

Octopuses of the Kermadec Islands: Discovery and description of a new member of the *Octopus 'vulgaris'* complex (*O. jollyorum*, sp. nov.) and the first description of a male *Callistoctopus kermadecensis* (Berry, 1914)

Amanda L. Reid Australian Museum Research Institute Nerida G. Wilson Western Australian Museum

Abstract

Two species of shallow-water octopuses were known to occur in the Kermadec Islands prior to the Kermadec Biodiscovery Expedition in May 2011: Callistoctopus kermadecensis (Berry, 1914) and Octopus oliveri (Berry, 1914). Representatives of both these species were collected during the expedition. Although O. oliveri is relatively well known and described, C. kermadecensis was previously known from only a few specimens, including the two dishevelled type specimens. A mature male animal had never been seen. One adult male C. kermadecensis was collected during the expedition and is described here. In addition, four specimens (two males and two females) belonging to the O. 'vulgaris' species-complex were discovered and molecular data was used to examine their relationships to other taxa in the complex. A phylogenetic analysis of COIII sequences showed that these Kermadec Island specimens are grouped in a clade with other O. 'vulgaris' from the tropical western Pacific (including Japan and Taiwan), and represent a unique species in the O. 'vulgaris' species-complex. The species is described here as O. jollyorum, sp. nov. Colour images of living specimens representing all three species are included, in addition to a checklist of all cephalopods known from the Kermadec Islands.

Keywords

Cephalopods; octopuses; vulgaris; new species; Callistoctopus

INTRODUCTION

Benthic shallow water octopuses belong to the largest benthic family of octopuses: Octopodidae. Our current understanding of the phylogeny and taxonomy of this group, particularly of the catch-all genus *Octopus*, is limited (Guzik *et al.* 2005), although considerable progress has been made in recent years (Norman & Hochberg 2005; Acosta-Jofré *et al.* 2012; Strugnell *et al.* 2013; Jereb *et al.* 2014). The Kermadec Biodiscovery Expedition 2011 provided a unique opportunity to collect these animals in a remote and comparatively unexplored region (Fig. 1) to contribute to our knowledge of the group and obtain tissue samples to contribute to future phylogenetic analyses.

The Kermadec Island cephalopods were first examined in detail by Berry, who in 1913 published a description of *Nematolampas regalis*, and in 1914

published a report based on specimens sent to him by T. Iredale and W. R. B. Oliver. Prior to Berry's (1913; 1914) publications, there were no reports of cephalopods from the Kermadec Islands in the literature, apart from three species listed by Hoyle (1886) that were obtained from very deep water in the vicinity during the HMS Challenger Expedition of 1873–1876 (Amphitretus pelagicus Hoyle, 1885; Cirroteuthis meangensis Hoyle, 1885; and Graneledone verrucosa Verrill, 1881). The shallow water specimens Berry (1914) described were collected on Raoul Island (then called Sunday Island) by Oliver (who published in 1915 the first list of molluscs from the Kermadec Islands) and R. S. Bell. The paper by Oliver (1915) included 15 cephalopod species, only three of which were dredged. One, O. oliveri (Berry, 1914), was found live among rocks and the rest were found washed up on beaches. Remarkably, according to Berry (1914: 135), apart from the "trifling circumstance"

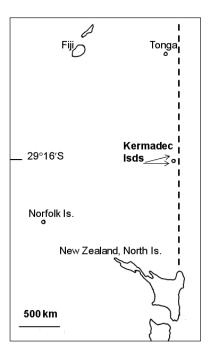


Figure 1. Location of the Kermadec Island chain. The islands lie within 29° to 31.5°S and 178°W, 800–1 000 km northeast of New Zealand's North Island, and a similar distance southwest of Tonga.

of the mantles of the specimens being partially filled with small pebbles and coarse gravel there was "little to indicate that the animals were not taken alive". This seemingly lucky circumstance enabled Berry to discern sufficient detail to describe the three new cephalopod species in his 1914 publication.

Since then, many more species have been added to the Kermadec Islands records. A checklist of all cephalopods currently known to occur in the Kermadec Islands is shown in Table 1. This paper provides an addition to the information on the octopods of the Kermadec Islands — the cephalopod group most readily obtained while SCUBA diving. The classification adopted here follows that proposed by Strugnell *et al.* (2013) and Jereb *et al.* (2014). These works review the current state of octopus taxonomy, resolve the status of many historical names and provide revised diagnoses for nominal species in the family.

In this paper, new data for two species previously known from the Kermadec Islands, C. kermadecensis (Berry, 1914) and O. oliveri, are provided, based on new material collected during the 2011 expedition. Both these species have been recently redescribed by O'Shea (1999), so only those characters that differ, or were not described in O'Shea's (1999) publication, are given here. In particular, a mature male *C. kermadecensis* was found. This species was previously known only from a female specimen, so male traits for this taxon are described and illustrated for the first time. In addition, four mature specimens of a third species that had not been recorded from the Kermadec Islands were discovered. The identity of this species was determined using morphological and molecular characters, and the new species, Octopus jollyorum, sp. nov., is fully described in this paper.

METHODS

Collection

All *O. oliveri* specimens were collected by hand from intertidal rock pools. The remaining specimens were hand collected while SCUBA diving. Most were found in their lairs under rocky ledges or hollows and one specimen (AIM MA119969) was found inhabiting the shell of a trochid, *Angaria delphinus* (Linnaeus, 1758). Two animals were obtained from fish rotenone stations, moving about outside their lairs. They may have been affected by rotenone, or perhaps attracted by a sudden supply of fish.

On board the RV *Braveheart*, specimens were photographed and relaxed in fresh water containing menthol crystals. Following death, mantle and arm tissue samples were taken and placed in 95% ethanol for future DNA analyses and animals were then preserved in 10% formalin in seawater until transportation to the Australian Museum in Sydney where they were transferred to 70% ethanol for detailed examination and measurement. Specimens were deposited either in the Auckland War Memorial Museum (New Zealand) or the Australian Museum (Sydney). Frozen, 95% ethanol-fixed tissue samples for all specimens have been retained by the Australian Museum.

Attempts were made to collect other cephalopods by utilising lights at night to attract them (the RV *Braveheart* floodlights and a Light & Motion Sola Video 1200, spot and floodlight [1200 lumen flood with a 500 lumen spotlight] suspended in the water). Fishing using squid jigs was also attempted. Unfortunately, only octopods were collected, and no other cephalopods were observed during this expedition.

Measurements and indices follow Roper and Voss (1983), and Huffard and Hochberg (2005), except for sucker counts; these included all suckers rather than those on the basal half of the arms. For clarity, these abbreviations and their definitions are given in Appendix 1.

In the taxonomy section below, the following abbreviations have been used: AIM, Auckland War Memorial Museum (New Zealand); AMS, Australian Museum, Sydney; EBU (Evolutionary Biology Unit), Australian Museum frozen tissue collection number. Where the whole animal is lodged at the Auckland Museum, tissue samples lodged at the Australian Museum are given individual collection registration numbers (preceded by 'AMS C.') in addition to an EBU number.

DNA Analyses

Tissue samples fixed in 95% ethanol were drained of liquid and deposited in the Australian Museum frozen (–80°C) tissue collection upon return to Sydney in preparation for molecular analyses. *Callistoctopus kermadecensis* could be readily identified based on morphological characters, and specimens were not subjected to molecular analyses for the purposes of this study. However, to confirm the identification of four large, unknown octopuses, suspected to belong to the *O. 'vulgaris'* species-complex (AIM MA119967, AIM MA119968, AMS C.477617,

Table 1. Kermadec Island Cephalopods. Sources of information: Australian Faunal Directory; Berry 1913, 1914, 1916; Bolstad 2007; Brooke 1998; Dell 1952; Imber 1978; Jereb and Roper 2010; Jereb *et al.* 2014; O'Shea 1999; Powell 1979; Voss 1976; this study.

