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The Marine Fauna of New Zealand:

Octopoda (Mollusca : Cephalopoda)

Steve O'Shea

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The Marine Fauna of New Zealand: Octopoda (Mollusca: Cephalopoda)

by

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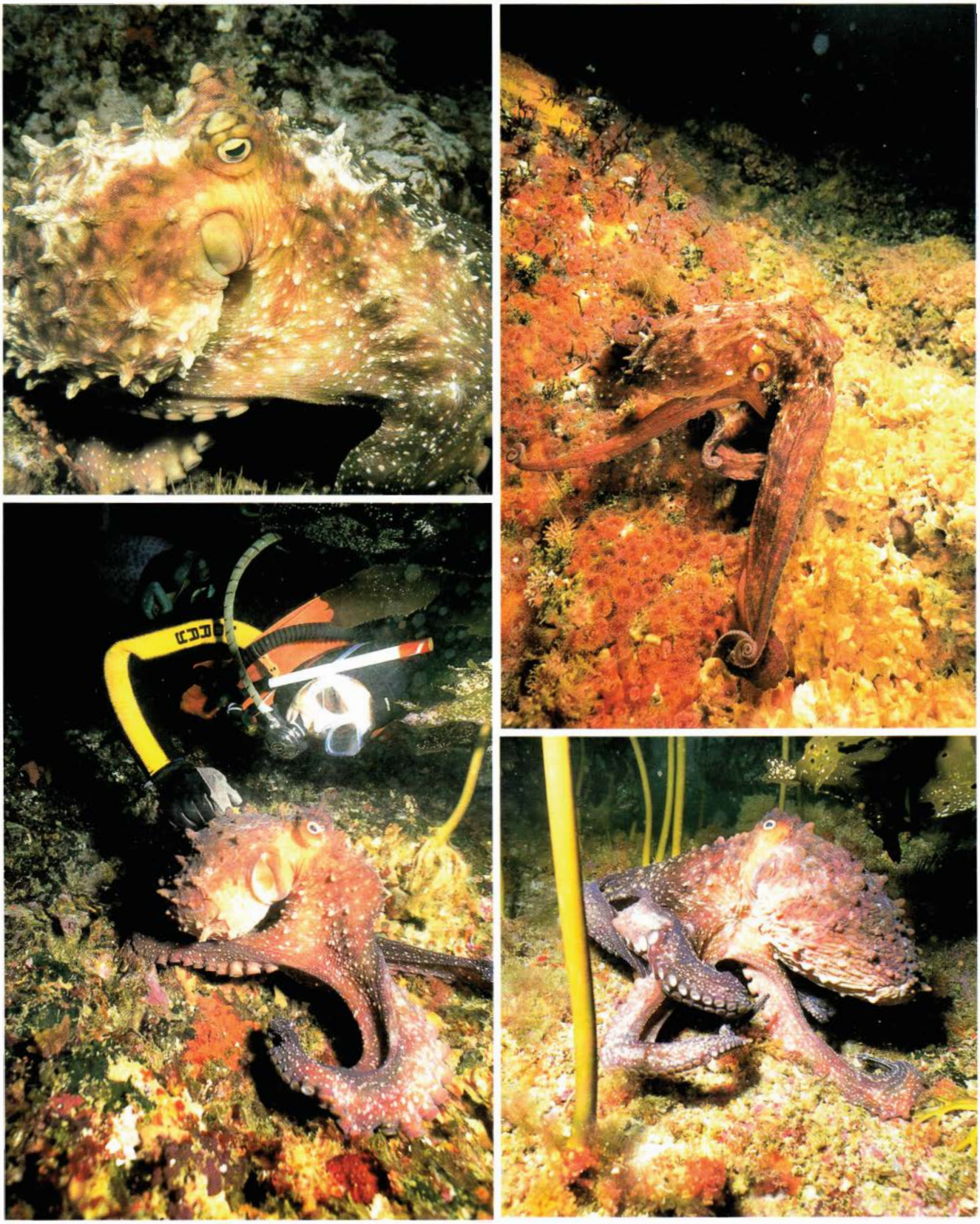

Frontis: ***Pinnoctopus cordiformis*** (Quoy & Gaimard, 1832).

Photos: A, Warren Farrelly. B, D, Jurgen Rötzell. C, David Stallworthy.

The Marine Fauna of New Zealand: Octopoda (Mollusca: Cephalopoda)

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ABSTRACT

The New Zealand octopod fauna (Mollusca: Cephalopoda: Octopoda) is revised, with a total of 39 species recorded and described. Several changes to established classifications of the Cirrata and the incirrate family Octopodidae are proposed. Six octopod families (two new), 14 genera (two new) and three species are newly recorded from New Zealand waters. Nine records of species from New Zealand are synonymised, and two species are removed from earlier synonymy and redescribed as distinct species.

The New Zealand finned (cirrate) octopod fauna as herein recognised comprises four families, seven genera and nine species; two new families are proposed, seven new species are described, with two additional species identified only to genus. Luteuthididae nov. is described to accommodate a single new genus *Luteuthis*. A second new family, Grimpoteuthididae, is proposed to accommodate two genera, *Grimpoteuthis* (revised) and a new genus, *Enigmatiteuthis*. The genus *Cirroctopus* Naef, 1921, is removed from the synonymy of *Grimpoteuthis*, and accommodated with *Opisthoteuthis* in a revised family Opisthoteuthididae. The fourth cirrate family represented in New Zealand waters, Cirroteuthididae, contains two species identified only to genus, *Cirroteuthis* sp. and *Cirrothauma* sp.

The New Zealand non-finned (incirrate) fauna comprises seven families, three subfamilies, 17 genera, and 30 species, including 12 that are new to science. Species previously admitted into the New Zealand fauna based solely on identifications of beak or tissue remains from gut contents of long-distance-foraging bird and whale species are critically evaluated: one family, genus and species are excluded from the New Zealand fauna. No changes are proposed to the classification of any of the seven incirrate families, although new records and minor nomenclatural changes are made for many species, and the classification of the Octopodidae is re-evaluated on the basis of apparent relationships between species with and without ink sacs. Three nominal subfamilies of the Octopodidae are recognised in New Zealand waters, Octopodinae, Bathypolypodinae, and Graneledoninae. Notable changes to previous classifications of the Octopodinae include removal of *Pinnoctopus* d'Orbigny from synonymy of *Octopus*, and recognition of four discrete groups of *Octopus* (*sensu lato*) morphology. Within the Bathypolypodinae, three species of *Benthoctopus* (*s.l.*) are described, and within the Graneledoninae a new species and a new subspecies of *Graneledone* are described, one is redescribed, and two new species of *Thaumeledone* are proposed.

After excluding several *Octopus* (*s.l.*) species common to both New Zealand and Australia, for which the distribution could be attributed to larval dispersal, there are clear biogeographic relationships between New Zealand and Australia, the central Pacific Islands, South Africa, South America, and Japan. No newly designated group of *Octopus* (*s.l.*) morphology is endemic to New Zealand. Biogeographic relationships between deep-sea octopods remain obscure.

Keywords: Cephalopoda, Octopoda, Cirrata, Incirrata, systematics, new families, new genera, new species, marine fauna, New Zealand, biogeography

INTRODUCTION

The New Zealand octopod fauna has only once been revised monographically (Dell 1952). Like any revision, this systematic work was incomplete and not without error; therein 14 octopus species were recognised from New Zealand waters, seven based on collections totalling only 46 specimens and a further seven cited from the literature. Substantial additions have been made to museum collections over the past 45 years, with marked increases in the number of specimens of many littoral species as well as many new deep-sea species. This material forms the basis of the present revision, with 39 species identified among nearly 1300 specimens. This revision fills a major gap in the knowledge of South Pacific Ocean octopod systematics, diversity, and distribution.

