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OCELLATE OCTOPUSES (CEPHALOPODA: OCTOPODIDAE) OF THE GREAT BARRIER REEF, AUSTRALIA: DESCRIPTION OF TWO NEW SPECIES AND REDESCRIPTION OF *OCTOPUS POLYZENIA* GRAY, 1849

By Mark D. Norman

Invertebrate Zoology, Museum of Victoria, 285 Russell Street, Melbourne, Vic. 3000, Australia

Abstract

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

Four species of ocellate octopuses are reported from the waters of the Great Barrier Reef, Australia. Ocellate octopuses exhibit a false eye-spot (or ocellus) on the arm crown below each eye. *Octopus polyzenia* Gray, 1849 is reported as an ocellate species for the first time and is redescribed based on examination of the type and specimens from tropical waters across northern Australia. Two new species, *O. exannulatus* and *O. mototi* spp. nov. are described and details of distribution and life history are presented. The widely distributed *O. cyanea* Gray, 1849 is the fourth ocellate species found on the Great Barrier Reef. *Octopus cyanea* shows different affinites to the other three species and may be of separate origin. A key for ocellate octopuses of Great Barrier Reef waters is provided. Delineation of Great Barrier Reef ocellate octopuses from others of the tropical Indo-West Pacific is discussed. Distribution patterns also are examined.

Introduction

Since the early 19th century, teuthologists have been familiar with ocellate octopuses, many authors discussing them in detail (Brock, 1887; Berry, 1912, 1912a; Robson, 1929; Sasaki, 1929; Adam, 1939, 1959, 1973; Pickford and McConnaughey, 1949; Voss and Solis Ramirez, 1966). Ocellate octopuses are shallow-water species characterised by the presence of a pair of dark false eye-spots (or ocelli) on the arm crown over the bases of arms 2 and 3, one below each eye. In many of these octopuses the dark ocelli each contain a fine ring of iridescent tissue, which is expressed as a brilliant metallic blue or gold ring in live animals.

Recent research into the shallow-water octopuses of the Great Barrier Reef, Australia has uncovered many octopus species (Norman, 1991, 1992a, 1992b), including four ocellate species: *Octopus cyanea* Gray, 1849, *O. polyzenia* Gray, 1849 and two new species, *O. exannulatus* and *O. mototi* spp. nov.

Octopus cyanea is a widely distributed tropical Indo-West Pacific species, found in coral reefs. It has previously been reported from Australian waters by Roper and Hochberg (1987, 1988) and Norman (1991). *Octopus polyzenia* was previously known only from the type specimen from Port Essington, Northern Territory (Gray, 1849) and a small male from Thursday I., northern Queensland (Smith, 1884). In examining these specimens in the British Museum (Natural History), it was discovered that both possess ocelli with an iridescent ring and both were mature males despite their small size (holotype: 12.3 mm ML, BMNH 1845.5.14.78 and Thursday I. specimen: 14.1 mm ML, BMNH 1882.2.23.568). An additional 14 specimens were found in Australian museum collections (NTM, AMS, WAM, NMV). *Octopus polyzenia* is here redescribed as a small ocellate species which lays large eggs and occurs in coastal waters across northern Australia. Species accounts are presented for two new ocellate species, *O. exannulatus* and *O. mototi*, along with information on distribution, life history and live animal attributes.

Material and methods

Field work on the Great Barrier Reef was carried out between May and November in 1989 and 1990. Live specimens of *O. cyanea* and *O. mototi* were encountered in the field during the day and at night on intertidal reef walks, snorkel and SCUBA dives and caught in octopus pots in deeper water. Individuals were observed in situ, collected, photographed, narcotised in fresh water, and fixed and preserved according to the techniques of Roper and Sweeney (1983). These specimens are now in the Museum of Victoria

(NMV). Preserved specimens of all four ocellate Reef species were found and examined in the collections of the Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QMB), Northern Territory Museum of Arts and Sciences (NTM), Western Australian Museum (WAM), National Museum of Natural History, Washington (USNM), Californian Academy of Science (CAS), British Museum (Natural History) (BMNH) and Muséum National d'Histoire Naturelle, Paris (MNHN).

In the description and tables, measurements and indices follow Voss (1963) and Roper and Voss (1983). Terminology has been modified by Hochberg and Mangold (in prep.) for several anatomical structures: "copulatory organ" replaces the term "hectocotylus" and "terminal organ" replaces the term "penis". The following additional or slightly modified indices also are employed:

Stage of Maturity (StM): Immature (I: sex indeterminate or reproductive organs minute), Submature (S: reproductive organs distinct but poorly developed) and Mature (M: developed spermatophores or eggs distinct); Head Width Index (HWI): head width as a per cent of ML; Head Mantle Width Index (HMWI): head width as per cent of mantle width; Arm Mantle Index (AMI): arm length as per cent of ML; Arm Width Index (AWI): maximum arm width at widest point on stoutest arm, as per cent of ML; Sucker Count (SC): total sucker count for the intact arm with the most suckers; Gill Count (GC): number of gill lamellae per demibranch not including the terminal lamella; Hectocotylized Arm Mantle Index (HAMI): length of hectocotylized arm as per cent of ML; Hectocotylized Arm Sucker Count (HASC): number of suckers on hectocotylized arm (see Toll, 1988); Terminal Organ Length Index (TOLI): length of terminal organ as per cent of ML; Diverticulum Length Index (DLI): diverticulum length as per cent of length of terminal organ; Spermatophore number (SpN): number of spermatophores in Needham's sac; Sperm Cord Whorls (SpCW): number of whorls in which sperm cord is coiled; Funnel Length Index (FLI): funnel length as per cent of ML; Free Funnel Index (FFI): length of free funnel portion as per cent of funnel length: Funnel Organ Index (FOI): length of outer limb of funnel organ as per cent of median limb length; Funnel Organ Length Index (FOLI): length of medial limb as per cent of funnel length; Ocellus Diameter Index (OcDI): diameter of ocellus as a per cent of ML (specified as referring to iridescent ring or entire dark web spot).

Indices are presented for both sexes combined, except where significant differences were found between the sexes (one-way ANOVA, $P = 0.05$ level). In these indices, range and mean for each sex are presented. Where ranges significantly overlap, standard deviations around the mean are also presented.

Two additional undescribed ocellate species have been recognised from northern Australian waters west of Cape York. Due to the scarcity of material and the apparent absence of these taxa from the Great Barrier Reef region, these forms have not been included in this work.

Table 8 summarises the key differences between ocellate octopuses of the Great Barrier Reef.

Key to ocellate octopuses of the Great Barrier Reef

1 Ocellus lacks iridescent ring; either simple black spot (figs 1a, 10c–f) or black spot surrounded by a fine dark outer ring (figs 1b, 2a) 2

— Ocellus consisting of dark spot containing narrow iridescent blue ring in live animal, visible as white or pink superficial ring over dark ocellus in preserved specimens (figs 1c, 6h, 14g–h) 3

2 9–11 gill lamellae per demibranch, typically 10; over 400 suckers on normal intact arms of submature and mature animals; approximately 200 suckers on hectocotylized arm; ocellus comprised of dark oval spot bound by additional thin dark ring (fig. 1b), iridescent tissue absent; dark zebra bars on ventral faces of all arms on submature and mature animals (fig. 2d); very large species (ML to 160 mm; weight to 6 kg; fig. 1h) .. .. *Octopus cyanea* Gray, 1849

— 7–8 gill lamellae per demibranch, typically 7; 120–190 suckers on normal intact arms of submature and mature animals; approximately 70 suckers on hectocotylized arm; ocellus plain black spot lacking an iridescent ring, oval shaped and clearly defined (figs 1a, 10e–f); 4 dark broad longitudinal stripes on dorsal body, continuing anteriorly on to dorsal arm crown

(figs 7a, 10a–d); moderate size species (ML to 50 mm; weight to 75 g; fig. 1f) ..... *Octopus exannulatus* sp. nov.

3 6–7 gill lamellae per demibranch, typically 6; 85–135 suckers on normal intact arms of submature and mature animals; approximately 50 suckers on hectocotylized arm; widely spaced dark transverse bars on all arms separated by approximately 3–4 suckers (figs 3a, 6d, g); pattern of faint crucifix of light patches on dorsal body (figs 3a); small species (ML to 38 mm; weight to 20 g; fig. 1a) ..... *Octopus polyzenia* Gray, 1849

— 9–11 gill lamellae per demibranch, typically 11; 143–176 suckers on normal intact arms of mature animals; approximately 100 suckers on hectocotylized arm; circular cluster of dark spots above each eye forming "flower" pattern (figs 11a, 14a); alarm pattern of dark longitudinal bars on dorsal body and arm crown over white base (figs 14b, e); well developed frontal white spot with prominent elongate papilla (figs 14a, 14d); moderate to large species (ML to 100 mm; weight to 300 g; fig. 1g) .. .. *O. mototi* sp. nov.

Octopodidae d'Orbigny, 1839

Subfamily **Octopodinae** d'Orbigny, 1839

Octopus cyanea Gray, 1849

Figs 1g, 2a–d, 15a

See Norman (1991) for full annotated synonymy. *Octopus marmoratus* Hoyle, 1885. *O. horsti* Joubin, 1898. *O. herdmani* (Hoyle, 1904), *O. cyanea* var. *gracilis* (Robson, 1928) and *Callistoctopus magnocellatus* Taki, 1964 are synonyms.

Diagnosis. Large robust species with black oval ocellus surrounded by pale ring and thin dark outer ring. Ring of iridescent tissue within ocellus absent. Dark bars on ventral surfaces of all 4 arms of larger specimens (ML > about 60 mm), forming stripes in alternation with base of suckers. 3–7 rows of cream spots on aboral arm surfaces from web margin to tips, containing small erectile skin ridges. Skin sculptured in irregular patch and groove system. 3 pronounced large circular patches on dorsal arm crown, especially in younger animals. 9–11 gill lamellae per demibranch, typically 10. More than 400 suckers on intact normal arms of submature and mature individuals, approximately 200 suckers on hectocotylized arm. Terminal organ small and fine (TOLI about 20). Spermatophores short, approximately 40% of ML and produced in large numbers (SpN >300). Eggs small, ovarian eggs to 2.7 mm [ELI(ov) to 1.7], and produced in very large numbers (EN >100 000).

Distribution. Octopus cyanea is recorded from tropical waters of northern Australia, from Moreton Bay, southern Queensland (27°23′S, 153°15′E) to Point Cloates, north-west Western Australia (22°42′S, 113°39′E). This species is widely distributed in the tropical Indo-West Pacific from Hawaii in the east to the east African coast in the west (fig. 15a).

Aspects of the life history of *O. cyanea* were treated in Van Heukelem (1983). Morphological description and observations of live Australian specimens were provided in Norman (1991).

Commercial exploitation. There is no commercial fishery for *O. cyanea* in Australian waters. The association of this species with coral and rocky reefs excludes it from trawl fisheries which work more open substrates. No small-scale local exploitation has been noted. Elsewhere throughout the tropical Indo-West Pacific, this species is commonly taken in local and subsistence fisheries (Hoyle, 1907; Berry, 1912; Sasaki, 1929; Rees, 1950; Van Heukelem, 1983; Roper et al., 1984).

Octopus polyzenia Gray, 1849

Figs 1d, 3–6, 15b

Octopus polyzenia Gray, 1849: 13. — Tryon, 1879: 122. — Cox, 1882: 787. — Smith, 1884: 34, pl. 4, figs A–A3. — Hoyle, 1886: 8, 80. — Lu and Phillips, 1985: 33.

Octopus granulatus (non Lamarek, 1798). — Brazier, 1892: 4.

Octopus rugosus (non Bosc, 1792). — Ortmann, 1891: 669. — Robson, 1929: 63, 65, 73. — Fleecker and Cotton, 1955: 3.

Material examined. 16 preserved specimens including the extant type (BMNH 1845.5.14.78) examined in Australian museum collections and the British Museum (Natural History).

Holotype: NT: 1♂: 12.3 mm ML, BMNH 1845.5.14.78, Port Essington, 11°16′S, 132°09′E, presented by the Earl of Derby.

Other material: NT: 3Imm: 7.4–8.8 mm ML, NTM P1393, Port Essington, Coral Bay (11°16′S, 132°09′E), 4.5–6 m, Helen Larson, 18 Oct 1981 (poison station,

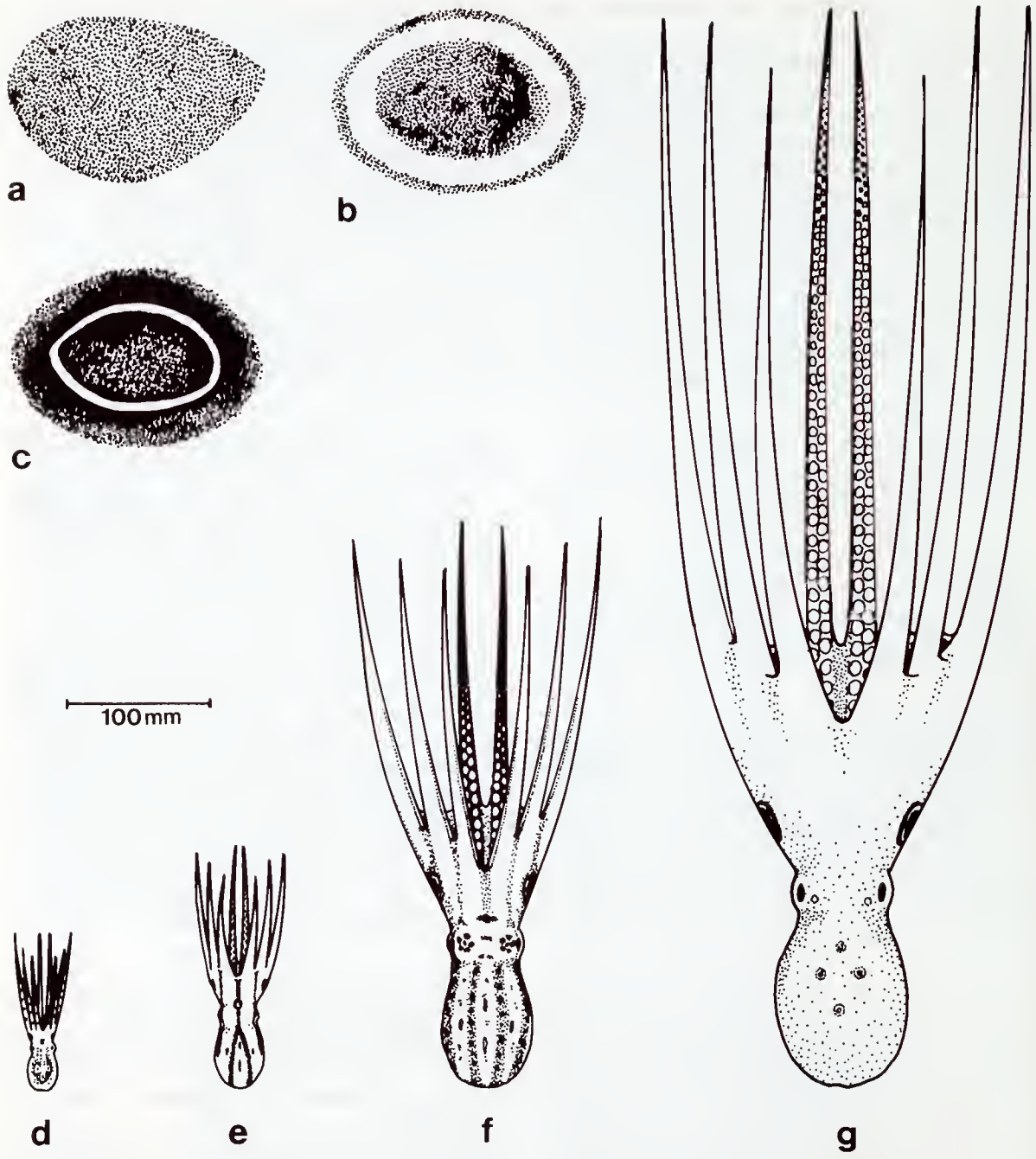

Figure 1. Occlli and body sizes of Great Barricr Reef ocellate octopuses. a–c. Ocellus types: a, occllus simple black spot, lacking iridescent ring or outer ring (as in *O. exannulatus*). b, dark ocellus contained within a light ring, which is bound by an additional thin black ring (as in *O. cyanea*). c, dark ocellus containing thin iridescent ring on surfacc of skin (as in *O. polyzenia* and *O. mototi*).
d–g. Comparative body sizes: d, *Octopus polyzenia* Gray, 1849. e, *Octopus exannulatus* sp. nov. f, *Octopus mototi* sp. nov. g, *Octopus cyanea* Gray, 1849.