Order	Family	Species	Type locality
Nautilida	Nautilidae	Nautilus pompilius Linnaeus, 1758	Pelsart I., Houtmans Abrolhus, and Rottnest I. Western Australia
Nautilida	Nautilidae	Nautilus macromphalus Sowerby, 1848	Not designated: unresolved
Octopoda	Amphitretidae	Amphitretus pelagicus Hoyle, 1885	Off Kermadec Is 29°55′S 178°14′W
Octopoda	Argonautidae	Argonauta argo Linnaeus, 1758	'Pelago, M. Indico, Mediterrane'
Octopoda	Argonautidae	Argonauta nodosus Solander, 1786	Portland I.: unresolved
Octopoda	Cirroteuthidae	Grimpoteuthis meangensis (Hoyle, 1885)	Pacific Ocean 4°33′N 127°06′E
Octopoda	Cirroteuthidae	Cirroteuthis muelleri Eschricht, 1836	Jakobshavn, West Greenland
Octopoda	Megaleledonidae	Graneledone challengeri (Berry, 1916)	Off Kermadec Is 29°45′S 178°11′W
Octopoda	Octopodidae	Callistoctopus kermadecensis (Berry, 1914)	Sunday [Raoul] I., Kermadec Is
Octopoda	Octopodidae	Octopus oliveri (Berry, 1914)	Sunday [Raoul] I., Kermadec Is
Octopoda	Octopodidae	Octopus sp. A Orbigny, 1834	Japan
Octopoda	Tremoctopodidae	Tremoctopus robsoni Kirk, 1884	Mayor I., New Zealand
Octopoda	Ocythoidae	Ocythoe tuberculata Rafinesque, 1814	?Sicily: not designated
Oegopsida	Cranchiidae	Bathothauma lyromma Chun, 1906	Not designated
Oegopsida	Cranchiidae	Cranchia scabra Leach, 1817	South Seas
Oegopsida	Cranchiidae	Galiteuthis armata Joubin, 1898	60°03′N 3°53′W (Atlantic Ocean)
Oegopsida	Cranchiidae	Megalocranchia maxima Pfeffer, 1884	Cape of Good Hope
Oegopsida	Cranchiidae	Liguriella pardus (Berry, 1916)	Sunday [Raoul] I., Kermadec Is
Oegopsida	Cranchiidae	Sandalops melancholicus Chun, 1906	NE Tristan da Cunha Island (32°8'S 8°28'W)
Oegopsida	Cranchiidae	Taonius belone (Chun, 1906)	10°08'S 97°14'E (Indian Ocean)
Oegopsida	Cranchiidae	Teuthowenia pellucida (Chun, 1910)	37°29′S 177°17′E (Pacific Ocean)
Oegopsida	Enoploteuthidae	Abralia astrolineata Berry, 1914	Kermadec Is
Oegopsida	Enoploteuthidae	Abraliopsis hoylei Pfeffer, 1884)	Mascarene Is (Indian Ocean)
Oegopsida	Enoploteuthidae	Abraliopsis tui Riddell, 1985	Kermadec Is
Oegopsida	Lycoteuthidae	Lampadioteuthis megaleia Berry, 1916	Sunday [Raoul] I., Kermadec Is
Oegopsida	Lycoteuthidae	Nematolampas regalis Berry, 1913	Sunday [Raoul] I., Kermadec Is
Oegopsida	Ommastrephidae	Ommastrephes bartramii (Lesueur, 1821)	'Barre de Lisbonne', Portugal
Oegopsida	Ommastrephidae	Sthenoteuthis oualaniensis (Lesson, 1830)	'found in a lot of salt, most probably from near Point Conception', California
Oegopsida	Onychoteuthidae	Onychoteuthis banksii (Leach, 1817)	Not designated ?Gulf of Guinea
Oegopsida	Pyroteuthidae	Pterygioteuthis giardi Fischer, 1896	Marocco [off Morocco]
Oegopsida	Pyroteuthidae	Pyroteuthis serrata Riddell, 1985	Kermadec Is
Spirulida	Spirulidae	Spirula spirula (Linnaeus, 1758)	Off Timor
Vampyromorpha	Vampyroteuthidae	Vampyroteuthis infernalis Chun, 1903	1°56.7′S 7°40.6′E (Atlantic Ocean)

AMS C.477618), a phylogenetic analysis based on molecular data was carried out.

Genomic DNA was extracted from each specimen using a DNeasy blood and tissue kit (Qiagen, Maryland, USA). PCR reactions were carried out to amplify a fragment of the Cytochrome Oxidase subunit III (COIII), using universal primers obtained from Boore and Brown (2000), because this marker has been used extensively to differentiate species in this complex and thus maximizes the breadth of comparisons using available data. In addition, to confirm specimens of Octopus oliveri from Hawaii and Japan were conspecific with specimens from the type locality, we also sequenced two specimens of O. oliveri. For this, we amplified Cytochrome Oxidase subunit I (COI), using universal primers (Folmer et al. 1994), because that was the existing data available for comparison. All amplicons were purified using Exo-SapIT prior to Sangar sequencing at Macrogen Korea. Forward and reverse sequences were reconciled and edited with Sequencher v4.10.1 (Gene Codes Corporation, MI, USA) and assembled in Se-Al (Rambaut 2002), together with all available sequences (as at mid 2012).

Octopus tetricus Gould, 1852 was included in the phylogenetic analysis as it has been identified in a number of studies to be a sister taxon to *O. vulgaris* Cuvier, 1797 (e.g. Guzik et al. 2005; Kaneko et al. 2011; Amor et al. 2014). Octopus tetricus sequences were obtained from GenBank and included together with a new sequence obtained from a specimen identified by the first author as *O. tetricus* from Bendalong, NSW, Australia (AMS C.469594, EBU 54808, GenBank accession JX680530). Two sequences from GenBank identified as *O. vulgaris* and *O. oculifer* Hoyle, 1904 were given updated identifications as *O. mimus* Gould, 1852 based on evidence from Acosta-Jofré et al. (2012).

COIII sequences were aligned using the strategy in MAFFT (Multiple Alignment using Fast Fourier Transform; Katoh 2008). The resulting alignment length of COIII data comprised 592 bp devoid of stop codons, indels or deletions. iModelTest v2.1.1 (Darriba et al. 2012) selected a GTR+Γ model as the best-fit model of nucleotide substitution using the Akaike Information criterion. This dataset was analysed with this model under a maximum likelihood (ML) criterion in the raxmlGUI v0.93 (Silvestro and Michalak 2011), which implements RAxML (Stamatakis 2006). Node support was assessed by carrying out 1000 thorough bootstrap replicates (option "-b" in RAxML). Cistopus indicus (Rapp, 1835) and Octopus cyanea Gray, 1849 were selected as outgroup taxa for the analysis following Guzik et al. (2005), Guerra et al. (2010) and Acosta-Jofré et al. (2012), which all suggest these two taxa are evolutionarily close to, but outside of, the O. 'vulgaris' clade. We also included available data for O. oliveri from Japan since its placement in Kaneko et al. (2011) suggested a close relationship with species in the O. 'vulgaris' group.

For *O. oliveri*, the new sequences were blasted to the Nucleotide database at NCBI (http://www.ncbi.nlm.nih.gov/) using the megablast algorithm for highly similar sequences.

RESULTS

Three octopus species were found at the Kermadec Islands: *Callistoctopus kermadecensis*, *Octopus oliveri* and *O. jollyorum*, sp. nov. The following descriptions only include traits for *C. kermadecensis* and *O. oliveri* that differ from previous descriptions, or were not described in detail in previous publications. *Octopus jollyorum*, sp. nov. is fully described based on morphological and molecular data.

The phylogenetic analysis of COIII data for octopuses of the O. 'vulgaris' species-complex demonstrated that all the Kermadec specimens from this complex form a monophyletic clade (Fig. 2, bootstrap support 100). This clade includes available GenBank data from specimens identified as O. vulgaris from the East China Sea (AB573218), Japan (complete mt genome, AB158363; AB573217; AB573219; AJ616311) and Taiwan (AJ250479). We use morphological and molecular data to delimit this clade as a unique species in the O. 'vulgaris' complex. The other occurrence of 'vulgaris' members in the west Pacific is attributed to O. tetricus, known to occur in both New Zealand and eastern Australia, and a distinct, but as yet unnamed, form from Western Australia (Amor et al. 2014). The clade that contains a specimen of O. vulgaris from the type locality (presumed to be the western Mediterranean Sea) occurs in the Mediterranean/Atlantic, southern Indian Ocean and southern Atlantic Ocean.

Molecular data confirms *Octopus oliveri* ranges widely in the Pacific Ocean. Two sequences generated from the type locality for *O. oliveri* blasted with 99% similarity to sequences from *O. oliveri* on GenBank from Hawaii (GQ900744) and Japan (AB430532).

Callistoctopus kermadecensis (Berry, 1914)

(Table 2; Figs 3–16)

Polypus (Pinnoctopus?) kermadecensis Berry, 1914: 138–139; pls 7, 8.

Pinnoctopus kermadecensis O'Shea, 1999: 143–145; pl. 91; Tables 68, 69.

Type data – Holotype, NMNH 816461.

Type locality – Sunday Island [Raoul Island], Kermadec Islands.

Material examined. Kermadec Islands: ♂ 49.5 mm ML, northwest corner of North Meyer Island, 29°14′29″S 177°52′43″W, 16–18 m, 19 May 2011, hand net at rotenone station, coll. C. Bedford and Kermadec Biodiscovery Expedition party (AIM MA119961: AMS C.477720, EBU 54841; AMS C.477721, EBU 54871); ♀ 78.0 mm ML, Raoul Island, 1910, coll. R. S. Bell (NMNZ M.256374); ♂ 15.7 mm ML juvenile, west-north-west side of Macauley Island, 30°13′54″S 178°26′33″W, 21–23 m, 21 May 2011, hand net at rotenone station, coll. Kermadec Biodiscovery Expedition party (AIM MA119962).