Whereas historic collections primarily comprised species inhabiting coastal littoral and pelagic environments, recent collections are numerically dominated by species and specimens typical of offshore bathyal to abyssal environments. Unfortunately, the systematics of deep-sea species are poorly known, as deep-sea octopods are comparatively rare in collections world wide. This dearth of information necessitated both regional analysis of diversity and a partial revision of many deep-sea octopod genera. As such, considerable effort has gone into defining many species, genera, and families, and identifying and resolving problems with existing classifications as they became apparent. Consequently substantial changes are proposed to classifications of deep-sea genera, far more so than changes proposed to littoral genera.

Since no comparable systematic treatment of the deep-sea fauna is available for any other part of the southern ocean, New Zealand species frequently had to be compared with relatively better-known faunas of the North Pacific and Atlantic Oceans. Monographic revisions such as those of Robson (1929, 1932), who redescribed the entire world fauna, and Sasaki (1929), who revised the Japanese fauna, are desperately needed for most of the world's oceans. Given this lack of information it is impossible to assess how the diversity of species now recognised from New Zealand waters compares with those from warmer or cooler seas.

Although littoral depths account for only the smallest fraction of the total seafloor environment surrounding New Zealand, it is within this depth range that a disproportionately large percentage (36%) of the recognised octopus species are found. Bathymetry off New Zealand (between coordinates 24°50–57°50' S, 157° E–167°00' W) from 0–1000 m depth accounts for *c.* 12% of the total sea floor area, 1000–2000 m for *c.* 13%, 2000–3000 m (*c.* 11%), 3000–4000 m (*c.* 11%), 4000–5000 m (*c.* 24%), 5000–6000 m (*c.* 25%), 6000–7000 m (*c.* 1%), 7000–8000 m (<1%), and 8000+ m (<1%) (NIWA, unpub.). The disproportionate number of species in littoral depths may be an artefact of collecting effort, since local seafloor depths over 1400 m have been inadequately sampled for cephalopods, with fewer than 10 octopus specimens known from depths in excess of it. New Zealand cirrates are known to 3150 m depth, elsewhere to 7279 m (Voss 1988b), and since depths of 3000–8000 m account for more than 50% of the total local seafloor environment, deep-sea octopod diversity will inevitably increase with increased collecting effort; the high ratio of littoral to deep-water taxa will thus probably decline. Currently, most New Zealand taxa are found on the lower continental shelf and slope.

Most systematic research undertaken on the New Zealand fauna subsequent to Dell's (1952) revision has focused on resolving the systematic status of several small-bodied littoral species attributed to the genus *Octopus sensu lato*. In the most recent compilation of valid molluscan taxa recorded from New Zealand (Spencer & Willan 1995), 17 species of octopod were recognised, compared with the 14 recognised by Dell. Two of the species recorded from New Zealand by Spencer and Willan (*loc. cit.*), *Haliphron atlanticus* (as *Alloposus mollis*) and *Octopus dofleini*, have since been excluded from the New Zealand fauna (O'Shea 1997b). These two species are not treated herein. The nomenclatural status of the remaining 15 species is substantially changed.

MATERIALS AND METHODS

The octopus fauna treated here is restricted to the area of the New Zealand Exclusive Economic Zone (EEZ), the fourth largest in the world, which includes diverse subtropical to subantarctic environments between 24°00–57°30' S latitude and 157°00' E–167°00' W longitude. The fauna is further restricted to that represented in collections to March 1997. With the exception of *Grimpoteuthis* (*s.l.*) *meangensis* Hoyle, representatives of all species recorded from the New Zealand EEZ, and almost every extant specimen previously recorded from it, have been re-examined.

Since live-animal photographs and descriptions of habitat and behaviour are not available for most species, the revision is based primarily on dead animals and description of preserved-animal characteristics. Although several species are described as new to science on the basis of one or two specimens, this is done only when available material is in exceptional condition and/or manifestly so different from previously known species that no confusion could result from their description. Several specimens that were impossible to identify have been deliberately excluded from the systematic treatment, given that apparent differences/similarities could be due to initial treatment history — the condition of the specimen at the time of fixation, whether live or at any one of a number of relaxed post-mortem stages (O'Shea 1997a).

Three categories of material examined are referred to in species descriptions. The first, Material Examined, includes all New Zealand specimens referred to a single species, presented in order of increasing latitude (north to south), then longitude (east to west). The second, Reference Material (after Cairns 1995), refers to closely related but not conspecific species examined to facilitate species description. Although some species referred to in this latter category are themselves poorly known, redescription falls outside the scope of this present study so that comparisons are made in abridged format only. The third, Foreign Material Examined, details material considered conspecific with New Zealand material but collected outside the New Zealand EEZ.

The two major collections from which material has been examined are those of the National Institute of Water and Atmospheric Research (NIWA, collection acronym NZOI) and Museum of New Zealand (NMNZ). These organisations accession specimens into collections in different ways. The NZOI system localises a specimen with an alphabetical-numeric code, with all taxa with common collection data prefixed by an NZOI Station number; holotype and paratype specimens receive a specimen-specific number, designated NZOI H- or NZOI P-. In contrast, material at NMNZ, and most other collections from which material has been examined, all employ a unique specimen- or lot-specific registration number.

International Acronyms

AIM	Auckland Institute and Museum, Auckland, New Zealand.
AMS	Australian Museum, Sydney, Australia.
BMNH	The Natural History Museum, London, UK
CM	Canterbury Museum, Christchurch, New Zealand.
FSFRL	Far Seas Fisheries Research Laboratory, Tokyo, Japan.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
NIWA	National Institute of Water and Atmospheric Research (formerly New Zealand Oceanographic Institute), Wellington, New Zealand.
NMNZ	Museum of New Zealand, (formerly National, Dominion, or Colonial Museum), Wellington, New Zealand.
NMV	Museum of Victoria, Melbourne, Australia.
NZOI	New Zealand Oceanographic Institute, now known as National Institute of Water and Atmospheric Research (NIWA).
OM	Otago Museum, Dunedin, New Zealand.
SAM	South African Museum, Cape Town, South Africa.
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
NSMT	National Science Museum, Tokyo, Japan.
UMML	University of Miami Marine Laboratory, Florida, USA.
USNM	National Museum of Natural History, Washington D.C., USA.

Other Acronyms

Where a single male or female specimen is represented within a given lot, it is simply denoted by M (male) or F (female), followed by the mantle length (ML) of the specimen. Where more than a single male or female is present within a sample, it is so enumerated, i.e., 4M, 2F, followed by respective ML in decreasing order. Where the sex of damaged or juvenile specimens is not obvious, and where sexing a specimen would be of limited value, a specimen is referred to as sex indeterminate (sex indet.).

When known, an initial treatment history (ITH) acronym follows mantle length, because of the effect this has on octopod morphology as detailed by O'Shea (1997a). ITH is provided in accordance with the following: FL, fixed live; FFN, fixed following narcotisation; FPM, fixed post-mortem; FPT, fixed post-thaw.