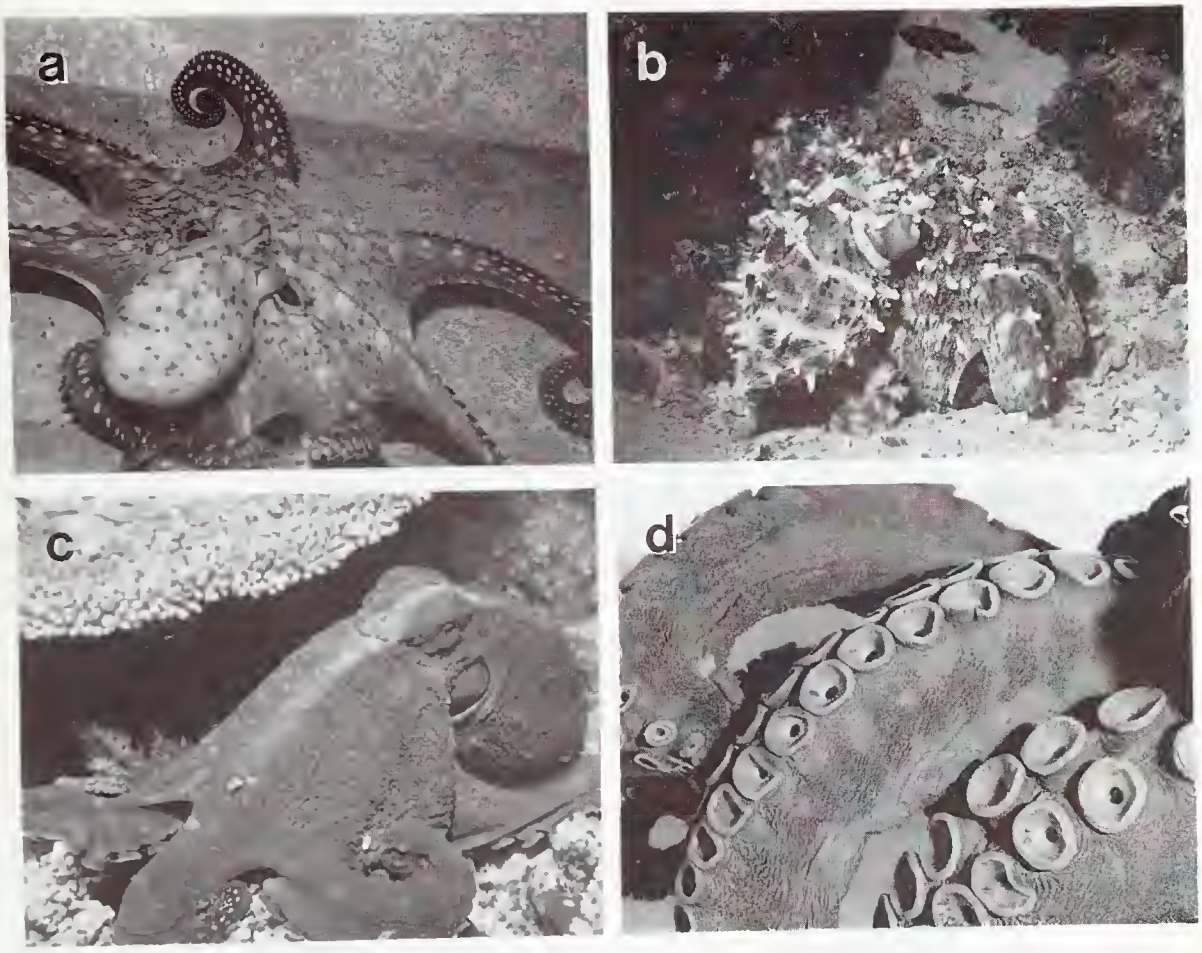

Figure 2. Photographs of *Octopus cyanea* Gray, 1849. a–c. Live colour patterns showing range in sculpture and colouration. a,warning posture with web flared and ocelli pronounced (NMV F57903: 86.7 mm ML submature female). b, "spiked" posture in wild specimen at Tryon I., southern Great Barrier Reef. c, chocolate brown colouration showing start of medial stripe in same specimen. d, dark bars on ventral arm faces of preserved specimen (NMV F57904: 100.0 mm ML mature male).

silty sand bottom, rock rubble with soft corals and gorgonians); 1♀: 32.8 mm ML, NTM P1451, Darwin, Casuarina Beach, Off Lee Point, (12°21′S, 130°52′E), C. Hood, 22 Jan 1986 (washed up in *Pinna* shell after storms).

WA: 1♀: 13.9 mm ML, WAM 363-88, Dampier Archipelago, Rosemary I., outside Norbill Bay, (20°29′S, 116°35′E), 5 m, Barry Wilson, WAM Crown of Thorns Survey, 21 May 1972 (dredged); 2♀: 17.7 mm, body missing from second specimen, ML, WAM 329-88, Dampier Archipelago, Rosemary I., Norbill Bay, (20°29′S, 116°35′E), 1–2 m, Barry Wilson, WAM Crown of Thorn Survey, 21 May 1972 (dredged on sand); 1♂: 24.4 mm ML, WAM 305-88, Monte Bello Is, northern end of Hermite I., (20°28′S, 115°31′E), F.E. Wells, 20 Aug 1986.

Qld: 1♂: 14.1 mm ML, BM 82.2.23.568, Torres Strait, Thursday I., (10°35′S, 142°13′E), 7.3–9.2 m, HMS "Alert"; 1♀: 24.9 mm ML, AM C48267, Bowen, 20°01′S, 148°15′E, E.H. Rainsford, no date; 3♀: 25.8–33.3 mm ML, AM C164168, Gulf of Carpentaria, Weipa, Albatross Bay, 12°40′S, 141°42′E, W. H. Foley, 1962; 1♂: 26.3 mm ML, AM C164179, Gulf of Carpentaria, off Karumba, (about 17°29′S, about 140°50′E), CSIRO Prawn Survey, 1963–1964 (trawl); 1♀: 37.7 mm ML, NMV F60112, Cleveland Bay, off Townsville, (19°11′S, 147°01′E), <20 m, G. Jackson, 1989 (trawled, RV "James Kirby").

Diagnosis. Small species with black oval ocellus containing an iridescent blue ring. Dark, widely-spaced, transverse bars along aboral and lateral faces of all arms, approximately 3–4 suckers between each bar. Light patches surrounding raised skin ridges form crucifix pattern on dorsal mantle. 6–7 gill lamellae per demibranch, typi-

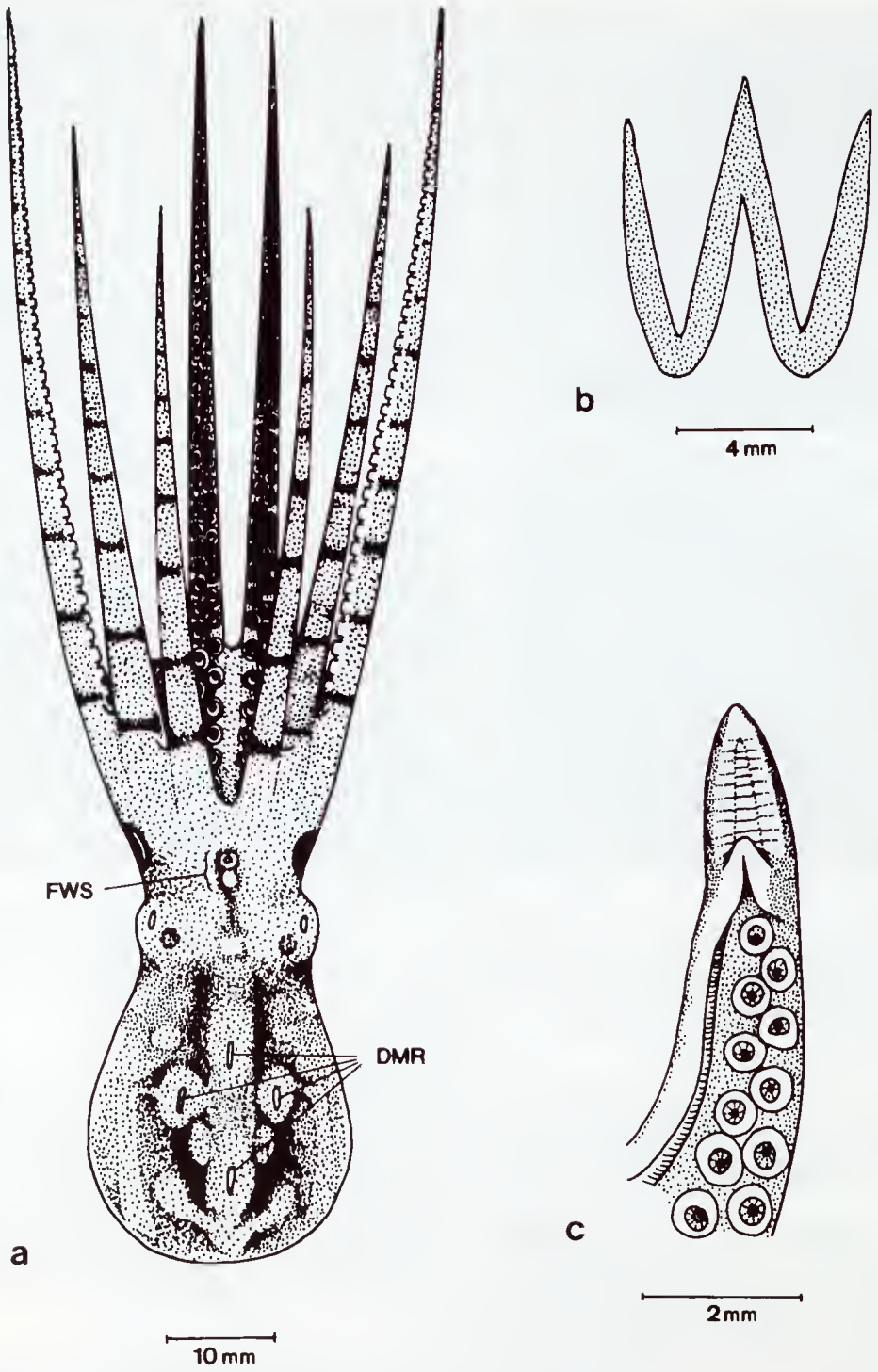

Figure 3. *Octopus polyzenia* Gray, 1849. a, dorsal view of 33.3 mm ML female (AM C164168): DMR = dorsal mantle ridges; FWS = frontal white spot complex. b, funnel organ of same specimen. c, copulatory organ of 26.3 mm ML male (AM C164179).

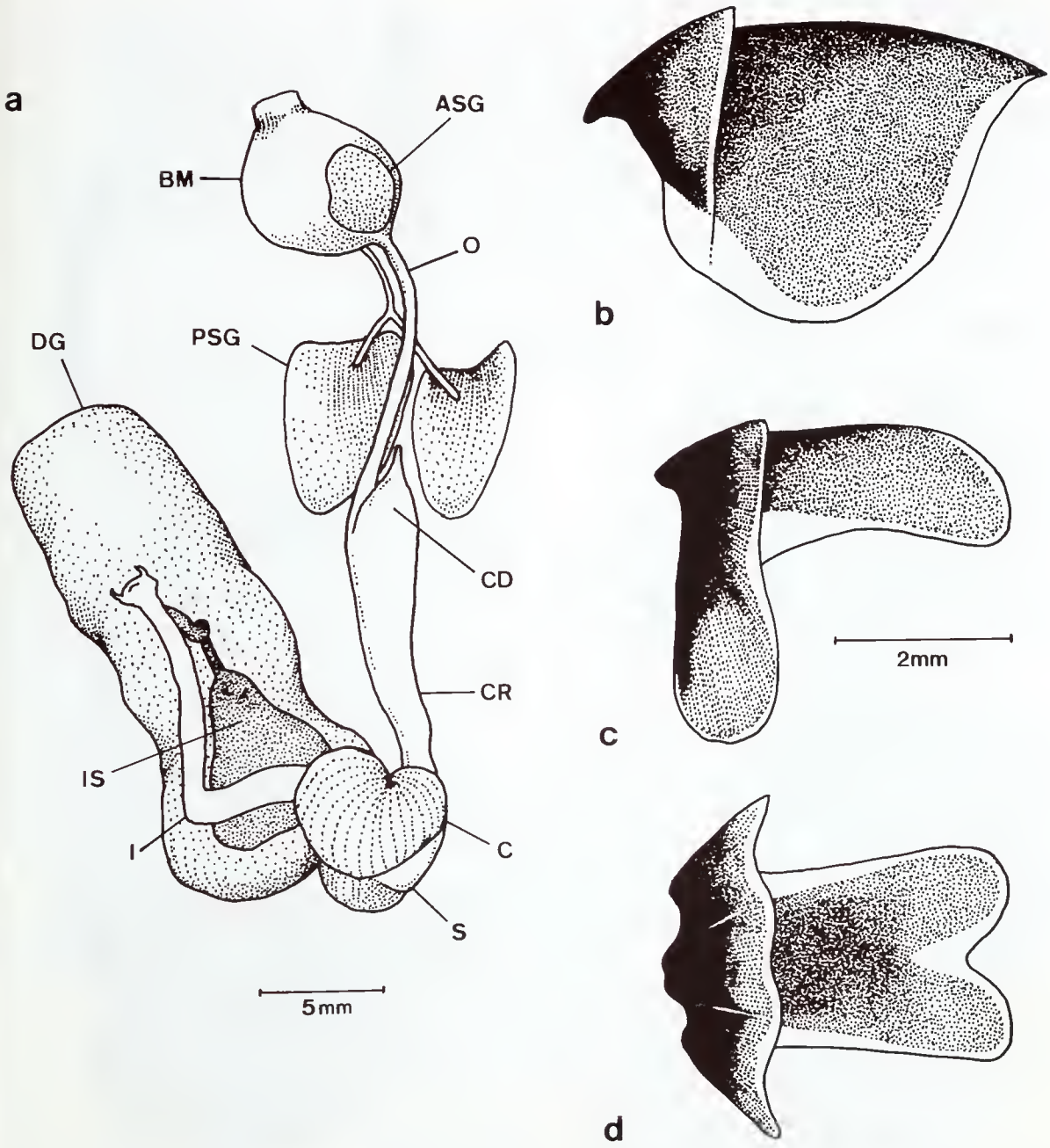

Figure 4. *Octopus polyzenia* Gray, 1849. a, digestive tract of 33.3 mm ML female (AM C164168): ASG = anterior salivary glands; BM = buccal mass; C = caecum; CD = crop diverticulum; CR = crop; DG = digestive gland; I = intestine; IS = ink sac; O = oesophagus; PSG = posterior salivary gland; S = stomach.
b–d, beaks of same specimen: b, upper beak, lateral view. c, lower beak, lateral view. d, lower beak, ventral view.

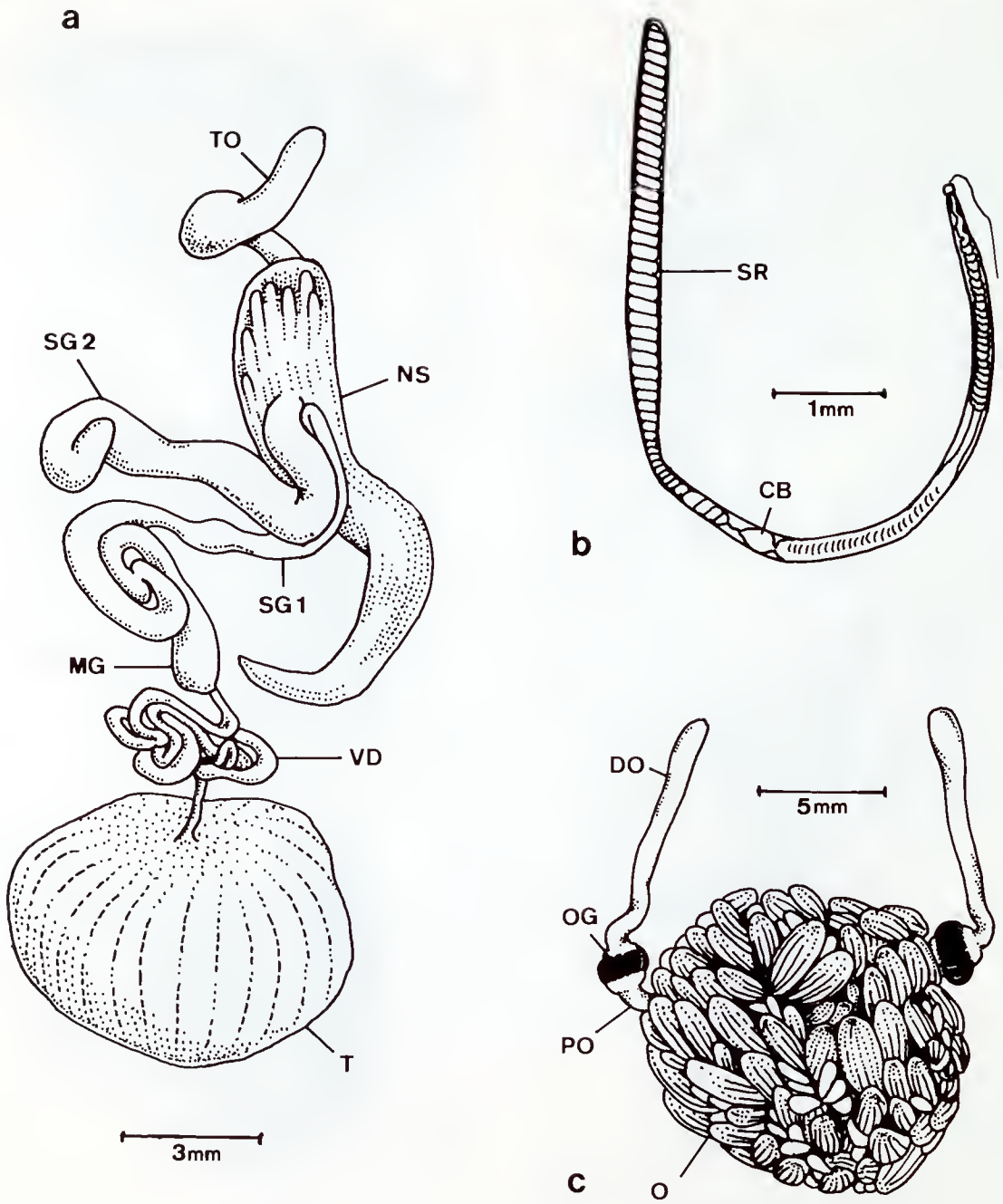

Figure 5. *Octopus polyzenia* Gray, 1849. a, reproductive tract of 26.3 mm ML male (AM C164179): MG = mucilaginous gland; NS = Needham's Sac; SG1 = spermatophoric gland I; SG2 = spermatophoric gland II; T = testes; TO = terminal organ; VD = vas deferens. b, spermatophore of same specimen: CB = cement body; SR = sperm reservoir. c, ovary of 33.3 mm ML female (AM C164168): DO = distal oviduct; O = ovary; OG = oviducal gland; PO = proximal oviduct.

cally 6. Approximately 115 suckers per arm in mature females (SC♀ 103–*115*–135, n = 9♀♀), slightly fewer in mature males (SC♂ 85, 86, 108), approximately 50 suckers on hectocotylized arm. Terminal organ short and robust (TOLI about 15). Spermatophores short, approximately one third of ML and produced in low numbers (SpN about 10). Eggs large, spawned capsules to 7.5 mm [ELI(sp) to 22.9] and produced in moderately low numbers (EN about 250).