Description (male). Counts and measurements for the mature male specimen described below are given in Table 2. Medium to large-sized (470 mm TL). Slender, saccular mantle with thin, muscular wall. Mantle elongate,

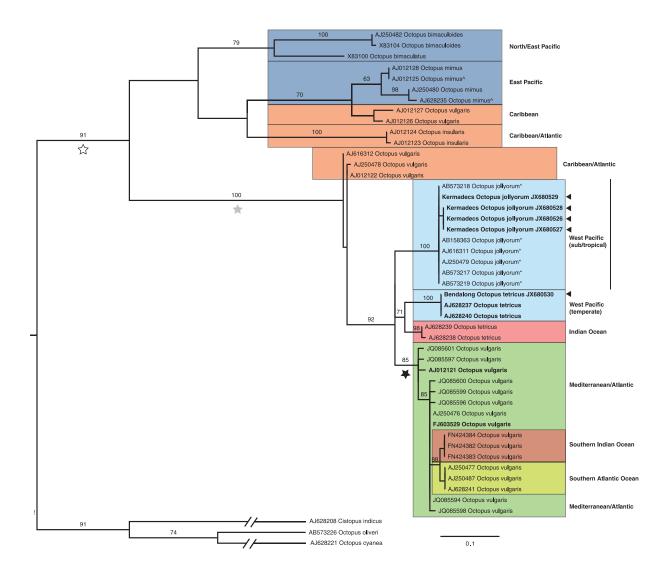


Figure 2. Maximum-likelihood tree showing relationships among the *Octopus 'vulgaris'* complex based on COIII data. Clade support assessed by 1 000 thorough bootstrap replicates. Arrows indicate new sequences; vertical bar shows the position of the new species. Open star, *Octopus sensu stricto*; grey star, *O. vulgaris* complex; solid star, *O. vulgaris sensu stricto*. Samples belonging to the clade containing the Kermadec Island octopuses were obtained from the following locations: AJ616311, Japan, Seto Inland Sea; AJ250479, northeast Taiwan (Warnke *et al.* 2004); AB158363, Japan Tokyo Fish Market (Yokobori *et al.* 2004); AB573218, East China Sea; AB573217, Japan, Seto Inland Sea; AB573219 Japan, Sagami Bay, Misaki (Kaneko *et al.* 2011).

flask-shaped, widest medially and tapers posteriorly to a blunt point. Pallial aperture of moderate width (PAI 119). Head relatively narrow (HWI 77). Eyes not prominent (Figs 3, 13–15). Funnel tubular (FLI 85). Well defined, W-shaped funnel organ, lateral limbs shorter than medial limbs; all four limbs of equal width, slender. Arms slender (AWI 33), relatively long (ALI 575–788; HAMI 505); arm formula variable. Third right arm hectocotylised, shorter than third left arm (OAI 80.6) bearing 106 suckers. Ligula small (LLI 3.3) (Fig. 4), robust and tapers to a blunt point (Figs 4, 5). (Note that the ligula in the preserved specimen is slightly folded at the tip. This is a preservation artefact.) Ligula groove deep without transverse furrows, calamus relatively long (CLI 39), broad, triangular. Total number of suckers on normal arms 182-196. Normal sucker diameter wide (SDIn 16.4–24.4); suckers slightly but not markedly enlarged on arms 2–3. Web moderately deep (WDI 19–21), shallower between dorsal and ventral arms (webs A and C deepest). Gills with 11–12 lamellae per demibranch.

Digestive tract not removed to avoid additional damage to specimen. Upper beak (Fig. 6) with short pointed rostrum, not distinctly hooked, jaw angle obtuse, hood narrow. Lower beak (Figs 7, 8) with long, pointed rostrum and obtuse jaw angle, hood narrow, wings widely spread with flared lateral walls, separated in the posterior half (Fig. 8). Radula with seven teeth in each transverse row (Fig. 9), marginal plates present. Rhachidian teeth long, scythe-like, broad-based with three cusps on each side, basal cusps largest, becoming smaller distally. First lateral tooth much smaller, triangular, asymmetrical with broad heel directed

toward midline of radula. Second lateral symmetrical, broad-based triangular, with concave margins, larger than first lateral. First marginal teeth slightly longer than second laterals, curved with tooth directed toward midline. Marginal plates flat, rectangular.

Testis large broad, in mature males (Fig. 10); vas deferens narrow, long, highly coiled and wrapped in membranous sac. Vas deferens opening into

Table 2. Counts and measurements (mm) for mature male *C. kermadecensis* (AIM MA119961) and juvenile male (AIM MA119962).

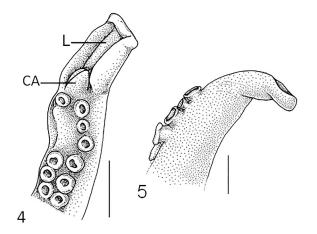
For definitions of counts, measurements and indices, see Appendix 1. –, not recorded; * excluding terminal lamella.

	C. kermadecensis ♂ AIM MA119961	C. kermadecensis ju ♂ AIM MA119962	
TL	470	70	
ML	49	16	
MW	49	10	
HW	38	9	
FL	42	6	
FFL	20	4	
FOL	82	53	
WD A	83	8	
WD B	81	9	
WD C	83	11	
WD D	73	7	
WD E	_	13	
WF	A=C.B.D	C.B.A.D.E	
AL 1	390	52	
AL 2	_	52	
AL 3	310	50	
SCh	250	47	
AL 4	285	41	
AF	1.3.4	1=2.3.4	
AW	16	3	
SD 1	12.1	1.2	
SD 2	10.5	1.0	
SD 3	9.3	0.9	
SD 4	8.1	0.9	
SC 1	182	116	
SC 2	-	112	
SC 3	186	105	
Нс	106	100	
SC 4	196	116	
GC	11	12	
GL	24	5	
LL	8.2	_	
CL	3.2	_	
SpL	75.0	_	
SpW	1.8	_	

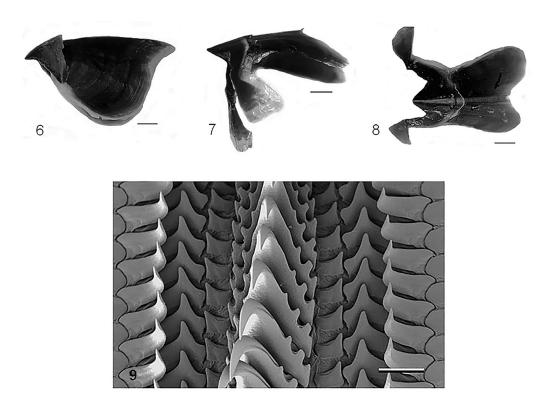
long spermatophore gland with distinct recurved coil; accessory gland robust, reflexed distally. Spermatophoric gland and accessory gland open into spermatophore storage sac. Blunt appendix at junction of spermatophore storage sac and spermatophoric ducts. Terminal organ short, tubular (Fig. 10). Spermatophores large (SpLI 151), narrow, (SPWI 2.4) (Figs 11, 12). Two spermatophores in storage sac of a mature male.



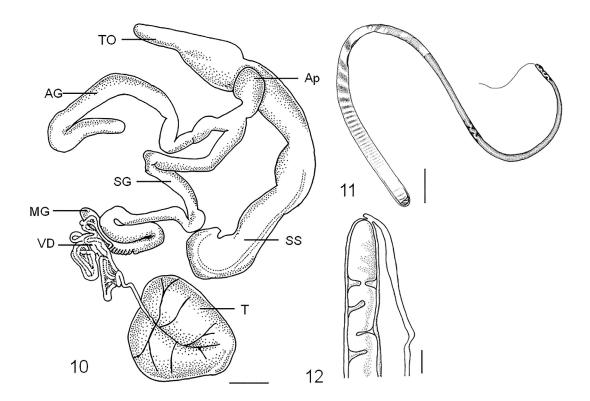
Figure 3. Callistoctopus kermadecensis (Berry, 1914), 3 49 mm ML (AIM MA119961): preserved animal, dorsal view. Scale bar = 2 cm.



Figures 4 and 5. Callistoctopus kermadecensis (Berry, 1914), 3 49 mm ML (AIM MA119961): 4. Copulatory organ, ventral view. Scale bar = 5 mm. 5. Copulatory organ, side view. Scale bar = 5 mm. CA, calamus; L, ligula.



Figures 6–9. Callistoctopus kermadecensis (Berry, 1914), 3 49 mm ML (AIM MA119961): 6. Upper beak, lateral view. 7. Lower beak, lateral view. 8. Lower beak, ventral view. Scale bars = 2 mm. 9 78 mm ML (NMNZ M.256374): 9. Radula. Scale bar = 300 μ m. (Note that the rhachidian teeth and third lateral teeth are abnormally curved due to problems with preparation for SEM.)



Figures 10–12. *Callistoctopus kermadecensis* (Berry, 1914), & 49 mm ML (AIM MA119961): 10. Male reproductive tract. Scale bar = 10 mm. Ap, appendix; AG, accessory gland; MG, mucilaginous gland; SG, spermatophoric gland; SS, spermatophore storage sac sac; T, testis; TO, terminal organ; VD, vas deferens. 11. Spermatophore. Scale bar = 5 mm. 12. Enlargement of oral end of spermatophore. Scale bar = 0.5 mm.

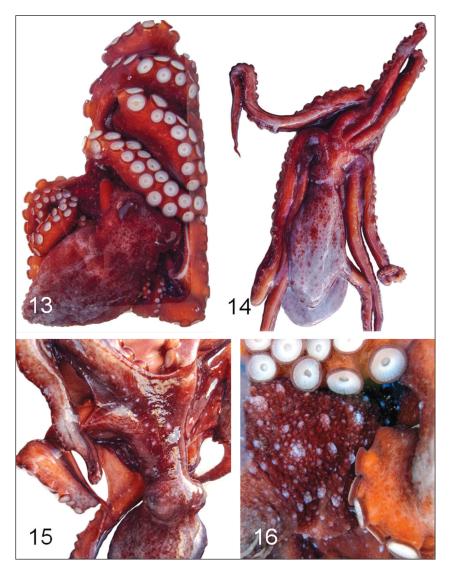
Colour and sculpture (Figs 3, 13–16). Live male specimen brick-red in colour over entire body and arms, with distinct, evenly spaced, large, lavender to electric blue spots, located on anterior half of head and arm crown (Figs 15, 16), that flashed 'on and off' when the animal was agitated. Preserved specimen creamy brown; blue spots not visible. Skin comparatively smooth. Dorsal surface covered with uniform low papillae, none appear to be particularly enlarged. Lavender blue spots composed of cluster of papillose bumps surrounding a larger, central papilla (Fig. 16). Specimen identified as a juvenile (which was not observed while alive) much paler in colour, evenly peppered with maroon chromatophores and darker underlying spots. It has uniform low papillae over mantle and arms.