Where capture detail has simply been identified by place name, latitude and longitude coordinates where possible are taken from the New Zealand gazetteer (1954), and prefixed by *circa* (*c.*). The prefix '*c.*' is also used to localise some commercial fisheries bycatch material where specimens have occasionally been pooled over the course of several trawls within a restricted area. Depths are given in metres (m); where the depth has not been recorded this is denoted by 'DepNR'. Dates are formatted by day/month/year; when unknown detailed as DatNR. Where recorded, bottom temperature (BT) is given in degrees Celsius (°C). Other acronyms recorded in the Material Examined section are defined as: f.v., fishing vessel; f.r.v., fisheries research vessel; m.f.v., motorised fishing vessel; F.R.D., Fisheries Research Division; r.v., research vessel.

The recognised distribution of a species is that known to 30 May 1997.

MEASURES, INDICES, AND COUNTS

Frequently cited anatomical characters, structures, organ systems, measures and ratios employed in descriptions of cirrate and incirrate octopods are depicted in Figures 1–6. As a detailed, annotated account was presented by Roper and Voss (1983), emphasis here is made on defining points of reference used to measure characters or ratios, and in defining new character states employed in species descriptions. Definitions of indices in **bold type** are modified from definitions provided by Roper and Voss (*l.c.*), and several additional characters denoted by an asterisk (*) are proposed as basic to descriptions of certain genera.

Root **Definitions and Derivatives**

AF *Arm Formula*: relative length of arms expressed numerically in decreasing order (see AL): arm 1 (dorsal), 2 (dorsolateral), 3 (ventrolateral), 4 (ventral); e.g., 1.3.4.2., 2.3=4.1.

AL *Arm Length* — arm length measured from beak to tip of arm. ALI, Arm Length Index — AL as a percentage of ML. ALI1–4, Arm Length Index arms 1 to 4 — range of arm length indices, longest to shortest.

AS *Arm Sucker diameter* — diameter of suckers (e = enlarged, n = normal). ASIe, Arm Sucker Index (enlarged) — diameter of largest enlarged arm sucker on each designated arm as a percentage of ML. ASIn, Arm Sucker Index (normal)— diameter of largest normal arm sucker (not enlarged) on each designated arm as a percentage of ML. ASIn1–4, Arm Sucker Index (normal) 1 to 4R/L — range of ASIn values arms 1 to 4 R or L.

ASC *Arm Sucker Count*— number of suckers along each entire intact designated arm (to arm tip)[1], e.g., ASC2R, total arm sucker count arm 2 right. ASC1–4, Arm Sucker Count 1 to 4R/L (ex. 3R or L male hectocotylised arm, see ASC 3R or L) — range of arm sucker counts excluding counts on hectocotylised arm of male 3R or L. ASC3R (or 3L), Hectocotylised Arm Sucker Count — number of suckers along entire arm (to calamus).

BL* *Areolar Spot frequency* (blotches) (CIRRATES only) — number of areolar spots in longitudinal row from mantle down designated arm.

CaL *Calamus Length* — measured from last (distalmost) sucker to calamus tip. CaLI, Calamus Length Index — calamus length (CaL) as a percentage of ligula length (LL).

Cf(x)* *Cluster f(x) dorsal mantle length* — genus *Graneledone* only.

CIf(x)* *Cluster f(x) interocular* — genus *Graneledone* only.

CiL *Cirrus Length* — length of longest cirrus on each arm. **CiLI**, Cirrus Length Index, CiL as a percentage of the diameter of the largest normal sucker (or mantle length[2], whichever designated).

DIC* *Diameter individual clusters* (mm) — genus *Graneledone* only.

EO *Eye Orifice diameter* — diameter of the opening of eye. EOI, Eye Orifice Index — EO as a percentage of ML.

FFL *Free Funnel Length* — the length of funnel free of ventral surface of head from the anterior opening to the point of the funnel attachment to ventral surface of head.

FFuI *Free Funnel Length Index* — FFL as a percentage of ML.

FL *Fin Length* — measured along axis of fin. FL In, Fin Length Inner, greatest length along anterior margin of fin measured in straight line. FL Out, Fin Length Outer, greatest length along posterior margin of fin measured in straight line. **FLI In**[3], Fin Length Index Inner, FL In as a percentage of ML. **FLI Out**, Fin Length Index Outer, FL Out as a percentage of ML.

FuL *Funnel Length* — the length of the funnel from the anterior opening to the posterior border measured along the ventral midline. FuLI, Funnel Length Index — FuL as a percentage of ML.

FW *Fin Width* (CIRRATES only) — greatest width across one fin perpendicular to axis of fin. FWI, Fin Width Index, FW as a percentage of fin length.

GiLC *Gill Lamella Count* — number of lamellae on inner and outer demibranchs excluding[4] the terminal lamella(e), e.g., 7 outer, 7 inner.

HdL *Head Length* — diameter of orbits along anteroposterior axis of body.[5] HdLI, Head Length Index —HdL as a percentage of ML.

HdW *Head Width* — greatest width of head at level of eyes. HdWI, Head Width Index — HdW as a percentage of ML.

LL *Ligula Length* — measured from distalmost sucker to tip of arm. LLI, Ligula Length Index — LL as a percentage of hectocotylised arm length.

ML *Mantle Length* — measured from midpoint between eyes to posterior end of mantle.

MW *Mantle Width* — greatest straight-line (dorsal) width of mantle. MWI, Mantle Width Index — MW as a percentage of ML.

OAI *Opposite Arm Length Index* — length of hectocotylised arm as a percentage of its fellow arm on opposite side.

[1] Differs in whole arm sucker counts instead of half arm sucker counts.

[2] Differs in not using mantle width.

[3] Differs by dividing fin length measures by mantle length as opposed to head width; head width in species of *Opisthoteuthis* is somewhat indefinable owing to the anteroposterior compression of the cephalopedal mass.

[4] Differs by excluding the terminal lamellae from inner and outer demibranch lamella counts.

[5] Differs because head length is indefinable in many instances in octopods.

PA *Pallial Aperture extent* — the distance between the points of attachment of the mantle to the head along the ventral margin of the mantle. PAI, Pallial Aperture Index — PA as a percentage of ML.

PCL* *f(x) of processes within individual cluster* — genus *Graneledone* only.

TL *Total Length* — measured from end of longest arm to posterior end of mantle.

WD *Web Depth* — measurement of deepest web sector from beaks to midpoint of sector (Web sector A, dorsal to dorsal arm; B, dorsal to dorsolateral arm; C, dorsolateral to ventrolateral arm; D, ventrolateral to ventral arm; E, ventral to ventral arm). WDIA–E, web depth range sectors A–E.

WF *Web Formula* — relative depth of each web sector expressed alphabetically in decreasing order (see WD). WFR/L, right and left web formulas.

The relative size of mature specimens is recognised as a function of total length and defined in Table 1.

Relative characters employed in text descriptions of buccal mass, posterior salivary gland size, and characters of beak morphology are defined in Tables 2–4.

The posterior salivary glands as referred to for cirrate octopods (Voss & Pearcy 1991) are here referred to as anterior salivary glands.

Table 1. Measures employed in text descriptions of animal absolute size.

Size	TL (mm)
Small	< 200
Small to moderate	200–300
Moderate	300–500
Moderate to large	500–600
Large	600–1000
Massive	>1000

Table 2. Measures employed in description of buccal mass and and posterior salivary gland relative size (Incirrata).

	Descriptor	Buccal Mass Length =
Buccal mass:	Small	17–23% ML
	Moderate	24–28% ML
	Large	29–32% ML
Posterior salivary glands	Vestigial	9–14% ML
	Small	15–19% ML
	Moderate	20–24% ML
	Large	25–29% ML
	Very large	30–45% ML

Table 3. Measures employed in description of beak relative characters (Incirrata).