Description. Based on 3 mature males, and 3 submature and 4 mature females. Counts and indices are in Tables 1 and 2.

Small robust species (figs 1d, 3a), males to at least 26 mm ML, females to 37.7 mm ML, TL to at least 130 mm; weight to at least 19 g. Mantle ovoid (MWI 50.4–*69.0*–85.4) with muscular walls. Stylets not found. Pallial aperture of moderate width, approximately half of mantle width. Funnel muscular and broad-based (FLI 34.1–*39.6*–51.2) with free portion usually greater than half funnel length (FFLI 44.0–*63.5*–78.1). Funnel organ W-shaped with moderate limbs (fig. 3b). Outer limbs slightly shorter than median limb (FOI 90.2–*95.1*–100.0). Funnel organ large, approximately 60% of funnel length (FOLI 48.0–*61.1*–73.5).

Head of moderate width (HWI 41.1–*49.5*–63.3), always narrower than mantle (HMWI 60.0–*72.3*–89.5). Neck distinct, slightly narrower than head. Eyes large and slightly pronounced.

Arms of moderate length, 2–3 times mantle length; from limited material arms appear slightly longer in females (AMI♂ 200.8, 209.1, 252.0; ♀ 236.4–*261.7*–309.4). Arms robust (AWI 13.0–*18.2*–25.9), roughly circular in cross section and taper evenly to fine tips. Dorsal arms shortest, lateral and ventral arms longer and more robust (AF generally 4=3.2.1 or 4.3.2.1). Suckers of moderate size, slightly elevated with distinct radial cushions and scalloped rim. Mature males can possess 1–3 enlarged suckers on all arms, beyond margin of webs at level of seventh sucker pair (SDI♂ 10.3, 11.7, 13.5; ♀ 7.7–*9.4*–12.9). Arm 4 possesses most suckers, approximately 115 suckers per arm in females (SC♀ 103–*115*–135, n = 9♀♀), slightly fewer in males (SC♂ 85, 86, 108). Webs moderate to deep (WDI 26.1–*31.4*–39.1), deepest laterally, dorsal web distinctly shorter (WF typically D.C=E.B.A or D=E.C.B.A). Web margins poorly developed, extending less than half way along ventral edge of arms.

Third right arm in males hectocotylized and slightly shorter than opposite arm (OAI: 76.9, 77.4; HAMI: 152.1, 155.7, 195.1). Spermatophore groove well developed and wide with fine transverse ridges. Spermatophore guide distinct with small papillae. Copulatory organ small and robust (fig. 3e: LLI 4.7, 5.4, 6.8), ligula roughly conical with blunt tip; groove shallow with raised longitudinal midrib. Calamus well developed and large (CLI 40.7, 44.4, 69.2). Approximately 50 suckers on hectocotylized arm (HASC: 45, 49, 52).

Gills with 6–7 lamellae, typically 6, on both inner and outer demibranchs, plus a terminal lamella.

Digestive tract illustrated in figure 4a. Anterior salivary glands moderately large, approximately half of buccal mass length. Posterior salivary glands well developed, slightly larger than buccal mass. Crop diverticulum distinct but not greatly developed. Stomach bipartite. Caecum striated, coiled in single whorl. Muscular intestine reflexed approximately one-third along length from proximal end. Ink sac well developed, embedded in ventral surface of digestive gland below iridescent tissue layer. Anal flaps present.

Upper beak with moderate hood and slightly hooked rostrum, concave on cutting edge (fig. 4b). Lower beak (figs 4c–d) with blunt rostrum, narrow hood, widely spread wings and slightly flared lateral walls. Ventral view of posterior margin moderately concave. Radula with seven teeth and two marginal plates in each transverse row (figs 6i–j). Rhachidian tooth typically has 1 lateral cusp on each side of medial cone (2 in every fourth row). Lateral cusps in symmetrical seriation, migrating from lateral to medial position over four transverse rows. First lateral teeth unicuspidate with cusp towards lateral edge; second lateral teeth unicuspidate and robust; lateral marginal teeth robust, straight and moderately short; marginal plates oblong and plain.

Male reproductive tract illustrated in figure 5a. Terminal organ in mature males short and robust (TOLI 14.4, 16.3, 16.8) with robust diverticulum (DLI 34.2, 56.1, 70.0), genital aperture subterminal. Vas deferens short and robust. Mucilaginous gland enlarged at point of attachment to vas deferens. Spermatophoric gland I short and robust with recurved coil approximately three-quarters along length. Spermatophoric gland II relatively short and robust with reflexed tip. No distinct appendix at junction of spermatophoric glands and Need-

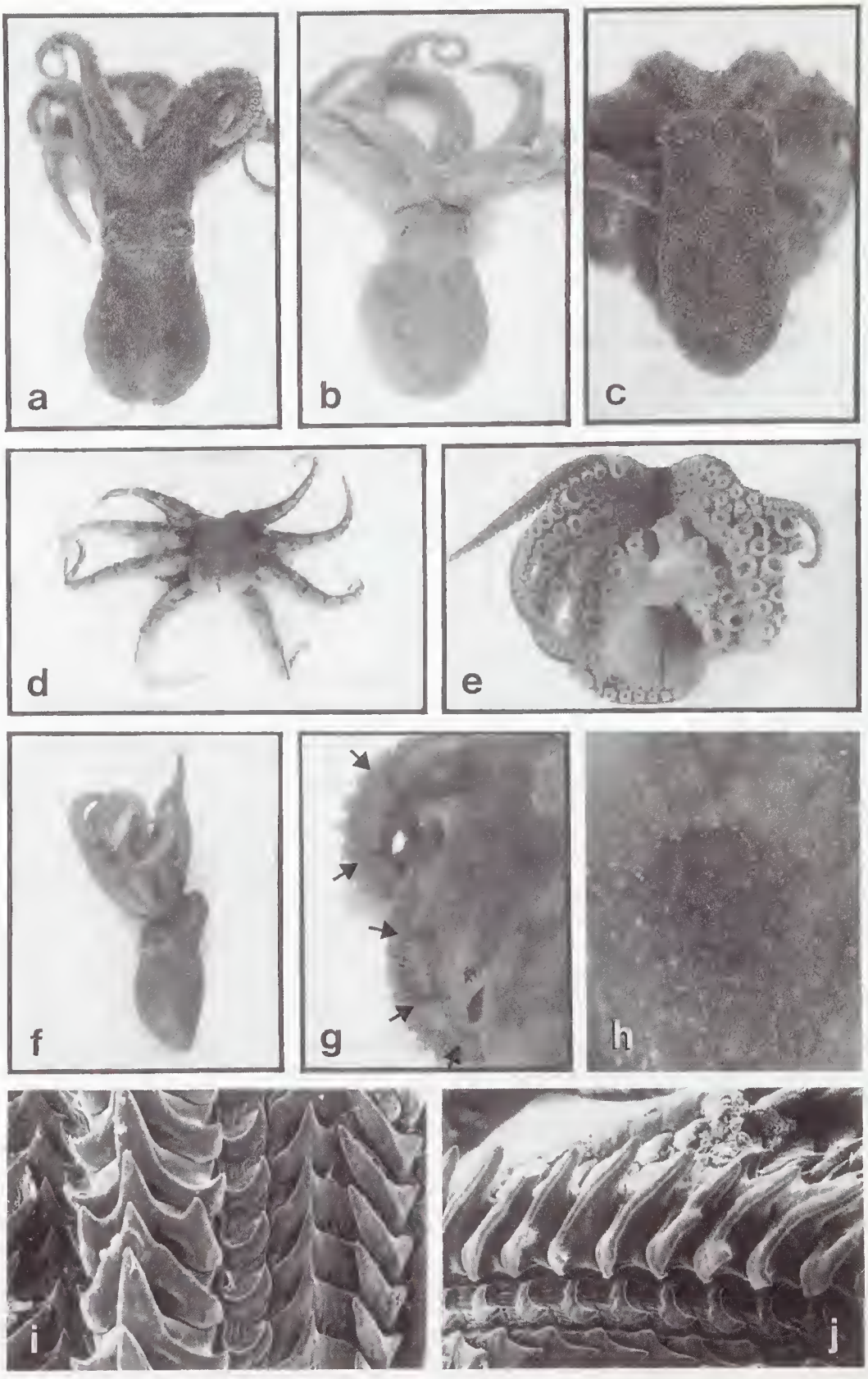
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Figure 6. Photographs of preserved specimens of *Octopus polyzenia* Gray, 1849. a, dorsal view of 25.8 mm ML female (AM C164168). b, dorsal view of 26.3 mm ML male (AM C164179). c, dorsal view of 24.4 mm ML male (WAM 305-88). d, posterior view of 13.9 mm ML female (WAM 363-88), indicating arm bars. e, enlarged suckers of 24.4 mm ML male (WAM 305-88). f, lateral view of 8.8 mm ML immature specimen (NTM 1393). g, arms and ocellus of 32.8 mm ML female (NTM P1451), indicating position of arm bars. h, ocellus of same specimen, containing iridescent ring. i–j, radula of 32.5 mm ML female (AM C164168).

ham's sac. Needham's sac relatively short and robust. Spermatophores (fig. 5b) short (SpLI 34.2) and moderately robust (SpWI 5.6), produced in low numbers (10 in Needham's sac of AM C164179). Sperm reservoir approximately half spermatophore length (SpRI 55.6). Sperm cord iridescent gold in colour and coiled in approximately 45 whorls. Oral cap with constricted collar bearing long cap thread.

Mature ovary oval shaped (fig. 5c). Oviducts short, robust and straight. Oviducal glands large with approximately 14 radiating (braiding) chambers. Eggs large, capsule of mature ovarian eggs to 4.9 mm long [ELI(ovarian) to 19.7], spawned eggs with capsule to 7.5 mm [ELI(spawned) to 22.9]. Eggs moderately wide [EWI(ovarian) to 6.8; EWI(spawned) to 9.1] and produced in low numbers (226 spawned eggs accompanying 32.8 mm ML female: NTM P1451). Approximately twelve follicular folds with cross striations on ovarian eggs. Ovarian eggs in 1 female at 2 distinct stages of development, suggesting spawning over an extended period. Eggs laid in short festoons attached by short stalks to a fine central thread.

Colour in life unknown. Base colour of preserved specimens generally cream to pink brown with dark mottlings and light patches on dorsal body. Dorsal mantle pattern of light coloured oval patches containing raised skin ridges, central four arranged in diamond shape forming faint crucifix pattern (fig. 3a). Dark brown rectangular block between and slightly behind eyes in some specimens. Dark brown to black oval ocellus on either side of arm crown between bases of arms 2 and 3, containing small iridescent blue ring (fig. 6h: OcDI for irideseent ring 6.1–9.7–14.6). Dark background spot of the ocellus may fade in preserved specimens leaving only irideseent ring visible. Dark transverse bars on aboral and lateral surfaces of all arms, widely spaced with 3–4 suckers between each bar (figs 3a, 6d, f–g). No dark longitudinal line along dorsal face of arms as found in *O. mototi* and *O. exannulatus*.

Frontal white spot complex of 2 light spots present on dorsal arm crown below midpoint of eyes (FWS in fig. 3a). Anterior spot cream coloured containing primary papilla. Posterior spot pink to peach coloured, clearly distinct from surrounding pigmentation.

Body, arms and arm crown covered in small round papillae, extending on to oral surface of

Table 1. Counts and indices of male *Octopus polyzenia* Gray, 1849.
(M = mature; D = damaged; — = not recorded; * = OcDI measured as diameter of iridescent ring).

Museum Reg. No.	BMNH 1845.5.14.78 (Holotype)	WAM 305-88	AM C164179
ML	12.3	24.4	26.3
StM	M	M	M
TL	46	75	84
MWI	85.4	50.4	70.3
HWI	60.2	45.1	45.2
HMWI	70.5	89.5	64.3
AMI: 1	195.1	151.6	174.9
2	243.9	168.0	205.3
3	252.0	D	197.7
H	195.1	155.7	152.1
4	252.0	200.8	209.1
AWI	13.0	14.3	20.2
SDI	11.4	13.5	10.3
WDI	32.2	34.9	32.7
GC	6	6	6
HAMI	195.1	155.7	152.1
OAI	77.4	D	76.9
HASC	45	49	52
LLI	5.4	4.7	6.8
CLI	69.2	44.4	40.7
TOLI	16.3	16.8	14.4
DLI	70.0	56.1	34.2
SpLI	—	—	34.2
SpWI	—	—	5.6
SpRI	—	—	55.6
SpN	—	—	10
FLI	40.7	32.8	36.5
FFLI	44.0	51.3	78.1
FOI	91.7	97.9	95.7
FOLI	48.0	58.8	71.9
OcDI*	14.6	6.1	8.0

Table 2. Counts and indices for female *Octopus polyzenia* Gray, 1849.
(S = submature; M = mature; D = damaged; — = not recorded; * = OcDI measured as diameter of iridescent ring).

Museum Reg. No.	WAM 363-88	AM C48267	AM C164168	AM C164168	NTM P1451	AM C164168	NMV F60112
ML	13.9	24.9	25.8	32.5	32.8	33.3	37.7
StM	S	M	S	S	M	M	M
TL	59	93	90	119	121	126	133
MWI	74.1	71.1	69.4	72.9	57.6	77.5	61.5
HWI	63.3	53.0	49.2	48.3	43.0	46.5	41.1
HMWI	85.4	74.5	70.9	66.3	74.7	60.0	66.8
AMI: 1	230.2	188.8	186.0	206.2	210.4	216.2	183.0
2	251.8	224.9	220.9	224.6	207.3	228.2	209.5
3	309.4	236.9	236.4	258.5	247.0	270.3	212.2
4	302.2	261.0	232.6	261.5	247.0	261.3	246.7
AWI	25.9	17.7	17.1	18.2	18.6	17.1	19.9
SDI	12.9	9.2	9.3	8.9	9.1	8.4	7.7
WDI	39.1	29.2	32.8	27.1	30.9	27.8	26.9
GC	6	6	6	6	7	7	7
ELI		19.7			22.9	12.6	—
EWI		6.8			9.1	3.9	—
EN		100s			226	100s	100s
FLI	48.9	34.1	41.5	40.0	38.7	46.8	36.1
FFLI	76.5	71.8	61.7	70.8	63.8	62.2	54.4
FOI	100.0	94.0	91.4	97.0	93.8	90.2	99.0
FOLI	60.3	58.8	65.4	51.5	63.8	59.0	73.5
OcDI*	12.9	9.2	9.7	9.5	8.5	9.0	9.5

dorsal and dorsolateral webs. Sculpturing present on ventral surface of body, but absent from ventral arm crown. Longitudinal raised skin ridges visible on dorsal body (fig. 3a), largest 4 forming diamond arrangement. Additional shorter raised ridges on dorsal and lateral mantle. 1 large and 2 small branching papilla above each eye.