Remarks. O'Shea (1999) placed this species in the genus *Pinnoctopus*. *Pinnoctopus* was diagnosed by Orbigny (1845) on the basis of a fin-like flap around the mantle margin. We concur with Norman and Hochberg

(2005) in concluding that this structure is a preservation artefact. The flap can clearly be seen in Fig. 14. This picture was taken when the live animal was placed on the deck of the RV *Braveheart* and so was not supported by water. It is easy to imagine that a specimen could be preserved in this condition. Norman and Hochberg (2005) place this species in the genus *Callistoctopus*, a genus that is well supported on the basis of morphology and via a recent phylogenetic analysis of molecular data (Kaneko *et al.* 2011).

The morphometric data reported here (Table 2) conforms with that given in O'Shea (1999). The high gill lamellae count in this species (11–12) is diagnostic and differs from other species found among the islands.

Distribution. Kermadec Islands endemic. Known only from Raoul, North Meyer and possibly Macauley Islands (if the identification of the juvenile specimen is correct) (Fig. 17).



Figures 13–16. Callistoctopus kermadecensis (Berry, 1914), & 49 mm ML (AIM MA119961)), live animal: 13. Dorsal view, photographed in tray under water. 14. Animal placed on deck, briefly out of water (note the flat flange around the posterior mantle). 15. Animal showing blue spots on arm crown and base of arms. 16. Close-up view of raised blue papillae.

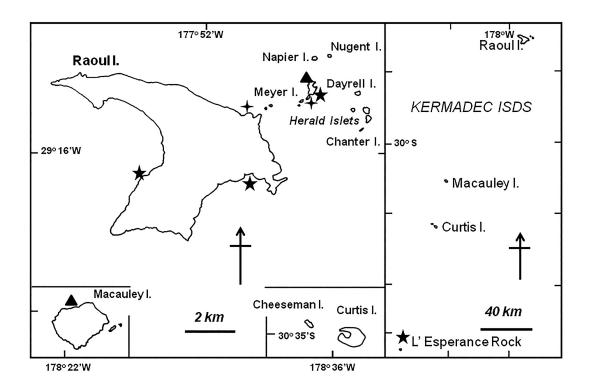


Figure 17. Distribution of Octopodidae collected during the expedition. Right-hand side map, the Kermadec Island chain; left-hand side map enlargement of Raoul and satellite islands with Macauley, Cheeseman and Curtis Islands shown as inserts at the bottom of the figure. Solid triangles, *C. kermadecensis* (Berry, 1914); five-pointed star, *O. jollyorum*, sp. nov.; four-pointed star, *O. oliveri* (Berry, 1914).

Octopus jollyorum, sp. nov. (Table 3; Figs 18–38)

Material examined. *Holotype.* ♂ 101.5 mm ML, Raoul Island, Boat Cove, 29°16'40"S 177°53'43"W, 10 m, 15 May 2011, hand collected, coll. M. Francis and A. Reid (AIM MA119967: AMS C.477711, EBU 54812; AMS C.477712, EBU 54844, GenBank accession JX680529; AMS C.477713, EBU 54811).

Paratypes. Kermadec Islands: ♀ 104.5 mm ML, northwest corner of North Meyer Island, 29°14'30"S 177°52'40"W, 10 m, 20 May 2011, hand collected, coll. S. Keable and A. Reid (AMS C.477617: EBU 54819, GenBank accession JX680527; EBU 54865, EBU 54885); \$\overline{9}\$ 93.0 mm ML, Raoul Island, Boat Cove, 29°16'48"S 177°53'50"W, 20–22 m, 15 May 2011, hand net at rotenone station, coll. Kermadec Biodiscovery Expedition Party (AIM MA119968: AMS C.477714, EBU 54843; AMS C.477715, EBU 54877, GenBank accession JX680528; AMS C.477716, EBU 54825); ∂ 102.3 mm ML, west side of L'Esperance Rock, 31°25'15"S 178°49'34"W, 18-22 m, 26 May 2011, hand net at rotenone station, coll. G. Wiren and Kermadec Biodiscovery Expedition Party (AMS C.477618: EBU 54889, GenBank accession JX680526; EBU 54884, EBU 54821).

Other material examined. ♂ 17.4 mm ML (juvenile), Raoul Island, southern Denham Bay, 29°16'57"S 177°57'10"W, 20–22 m, 19 May 2011, in trochid (*Angaria delphinus*) shell, coll. C. Bedford and Kermadec Biodiscovery Expedition Party (AIM MA119969: AMS

C.477717, EBU 54850; AMS C.477718, EBU 54860; AMS C.477719, EBU 54862).

Description. Counts and measurements for this species are given in Table 3.

The following description is based on two mature males and two mature females. Medium to largesized adults up to 600 mm TL. Broad saccular mantle with muscular wall (Figs 18, 19, 35). Pallial aperture of moderate width (PAI 92-131). Head wide (HWI 43-62). Eyes moderately prominent (Figs 18, 35, 36). Funnel tubular (FLI 45-49). Well defined W-shaped funnel organ, lateral limbs shorter than medial limbs; all four limbs of approximately equal width (Fig. 21). Arms thick (AWI 20–29), relatively long (ALI 319–539; HAMI 330-336); arm formula variable. Lateral arms longer than dorsal and ventral arms. Third right arm of males hectocotylised (OAI unknown, left arm three missing in both specimens) bearing 178-185 suckers. Copulatory organ (Figs 22-25) tiny (LLI 0.96-1.01), roughly triangular, pointed distally, outer walls slightly (Fig. 22) to markedly (Fig. 24) swollen, slightly flared toward posterior margin, and may meet medially to conceal calamus (Fig. 24); ligula groove without obvious transverse grooves. Spermatophore groove well developed. Calamus distinct, relatively long (CLI 43.7-38.5) with U-shaped distal margin and deep median groove (Figs 22, 24).

Total number of suckers on normal arms 230–300. Normal sucker diameter moderate (SDIn 8.7–14.7 \Diamond ; 6.6–18.9 \updownarrow).

Table 3. Counts and measurements (mm) for mature *O. jollyorum*, sp. nov. males, females and juvenile from the Kermadec Islands.

For definitions of counts, measurements and indices, see Appendix 1. D, damaged; –, not recorded; * excluding terminal lamella.

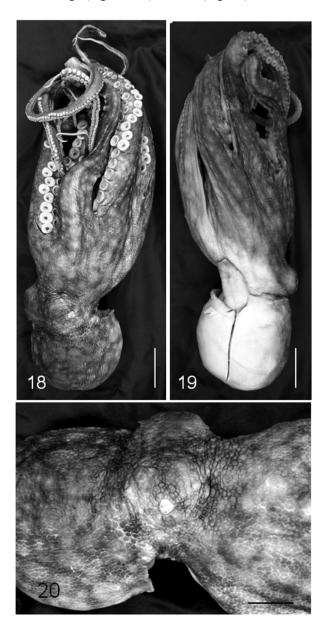
	O. jollyorum, sp. nov. ♂, paratype, AMS C.477618	O. jollyorum, sp. nov. ♂, holotype, AIM MA119967	O. jollyorum, sp. nov. ♀, paratype, AMS C.477617	O. jollyorum, sp. nov. ♀, paratype, AIM MA119968	O. jollyorum, sp. no juv. උ, AIM MA119969
TL	600	430	480	480	46
ML	102	101	104	93	17
MW	92	68	93	56	11
HW	63	44	55	50	9
FL	47	43	48	46	7
FFL	32	38	38	30	4.0
FOL	122	=	=	134	=
WD A	75	70	60	60	4.5
WD B	95	76	80	80	8.5
WD C	100	100	100	100	8.8
WD D	80	82	83	83	11
WD E	73	75	50	50	9
WF	C.B.D.A.E	C.D.B.E.A	C.D.B.A.E	C.D.B.A.E	D.E.C.B.A
AL 1	420	324	336	336	34
AL 2	473	332	359	359	39
AL 3	D	D	448	448	34
Нс	385	335	D	D	_
AL 4	347	340	307	307	42
AF	2.1.4	4.3.2.1	3.2.1.4	3.2.1	4.2.1.3
AW	28	20	34	21.7	3.3
SD 1	15.0	8.8	15	13.2	1.6
SD 2	17.7	9.0	18	11.0	1.9
SD 3	12.4	9.3	14.0	11.2	1.8
SD 4	13.5	10.0	13.2	6.1	1.7
SC 1	268	248	256	288	116
SC 2	_	273	D	300	130
SC 3	_	278	264	284	90
ScH	178	185	_	_	90
SC 4	230	280	280	278	116
GC	8	9	9	9	8
GL	27	38	38	26	27
LL	3.9	3.2	_	_	-
CL	1.5	1.1	_	_	-
Sp Count	>50	-	_	_	-
SpL	45	-	-	_	-
SpW	0.8	_	_	_	_

Suckers very slightly, but not markedly, enlarged on arms 2–3 in both sexes over rows 5–10. Web moderately deep (WDI 11–29), shallower between dorsal and ventral arms (webs C and D deepest; webs A and C shallowest). Gills with 8–9 lamellae per demibranch.