	LB Hood L	UB Hood L
Very shallow	< 25%	< 30%
Shallow	26–30%	31–35%
Moderate	31–35%	36–40%
Deep	36–40%	41–45%
Very deep	>41%	>46%

Table 4. Measures employed in description of beak relative characters (Incirrata).

	LB Height	UB Height	LB Wing Length	
Very depressed	<65%	<85%	<85%	Very short
Depressed	66–70%	86–90%	86–90%	Short
Moderately tall	71–75%	91–100%	91–95%	Moderately long
Tall	76–80%	101–110%	96–100%	Long
Very tall	>81%	>111%	>100%	Very long

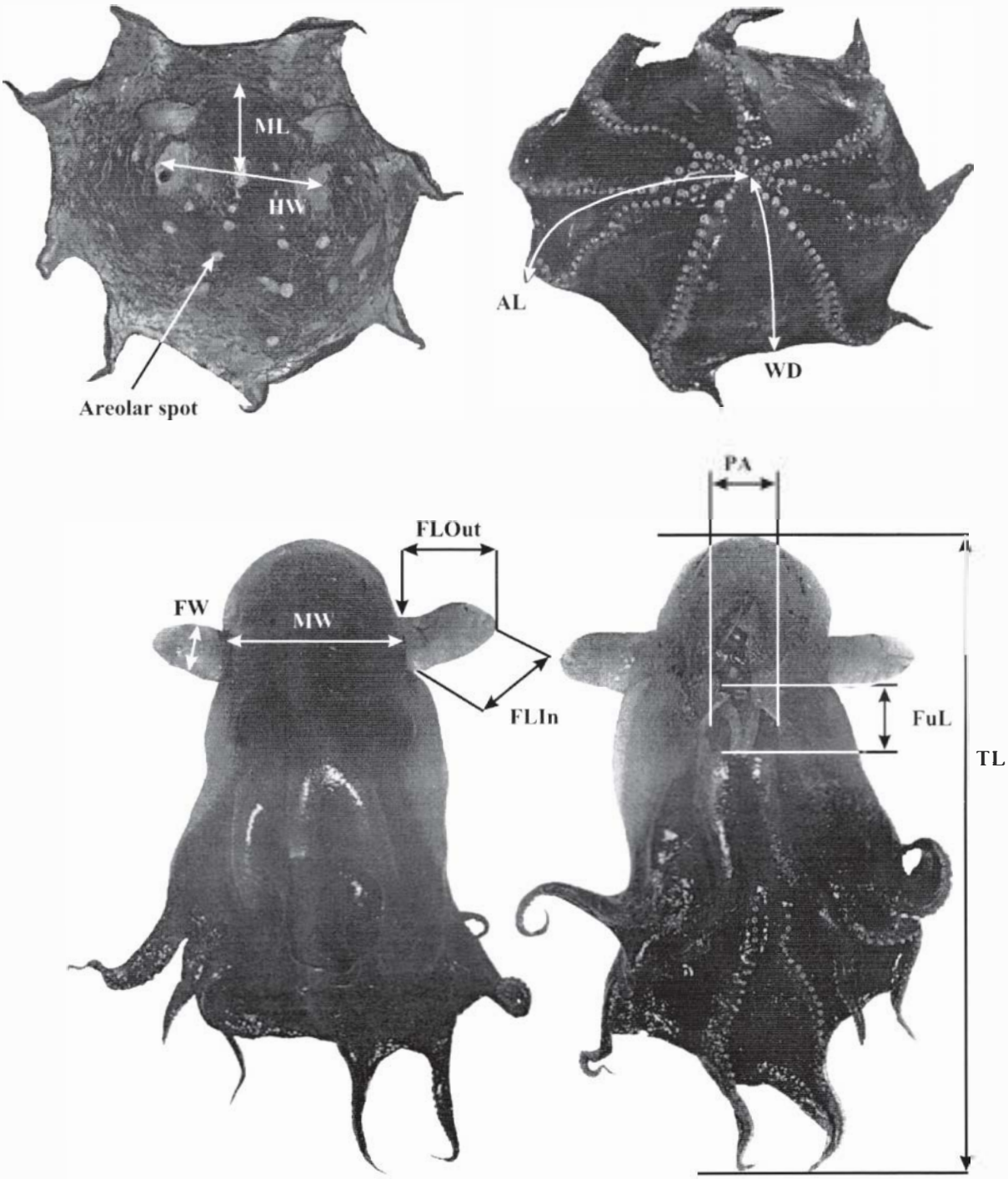


Figure 1. Top: ***Opisthoteuthis*** sp.; Bottom: ***Grimpoteuthis*** sp. Raw measure delineation points. Legend: AL (arm length), FLIn (fin length inner), FLOut (fin length outer), FuL (funnel length), FW (fin width), HW (head width), ML (mantle length), MW (mantle width), PA (pallial aperture width), TL (total length), WD (web depth).