Sexual dimorphism not marked in the few specimens available. Mature males can possess 1–3 enlarged suckers on all arms at level of seventh sucker pair. Two other trends are visible in the limited material: i) mature males appear to have longer arms than females (AMI♂ mean *220.6*; ♀ mean *261.7*); yet, ii) females appear to have higher sucker counts than males (SC♀ mean *115*; ♂ mean *93*). When converted to a ratio of sucker count/arm length, the trend is clearer (SC/AL♀ 130.0-*154.4*-193.3, n = 6♀♀, ♂ 175.5, 207.7, 274.2). Additional material is required to confirm this trend.

Distribution. Octopus polyzenia is recorded from shallow, tropical waters across northern Australia (fig. 15b), from Bowen, Queensland (20°01′S, 148°15′E) west to Rosemary I., Dampier Archipelago, Western Australia (20°29′S, 116°35′E).

Life history. This taxon appears restricted to shallow, coastal waters on open substrata of sand or mud. Most specimens were collected by trawl or dredge between 1 and 20 m. The large eggs and well developed arms in very small juveniles from the type locality (3Imm: 7.4-8.8 mm ML, NTM P1393) indicate hatchlings adopt a benthic habit.

Two specimens were accompanied by eggs laid in bivalve shells.

Commercial exploitation. There is no known exploitation of this species although it is likely to occur in low numbers in prawn trawl by-catch, particularly in the Gulf of Carpentaria.

Remarks. Brazier (1892) placed *O. polyzenia* in the synonymy of *O. granulatus* Lamarck, 1798, a species with no known type material or type locality. Other authors placed *O. polyzenia* in the synonymy of *O. rugosus* (Bosc, 1792) described from West Africa (Ortmann, 1891;

Robson, 1929; Fleeker and Cotton, 1955), a species also lacking type material. The type locality of *O. rugosus*, and the absence of reference to ocelli in both *O. granulatus* and *O. rugosus* justify removing *O. polyzenia* from the synonymies of these species. The status of these two nominal taxa requires review.

Octopus exannulatus sp. nov.

Figs 1c, 7–10, 15c

Octopus membranaceus (non Quoy and Gaimard, 1832). — Lu and Phillips, 1985: 33.

Material examined. 137 preserved specimens examined in Australian museum collections and the National Museum of Natural History, Washington (USNM). The material listed was used to generate the description.

Holotype: Qld: 1♂: 46.7 mm ML, NMV F60143, Moreton Bay, 3 mi (5 km) N of E corner of Mud I., (about 27°23′S, about 153°15′E), W. Stephenson, 9 Dec 1966.

Paratypes: Qld: 1♂: 39.8 mm ML, QMB Mo29473, off Cairns, about 15 km SE of Fitzroy I., (about 17°00′S, about 146°05′E), 30 m, C. Jones, 25 Apr 1982 (Seibenhausen net); 1♂: 41.5 mm ML, USNM 817673, Moreton Bay, 3 mi N of E corner of Mud I., (about 27°23′S, about 153°15′E), W. Stephenson, 9 Dec 1966; 1♀: 41.8 mm ML, NMV F60105, Gulf of Carpentaria, 130 km W of Prince of Wales I., 10°56′S, 140°55′E, 44 m, C.C. Lu, 10 Sep 1982 (trawl, 1900–2000 hr); 1♀: 48.0 mm ML, QMB Mo29329, Moreton Bay, Peel I., Horseshoe Bay, (about 27°23′S, about 153°15′E, J.M. Raven, 9 Oct 1975; 1♀: 53.3 mm ML, NMV F60107, Gulf of Carpentaria, 50 km W of Port Musgrave, 11°57.5′S, 141°22′E, 38 m, C.C. Lu, 7 Sept 1982 (prawn trawl, 2052–2137 hr).

Other material: Qld: 1♂: 17.7 mm ML, QMB Mo29469, Moreton Bay, Middle Banks, (about 27°23′S, about 153°15′E), W. Stephenson, Mar, 1974; 2♂, 3♀: 27.5–41.5 mm ML, NMV F60104, Moreton Bay, (about 27°23′S, about 153°15′E), M. Potter, 22 Jul 1981; 1♂: 38.9 mm ML, QMB Mo29468, E of Cairns, 17°03.0′S, 146°07.8′E, 30.6 m, Queensland Fisheries Service, FRV "Southern Ocean", 28 Jan 1981 (single rigged try nets with tickler chains); 1♂: 39.3 mm ML, NMV F60106, Gulf of Carpentaria, 175 km W of Thursday I., 10°27′S, 140°45′E, 47 m, C.C. Lu, 13 Sep 1982 (trawl, 1900–2000 hr); 2♂: 41.3, 41.7 mm ML, NMV F60103, Moreton Bay, (about 27°23′S, about 153°15′E), Jan or Feb 1982.

WA: 1♀: 24.4 mm ML, WAM 352-88, Dampier Archipelago, 5–6 mi off "Brazont I.", 43 m, B.R. Wilson, FV "Daveno", 5 Jun 1960, (honolulu dredge on sand); 2♀: 23.6, 31.1 mm ML, NMV F60109, North West Shelf, 19°55.5′S, 117°55.5′E, 42 m, CSIRO, 22 Apr 1983 (beam trawl, 0845hrs); 1♀: 44.5 mm ML, NMV F60108, 50 km off Wickham, 20°15′S, 117°12′E, 40 m, CSIRO, 2 Jun 1990 (trawl, 1718 hr); 1♂: 45.4 mm ML, WAM 276-88, Shark Bay, 15 mi W of Carnarvon, (about 24°53′S, 113°40′E), L. Marsh and M. Sinclair, 3–4 Jul 1975 (trawl).

Diagnosis. Small to moderate sized species with simple black ocellus lacking an iridescent ring. 4 dark broad longitudinal stripes present on dorsal body extending on to arm crown. Dark leading edges present along length of dorsal edges of all arms. 7–8 gill lamellae per demibranch. Approximately 150 suckers per arm in females (SC♀ 136–*154*–188, n = 8), slightly fewer in males (SC♂ 123–*137*–162, n = 8); approximately 70 suckers on hectocotylized arm. Terminal organ large and recurved (TOLI about 40). Spermatophores very long, up to 1.5 times mantle length and produced in low numbers (SpN <10). Eggs moderately small, ovarian eggs to 3.9 mm [ELI(ov) to 7.3] and produced in large numbers (>5000).

Description. The following description based on 9 mature males, and 6 submature and 4 mature females. Counts and indices in Tables 3 and 4, with data from an immature male (17.1 mm ML, QMB Mo29469).

Small to medium-sized robust species (figs 1e, 7a, 10a): ML to at least 50 mm for both sexes, TL to at least 200 mm; weight to at least 75 g. Mantle round to ovoid (MWI 56.2–*67.4*–79.3), mantle walls thick and muscular. Stylets not found. Pallial aperture of moderate width, approximately half mantle width. Funnel muscular and broad based (FLI 31.8–*38.0*–45.0) with free portion usually greater than half funnel length (FFLI 40.4–*57.5*–78.6). Funnel organ W-shaped with broad limbs (fig. 7b). Outer limbs slightly shorter than median limb (FOI 79.4–*89.6*–97.2). Funnel organ large, approximately two-thirds of funnel length (FOLI 53.3–*67.0*–85.9).

Head of moderate width (HWI 41.7–*50.1*–60.7), narrower than mantle except in smallest specimen (HMWI 53.3–*74.9*–91.7). Neck distinct, slightly narrower than head. Eyes large and slightly pronounced.

Arms of moderate length, approximately 2–3 times ML (AMI 214.5–*245.2*–285.4), robust (AWI 13.3–*16.8*–20.1), roughly circular in cross section and tapering rapidly to fine tips in distal third. Dorsal arms shortest, lateral and ventral arms longer and more robust (AF generally 4.3.2.1 or 3.4.2.1). Suckers of moderate size, slightly elevated with distinct radial cushions, rim scalloped and often incurved. Mature males possess 2–4 considerably enlarged suckers at level of third sucker pair on arms 2 and 3 (SDI♂ 10.2–*14.3*–18.8; ♀ 7.1–*8.4*–9.5). Arm 3 or 4 possesses most suckers, approximately 150 per arm

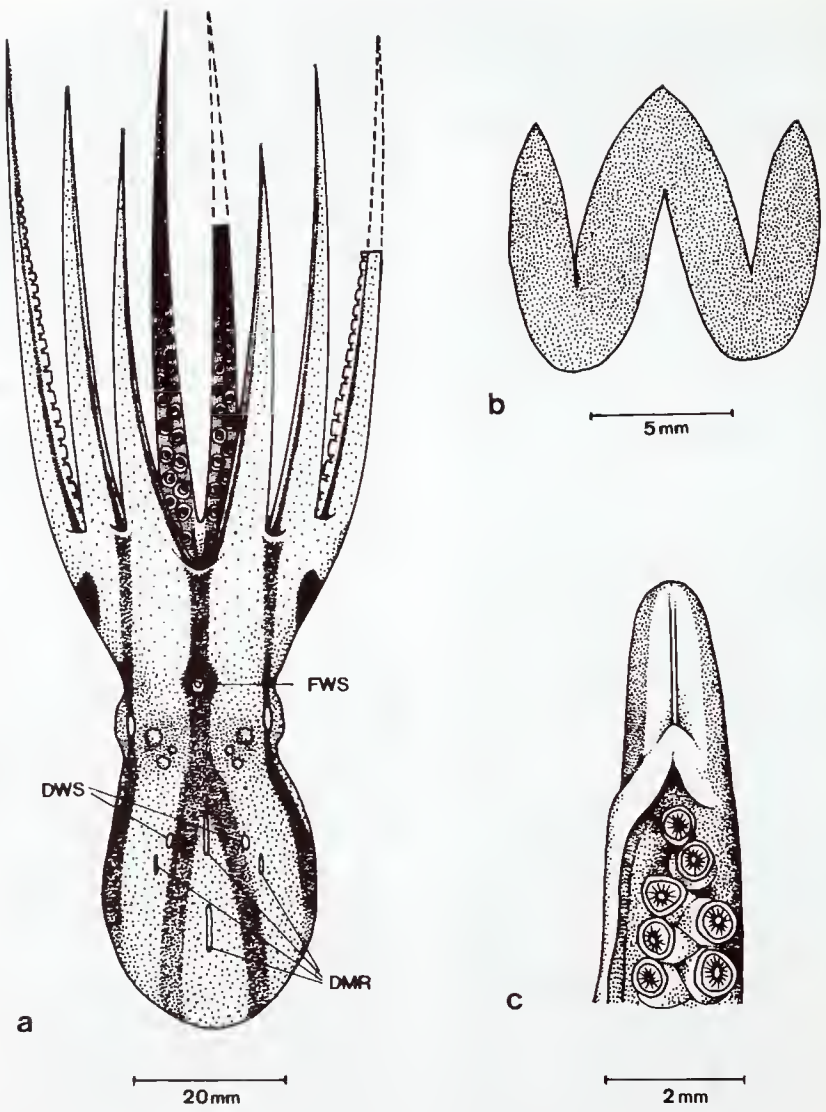

Figure 7. *Octopus exannulatus* sp. nov. a, dorsal view of 41.5 mm ML female (NMV F60104): DMR = dorsal mantle ridges; DWS = dorsal white spots; FWS = frontal white spot. b, funnel organ of 41.7 mm ML male (NMV F60103). c, copulatory organ of same specimen.

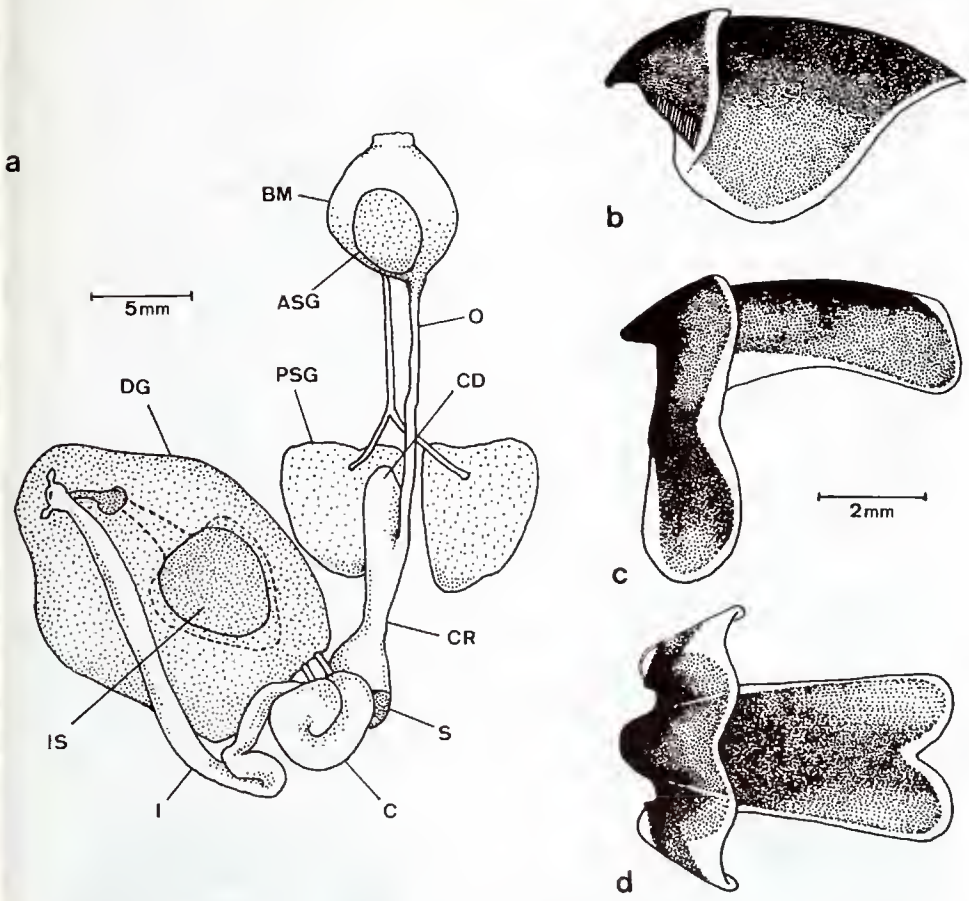

Figure 8. *Octopus exannulatus* sp. nov. a, digestive tract of 37.2 mm ML male (NMV F60104): hatched line indicates extent of ink sac embedded within digestive gland (for key to symbols see fig. 4). b, upper beak, lateral view of 34.9 mm ML female (NMV F60104). c, lower beak, lateral view of same specimen. d, lower beak, ventral view of same specimen.

in females (SC♀ 136–*154*–188, n = 8♀♀), slightly (not significantly) fewer in males (SC♂ 123–*137*–162, n = 7♂♂). Webs moderate to deep (WDI 24.3–*29.8*–37.1), deepest laterally, dorsal web distinctly shorter (WF typically D.C=E.B.A or D=C.E.B.A). Web margins well developed on ventral edges of arms, extending along approximately 80% of arm length.