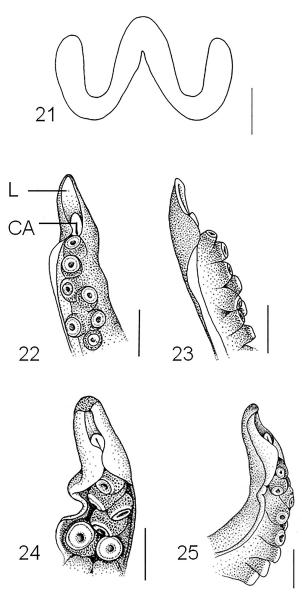
Typical *Octopus* digestive tract (Fig. 26). Large buccal mass; pair of flattened, medium-sized anterior salivary glands joined by salivary ducts to posterior portion of buccal mass; posterior salivary glands triangular. Narrow oesophagus followed by crop diverticulum; stomach wide. Spiral caecum connected by two ducts to large digestive gland; ink sac embedded in digestive gland surface. Intestine long, curved, ending in muscular rectum. Strong beaks; prominent rostrum and thick wings (Figs 27–29). Radula (Fig. 30) with seven

teeth and two marginal plates in each transverse row. Rhachidian tooth with 1–2 symmetrical lateral cusps migrating from medial to lateral position over 6–8 rows (Figs 30, 31). First lateral teeth elongate with single cusp displaced towards second lateral teeth. Second lateral teeth with large pointed cusp displaced toward midline of radula ribbon. First marginal teeth narrow, elongate, blade-shaped. Marginal plates small, flat, rectangular (folded under margin of radula ribbon in Fig. 30).

Male reproductive system. Testis large, broad in mature males (Fig. 32); vas deferens narrow, long, highly coiled and wrapped in membranous sac. Vas deferens opening into long spermatophore gland with distinct recurved coil; accessory gland robust, reflexed distally. Spermatophoric gland and accessory gland opening into



Figures 18–20. Octopus jollyorum, sp. nov., paratype $\ 93$ mm ML (AIM MA119968), preserved specimen: 18. Dorsal view. 19. Ventral view. Scale bar = 40 mm. 20. Enlargement of integument to show pavement-like sculpture. Scale bar = 20 mm.



Figures 21–25. Octopus jollyorum, sp. nov., paratype & 102 mm ML (AMS C.477618): 21. Funnel organ. Scale bar = 10 mm. 22. Copulatory organ, ventral view. 23. Copulatory organ, side view. Holotype & 101 mm ML (AIM MA119967): 24. Copulatory organ, ventral view. 25. Copulatory organ side view. Scale bars = 5 mm. CA, calamus; L, ligula.

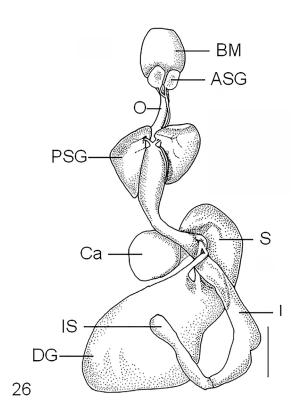


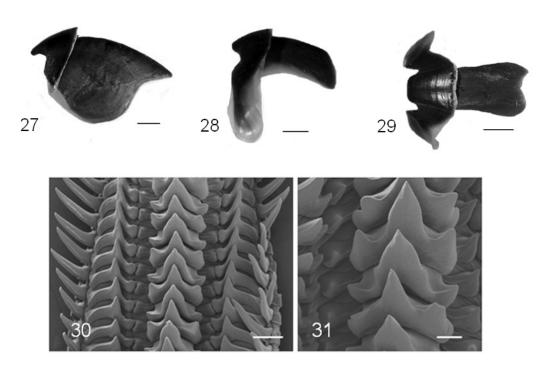
Figure 26. Octopus jollyorum, sp. nov., paratype & 102 mm ML (AMS C.477618): Digestive tract, ventral view. Scale bar = 20 mm. ASG, anterior salivary gland; BM, buccal mass; Ca, caecum; DG, digestive gland; I, intestine; IS, ink sac; O, oesophagus; PSG, posterior salivary gland; S, stomach.

spermatophore storage sac. Blunt appendix at junction of spermatophore storage sac and spermatophoric ducts. Terminal organ short, tubular; diverticulum spherical. Spermatophores medium-sized (SpLI 44.1), narrow (SPWI 1.78) (Figs 33, 34). More than 100 spermatophores in storage sac of a mature male.

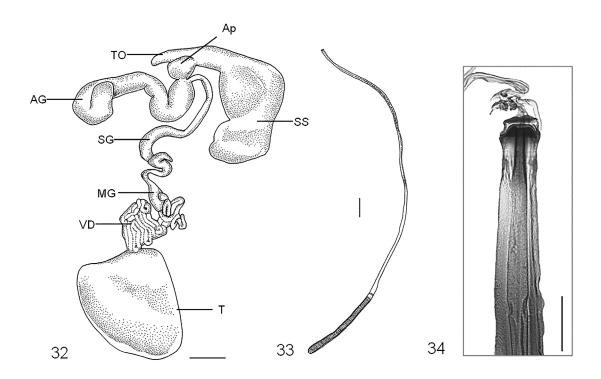
Colour and sculpture. Skin pavement-like on dorsal surface (Fig. 20). Ventral surface smoother than dorsal surface (Figs 18, 19). Colour varying from yellowish brown to dark purplish on dorsal surface and from cream to brownish on ventral surface. Dorsal surfaces of mantle, head and web covered with evenly-spaced papillae. One large papilla dorsal to each eye and one smaller flap-like papilla posterior to each eye and one spike-like cirri ventral to eyes.

Live animals mottled grey to orange brown (Figs 35, 36) with distinct pavement-like patches, and large papillae that can be raised over the body to produce a spiky appearance (Fig. 36). Eye iris white (Figs 35, 36); arms and arm webs bright orange orally (Fig. 37). Live juvenile specimen found inhabiting a trochid shell had distinct white patches between the eyes, joined by a paler bar and two white spots on the dorsal mantle (Fig. 38). These are not visible in the preserved specimen.

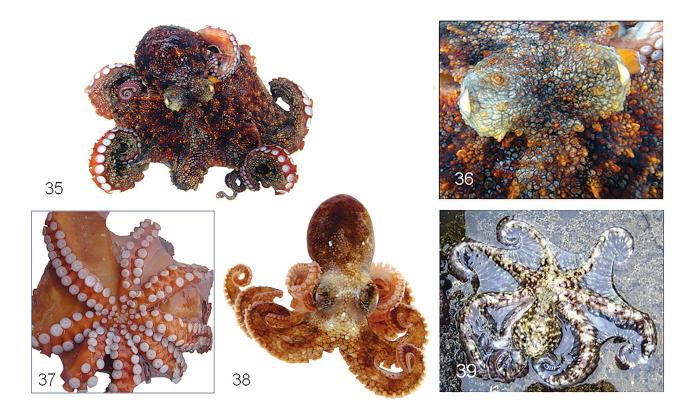
Habitat and Biology. One specimen, the large female (AMS C.477617) was brooding thousands of minute eggs that were attached in festoons to the underside of a large rock ledge. This female was visible in the mouth of its lair displaying the orange colour of the oral surfaces of the arms and a white eye pupil, a posture very similar to that known for its sibling species *O. tetricus*. The eggs were about to hatch and when disturbed, large numbers



Figures 27–31. Octopus jollyorum, sp. nov., \bigcirc 93 mm ML (AIM MA119968): 27. Upper beak, lateral view. 28. Lower beak, lateral view. 29. Lower beak, ventral view. Scale bars = 2 mm. 30. \bigcirc radula. Scale bar = 200 μ m. 31. Enlargement of rhachidian teeth. Scale bar = 100 μ m.



Figures 32–34. Octopus jollyorum, sp. nov., paratype 3 102 mm ML (AMS C.477618): 32. Reproductive tract. Scale bar = 10 mm. Ap, appendix; AG, accessory gland; MG, mucilaginous gland; SG, spermatophoric gland; SS, spermatophore storage sac; T, testis; TO, terminal organ; VD, vas deferens. 33. Spermatophore. Scale bar = 2 mm. 34. Enlargement of oral end of spermatophore. Scale bar = 0.1 mm.



Figures 35–39. Octopus jollyorum, sp. nov., paratype & 102 mm ML (AMS C.477618): 35. Live animal. 36. Enlargement of head. 37. Oral arm crown. Juvenile & 17 mm ML (AIM MA119969): 38. Live animal. Octopus oliveri (Berry, 1914) & 53 mm ML (AMS C.475899): 39. Live animal dorsal view photographed in rock pool at Fishing Rock.

of hatchlings emerged and swam into the water column. Some hatchlings and a clump of eggs were collected and placed in 95% ethanol.

Distribution. Subtropical west Pacific. Kermadec Islands: Raoul Island: Boat Cove, Denham Bay, North Meyer Island and Esperance Rock (Fig. 17). The specimens collected here are from the extreme north to the extreme south of the Kermadec Island chain, suggesting that the species is likely to be distributed throughout the Kermadec Islands. Also Japan, Taiwan and the East China Sea.

Etymology. The species is named for the owner of the RV *Braveheart*, Nigel Jolly, and the ship's master, Matthew Jolly. The involvement of these two men — Nigel in helping to facilitate the expedition and Matt's skilled handling of the ship at sea — assisted in the discovery of this new species.