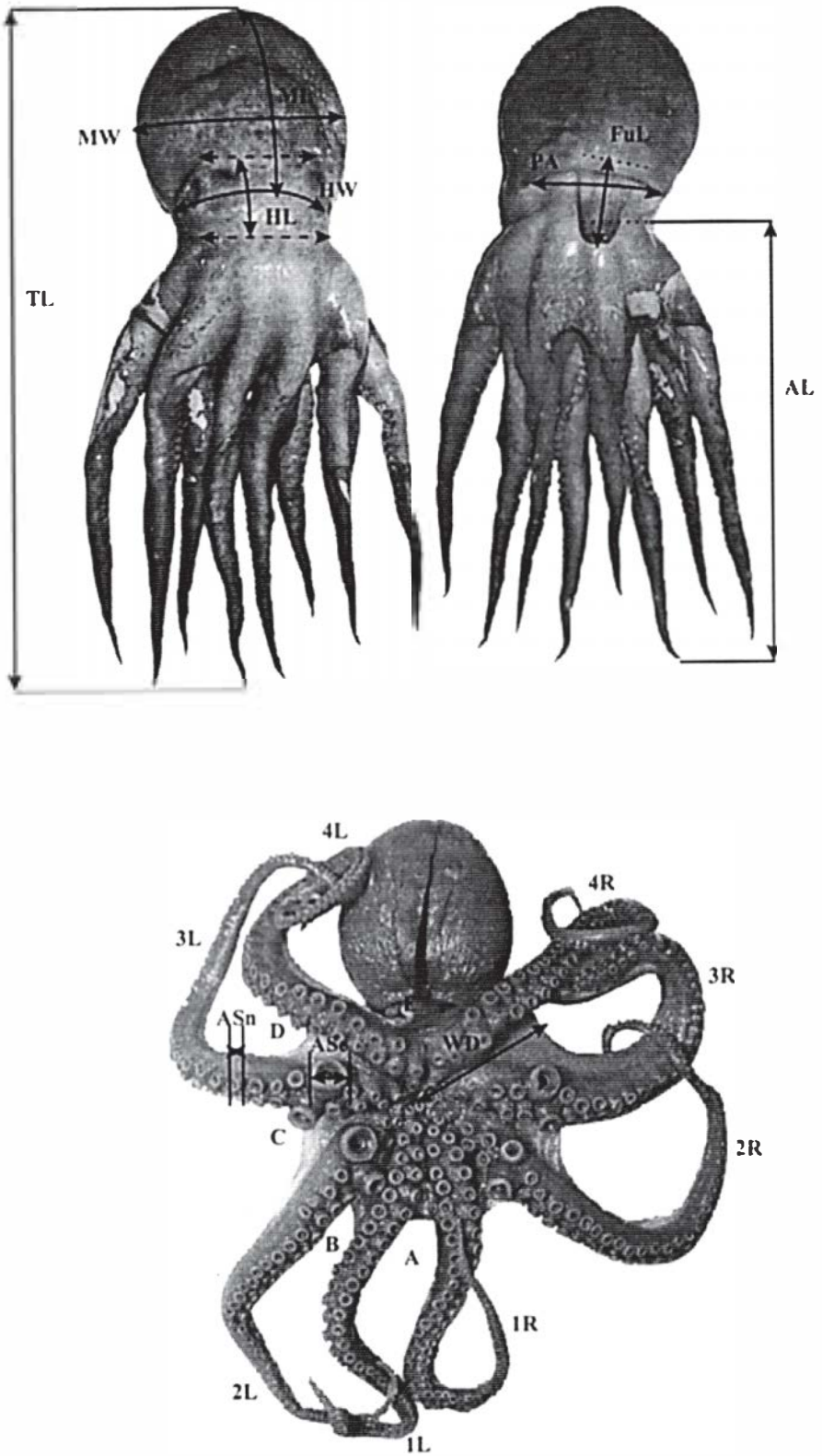


Figure 2. Top: ***Graneledone*** sp.; Bottom: ***Octopus*** (s.l.) ***campbelli*** (Smith). Raw measure delineation points. Legend: **A–E** (web sectors A through E), AL (arm length), ASe (enlarged sucker diameter), ASn (normal sucker diameter), FuL (funnel length), HW (head width), ML (mantle length), MW (mantle width), PA (pallial aperture width), TL (total length), WD (web depth), **1–4R/L** (arms 1 through 4 right or left).

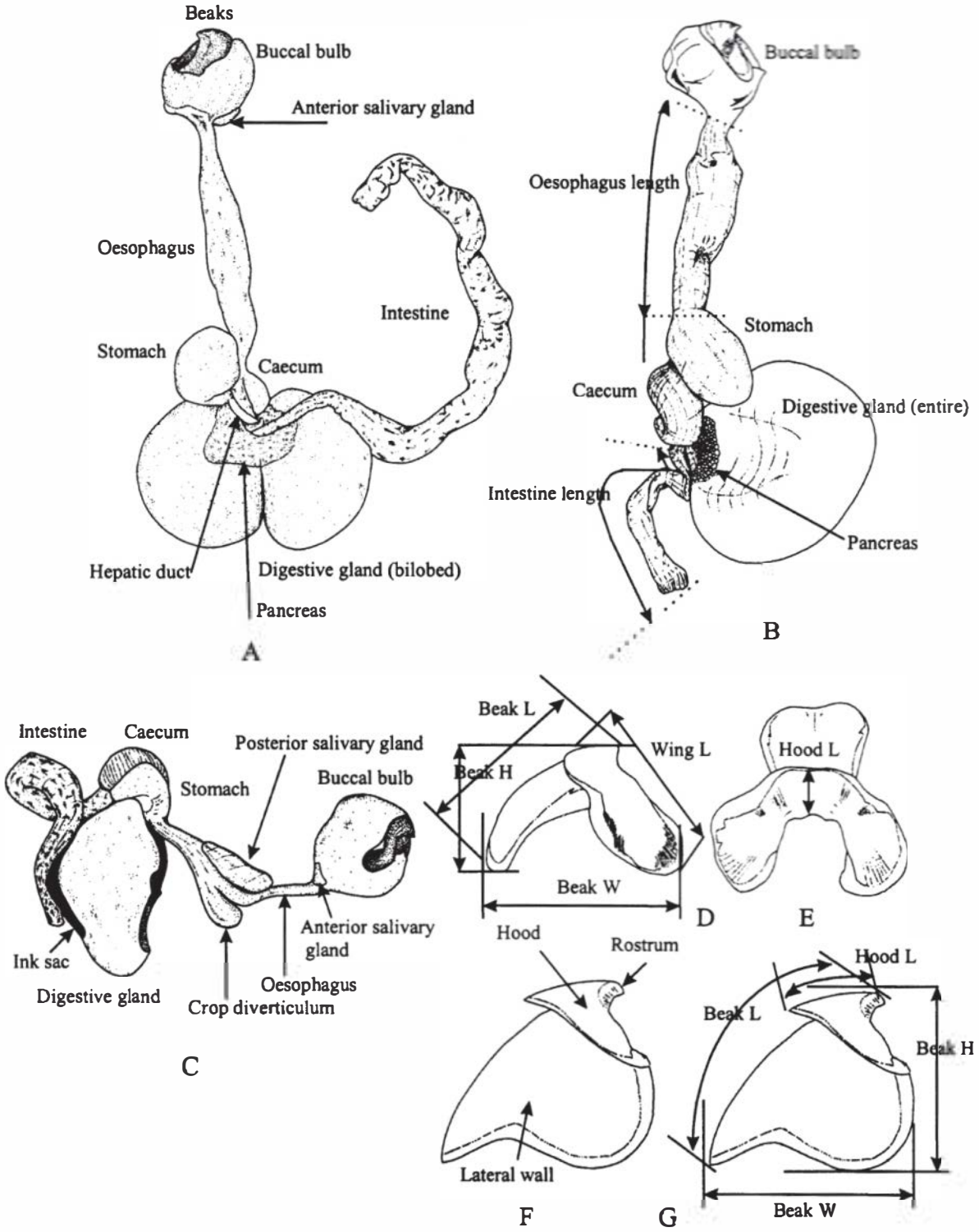


Figure 3. Terminology, ratios, and measures employed in anatomical description of alimentary canal and beak structures. **A–C**, alimentary canal: **A**, *Opisthoteuthis* sp.; **B**, *Grimpoteuthis* sp.; **C**, *Octopus* sp.; **D–G**, beaks, *Cirroctopus* sp.; **D**, **F**, lower beak. **E**, **G**, upper beak. Legend: Beak H/L/W (beak height, length, width), Hood L (hood length), Wing L (wing length).