Third right arm in males hectocotylized and slightly shorter than opposite arm (OAI: 74.6–*83.0*–97.6; HAMI: 158.6–*187.5*–218.5). Spermatophore groove well developed and wide with fine transverse ridges. Spermatophore guide deep with elevated square papillae. Mature copulatory organ small (fig. 7c: LLI 3.5–*4.3*–5.8), ligula roughly conical with blunt tip; groove

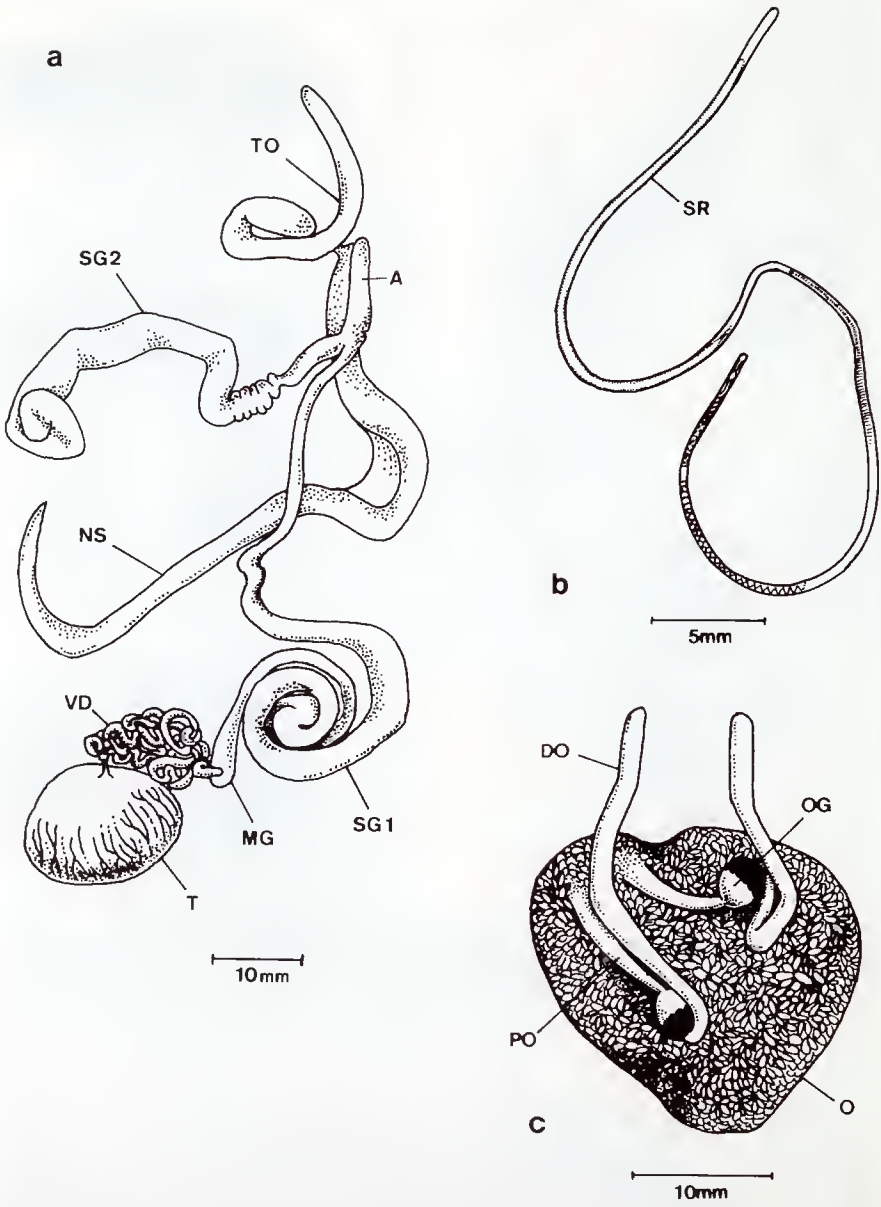

Figure 9. *Octopus exannulatus* sp. nov. a, male reproductive tract of 37.2 mm ML specimen (NMV F60104); for key to symbols see fig. 5.; A = appendix. b, spermatophore of 39.8 mm ML specimen (QMB Mo29473): SR = sperm reservoir. c, ovary of 44.5 mm ML specimen (NMV F60108): DO = distal oviduct; O = ovary; OG = oviducal gland; PO = proximal oviduct.

wide and shallow with a raised longitudinal midrib. Calamus medium size, slightly raised (CL1 19.4–*26.2*–34.2). Approximately 70 suckers on hectocotylized arm (HASC: 62–*69*–77).

Gills with 7–8 lamellae on both inner and outer demibranchs, plus a terminal lamella.

Digestive tract illustrated in figure 8a. Anterior salivary glands large, approximately 60% of buccal mass length. Posterior salivary glands well developed, slightly larger than buccal mass. Crop diverticulum distinct but not greatly developed. Stomach bipartite. Caecum coiled in single whorl. Muscular intestine reflexed approximately one-third of intestine length from proximal end. Ink sac well developed, embedded in ventral surface of digestive gland below iridescent tissue layer. Anal flaps present.

Upper beak (fig. 8b) with moderate hood and slightly hooked rostrum, concave on cutting edge. Ventral edge of hood with regular vertical ridges. Lower beak (figs 8c–d) with blunt rostrum, narrow hood, widely spread wings and slightly flared lateral walls. Ventral view of posterior margin moderately concave. Radula with seven teeth and two marginal plates in each transverse row (figs 10e–f). Rhachidian tooth with 1–2 lateral cusps, typically 1, on either side of a short robust medial cone. Lateral cusps are in symmetrical seriation, migrating from lateral to medial position over 2–3 rows. First lateral teeth unicuspidate with cusp towards lateral edge; second lateral teeth unicuspidate and long with curved base; lateral marginal teeth long, straight and robust; marginal plates oblong and plain.

Male reproductive tract illustrated in figure 9a. Terminal organ in mature males very long, thin and recurved (TOL1: measured from tip to apex of curve: 34.1-*41.3*-48.1) with robust diverticulum (DL1 27.3-*34.4*-38.1), genital aperture subterminal. Vas deferens relatively robust and short. Mucilaginous gland enlarged at point of attachment to vas deferens. Spermatophoric gland I elongate and narrow with large recurved coil approximately 80% along length. Spermatophoric gland II long and narrow with reflexed tip. Appendix present at junctions of spermatophoric glands and Needham's sac. Needham's sac greatly elongated and narrow curved to follow curve of spermatophoric glands. Spermatophores (fig. 9b) very long (SpL1 136.8, 152.3, 162.4) and fine (SpW1 0.8–1.1), produced in low numbers (<10 in Needham Sacs of dissected males). Oral cap simple bearing cap thread. Sperm reservoir one third to one half spermatophore length (SpR1 37.4, 46.5, 46.9), retracted from tip of oral end in all preserved material examined. Sperm cord very fine and irregularly packed within the sperm reservoir, not forming regular whorls in material examined. Cement body not distinct in material examined.

Mature ovary oval shaped (fig. 9c). Oviducts robust and of moderate length. Oviducal glands large with approximately 15 radiating (braiding) chambers. Eggs small, ovarian eggs to 3.9 mm long [EL1(ovarian) to 7.3], moderately wide [EW1(ovarian) to 1.9] and produced in large numbers (at least 5000 ovarian eggs estimated from 1 specimen). 4–5 follicular folds on ovarian eggs.

Live specimens not witnessed. Preserved specimens exhibit 4 broad dark brown to black longitudinal stripes on dorsal body, over cream to red-brown base colour (fig. 7a). Inner pair of stripes extend along length of body joining at midpoint above eyes, continuing as single medial stripe to margin of dorsal web. Lateral body stripes commence from midway along lateral mantle, pass through the eye and extend on arm crown to margin of dorsolateral web. Thin dark brown to black lines extend along bases of suckers on dorsal faces of all arms. Plain dark brown to black ocellus present on each side of arm crown between bases of arms 2 and 3 (figs 10e-f: OcD1 of black spot 14.8-*20.6*-28.8). Ring of iridescent tissue absent.

Several small circular pink spots are visible over base colour, 1 pair on dorsal body approximately one-third along body from level of eyes (fig. 7a). Circular frontal white spot on dorsal arm crown present just below eyes, in centre of medial dark stripe. Pigmentation reduced on ventral body and arm crown surfaces, but well developed on oral surface of dorsal web.

Body, arms and arm crown covered in small oval to round papillae, extending to arm faces and oral surface of dorsal and dorsolateral webs. Sculpturing present on ventral surface of body, but papillae almost twice diameter of those on dorsal surfaces. Sculpturing absent from ventral arm crown. 4 longitudinal raised skin ridges visible on dorsal body, in diamond arrangement (fig. 7a). Single large branching papilla above and slightly behind each eye, surrounded by additional smaller papillae (fig. 10a). Raised papilla present in centre of frontal white spot on dorsal arm crown.

Photographs of a live juvenile (15.1 mm ML, AM C168950) were provided by I. Loch (AM). Resting colour was orange-brown with longitudinal bars partially suppressed and dorsal mantle white spots clearly visible. Alarm color-

Table 3. Counts and indices for male *Octopus exannulatus* sp. nov.
(I = immature; S = submature; M = mature; D = damaged; ID = indistinct; — = not recorded; * = OcD1 measured as diameter of black spot).

Museum Reg. No.	QMB Mo29469	NMV F60104	NMV F60104 (Paratype)	QMB Mo29468	NMV F60106 (Paratype)	QMB Mo29473 (Paratype)	USNM 817673 (Paratype)	NMV F60103	WAM 276-88	NMV F60143 (Holotype)
ML	17.7	27.5	37.2	38.9	39.3	39.8	41.5	41.7	45.4	46.7
StM	I	M	M	M	M	M	M	M	M	M
TL	60	90	121	146	140	144	149	142	173	146
MWI	60.5	70.2	65.1	77.6	63.6	59.8	68.4	63.5	62.3	63.2
HWI	65.0	60.7	59.7	48.6	44.5	46.5	51.8	47.7	50.2	48.2
HMWI	107.4	86.5	91.7	62.6	70.0	77.8	75.7	75.1	80.6	76.3
AMI: 1	180.8	167.3	174.7	223.7	239.2	228.6	180.7	175.1	209.3	D
2	169.5	210.9	198.9	239.1	241.7	241.2	204.8	194.2	233.5	D
3	214.7	214.5	198.9	233.9	208.7	D	226.5	247.0	251.1	D
H	169.5	160.0	158.6	218.5	203.6	193.5	197.6	187.1	193.8	192.7
4	220.3	229.1	215.1	259.6	231.6	213.6	238.6	225.4	270.9	D
AWI	15.8	16.4	18.3	20.1	17.3	15.3	15.9	15.6	16.5	15.6
SDI	7.3	10.2	13.2	17.5	11.7	12.1	18.8	15.6	10.6	18.8
WDI	34.4	30.2	27.5	34.7	28.4	32.3	30.3	26.2	27.6	32.6R
GC	7	8	8	7	8	8	8	8	7	7
HAMI	169.5	160.0	158.6	218.5	203.6	193.5	197.6	187.1	193.8	192.7
OAI	78.9	74.6	79.7	93.4	97.6	D	87.2	75.7	77.2	D
HASC	68	68	66	68	74	76	70	62	77	68
LLI	1.3	5.5	5.8	3.5	3.9	3.6	3.7	4.1	4.1	4.2
CLI	ID	25.0	35.3	23.3	19.4	21.4	30.0	28.1	19.4	34.2
TOLI	ID	38.2	37.4	48.1	34.1	46.5	42.2	46.0	36.8	42.8
DLI	ID	38.1	27.3	31.6	33.6	36.8	32.0	28.6	49.1	32.5
SpLI		—	162.4	—	—	—	—	152.3	136.8	—
SpWI		—	0.8	—	—	—	—	0.8	1.1	—
SpRI		—	46.5	—	—	—	—	46.9	37.4	—
SpN		—	—	—	—	—	—	9	—	—
FLI	39.5	33.5	34.1	38.3	37.4	37.7	39.5	41.2	35.9	38.1
FFLI	42.7	61.8	54.3	53.0	57.2	55.4	57.3	49.5	78.6	40.4
FOI	93.5	92.4	89.2	87.5	90.5	91.3	86.1	85.7	ID	94.6
FOLI	65.7	85.9	73.2	64.4	64.6	53.3	65.6	61.0	ID	62.4
OcDI*	20.9	20.0	14.8	21.9	27.5	17.6	21.7	22.1	19.8	18.2

Table 4. Counts and indices for female *Octopus exannulatus* sp. nov.
(S = submature; M = mature; D = damaged; ID = indistinct; — = not recorded; * = OcDI measured as diameter of black spot).

Museum Reg. No.	NMV F60109	WAM 352-88	NMV F60109	NMV F60104	NMV F60104	NMV F60104	NMV F60105 (Paratype)	NMV F60108	QMB Mo29329 (Paratype)	NMV F60107 (Paratype)
ML	23.6	24.4	31.1	34.9	34.9	41.5	41.8	44.5	48.0	53.3
StM	S	S	S	S	S	M	M	M	S	M
TL	96	87D	111	110	114	129	155	181	161	205
MWI	72.0	79.3	76.5	66.8	65.0	68.2	56.2	72.8	60.8	79.2
HWI	57.6	57.9	48.2	56.4	55.6	54.5	43.1	41.8	41.7	42.2
HMWI	80.0	73.0	63.0	84.4	85.1	79.9	76.7	57.4	68.6	53.3
AMI: 1	254.2	231.4	199.4	163.3	166.2	178.3	196.2	206.7	175.0	245.8
2	275.4	D	228.3	197.7	194.8	200.0	220.1	262.9	191.7	251.4
3	296.6	D	241.2	209.2	206.3	209.6	256.0	262.9	208.3	264.5
4	279.7	D	247.6	214.9	217.8	214.5	251.2	285.4	220.8	285.2
AWI	17.4	19.4	16.7	18.1	16.9	18.6	16.5	16.6	13.3	15.2
SDI	8.5	9.5	7.1	8.9	8.3	9.4	7.9	8.8	8.3	7.5
WDI	37.1	—	32.5	32.0	26.3	29.2	25.2	32.3	28.3	24.3
GC	7	7	7	7	8	8	7	8	8	8
ELI						5.5	—	4.9		7.3
EWI						1.7	—	1.6		1.9
EN						>5000	>>1000	>>1000		>>1000
FLI	42.4	45.0	36.0	37.8	34.4	31.8	39.0	38.2	39.6	39.6
FFLI	59.9	D	68.9	69.0	57.6	47.8	57.7	61.8	63.1	53.0
FOI	ID	79.4	ID	87.9	94.7	97.2	93.1	85.1	87.6	90.3
FOLI	ID	62.4	ID	75.0	78.3	80.3	62.6	59.4	67.9	58.8
OcDI*	28.8	28.5	18.0	18.3	16.9	15.9	22.7	19.3	19.6	21.2

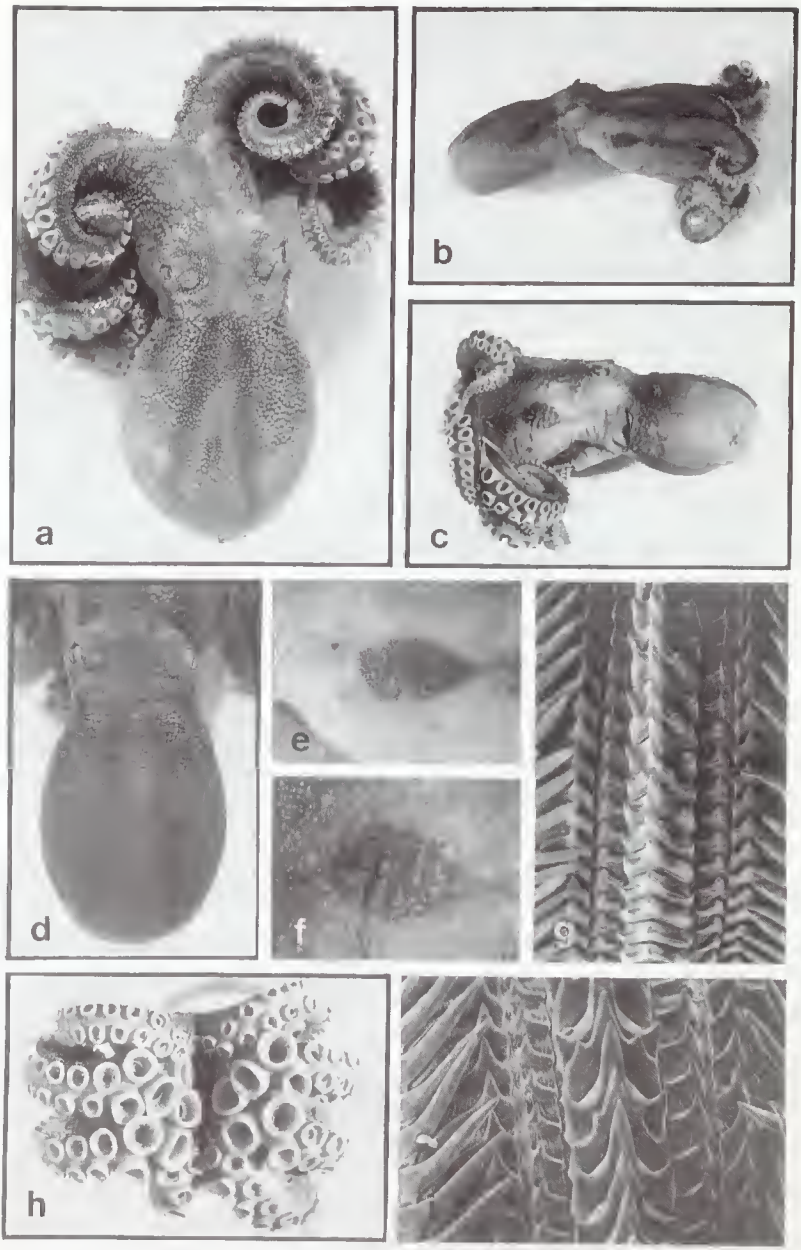
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Figure 10. Photographs of preserved specimens of *Octopus exannulatus* sp. nov. a, dorsal view of 41.5 mm ML male (USNM 817673). b, lateral view of 41.8 mm ML female paratype (NMV F60105). c, lateral view of 46.7 mm ML male paratype (USNM 817673). d, dorsal view of 41.8 mm ML female (NMV F60105). e, ocellus of 41.8 mm ML female paratype (NMV F60105). f, ocellus of 46.7 mm ML male paratype (USNM 817673). g, i, radula of 34.9 mm ML female (NMV F60104). h, enlarged suckers of 41.5 mm ML mature male (USNM 817673).

ation consisted of red-brown longitudinal bars over white base colour.

Sexual dimorphism is not marked in this species. Both sexes attain approximately equal maximum size. Mature males possess 2–4 enlarged suckers on arms 2 and 3 at level of third sucker pair (SDI♂ mean *14.3*; ♀ mean *8.4*). Females appear to possess more suckers than males (SC♀ 136-*154*-188; ♂ mean 123-*137*-162, difference not significant at P = 0.05 level).