Remarks. Morphological examination of the four adult specimens collected suggested they belonged to the O. 'vulgaris' species-group as defined in Norman et al. (2014). They are all medium-sized, muscular, and the skin sculpture consists of regular pavements of raised patches separated by distinct grooves. One female was found brooding vast festoons of tiny eggs that hatched into planktonic young — typical of the representatives of this group. These generalised traits are also typical of O. tetricus Gould, 1852, which occurs in Australia and New Zealand (Amor et al. 2014). However, O. tetricus differs from O. jollyorum, sp. nov. in a number of characters. The arms are relatively longer in O. tetricus (the ALI in O. jollyorum, sp. nov. ranges from 319-539 vs 550-740 in O. tetricus according to Stranks (1998)). Octopus tetricus males have 3-5 enlarged suckers from approximately the 13th sucker row. The suckers are not markedly enlarged in O. jollyorum, sp. nov. The new species also appears to have a greater number of suckers on each arm than O. tetricus, however, more Kermadec Island specimens need to be examined to confirm these differences.

There is an available name for one Japanese O. 'vulgaris': Octopus sinensis d'Orbigny, 1834. Octopus sinensis was synonomised with Octopus vulgaris by Sasaki (1929) and most authors since have followed Sasaki's lead (e.g. Gleadall & Naggs 1991), but Toll and Voss (1998: 514) did not support this synonymy, stating: "there is some doubt about whether O. vulgaris occurs in the western Pacific". According to Gleadall (pers. comm.) there are at least two representatives from the O. 'vulgaris' complex occurring in Japan. Unfortunately, no comparative type material of *O. sinensis* is available. Lu et al. (1995) state that the type species of O. sinensis is not in the Muséum national d'Histoire naturelle where it was thought to be originally deposited along with other material collected during the 1826-1829 Voyage de l'Astrolabe (Tiller & Boucher-Rodoni 1993). Norman and Hochberg (2005) described its status as unresolved. The original description contains only scant information about O. sinensis and no type specimen or type locality is designated. Unless the type material can be found, it will not be possible to reconcile d'Orbigny's description of *O. sinensis* with any of the species from Japan.

At present, it is not possible to morphologically distinguish Octopus jollyorum, sp. nov. from the Mediterranean/Atlantic O. vulgaris, and the differences between O. tetricus and O. jollyorum sp. nov. are minor. However, the phylogenetic analysis clearly indicates the independent nature of these taxa. Importantly, comprehensive descriptions and illustrations are still lacking for O. sinensis, O. tetricus and O. vulgaris, and types were either not designated in the original descriptions or have been lost; in each case the type locality is unknown, or known only generally (for example, the type locality of O. tetricus is known only as 'near Sydney'). In the case of O. vulgaris, Mangold (1998) selected a neotype from the western Mediterranean Sea (Banyuls-sur-Mer, France) but it was not formally described. Some partial descriptions of O. vulgaris are given in Toll and Voss (1998), Mangold (1998) and Stranks (1998). Based on the description of O. vulgaris given in Mangold (1998), Octopus jollyorum, sp. nov. from the Kermadec Islands shows some differences in morphometric characters, although most of the ranges overlap. It seems that O. vulgaris may attain greater sizes than O. jollyorum, sp. nov. at maturity (up to 250 mm ML in O. vulgaris vs ~100 mm ML in O. jollyorum, sp. nov.). However, given that so few specimens were collected from the Kermadec Islands, it is not possible to determine whether this difference is meaningful. The arms in O. jollyorum, sp. nov. (as is true for O. tetricus) are proportionally much longer than the mantle (as stated above, ALI in mature specimens ranges from 319-539 in the Kermadec Island specimens vs 76-89 in O. vulgaris from the Mediterranean as defined by Mangold (1998)). The arm sucker counts are also greater in O. jollyorum, sp. nov. (268-300 vs 140–180 in O. vulgaris). It appears that the web depths are generally greater in O. jollyorum, sp. nov. than in O. vulgaris but more O. jollyorum, sp. nov. specimens need to be examined to check this.

The lack of an available name for the well-supported clade that includes the Kermadec Island octopuses described above and others from the tropical west Pacific is in need of redress. By providing a full description we are recognising the members of that clade as a species worthy of formal nomenclatural recognition.

Octopus oliveri (Berry 1914)

(Table 4; Figs 16, 39–44)

Polypus oliveri Berry 1914: 136–137; Oliver 1925: 560, 564; Berry 1916: 49, pl. 6, Fig. 2; Sasaki 1929: 42, 43, text Figs 15, 16, pl. 4, Fig. 2, pl. 9, Figs 14–18.

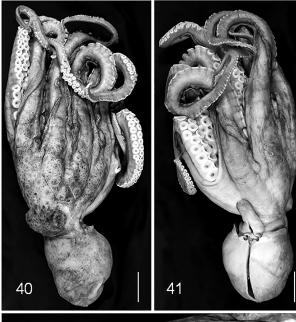
Octopus oliveri — Robson 1929: 100–101; Okutani et al. 1987: 166–167, Fig. 65A, B; O' Shea 1999: 114–119, Figs 74, 75; Ylitalo et al. 2014: 79–83, Figs 1, 2; Ylitalo-Ward 2014: 10–11, Fig. 1.

Type data – Holotype NMNH 816455, paratype CASIZ

Type locality – Sunday Island [Raoul Island], Kermadec Islands.

Table 4. Counts and measurements (mm) for mature *O. oliveri*. For definitions of counts, measurements and indices, see Appendix 1. . Indices are shown in brackets. –, not recorded; * excluding terminal lamella.

	<i>O. oliveri</i> , ੍ਰੈ, AIM MA119963	<i>O. oliveri</i> , ♂, AMS C.475899	<i>O. oliveri</i> , ♀, AMS C.475900	<i>O. oliveri</i> , ♀, AIM MA119964
TL	275	235	255	215
ML	63	53	43	39
MW	42 (68)	38 (71)	23 (53)	28 (70)
HW	26 (42)	25 (48)	23 (52)	20 (52)
FL	23 (37)	20 (38)	22 (51)	17 (43)
FFL	16 (25)	17 (32)	11 (50)	15 (38)
WD A	52 (20)	46 (22)	25 (11)	46 (21)
WD B	59 (23)	46 (22)	40 (17)	35 (16)
WD C	50 (19)	46 (22)	37 (16)	36 (16)
WD D	63 (24)	36 (17)	-	38 (17)
WD E	55 (21)	26 (13)	_	32 (15)
WF	D.B.E.C.A	A=B=C.D.E	B.C.A	A.D.C.B.E
AL 1	236 (376)	206 (389)	_	210 (532)
AL 2	245 (391)	152 (287)	233 (536)	218 (552)
AL 3	254 (405)	_	217 (499)	203 (514)
Нс	212 (338)	156 (294)	_	_
AL 4	258 (411)	198 (374)	191 (439)	193 (489)
AF	4.3.2.1	1.4.2	2.3.4	2.3.1.4
AW	14	11	11	13
SD 1	8.8 (14.0)	6.8 (12.8)	_	6.0 (15.2)
SD 2	8.7 (20.0)	8.5 (22.4)	8.3 (19.1)	7.9 (20.0)
SD 3	9.1 (14.5)	8.9 (35.2)	8.2 (18.9)	7.0 (17.7)
SD 4	7.6 (12.1)	7.3 (15.9)	7.0 (16.1)	5.8 (14.7)
SC 1	204	168	_	180
SC 2	207	140	184	181
SC 3	205	_	188	182
Нс	125	100		
SC 4	207	179	178	183
GC	6	7	6	6
GL	13 (20)	_	18 (42)	13 (33)
LL	4.3 (2.0)	4.0 (2.6)		
CL	1.5 (34.5)	0.9 (22.5)		
SpL	_	40 (75.5)		
SpW	_	1.0 (2.5)		
SpRL	_	6.3		

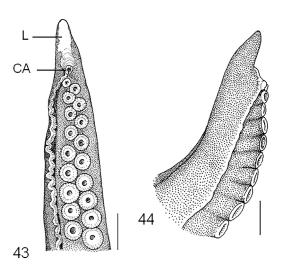




Figures 40–42. Octopus oliveri (Berry 1914), ♂ 63 mm ML (AIM MA119963), preserved animal: 40. Dorsal view. 41. Ventral view. Scale bar = 20 mm. 42. Enlargement of integument to show 'warty' spots. Scale bar = 10 mm.

Material examined. Kermadec Islands: ♂ 62.7 mm ML, Raoul Island, Fishing Rock Landing, 29°15'03"S 177°54'12"W, <1 m, 18 May 2011, hand collected from shallow rock pools and ledges in intertidal splash zone, coll. M. Francis and A. Reid (AIM MA119963: AMS C.477708, EBU 54863, GenBank accession KP164810; AMS C.47709, EBU 54853; AMS C.477710, EBU 54891); ♂, 53.0 data as previous (AMS C.475899: EBU 54878, EBU 54804, EBU 54879); ♀ 39.5 mm ML, data as previous (AIM MA119964: AMS C.477705, EBU 54864; AMS C.477706, EBU 54809; AMS C.477707, EBU 54849); ♀ 43.5 mm ML, South Meyer Island, 29°14'50"S 177°52'49"W, 0.25 m, 13 May 2011, hand collected from rock pool, coll. W. Chinn and P. de Lange (AMS C.475900: EBU 54859, GenBank accession KP164809; EBU 54890, EBU 54872).

Description. Counts and measurements for this species are given in Table 4.