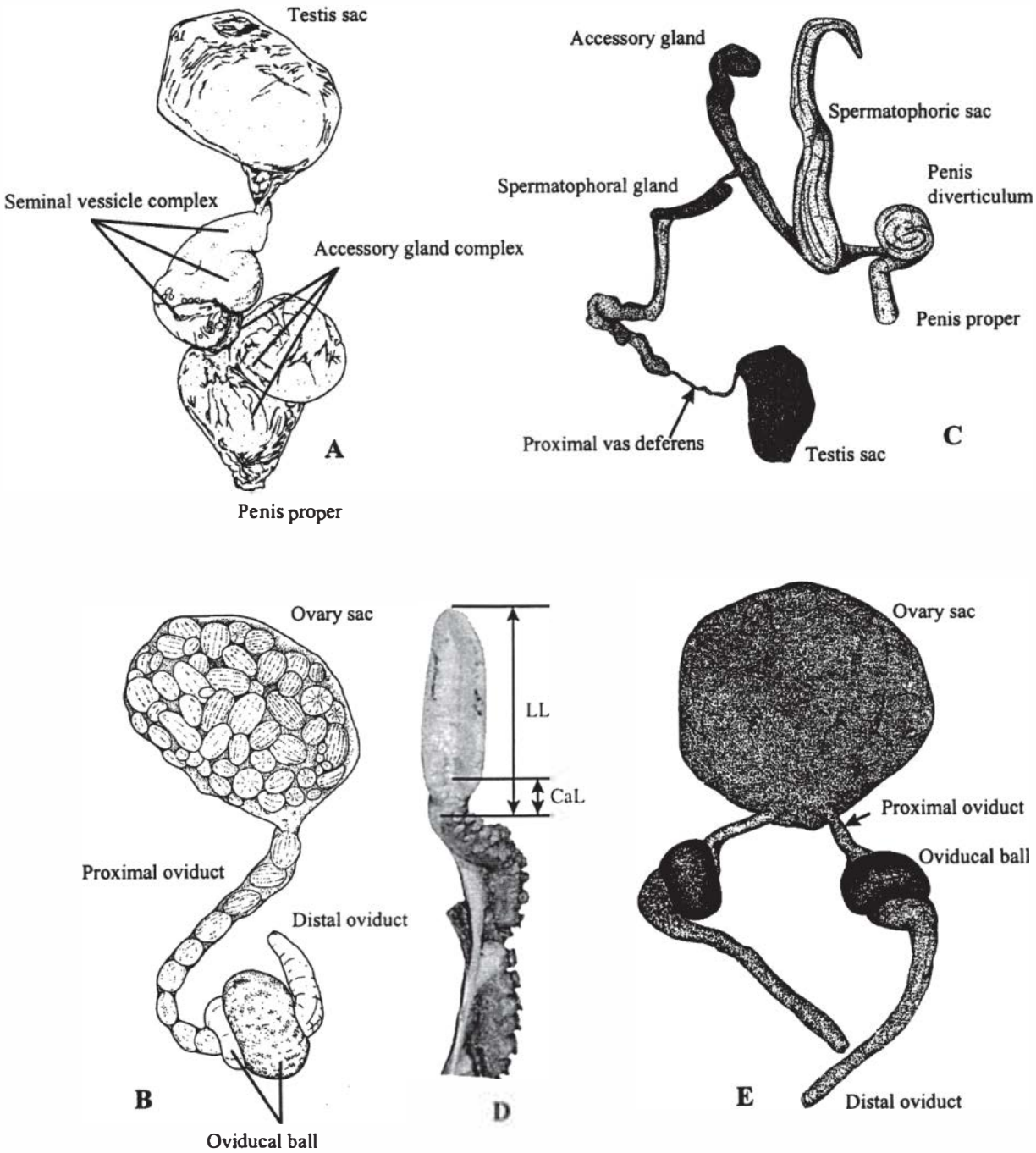


Figure 4. Terminology, ratios, and measures employed in anatomical description of reproductive system and hectocotylus characters. **A, B**, ***Opisthoteuthis*** sp., **A**, male system, **B**, female system; **C**, male system ***Graneledone*** sp.; **D**, hectocotylus ***Pinnoctopus*** sp.; **E**, female system ***Benthoctopus*** sp. Legend: CaL (calamus length), LL (ligula length).

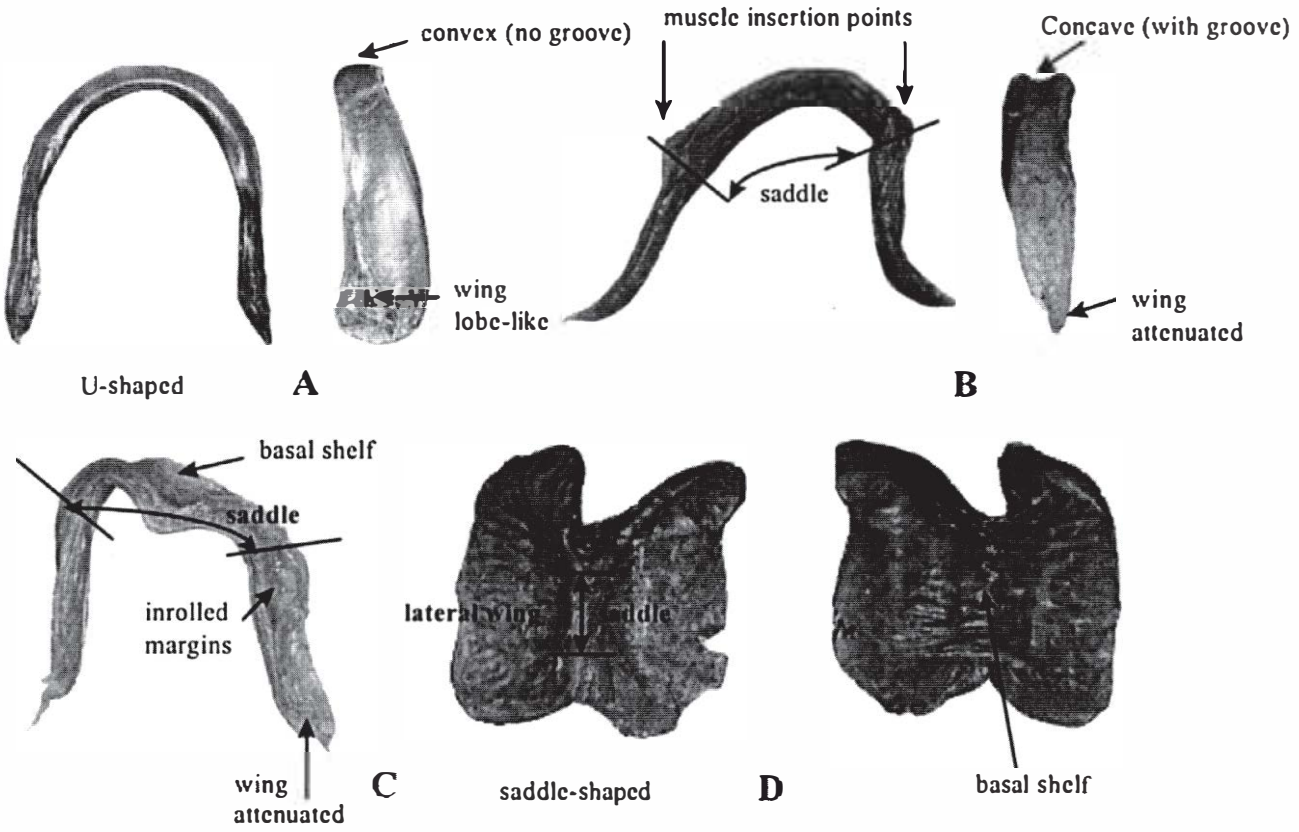


Figure 5. Terminology employed in description of shell structures in cirrate taxa. **A**, *Grimpoteuthis*. **B**, *Opisthoteuthis*. **C**, *Luteuthis* n. gen. **D**, *Cirroteuthis*.

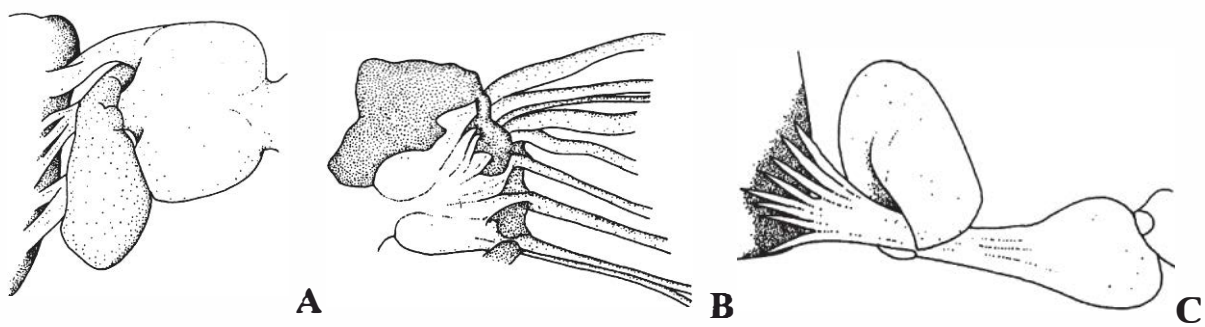


Figure 6. Optic lobe shapes: **A**, *Opisthoteuthis*, kidney-shaped (optic nerves 3). **B**, *Cirroctopus*, kidney-shaped (optic nerves 9). **C**, *Grimpoteuthis*, ovoid (optic nerves 1).