Distribution. *Octopus exannulatus* is recorded from tropical Australian waters (fig. 15e), from Shark Bay, Western Australia (24°49′S, 113°33′E) to Gulf of Carpentaria, Torres Strait and south to Moreton Bay, southern Queensland (27°15′S, 153°15′E).

Life history. It has been collected from exposed intertidal mudflats to 84 m deep, on muddy, sandy and shelly sand substrata. This species appears to inhabit open bottom substrata and seagrass beds.

Prawn trawler operators fishing within Great Barrier Reef waters report catches of this distinctive species in trawls on sand or muddy substrates.

Commercial exploitation. *Octopus exannulatus* occurs in fairly low numbers in the by-catch of Moreton Bay, Great Barrier Reef and Gulf of Carpentaria trawl fisheries, particularly prawn fisheries. This species is often retained for use as bait. No information is available on scale of catch.

Etymology. From the Latin, *ex* (without) and *annulus* (ring), referring to the simple black ocellus which lacks an iridescent ring.

Remarks. Lu and Phillips (1985) reported this species under the name *O. membranaceus* Quoy and Gaimard, 1832. Despite the poor condition of the type of *O. membranaceus*, it clearly possesses an iridescent ring within its ocellus, easily distinguishing it from *O. exannulatus*.

Octopus mototi sp. nov.

Figs 1f, 11–14, 15d

Octopus membranaceus. — Loch, 1987: 8, textfigs. (non Quoy and Gaimard, 1832)

Material examined. 2 live *O. mototi* were encountered on offshore islands at the southern end of the Great Barrier Reef. 8 preserved specimens were examined in Australian museum collections, the National Museum of Natural History, Washington and the Muséum National d'Histoire Naturelle, Paris.

Holotype: Qld: 1♂; 66.2 mm ML, NMV F60101, Capricorn Bunker Group, Heron I., 23°50′S, 152°25′E, 31 m, M. Norman and R. Fenwick, 30 Aug 1990 (raised in pot at 0945 hr, on sandy bottom in channel on N side of island).

Paratypes: Qld: 1♀: 58.6 mm ML, NMV F60102, Capricorn Bunker Group, One Tree I., 23°30′S, 152°05′E, 1 m, M. Norman and R. Fenwick, 7 Sep 1990 (deep in lair, 1415 hr, in dead coral within lagoon, on sand, flushed with $CuSO_4$); 1♀: 73.3 mm ML, AM C154277, Coral Sea, Wreck Reef, NE of West Islet, 22°12′S, 155°10′E, 12 m, P. Cook and B. Bately, 30 Oct 1983 (in lair during day, under dead staghorn clump on sand, caught by hand on SCUBA); 1♀: 76.7 mm ML, QMB Mo29325, Swains Reef, 21°46.9′S, 152°50.0′E, 54 m, C. Jones, Swains Reef Survey Station 12, 27 July 1987 (trawled with Seibenhausen net).

Austral Is: 1♂: 70.5 mm ML, USNM 817681, Rapa I., about 27°36′S, 144°20′W, G. Paulay, 6 Jun 1980 (captured by local islanders).

Other material: Qld: 1♂: about 55 mm ML (in two pieces, arm crown with intact arms and bulk of body; head missing), QMB Mo29466, no locality data; 1♂: 60.6 mm ML, NMV F60142, off Caloundra, 26°40′S, 153°16′E, 22 fm (40.3 m), Adam Butcher, QDPI, "San Antone", 22 Jul 1991 (prawn trawl, just before dusk).

New Caledonia: 1♀: 100.0 mm ML, MNHN 2010, off Noumea, (about 22°30′S, 166°40′E), Alan Gerbault, no date; 1♀: 100.5 mm ML, MNHN 2011, North Lagoon, (about 22°30′S, 166°40′E), 1990.

Diagnosis. Moderate sized species with black oval ocellus containing irideseent blue ring. Circular cluster of dark spots above each eye forms "flower" pattern. Alarm colour pattern of white base colour and 6 dark maroon longitudinal stripes on dorsal body and arm crown. 9–11 gill lamellae per demibranch, typically 11. Approximately 160 suckers per arm, roughly equal in number in both sexes in the material available (SC♂ 149, 176; ♀ 143–*159*–172, n = 4♀♀), approximately 100 suckers on hectocotylized arm. Terminal organ short and robust (TOLI about 20). Spermatophores of moderate length (SpLI about 70) and produced in low numbers

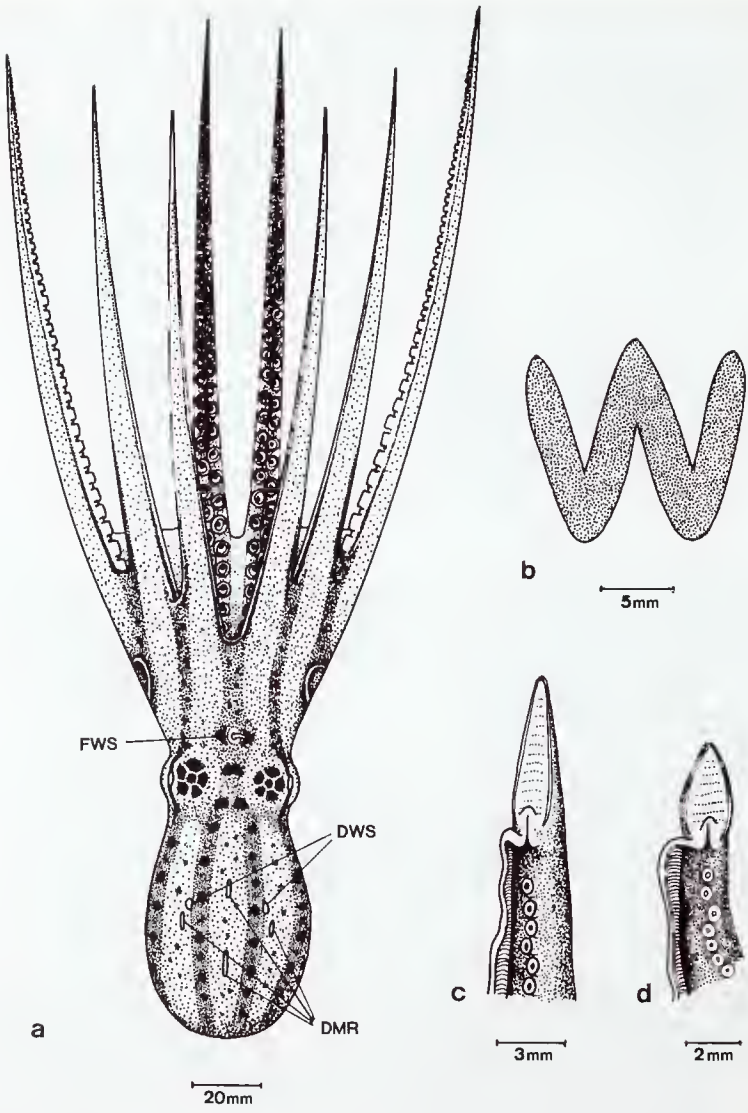

Figure 11. *Octopus mototi* sp. nov. a, dorsal view of 73.3 mm ML female paratype (AM C154277): DMR = dorsal mantle ridges; DWS = dorsal white spots; FWS = frontal white spot. b, funnel organ of 58.6 mm ML female paratype (NMV F60102). c, copulatory organ of 66.2 mm ML holotype (NMV F60101). d, copulatory organ of 70.5 mm ML paratype (USNM 817681).

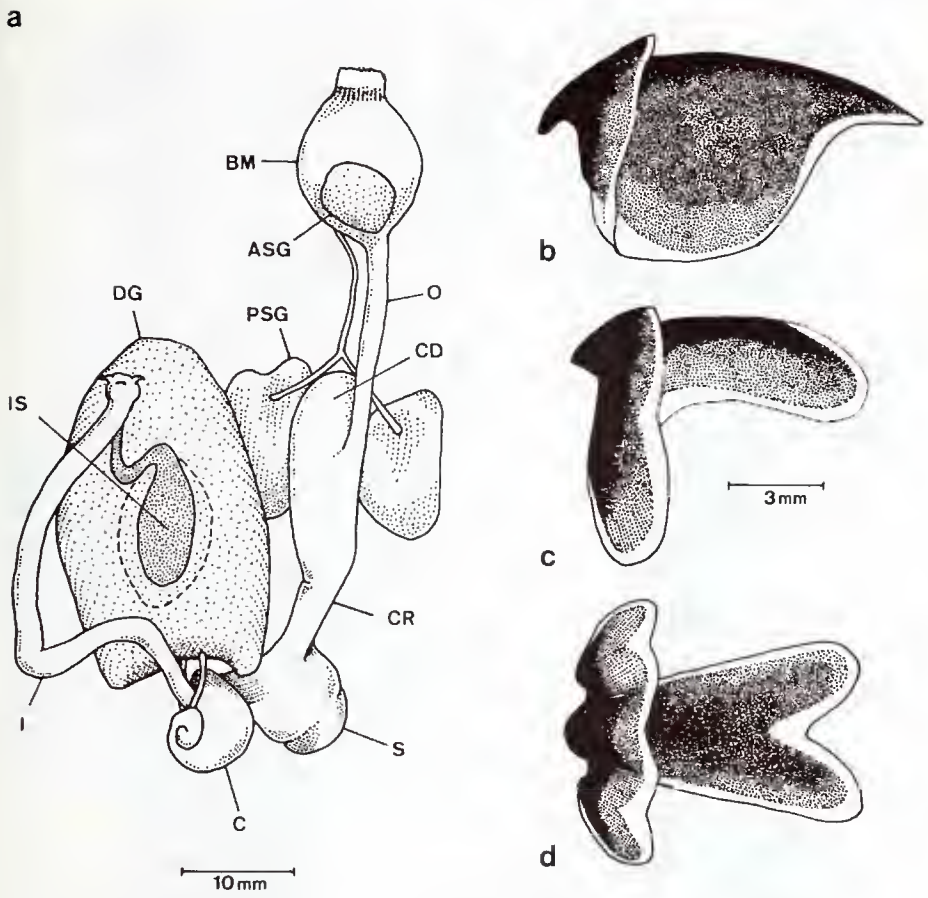

Figure 12. *Octopus mototi* sp. nov. a, digestive tract of 58.6 mm ML female paratype (NMV F60102); hatched line indicates volume of ink sac embedded within digestive gland (for key to symbols see fig. 4). b, upper beak, lateral view of same specimen. c, lower beak, lateral view of same specimen. d, lower beak, ventral view of same specimen.

numbers (SpN <10). Eggs moderately small, ovarian eggs to 6 mm, spawned egg capsules to 3.2 mm [ELI(ov) to 7.8, ELI(sp) to 4.2], produced in large numbers (EN >10 000).

Description. Based on 3 mature males, and 1 submature/mature and 4 mature females. Counts and indices in Table 5 and 6.

Moderate sized, robust species (figs 1f, 11a): ML to at least 70 mm for males and 100 mm for females, TL to at least 320 mm; weight to at least 300 g. Mantle ovoid (MWI 52.8–*64.3*–70.4), mantle walls thick and muscular. Stylets not found. Pallial aperture of moderate length, approximately half mantle width. Funnel muscular and broad based (FLI 34.5–*37.1*–40.0) with free portion usually greater than half funnel length (FFLI 43.5–*64.0*–82.6). Funnel organ W-shaped with broad limbs (fig. 11b). Outer limbs slightly shorter than median limb (FOI

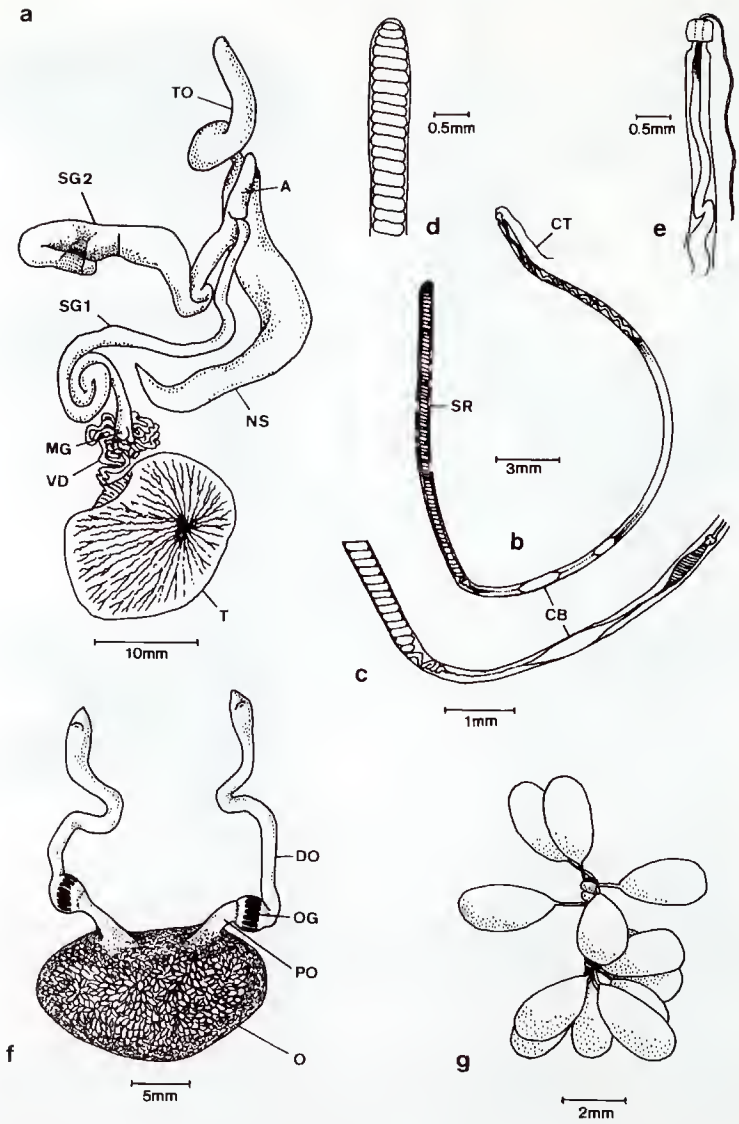

Figure 13. *Octopus mototi* sp. nov. a, male reproductive tract of 66.2 mm ML holotype (NMV F60101): for key to symbols see fig. 5.; A = appendix. b–e, spermatophore from same specimen. b, entire spermatophores: CB = cement body; CT = cap thread; SR = sperm reservoir. c, midsection indicating position of cement body. d, oral cap. e, aboral cap bearing cap thread. f, ovary of 58.6 mm ML female paratype (NMV F60102): DO = distal oviducts; O = ovary; OG = oviducal gland; PO = proximal oviduct. g, section of festoon of spawned eggs from 76.7 mm ML female paratype (QMB Mo29325).

Table 5. Counts and indices for male *Octopus mototi* sp. nov.
(M = mature; D = damaged; — = not recorded; ID = indistinct; # = specimen frozen, hectocotylized arm distorted at tip; * = OcD1 measured as diameter of iridescent ring).

Museum Reg. No.	NMV F60101 (Holotype)	USNM 817681 (Paratype)	NMV F60142	QMB Mo29466
ML	66.2	70.5	60.6	~55
StM	M	M	M	M
TL	255	260	D	~192
MWI	70.4	65.7	52.8	D
HWI	52.7	46.4	42.7	D
HMWI	74.8	70.6	80.9	D
AMI: I	226.6	228.4	D	~201.8
2	271.9	235.5	D	~232.7
3	268.9	249.6	D	D
H	250.8	217.0	236.0	~221.8
4	249.2	252.5	D	~258.2
AWI	18.6	14.9	13.4	~12.4
SDI	13.0	9.4	10.1	~6.9
WDI	25.6	29.8	D	D
GC	11	11	10	10
HAMI	250.8	217.0	236.0	~221.8
OAI	93.3	86.9	D	D
HASC	100	106	95	103
LLI	5.4	3.1	6.7#	~2.0
CLI	36.7	48.9	54.2#	D
TOLI	25.7	20.0	24.9	~15.5
DLI	37.1	30.5	46.4	49.4
SpLI	70.2	59.4	D	—
SpWI	1.3	1.2	D	—
SpRI	34.8	35.3	D	—
SpN	—	5	6	—
FLI	40.0	35.9	34.5	D
FFLI	82.3	43.5	49.3	D
FOI	ID	86.6	100	D
FOLI	ID	56.1	63.6	D
OcDI*	14.4	15.9	18.2	~15.6

85.5–*91.0*–100.0). Funnel organ large, approximately 60% of funnel length (FOLI 56.1–*61.1*–63.9).

Head of moderate width (HWI 46.4–*49.3*–56.6), always narrower than mantle (HMWI 70.6–*76.7*–81.1). Neck distinct, slightly narrower than head. Eyes large and slightly pronounced.