Figures 43, 44. Octopus oliveri (Berry 1914), ♂ 53 mm ML (AMS C.475899) copulatory organ: 43. Ventral view. 44. Side view. CA, calamus: L, ligula. Scale bar = 3 mm.

Colour and sculpture (Figs 39, 42). Specimens collected at Fishing Rock Landing were highly papillose in life, and, when captured, raised their greenish yellow, wart-like papillae and flattened the arm webs (Fig. 39). In contrast, the South Meyer Island specimen flashed with vivid blue spots on the mantle and arms when captured (Chinn and de Lang pers. comm.). In other respects, this specimen does not markedly differ from those collected at Fishing Rock. Preserved specimens pale grey with darker grey spots dorsally and over arm crown and arms; pale cream to white ventrally (Figs 40–42).

The copulatory organ is illustrated here (Figs 43, 44) to complement the illustration provided in O'Shea (1999).

Remarks. This species was redescribed in detail by O'Shea (1999). The specimens examined here do not differ markedly from those O'Shea (1999) described, however, a few additional observations follow. Most measurements and counts fall within the ranges O'Shea listed; however, three specimens have arm sucker counts that fall outside the range given by O'Shea (1999): 95–180 suckers for the non-modified arms (see Table 4). The hectocotylised arm of one animal (AIM MA119963) has 125 suckers, thus falls outside the range 76–110 cited in the former work. He also describes preserved specimens as being dark red to purple, while the preserved specimens examined here are pale to mid-grey.

Specimens were extremely easy to find in shallow pools in the splash zone of the sloping rocky shore at Fishing Rock Landing. Three specimens were collected in a short period of time. The specimen at South Meyer Island was found in a rock pool at low tide.

A recent molecular study (Kaneko *et al.* 2011) placed *O. oliveri* in a clade with *O. 'vulgaris'* in both maximum parsimony and maximum likelihood analyses (although support for this clade was fairly low: MP 62; ML 77). As *O. vulgaris* is the type species for the genus, the generic placement of *O. oliveri* within the genus

Octopus would seem to be correct based on Kaneko's (2011) work. Norman *et al.* (2014), however, concluded that although currently treated under the genus *Octopus*, the generic placement of this taxon awaits a major revision of the family.

In addition, the specimen from South Meyer Island (AMS C.475900) demonstrates variation in mantle colouration. The vivid blue spots on the mantle of this specimen were not present on the conspecific specimen sequenced from the type locality (AMS C. 477708), and no mention of these spots was made in the original description.

Habitat and Biology. Rock pools and rock ledges in shallow intertidal areas with mid to high wave action. Benthic, intertidal and shallow subtidal to "several metres depth" (O'Shea 1999: 115).

Ylitalo *et al.* (2014) described the hatchlings and eggs of three *O. oliveri* from Hawaii. Eggs were laid in strings in large numbers (~400–2000) attached to a hard substrate, which the female covered with her mantle and arms. The hatchlings emerged after 35–40 days and moved up into the water column, suggesting a planktonic lifestyle. The chromatophore pattern could be used to distinguish *O. oliveri* paralarvae from other Hawaiian cephalopod paralarve. Mating behaviour was described by Ylitalo-Ward (2014). The behaviour was described as typical for the genus *Octopus*.

Distribution. Kermadec Islands: South Meyer Island, Raoul Island (Fig. 17). Japan and Hawaii.

DISCUSSION

Three species of Octopodidae are now known from the Kermadec Islands. The collection of shallow water octopuses during the Kermadec Biodiscovery Expedition in May 2011 has enabled the description of a male *Callistoctopus kermadecensis* and has also resulted in the description of a new species, *Octopus jollyorum*. *Octopus oliveri* was collected from its type locality, and DNA sequences were generated from the latter two species.

Members of the clade including *Octopus jollyorum* have formerly been identified as *Octopus 'vulgaris'* from material collected in Japan and Taiwan (see Kaneko *et al.* 2011; Warnke *et al.* 2004; Amor *et al.* 2014). However, molecular analyses show that *O. 'vulgaris'* forms an extremely widespread taxon thought to comprise a number of species. With the assistance of molecular data, many monophyletic clades in this complex have now been distinguished from *O. vulgaris sensu stricto*. These include *O. insularis* (Leite *et al.* 2008), *O. mimus* (Söller *et al.* 2000; Acosta-Jofré *et al.* 2012) and *O. tetricus* (Guzik *et al.* 2005; Amor *et al.* 2014).

The phylogenetic position of O. *jollyorum* has differed among previous phylogenetic analyses. Warnke *et al.* (2004) showed a single *O. 'vulgaris'* from Japan as the sister to *O. 'vulgaris'* from the Mediterranean but lacked representatives of *O. tetricus* and had fairly limited

overall sampling. Congruent with our results (Fig. 2), COIII data from Guerra et al. (2010) and Acosta-Jofré et al. (2012) also showed a well-supported polytomy among O. vulgaris sensu stricto, the Australian O. tetricus and a western Pacific clade from Japan+Taiwan (= O. jollyorum). They included good geographic sampling and many representatives from the O. 'vulgaris' species-group. Kaneko et al. (2011) analysed the phylogenetic relationships among the shallow water octopuses of Japan and adjacent waters, and showed three O. 'vulgaris' from Japan (= O. jollyorum) as the sister group to one O. vulgaris from the type locality but lacked representatives of O. tetricus. Amor et al. (2014) show a few individuals of O. 'vulgaris' from Japan and China (= O. jollyorum) to be the sister group to O. tetricus and O. cf. tetricus. In our analyses O. jollyorum forms a polytomy with the O. tetricus clade and the clade that contains O. vulgaris sensu stricto. Using a single mitochondrial gene is somewhat limiting in the sense that it is a maternally-inherited gene, and thus multi-marker phylogenies better represent evolutionary histories of taxa. However, using this gene maximised taxon coverage, and our results agreed with the three COIII clades found by previous authors (Guerra et al. 2011; Acosta-Jofré et al. 2012) and subsequently demonstrated that the west Pacific O. jollyorum and O. tetricus are distinct from the Mediterranean O. vulgaris.

Studies in recent years have compared O. vulgaris from the Mediterranean (the type locality for the genus and species) and Japan (= O. jollyorum) using both morphological and molecular data (e.g. Warnke et al. 2004; Amor et al. 2014). Samples from these two disjunct locations show relatively low pairwise population sequence divergences. This is despite the fact that populations of O. jollyorum from Japan and O. vulgaris from the Mediterranean must have been separated for about 10 million years — the approximate time of the final closure of the Tethys Sea, which once linked the Indo-Pacific with the Mediterranean. Amor et al. (2014) used a generalised rate of evolution applied to genetic distances to estimate the Australian O. *tetricus* complex had separated from representatives now recognised as O. jollyorum ~5.4–11.6 million years ago.

Rather than supporting the definition of O. vulgaris as a single species with a very wide and disjunct distribution Norman et al. (2014) recognise the 'Octopus vulgaris group' with O. vulgaris sensu stricto having a geographic range from the northeast Atlantic Ocean, south to the midcoast of western Africa, as well as to offshore central Atlantic islands. They state that "the species name Octopus vulgaris is also currently applied to at least four additional but morphologically similar but unresolved taxa" (Norman et al. 2014: 41). One of these is Octopus 'vulgaris' type IV with a distribution including subtropical east Asia. We propose the name O. jollyorum for this form and extend its range to include the Kermadec Island group. If this conclusion is supported by future studies, it implies a broad distribution for this taxon and the likelihood of finding more representatives of this group elsewhere throughout the western Pacific.

ACKNOWLEDGMENTS

We would particularly like to thank Dr Tom Trnski of the Auckland Museum for offering the Australian Museum three berths on the Kermadec Biodiscovery Expedition and for including the first author (AR) among the three participants. We would also like to thank members of the Australian Museum Trust for supporting our participation in this expedition. We also wish to thank Mike Shea for producing some of the line drawings in this paper and Ian Gleadall for his review and suggestions and thoughts concerning O. vulgaris. Cintia Mayel also assisted with generating DNA sequences. Another anonymous reviewer also contributed useful suggestions. The first author would particularly like to thank the other members of the expedition who looked for cephalopods and collected some of the octopus specimens that are discussed in this paper.