CHECKLIST OF OCTOPODA
Known from the New Zealand Region

Suborder CIRRATA
Family OPISTHOTEUTHIDIDAE
Opisthoteuthis (*s.s.*) *mero* sp. nov.
Opisthoteuthis (*s.l.*) *chathamensis* sp. nov.
Opisthoteuthis (*s.l.*) *robsoni* sp. nov.
Cirroctopus hochbergi sp. nov.

Family GRIMPOTEUTHIDIDAE new family
Grimpoteuthis abyssicola sp. nov.*
Enigmatiteuthis innominata gen. et sp. nov.

Family LUTEUTHIDIDAE new family
Luteuthis dentatus gen. et sp. nov.

Family CIRROTEUTHIDIDAE
Cirroteuthis cf. *muelleri* Eschricht, 1836
Cirrothauma sp. cf. *Cirroteuthis magna* Hoyle, 1885

INCERTAE SEDIS
Cirrate eggs, gen. et sp. indet. Boletzky, 1982
'*Grimpoteuthis*' *meangensis* (Hoyle, 1885)

Suborder INCIRRATA
Family AMPHITRETIDAE
Amphitretus pelagicus Hoyle, 1885
Amphitretus thielei Robson, 1930

Family BOLITAENIDAE
Bolitaena microtyla Steenstrup, 1886
Japetella diaphana (Hoyle, 1885)
Eledonella pygmaea Verrill, 1884

Family OCYTHOIDAE
Ocythoe tuberculata Rafinesque, 1814

Family ARGONAUTIDAE
Argonauta argo Linnaeus, 1758
Argonauta nodosa Solander, 1786

Family TREMOCTOPODIDAE
Tremoctopus robsonianus Kirk, 1883

Family VITRELEDONELLIDAE
Vitreledonella richardi Joubin, 1918

Family OCTOPODIDAE
Subfamily Octopodinae
Octopus (*s.s.*) *oliveri* Berry, 1914
Octopus (*s.s.*) *gibbsi* sp. nov.
Octopus (*s.l.*) sp. 1
Octopus (*s.l.*) sp. 2
Pinnoctopus cordiformis (Quoy & Gaimard, 1832)
Pinnoctopus kermadecensis (Berry, 1914)
Octopus (*s.l.*) *huttoni* (Benham, 1943)
Octopus (*s.l.*) *campbelli* (Smith, 1902)
Octopus (*s.l.*) *mernoo* sp. nov.
Octopus (*s.l.*) *kaharoa* sp. nov.
Enteroctopus zealandicus (Benham, 1944)

Subfamily Bathypolypodinae
Benthoctopus (*s.l.*) *tegginmathae* sp. nov.
Benthoctopus (*s.l.*) *tangaroa* sp. nov.
Benthoctopus (*s.l.*) *clyderoperi* sp. nov.

Subfamily Graneledoninae
Graneledone challengeri (Berry, 1916)
Graneledone taniwha taniwha sp. nov.
Graneledone taniwha kubodera ssp. nov.
Thaumeledone zeiss sp. nov.
Thaumeledone marshalli sp. nov.
?Pareledone sp.

* Known from immediately outside the New Zealand Exclusive Economic Zone only.

SYSTEMATICS

Order **OCTOPODA** Leach, 1818
Suborder **CIRRATA** Grimpe, 1916
Family **OPISTHOTEUTHIDIDAE** Verrill, 1896

DIAGNOSIS (revised): Small- to moderate-sized cirrates. Fins short to long, terminal; body anteroposteriorly compressed, with mantle, head and pedal mass bell to disc shaped; areolar spots present, variably extending over mantle, head and arms 1-4. Arms long; web deep, single; web nodules variably developed. Cirri commence between suckers 1-4; cirrus length less than twice greatest sucker diameter; sucker size sexually dimorphic, enlarged in male in either distal and /or proximal fields; suckers with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, and simple aperture. Gills of 'half orange' type. Shell simple; lateral wings taper to acute points. Intestine about 1.5–2.5 times longer than oesophagus; radular and palatine teeth absent. Optic lobe kidney shaped; optic nerves few to many (2–9).

REMARKS: While specimens fixed live tend to be bell shaped, specimens fixed post-mortem assume the classic disc-shaped morphology; the distinction between the two morphologies is of limited systematic value when dealing with specimens of unknown ITH. The apparent absence of areolar spots in some species is likely attributable to preservation artefact.

To facilitate the description of novel *Opisthoteuthis* species three 'types' of *Opisthoteuthis* are diagnosed and, where possible, species referable to each are identified. Although species within an organisational type probably are more closely related to each other than to those between types, it is premature to portray any type as a distinct genus or subgenus. Resolving systematic relationships between the three recurring types of *Opisthoteuthis* morphology is presently difficult given the generally conservative body plan and preliminary nature of the systematic treatment offered herein. Although those characters employed to differentiate the three types of *Opisthoteuthis* may appear quite trivial, additional characters or character combinations may become apparent when both the comparative anatomy of these animals is better understood and more species are described.

Opisthoteuthis Verrill, 1883

TYPE SPECIES: *Opisthoteuthis agassizii* Verrill, 1883, by original designation.

DIAGNOSIS (type 1): With the characters of the family. Cirri commence between suckers 1 and 2; male sucker enlargement greatest in proximal field, weak in distal field. Mantle transversely divided by mantle margin invagination. Shell simple, non-vacuolate; lateral wings laminar, with terminal prolongation into fine-pointed tips. Digestive gland bilobed; male accessory gland 3 dominates accessory gland complex.

REMARKS: Voss (1988a: 254, 266) recognised 10 species of *Opisthoteuthis*: *O. agassizii* Verrill, 1883, *O. depressa* Ijima & Ikeda, 1895, *O. grimaldi* (Joubin, 1903), *O. extensa* Thiele, 1915, *O. medusoides* Thiele, 1915, *O. pluto* Berry, 1918, *O. persephone* Berry, 1918, *O. californiana* Berry, 1949, *O. japonica* Taki, 1962, and *O. philippi* Oommen, 1976, to which can be added *O. vossi* Sanchez & Guerra, 1989. Three additional *Opisthoteuthis* species are recognised from New Zealand waters. While comparing New Zealand and foreign material it became apparent that at least three recurring morphological and anatomical types exist. The three *Opisthoteuthis* types are enumerated 1, 2, and 3, with 1 considered *Opisthoteuthis* (*sensu stricto*), and 2 and 3 considered *Opisthoteuthis* (*sensu lato*). Type 2 groups the same species identified by Berry (1949, 1952) as related to each other: *O. californiana* (= ?*O. albatrossi*) and *O. pluto* (Berry 1949, 1952). Unfortunately, the characters which led Berry to draw a relationship between these two species were not discussed. Whatever they were, however, they could not have included the morphology of male *O. californiana*, for this was only subsequently described (Berry 1955).