Arms of moderate length, 2.5–3 times ML, slightly longer in females of material examined (AMI♂ 252.5, about 258, 268.9; ♀ 261.7–*292.2*–314.0). Arms robust (AWI 10.5–*15.5*–24.6), square in cross section and tapering rapidly to fine tips in distal third. Dorsal arms shortest, lateral and ventral pairs longer and more robust (AF typically 4=3.2.1). Suckers of moderate size, slightly elevated with distinct radial cushions and scalloped rim. Suckers approximately equal in size for both sexes in limited specimens available (SDI♂ about 6.9, 9.4, 10.1, 13.0; ♀ 10.5–*11.3*–13.6). The holotype exhibits slight enlargement of several suckers at level of fifth to sixth sucker pair on arms 2 and 3. Arms 3 or 4 possess most suckers, approximately 160 per arm, roughly equal in number in both sexes in available material (SC♂ 149, 176; ♀ 143–*159*–172, n = 4). Webs moderate to deep (WDI 25.6–*30.4*–38.8), deepest laterally, dorsal web distinctly

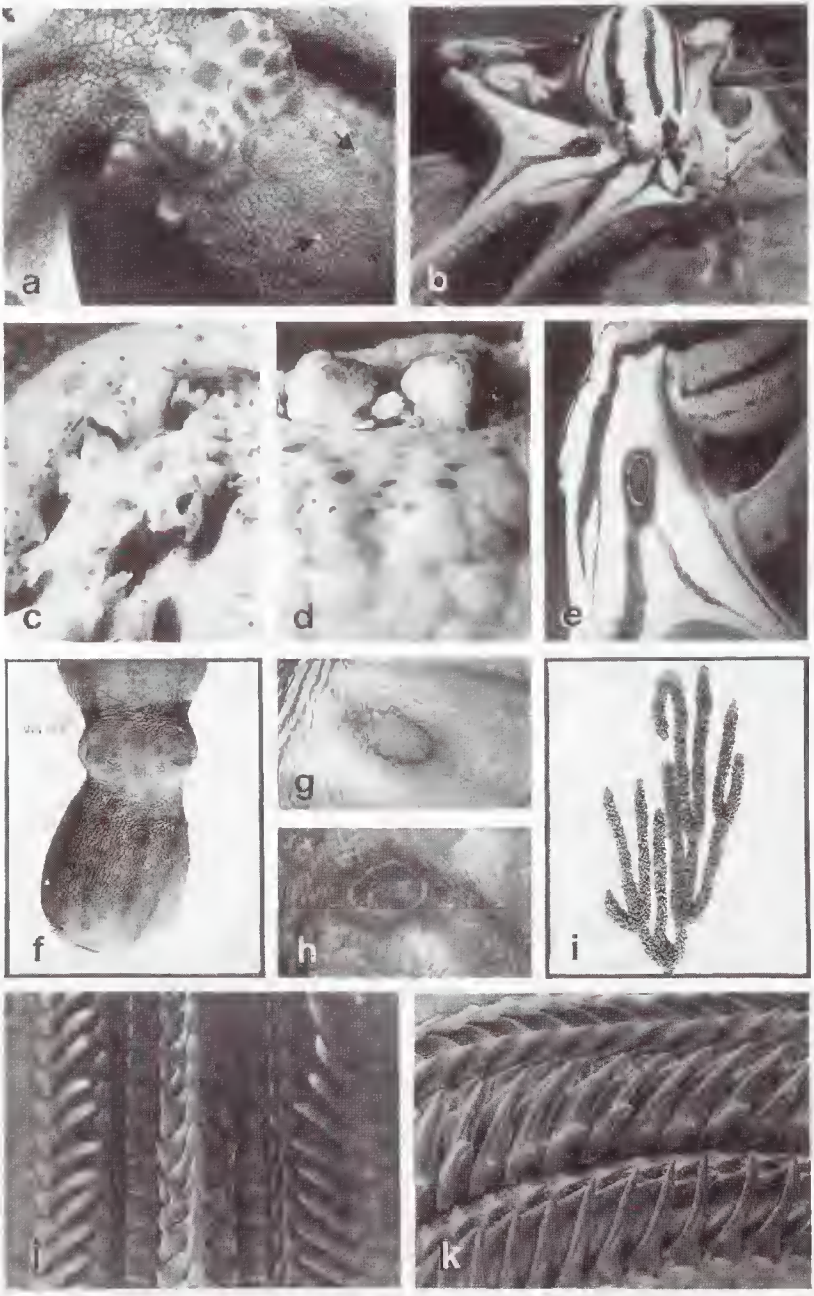
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Figure 14. Photographs of *Octopus mototi* sp. nov. a–e, colour patterns of live animals: a, resting colouration of 66.2 mm ML male holotype (NMV F60101); arrows indicate dorsal white spots. b, alarm coloration of 58.6 mm ML female paratype (NMV F60102). c, wild animal in Coral Sea, emerging from conch shell displaying eye bar and "flower" pattern above each eye (Photo courtesy of Neville Coleman). d, posture of arms drawn back along body exposing suckers, beak and displaying frontal white spot and spotted oral surface of dorsal web (58.6 mm ML female paratype: NMV F60102). e, alarm colouration of same specimen. f, colour pattern in preserved 73.3 mm ML female paratype (AM C154277). g, preserved ocellus of same specimen. h, preserved ocellus of 76.7 mm ML female paratype (QMB Mo29325). i, festoon of spawned eggs from same specimen. j, k, radula of 58.6 mm ML female paratype (NMV F60102).

shorter (WF typically D.C=E.B.A). Web margins extend along approximately 60% of ventral edges of arms.

Third right arms in males hectocotylized and slightly shorter than opposite arm (OAI: 86.9, 93.3; HAMI: 217.0, about 222, 236.0, 250.8). Spermatophore groove well developed and wide with fine transverse ridges. Spermatophore guide distinct with cross ridges but no obvious papillae. Copulatory organ small (fig. 11c: LLI 3.1, 5.4 for 2 mature males, 6.7 in distorted frozen specimen, NMV F60142), ligula roughly conical; groove wide and shallow bordered laterally by fine skin ridges. Calamus medium size and slightly raised (CLI 36.7, 48.9). Copulatory organ on male from Rapa I. (USNM 817681) slightly shorter and broader (fig. 11d) than that of holotype, but still bears distinctive skin ridges bordering ligular groove. Approximately 100 suckers on hectocotylized arm (HASC: 95–*101*–106).

Gills with 9–11 lamellae, typically 11, on both inner and outer demibranches, plus a terminal lamella.

Table 6. Counts and indices for female *Octopus mototi* sp. nov.
(S = submature; M = mature; D = damaged: — = not recorded; ID = indistinct: # = from ovarian eggs, capsule of spawned eggs much shorter; ## = counted from festoons of spawned eggs; * = OcDI measured as diameter of iridescent ring).

Museum Reg. No.	NMV F60102 (Paratype)	AMS C154271	QMB Mo29325 (Paratype)	MNHN 2010	MNHN 2011
ML	58.6	73.3	76.7	100.0	100.5
StM	M	S/M	M	S/M	M
TL	228	290	324	425	366
MWI	69.6	65.3	69.8	D	56.5
HWI	51.9	52.7	56.6	D	41.9
HMWI	74.6	80.7	81.1	D	74.1
AMI: 1	240.6	252.4	D	271.0	210.0
2	261.1	274.2	286.8	294.0	D
3	D	307.0	305.1	293.0	261.7
4	273.0	286.5	D	314.0	243.8
AWI	16.2	10.5	24.6	16.1	12.8
SDI	11.6	10.5	13.6	10.5	10.5
WDI	26.9	32.0	29.5	38.8	D
GC	11	10	9	10	10
ELI	—	—	7.8#	—	—
EWI	—	—	1.7#	—	—
EN	—	—	~10 700##	—	>>1000
FLI	39.2	38.5	34.6	36.7	D
FFLI	73.5	58.2	82.6	58.3	D
FOI	91.8	85.5	ID	ID	ID
FOLI	63.9	61.0	ID	ID	ID
OcDI*	13.7	19.1	16.6	14.3	14.0

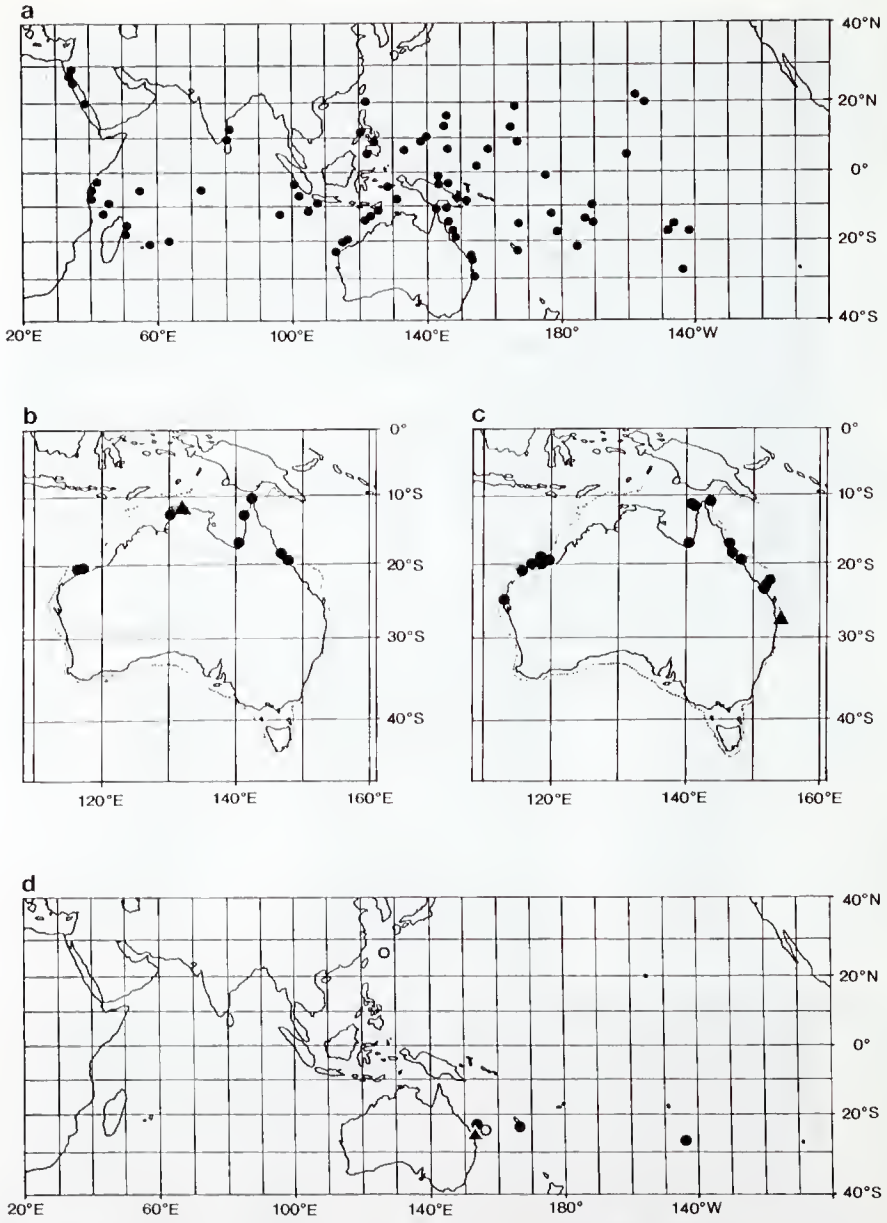

Figure 15. Distributions of Great Barrier Reef ocellate octopuses. a, *Octopus cyanea* Gray, 1849: ● = material examined. b, *Octopus polyzenia* Gray, 1849: ▲ = type locality; ● = other material examined. c, *Octopus exannulatus* sp. nov.: ▲ = type locality; ● = other material examined. d, *Octopus mototi* sp. nov.: ▲ = type locality; ● = other material examined; ○ = photographic records.

Digestive tract illustrated in figure 12a. Anterior salivary glands of moderate size, approximately half buccal mass length. Posterior salivary glands well developed, approximately equal in length with buccal mass. Crop diverticulum distinct. Stomach bipartite. Caecum coiled in single whorl. Intestine poorly preserved in dissected specimen, reflexed at proximal third, rectum not distinct. Ink sac well developed, embedded in ventral surface of digestive gland. Anal flaps present and fine. Membrane on dorsal surface of visceral mass pigmented with large dark chromatophores, remnants of larval or founder chromatophores.

Upper beak (fig. 12b) with moderate hood and short hooked rostrum, concave on cutting edge. Lower beak (figs 12c–d) with blunt rostrum, narrow hood, widely spread wings and moderately flared lateral walls producing moderately concave posterior margin from ventral view. Radula with seven teeth and two marginal plates in each transverse row (figs 14j–k). Rhachidian tooth with 1–2 lateral cusps, typically 1, on either side of a robust medial cone. Lateral cusps are in symmetrical seriation, migrating from lateral to medial position over 4–6 rows. First lateral teeth unicuspidate with cusp towards lateral edge; second lateral teeth unicuspidate and long with curved base; lateral marginal teeth long, straight and robust; marginal plates oblong and plain.

Male reproductive tract illustrated in figure 13a. Terminal organ in mature males moderate to large and robust (TOLI about 15.5, 20.0, 24.9, 25.7), diverticulum moderate sized (DLI 30.5–40.9–49.4), genital aperture subterminal. Vas deferens thin and of moderate length. Mucilaginous gland enlarged at point of attachment to vas deferens. Spermatophoric gland I robust with large recurved coil approximately three-quarters along length. Spermatophoric gland II long and robust, tip reflexed. Appendix present at junction of spermatophoric glands and Needham's sac. Needham's sac moderately short, tapering to fine point at posterior end. Spermatophores (fig. 13b–e) of medium length (SpLI 59.4, 70.2) and fine (SpWI 1.2, 1.3), produced in low numbers (<10 in Needham's sac of holotype; 4 in Rapa I. male, 6 in NMV F60142). Oral cap simple, showing slight restriction below tip, bearing long cap thread. Sperm reservoir approximately one third of spermatophore length (SpRI 34.8, 35.3). Sperm cord coiled in approximately 75 coils (holotype: 76; Rapa I. male: 75).

Mature ovary oval shaped (fig. 13d). Distal oviducts robust and reflexed midway along length, extending to level of anus and flattened distally. Proximal oviducts originate laterally on ovary, not obviously from common origin in specimen examined. Oviducal glands large with 16–20 radiating (braiding) chambers. Eggs (fig. 13g) medium sized, ovarian eggs to 6 mm total length [ELI(ovarian) to 7.8], spawned eggs with smaller capsule to 3.2 mm [ELI(spawned) to 4.2]. Eggs moderately wide [EWI(ovarian) 1.7; EWI(spawned) 2.0] and produced in large numbers (about 10,700 eggs accompanied 76.7 mm ML female, QMB Mo29325). Eggs laid in long branching festoons (fig. 14i). Approximately 6 follicular folds on immature ovarian eggs.

Colour in life variable. Ocellus on each side of arm crown between bases of second and third arms, each containing a large iridescent blue ring (figs 14e, g–h; OcDI for iridescent ring 13.7–15.9–19.1). Iridescent ring masked in some colour patterns, exaggerated by dark background in alarm colouration (fig. 14e).

Resting animals exhibit orange-cream base colour with darker brown spots in six longitudinal series along dorsal body (fig. 14a). Cluster of 5 large spots around a central spot above each eye, form "flower" pattern (fig. 11a, 14a). "Flower" pattern often visible in specimens within, or partially emerged from, lairs (fig. 14c). Circular frontal white spot visible on dorsal arm crown just below eyes, containing thin erectile papilla (fig. 11a). Small pair of dorsal white spots midway along dorsal mantle visible over darker resting base colour (fig. 11a, 14a).

Alarm display of distinctive striped colour pattern over white base (fig. 14b, e). 6 solid dark maroon longitudinal stripes form on dorsal body extending on to arm crown and down ventral edges of arms. Median pair of dorsal stripes extend to near eyes, dorsolateral pair continue through eyes down ventral edge of arm 1, and lateral pair cease at pallial aperture. Additional medial stripe commences between eyes, divides each side of frontal white spot and rejoins to continue to margin of dorsal web, fine stripe continuing down dorsal edge of arm 1. Dark oval spot can be expressed under iridescent ring of ocelli, extending distally to form wide stripe down ventral edge of arm 2 and fine stripe down dorsal edge of arm 3 (fig. 14e). "Flower" pattern of spots above eyes sometimes pronounced in alarm displays, other times suppressed. Alarmed individuals often retreat into crevices or corners and raise arms over body to display frontal white

spot, suckers and beak. In this posture, dark spots are clearly visible against white base on oral face of dorsal and dorsolateral webs (fig. 14d). This characteristic pattern is clearly visible on individuals deep within lairs.

Skin sculptured in patch and groove system consisting of oval to round patches (fig. 14a), extending on to oral surface of dorsal and dorsolateral webs and arm faces. Raised erectile papilla in centre of frontal white spot distinct in most colour patterns. 4 longitudinal skin ridges in diamond arrangement on dorsal mantle (fig. 11a). Single small supraocular papilla above and slightly behind each eye in centre of "flower" pattern of spots.

Skin sculpturing and some colour patterns are visible in preserved specimens (figs 14f–h).