REFERENCES

- Acosta-Jofré, M.S., R. Sahade, J. Laudien and M. Chiappero 2012. A contribution to the understanding of phylogenetic relationships among species of *Octopus* (Octopodidae: Cephalopoda). *Scientia Marina* 76(2): 311–318.
- Amor, M.D., M.D. Norman, H.E. Cameron and J.M. Strugnell 2014. Allopatric speciation within a cryptic species complex of Australasian octopuses. PLoS ONE 9(6). DOI:10.1371/journal.pone.0098982.
- Berry, S.S. 1913. Nematolompas, a remarkable new cephalopod from the South Pacific. Biological Bulletin 25(3): 208–212.
- Berry, S.S. 1914. Notes on a collection of cephalopods from the Kermadec Islands. *Transactions of the New Zealand Institute* XXIV: 134–149.
- Berry, S.S. 1916. Cephalopoda of the Kermadec Islands. Proceedings of the Academy of Natural Sciences of Philadelphia 68: 45–66.
- Bolstad, K.S. 2007. Systematics and distribution of the New Zealand onychoteuthid fauna (Cephalopoda: Oegopsida), including a new species, *Notonykia nesisi*, sp. nov. *Reviews in Fish Biology and Fisheries* 17: 305–335.
- Boore, J.L. and W.M. Brown 2000. Mitochondrial genomes of *Galathealinum*, *Helobdella*, and *Platynereis*: Sequence and gene arrangement comparisons indicate that Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. *Molecular Biology and Evolution* 17(1): 87–106.
- Brooke, F.J. 1998. The coastal molluscan fauna of the northern Kermadec Islands. *Journal of the Royal Society of New Zealand* 28: 185–233.
- Darriba, D., G.L. Taboada, R. Daollo and D. Posada 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- Dell, R.K. 1952. The recent cephalopoda of New Zealand. Dominion Museum [N.Z.] Bulletin.
- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

- Gleadall, I.G. and F.C. Naggs 1991. The Asian ocellate octopuses, II: The validity of *Octopus fangsiao* Orbigny. *The Annals of Applied Information Sciences* 16(2): 173–180.
- Guerra, Á., Á. Roura, Á. González, S. Pascual, Y. Cherel and M. Pérez-Losada 2010. Morphological and genetic evidence that *Octopus vulgaris* Cuvier, 1797 inhabits Amsterdam and Saint Paul Islands (southern Indian Ocean) *ICES Journal of Marine Science* 67: 1401–1407.
- Guzik, M.T., M.D. Norman and R.H. Crozier 2005. Molecular phylogeny of the benthic shallow-water octopuses (Cephalopoda: Octopodinae). *Molecular Phylogenetics and Evolution* 37: 235–248.
- Hoyle, W.E. 1886. Report on the Cephalopoda. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. *Zoology* 16(44): 1–245, 33 pls.
- Huffard, C.L. and F.G. Hochberg 2005. Description of a new species of the genus *Amphioctopus* (Mollusca: Octopodidae) from the Hawaiian Islands. *Molluscan Research* 25: 134–135.
- Imber, M.J. 1978. The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidea) in the New Zealand region. *New Zealand Journal of Zoology* 5: 445–484.
- Jereb, P., and C.F.E. Roper (eds) (2010). Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. 2010. 605 pp. 10 colour plates.
- Jereb, P., C.F.E. Roper, M.D. Norman and J.K. Finn (eds) (2014). Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids. *FAO Species Catalogue for Fishery* Purposes. No. 4, Vol. 3. FAO, Rome. 370 pp. 11 colour plates.
- Kaneko, N., T. Kubodera and A. Iguchi 2011. Taxonomic study of shallow-water octopuses (Cephalopoda: Octopodidae) in Japan and adjacent waters using mitochondrial genes with perspectives on octopus DNA barcoding. *Malacologia* 54(1–2): 97–108.
- Katoh, T. 2008. Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. *BMC Bioinformatics* 9: 212.
- Leite, T.S., M. Haimovici, W. Molina and K. Warnke 2008. Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *Journal of Molluscan Studies* 74: 63–74.
- Lu, C.C., R. Boucher-Rodoni and A. Tiller 1995. Catalogue of types of recent Cephalopoda in the Muséum d'Histoire naturelle (France). *Bulletin of the Muséum d'Histoire naturelle*, *Paris*, 17: 307–343.
- Mangold, K. 1998. The Octopodinae from the eastern Atlantic Ocean and the Mediterranean Sea. *Smithsonian Contributions to Zoology* 586: 521–528.
- Norman, M.D. and F.G. Hochberg 2005. The current state of octopus taxonomy. *Phuket Marine Biological Centre Research Bulletin* 66: 127–154.
- Norman, M.D., J.K. Finn and F.G. Hochberg 2014. Family Octopodidae. Pp. 36–215, *in*: Jereb, P., C.F.E. Roper, M.D. Norman and J.K. Finn (eds) *Cephalopods of the world*.

- An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. FAO, Rome. 370 pp. 11 colour plates.
- Oliver, W.R.B. 1915. The Mollusca of the Kermadec Islands. Transactions and Proceedings of the Royal Society of New Zealand 47: 534.
- 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.
- Powell, A.W.B. 1979. *New Zealand Mollusca*. Pp. 500. Collins. Auckland.
- Rambaut, A. 2002. Se-Al. Department of Zoology, University of Oxford. Oxford.
- Roper, C.F.E. and G.L. Voss 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* 44: 48–63.
- 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.
- Silvestro, D. and I. Michalak 2011. RaxmlGUI: A graphical front-end for RAxML. *Organisms Diversity and Evolution*. doi: 10.1007/s13127-011-0056-0.
- Söller, R., K. Warnke, U. Saint-Paul and D. Blohm 2000. Sequence divergence of mitochondrial DNA indicates cryptic biodiversity in *Octopus vulgaris* and supports the taxonomic distinctiveness of *Octopus mimus* (Cephalopoda: Octopodidae). *Marine Biology* 136(1): 29–35.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22(21): 2688–2690.
- Stranks, T.N. 1998. The systematic and nomenclatural status of the Octopodinae described from Australia (Mollusca:

- Cephalopoda). Smithsonian Contributions to Zoology 586: 529–547.
- Strugnell, J., M.D. Norman, M. Vecchione, M. Guzic and A.L. Allcock 2013. The ink sac clouds octopod evolutionary history. *Hydrobiologia* http://dx.doi.org/10.1007/s10750-013-1517-6.
- Tiller, A. and R. Boucher-Rodoni 1994. Ferrusac and d'Orbigny's "Histoire naturelle générale et particulière des Céphalopodes acétabulifères": Dates of Publication of Plates and Text. *Nautilus* 107(3): 97–103.
- Toll, R.B. and 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. 1976. Two new species of octopods of the genus *Graneledone* (Mollusca: Cephalopoda) from the Southern Ocean. *Proceedings of the Biological Society* of Washington 92: 447–458.
- Warnke, K., R. Söller, D. Blohm and U. Saint-Paul 2004. A new look at geographic and phylogenetic relationships within the species group surrounding *O. vulgaris* (Mollusca, Cephalopoda): indications of a very wide distribution from mitochondrial DNA sequences. *Journal of Zoological Systematics and Evolutionary Research* 42: 306–312.
- Ylitalo, H.A., L. Watling and R.J. Toonen 2014. First description of hatchlings and eggs of *Octopus oliveri* (Berry, 1914) (Cephalopoda: Octopodidae). *Molluscan Research* 34(2): 79–83.
- Ylitalo-Ward, H. 2014. Notes on the mating behaviour of Octopus oliveri. Malacological Society of Australiasia Newsletter No. 51 July 2014: 10–11.
- Yokobori, S., N. Fukuda, M. Nakamura, T. Aoyama and T. Oshima (2004). Long-term conservation of six duplicated structural genes in cephalopod mitochondrial genomes. *Molecular Biology and Evolution* 21(11): 2034–2046.
- Amanda L. Reid, Australian Museum Research Institute, 6 College Street, Sydney 2010, Australia. Email: mandy.reid@austmus.gov.au
- Nerida G. Wilson, Western Australian Museum, 49 Kew Street Welshpool WA 6106, Australia.

Article submitted: 14 June 2012; revised and accepted: 20 November 2014.

APPENDIX 1: Definitions of Counts, Measurements and Indices.

- AF Arm Formula (arm numbers ordered from longest to shortest).
- ALI 1-4 and Hc Arm Mantle Index: Arm length as a percentage of mantle length (listed by arm numbers 1-4).
- AWI Arm Width Index: Arm width at widest point on stoutest arm as a percentage of mantle length.
- CLI Calamus Length Index: length of the calamus measured from the last (distal-most) sucker to its distal tip as a percentage of ligula length.
- FFLI Free Funnel Index: Length of free funnel portion as a percentage of funnel length.
- FLI Funnel Length Index: Funnel length as a percentage of mantle length.
- FOLI Funnel Organ Index: Length of outer limb of funnel organ as a percentage of median limb length.
- FOLI Funnel Organ Length Index: Length of median limb of funnel organ as a percentage of funnel length.
- GC Gill Count: Number of gill lamellae per demibranch (not including the medial terminal lamella).
- GLI Gill length as a percentage of mantle length.
- HAMI Hectocotylised Arm Mantle Index: length of hectocotylised arm as a percentage of mantle length. (Hc: hectocotylus.)
- HWI Head Mantle Width Index: Head width as a percentage of mantle width.

- LLI Ligula Length Index: Length of ligula measured from the distal-most sucker to the tip of the arm as a percentage of the length of the hectocotylised arm.
- ML Mantle Length: Dorsal mantle length measured from the midpoint between the eyes to the posterior end of the mantle.
- MWI Mantle Width Index: Greatest straight-line (dorsal) width of mantle as a percentage of mantle length.
- OAI Opposite Arm Index: length of hectocotylised arm as a percentage of left arm 3 length.
- PAI Pallial Aperture Index: Measurement between the points of attachment of the mantle to the head along the ventral margin of the mantle as a percentage of mantle length.
- SC Sucker Count: number of suckers on normal arms.
- SCH Number of suckers on hectocotylised arm of male.
- SDIn Sucker Diameter Index: Diameter of largest sucker measured across the aperture from rim to rim as a percentage of mantle length.
- SpLI Spermatophore Length Index: Length of spermatophore as a percentage of mantle length.
- SpWI Spermatophore Width Index: Greatest width of spermatophore as a percentage of spermatophore length.
- TL Total Length: measured from the tip if the longest arm to the posterior end of the mantle.
- WDI A-E (l and r) Web Depth Index: deepest sector of web as a percentage of the longest arm length (web sectors: A, dorsal to dorsal-E, ventral to ventral).
- WF Web Formula: web sectors ordered from deepest to shallowest.