Sexual dimorphism is not marked in the few specimens examined. Females attained largest size in available material, 100 mm ML versus 70 mm ML in males. Females appear to have slightly longer arms than males (AMI♂ 252.5, about 258.2, 268.9; ♀ 261.7–*292.2*–314.0).

Distribution. *Octopus mototi* is reported from eastern Australian waters: Capricorn-Bunker Group, southern end of the Great Barrier Reef; Swains Reefs and Wreck Reef, Coral Sea. Neville Coleman (pers. comm.) provided an additional record of this species from Saumarez Reef, Coral Sea (21°45′S, 153°40′E), photographing an individual at 10 m on sand occupying a large gastropod shell (fig. 14c). This species is also recorded from the South Pacific (fig. 15d): New Caledonia (22°33′S, 166°40′E) and Rapa I. (27°36′S, 144°20′W). Dr Okutani (Tokyo University of Fisheries) has a 77 mm ML female specimen of this species from Okinawa, south of Japan (26°30′N, 128°00′E). Photographs of this specimen kindly provided by Dr Okutani show the characteristic "flower" pattern above the eyes, longitudinal rows of spots on dorsal mantle and display of black spots on oral surface of dorsal web.

Octopus mototi has been collected from shallow subtidal depths (<1 m) down to 54 m, on sandy substrates near coral or coral rubble in clear water.

Life history. *Octopus mototi* appears to favour sandy substrata, often associated with coral heads or rubble. Deep lairs are excavated under coral heads or coral rubble. From limited observations, this species appears to have crepuscular activity patterns.

Examination of stomach and intestine contents found a high proportion of crustacean exoskeleton fragments. The lair of one specimen collected from One Tree I. lagoon was surrounded by discarded gastropod shells. It is likely that *O. mototi* preys on hermit crabs, discarding empty gastropod shells outside the mouths of lairs. Loch (1987) documented the shells surrounding the lair of the Swains Reef specimen (AM C154277) which included 15 gastropod species, predominantly *Fusinus undatus* and *Strombus* spp. Loch noted many shells exhibited two drill holes, one produced by naticid gastropods, the other by an octopus. Loch suggested that this was consistent with this octopus species drilling these shells to prey on secondary occupants, namely hermit crabs.

Eggs are laid in large numbers in festoons (fig. 14i). It is not known whether eggs are attached to the substrate or carried in the web of the female. This species lays small eggs indicating hatchlings are planktonic.

Octopus mototi may prove to be venomous. This species has a prominent warning colouration and is known locally on Rapa I. as the "poison octopus" (G. Paulay, pers. comm.). The two specimens encountered in the field showed a willingness to bite objects such as aquarium nets, a behaviour not observed in other Great Barrier Reef octopuses.

Etymology. On Rapa I., South Pacific (27°36′S, 144°20′W) the local name attributed to this octopus is "*fe'e mototi*", "*fe'e*" meaning octopus and "*mototi*" meaning poison, referring to the reported poisonous nature of this distinctive species (G. Paulay, USNM, pers. comm.) (noun in apposition).

Discussion

Systematics. Ocellate octopuses are found in two separate regions of the world: i) the Indo-West Pacific centred in the tropical waters of southeast Asia and tropical Australia; and ii) the Americas, centred on the east and west coasts of central America.

Fifteen species and three subspecies of ocellate species have been described from Indo-West Pacific waters (Table 7). Of these many are inadequately described, lack type material or are synonymous with others. The list can be reduced to eight apparently valid taxa from these waters (including the two new species described here): "iidako" (*O. areolatus* d'Orbigny, 1839 / *O. fangsiao* d'Orbigny, 1839 / *O. ocellatus* Gray, 1849); *O. polyzenia* Gray, 1849; *O. cyanea* Gray, 1849; *O. ovulum* Sasaki, 1917; *O. robsoni* Adam,

Table 7. List of nominal species of ocellate octopuses described from Indo-West Pacific waters.

Species		Type locality	Remarks
Octopus membranaceus Quoy and Gaimard, 1832		Papua New Guinea	Nomen dubium: type damaged
Octopus pulcher Brock, 1887		Amboina	Nomen dubium: type lost
"iidako": Probable synonyms			
	Octopus areolatus d'Orbigny, 1839	Japan	Valid
	Octopus fangsiao d'Orbigny, 1839	Japan	—
	Octopus ocellatus Gray, 1849	China	—
	Octopus brocki Ortmann, 1888	Japan	—
	Polypus fangsiao typicus Sasaki, 1929	Japan	—
	Polypus fangsiao etchuanus Sasaki, 1929	Japan	—
Octopus polyzenia Gray, 1849		Australia, Nth Territory	Valid
Octopus cyanea Gray, 1849		"Coasts of New Holland" (= Australia)	Valid
Synonyms	*Octopus marmoratus* Hoyle, 1885	Hawaii	—
	Octopus horsti Joubin, 1898	Red Sea	—
	Octopus herdmani Hoyle, 1904	Ceylon	—
	Octopus cyanea gracilis Robson, 1929	Madras	—
	Callistoctopus magnocellatus Taki, 1964	Japan	—
Octopus ovulum Sasaki, 1917		"Japan" (questionable)	Status unclear
Octopus robsoni Adam, 1941		Red Sea	Valid
Octopus varunae Oommen, 1971		West coast of India	Possible synonym of *O. robsoni*

1941, *O. varunae* Oommen, 1971, *O. exannulatus* sp. nov.; and *O. mototi* sp. nov.

The presence of an iridescent ring (ie. metallic blue, gold, silver or green colours produced by iridophores) within the ocellus of some species has been noted by many workers (e.g., Brock, 1887; Robson, 1929; Sasaki, 1929; Adam, 1959, Okutani et al., 1987). Voss (1963) suggested that the presence of this ring depended on the nature and duration of preservation. Adam (1973) disputed this and proposed that this character was constant within and between species. Adam's proposal holds true for the material examined in this study. There were no inconsistencies in the several hundred specimens examined. The iridescent ring found in the ocellus of species such as *O. polyzenia* and *O. mototi* was always visible even in poorly preserved material. Similarly, more than 200 specimens of *O. cyanea* and *O. exannulatus* were examined and none possessed an iridescent ring.

The absence of the iridescent ring in *O. cyanea* and *O. exannulatus* is sufficient to distinguish these taxa from those listed above, as all of the remaining species possess this iridescent ring. Several taxa require additional comment.

(1) "tidako". There appears to be a single common ocellate species in shallow coastal waters from Japan to Hong Kong, which in Japan goes under the common name "tidako". It is characterised by a large green to gold iridescent ring within each ocellus, a dumbbell-shaped head patch, 7–8 gill lamellae and large eggs (7–10 mm). Gleadall and Naggs (1991) proposed that this species should be assigned the name *O. fangsiao* d'Orbigny, 1839, a name d'Orbigny derived from earlier Japanese descriptions of this distinctive species (Terajima, 1713; Katsuma, 1762). No type material was designated. *Octopus areolatus* also was described by d'Orbigny in the same work (1839) and has page priority. The original description is inadequate, having been based on a description provided in a letter from De Haan but the two syntypes of *O. areolatus* collected by De Haan from Japan are in the Royal Museum in Leiden (collection numbers 490 and 2438). These types are clearly specimens of "tidako". The latter name is therefore the valid senior synonym but the status of these two names requires further clarification. In this discussion, this taxon is referred to by the vernacular name, "tidako". The following nominal taxa are considered synonymous:

Octopus areolatus d'Orbigny, 1839, *Octopus fangsiao* d'Orbigny, 1839; *Octopus ocellatus* Gray, 1849, *Octopus brocki* Ortmann, 1888; *Polypus fangsiao typicus* Sasaki, 1929; *Polypus fangsiao etchuanus* Sasaki, 1929.

Octopus polyzenia is similar to "tidako" in sharing large eggs, iridescent ring within ocellus and moderately low gill count (6–7 vs 7–8). However it differs in possessing widely spaced transverse bars on all arms and lacks the gold/brown dumbbell-shaped patch on the head between the eyes, characteristic of "tidako". These colour patterns are consistent on all specimens examined of both *O. polyzenia* and "tidako" (over 30 of the latter species have been examined in NMV, AM, QMB, NMNH, CAS, BMNH and MNHN collections). *Octopus polyzenia* is also distinct from this taxon in having a lower hectocotylized arm sucker count (about 50 vs 90+) and in possessing enlarged suckers on all arms at the level of the seventh row (vs. enlarged suckers on arms 2 and 3 only at the third row in "tidako"). "tidako" occurs in northern hemisphere warm temperate waters and consequently its distribution is unlikely to extend to Australia.

(2) *Octopus membranaceus* Quoy and Gaimard, 1832 has been reported widely throughout the Indo-West Pacific region. The type is in the Muséum d'Histoire Naturelle, Paris (MNHN 4-7-922) and was examined in November 1991. It is a small immature female (22.0 mm ML) in poor condition. Despite this condition, an iridescent ring within each ocellus is still clearly visible. The inadequate original description and the badly damaged type do not allow further clarification of this species. The name is here proposed as *nomen dubium*. All previous reports of this species and, where possible, the original specimens need to be re-examined. The name has been used in Japan and Hong Kong, applied to "tidako" (Tryon, 1879; Cox, 1882; Voss and Williamson, 1971; Lam and Chiu, 1983; Roper, Sweeney and Nauen, 1984; Khromov, 1990). Voss (1963) reported this species from the Philippines based on a single female specimen (20.0 mm ML, USNM 575405). This specimen was examined in the USNM in October 1990. It lacks the iridescent ring in the ocellus and appears to be an undescribed species.

There are two reports of *O. membranaceus* from Australian waters. Odhner (1917: 12, 70) reported this species from the north west coast of Western Australia on the basis of three small ocellated specimens, the largest with a mantle length of 17 mm. No description was provided and the specimens have not been traced to date. At least four species of ocellated octopus occur in these waters and Odhner's specimens may

belong to one or more of these taxa. It is unlikely that this record will be resolved unless the original material surfaces. Lu and Phillips (1985: 33) reported *O. membranaceus* from Moreton Bay and the Gulf of Carpentaria. These reports refer to specimens of the new species, *O. exannulatus*.

(3) *Octopus ovulum* Sasaki, 1917 was described as a small-egg species based on material purchased from Tokyo Fish Market. No subsequent records of a small-egg ocellate species in Japanese waters have emerged and it is possible that Sasaki's material originated from outside Japanese waters. The type material may have been collected from tropical Indo-West Pacific waters and transported to Japan for sale. Sasaki's description of this species shows some similarities with an undescribed species from Thai waters. Further study will be required to resolve the status of this taxon.

(4) *Octopus robsoni* Adam, 1941 was described from the Red Sea. The type material is in the Muséum National d'Histoire Naturelle, Paris and was examined in November 1991. This moderately small species is aligned with the small Indo-Malayan ocellates. It lays moderately small eggs (ovarian eggs about 5 mm long), has 10 gill lamellae per demibranch and a fine purple iridescent ring in the ocellus. Mature males possess a very long fine copulatory organ (LLI 9.0) and two to three enlarged suckers at the level of the third sucker pair on arms 2 and 3, with slightly enlarged suckers on arm 4. This combination of characters distinguishes this species from the ocellate species of the Great Barrier Reef.

(5) *Octopus varunae* Oommen, 1971 was described from four males and two females collected from 125–135 m off the west coast of India. This species is known only from the original description. It possesses an ocellus with an iridescent ring, lays small eggs (ovarian eggs about 2 mm long), has 10 gill lamellae per demibranch and a long narrow copulatory organ. No material of this species has been examined by the author. *Octopus varunae* shows many similarities with *O. robsoni* and further study is required to delineate these forms. It is distinct, however, from Great Barrier Reef ocellate octopuses.

Table 8 summarises the character states of the Great Barrier Reef ocellate octopuses and compares them with known characters for other Indo-West Pacific ocellates. Data for the latter group of species is taken from original descriptions ("iidako" from Sasaki, 1929 as *O. fangsiao*

Table 8. Comparison of Great Barrier Reef and other ocellate octopuses of the Indo-West Pacific region.

	Great Barrier Reef species				Indo-West Pacific species			
	O. cyanea	*O. polyzenia*	*O. exannulatus*	*O. mototi*	"iidako"	*O. ovulum*	*O. robsoni*	*O. varunae*
Size (ML)	to 160 mm	to 38 mm	to 50 mm	to 100 mm	>50 mm	to 40 mm	to 60 mm	to 60 mm
Arm length (AMI)	400–580	200–310	215–290	250–310	220–360	180–280	240–280	160–230
Iridescentring	no	yes	no	yes	yes	yes	yes	yes
Gill count (GC)	9–10–11	6–7	7–8	9–11	7–8	7–8	8–10	10
Sucker count (SC)	>400	103–135	120–190	140–180	—	—	110–150	—
Hect. Arm SC (HASC)	160–*199*–229	45–*50*–52	62–*70*–77	95–*101*–106	90–140	120–140	61	—
Egg size (mm)	2.7 ov	7.5 sp	3.9 ov	3.2 sp	10 ov.	3 ov.	5.2 ov.	2 ov.
Egg Length Index (ELI)	1.7 ov	22.9 sp	7.3 ov	4.2 sp	~20 ov.	6.7 ov.	8.8 ov.	3.3 ov.
Spermatophore length (SpLI)	32–50	~35	135–160	60–70	60–70	>100	~60	—

var. *typicus*) and supplemented with counts and measurements taken from the type of *O. robsoni* and specimens of "iidako" from NMNH and CAS.

Great Barrier Reef ocellate octopuses fall into two groups of potentially different origin. *Octopus polyzenia*, *O. exannulatus* and *O. mototi* show close affinities with all other Indo-Malayan ocellates in sharing: small body size, short arms (AMI about 200–280), body patterns that often include four to six wide longitudinal stripes on the dorsal mantle and arm crown, moderately low sucker counts (SC about 100–200, HASC about 50–100), and medium sized copulatory organs (LLI about 5+).

Octopus cyanea, despite possessing ocelli, is clearly of different origin from the above ocellate species. It shares greater affinities with *O. vulgaris* Lamarck, 1798 and several ocellate species of the Americas [*O. bimaculatus* Verrill, 1883, *O. bimaculoides* Pickford and McConnaughy, 1949; *O. maya* Voss and Solis Ramirez, 1966 and *O. oculifer* Hoyle, 1904 (senior synonym of *O. roosevelti* Stuart, 1941, *fide* Hochberg, in prep.)]. *Octopus cyanea* shares the following characters with many of these species: larger body size, long arms (AMI about 300–500), absence of four to six wide longitudinal stripes in body patterns, high sucker counts (SC >400, HASC about 200), and tiny copulatory organ (LLI <2).

Biogeography. Distributions of the four ocellate octopuses in the Great Barrier Reef region fall into three patterns.

Octopus cyanea is a widely-distributed species found in clear tropical waters of the Pacific and Indian oceans, from Hawaii in the east to the African coast in the west (fig. 15a). This distribution spans the Indo-West Pacific region (Briggs, 1974). Such a distribution is seen in a wide range of tropical marine organisms and is characteristic of fauna or flora with a lengthy planktonic phase in their life cycles (Ekman, 1967; Briggs, 1974). *Octopus cyanea* lays very small eggs (2 mm long, ELI 1.7) and the young enter the plankton on hatching (Van Heukelem, 1976). The duration of this planktonic phase is not known but must be sufficiently long to enable hatchlings to traverse the extensive areas of open ocean between island groups.

The distribution of *O. mototi* is also wide ranging (fig. 15d), apparently limited to the tropical Pacific Ocean. In the east, specimens have been collected from the South Pacific, the east coast of Australia and south of Japan. This species may prove to have a distribution restricted to the rim of the Pacific Plate as reported for certain fish species in Springer (1982). The eggs of *O. mototi* are moderately small (ovarian eggs to 5 mm, ELI 7.8) indicating that hatchlings are planktonic.

Octopus exannulatus and *O. polyzenia* exhibit distributions restricted to the tropical coastal waters of northern Australia, referred to as the "Northern Tropical Zone" or "Northern Australian Region" by Wilson and Allen (1987). Many other tropical Australian marine biota exhibit this distribution, including fishes (Wilson and Allen, 1987), echinoderms (Rowe, 1985) and another octopus species, *Ameloctopus litoralis* Norman, 1992 (Norman, 1992a). Both *O. polyzenia* and *O. exannulatus* occur in shallow and muddy coastal waters, on sand and/or mud substrates. These habitats are continuous from southern Queensland to Shark Bay, Western Australia. *Octopus exannulatus* lays moderately small eggs (ovarian eggs to 4 mm long, ELI 7.3) suggesting that hatchlings spend at least some time in the plankton. This species could potentially disperse across its range in the plankton, and may prove to also occur along the southern Papua New Guinea coastline where similar habitats exist. *Octopus polyzenia* lays relatively large eggs (spawned egg capsules to 8 mm long, ELI >20) indicating hatchlings spend little time in the plankton. In this species, dispersal must be limited to the distribution of shallow mud and sand substrata in tropical Australian waters.

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