With the exception of *O. medusoides*, the 11 recognised species of *Opisthoteuthis* are divided amongst the three types of *Opisthoteuthis* as diagnosed by a combination of direct examination for some species and a literature review for others. *Opisthoteuthis agassizii*, *O. vossi*, *O. persephone*, and *O. mero* sp. nov. are included in type 1 after direct examination of specimens, while *O. extensa*, *O. phillipi*, and *O. depressa* are included on the basis of literature accounts of morphology and anatomy. This *Opisthoteuthis* type occurs in the South Pacific (including Tasman Sea), Northeast Pacific (Japan), Indian Ocean, and North and South Atlantic (including Caribbean Sea and Gulf of Mexico). Types 2 and 3 are dealt with in respective systematic sections.

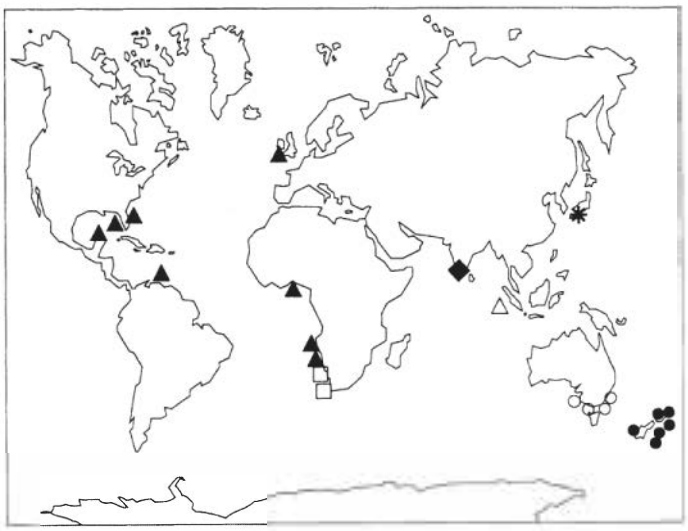


Figure 7. Recognised distribution of *Opisthoteuthis* Group 1. ▲ *O. agassizii* Verrill, 1883; Δ *O. extensa* Thiele, 1915; • *O. mero* sp. nov.; ○ *O. persephone* Berry, 1918: ♦ *O. phillipi* Oommen, 1976; □ *O. vossi* Sanchez & Guerra, 1989; ✳ *O. depressa* Ijima & Ikeda, 1895[1].

Opisthoteuthis mero sp. nov. (Figs 9, 10) (Tables 5–9)

TYPE MATERIAL (92 specimens, 43 male [M], 42 female [F], 7 sex indet.): Holotype: NZOI H-673, M, ML 70 mm, FPT, 36°51.84–54.84' S, 176°18.94–19.15' E, 509–514 m, BT 9.0°C, 07/04/1996, f.r.v. *Kaharoa* Stn KAH9604/004, NZOI Stn Z8528. Paratype: NZOI P-1108, F, ML 76 mm, FPT, 36°09.61–12.57' S, 176°17.50–16.91' E, 527–570 m, 06/01/1995, BT 8.4°C, f.r.v. *Kaharoa* Stn KAH9501/10, NZOI Stn Z8417; NZOI P-1109, F, ML 42 mm, FPT, 36°55.38–54.97' S, 176°17.32–18.43' E, 360–430 m, BT 10.1°C, 30/09/1995, f.r.v. *Kaharoa* Stn 9511/061, NZOI Stn Z8418.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.95264, BS 419, M, ML 30 mm, 34°47' S, 174°17' E, 417–483 m, otter trawl, 24/02/1974, r.v. *Acheron*; NMNZ M.131718, F, ML 20 mm, 35°23' S, 175°06' E, 402–475 m, 10/01/1969; NMNZ M.131719, M, ML 59 mm, 36°26.50–24.60' S, 173°35.60–34.70' E, 841–866 m, BT 8.2°C, datNR, f.r.v. *James Cook* Stn J3/25/84; NMNZ M.95258, F, ML 57 mm, 37°26.8' S, 177°43.5' E, 815–843 m, 17/04/1981, f.r.v. *James Cook* Stn J06/018/81; NZOI Stn D237, sex indet., ML 6.2 mm, 38°02' S, 167°42' E, 675 m, 01/10/1964; NMNZ M. 118293, 3M, ML 27, 25, 23 mm, 2F, ML 43, 25 mm, FPT, 39°00' S, 178°20' E, -/09/1993, 1000 m, f.v. *Peterson*; NMNZ M.118292, 2 sex indet., ML 18, 15, mm, FPT, 39°50–58' S, 168°04–10' E, 850–865 m, f.r.v. *San Hauraki*, 16/07/1994; NMNZ M.118240, M, ML 38 mm, sex indet, ML 15 mm, FPT, *c.* 40°00' S, 168°00' E, 900 m, -/08/1994, f.v. *San Hauraki*; NMNZ M.118294, M, ML 27 mm, 2 sex indet., FPT, ML 16, 15 mm, 40°00' S, 168°02' E, 900 m, -/07/1994, f.v. *San Hauraki*; NMNZ M.118296, M, ML 46 mm, FPT, 40°16.4' S, 177°06.2' E, 480 m, -/01/1994; NMNZ M.118297, M, ML 47 mm, FPT, 40°24' S, 177°18.4' E, 440 m, BT 7.5°C, -/01/1994, f.r.v. *Kaharoa* Stn KAH9401/59; NMNZ M.95288, M, ML 72 mm, 42°00.7–41°58.6' S, 170°21.8–21.6' E, 590–600 m, 18/05/1978, f.r.v. *James Cook* Stn J08/13/1978; NMNZ M.95271, M, ML *c.* 55 mm, sperm whale stomach contents, *c.* 42°26' S, 173°42' E, 1963/1964, coll. M.W. Cawthorn; NMNZ M.95272, 2F, ML *c.* 55, 46 mm, sperm whale stomach contents, *c.* 42°26' S, 173°42' E, 1963/64, coll. M.W. Cawthorn; NMNZ M.95294, F, ML 69 mm, 42°54.0' S, 175°12.0' E, 613–618 m, 08/11/1975, f.v. *Shinkai Maru* Stn 2/43; NMNZ M.118992, 3F, ML 40, 35, 29 mm, FPT, 42°54–43°08' S, 176°26–177°05' E, 368–411 m, 27/12/1994–18/01/1995; NZOI Stn Z8416, 2M, ML 45, 30 mm, 2F, ML 28, 27 mm, FPT, 43°10' S, 175°44' E, 450 m, -/10/1995, f.v. *Peterson*; NMNZ M.131720, M, ML 58 mm, 43°27.10' S, 168°53.70–52.30' E, 911–916 m, 15/12/1983, BT 6.3°C, f.r.v. *James Cook* Stn J16/23/83; NMNZ M.117553, F, ML 66 mm, 43°52.0' S, 178°43.6' E, 518 m, 13/04/1992, f.v. *Akagi Maru* Stn 520/139, coll. N. Allred; NMNZ M.131721, M, ML 68 mm, 44°34.4–39.5' S, 173°35.2–09.3' E, 682 m, 22/09/1989, f.v. *Oyang 76* Stn NZKOR 382, Tow 70; NMNZ M.117988, sex indet., ML *c.* 68 mm, 47°36.55' S, 178°38.37' E, 295–387 m, 17/11/1992, f.r.v. *Tangaroa* Stn 9211/04; NMNZ M.117880, F, ML 121 mm, FPT, 48°27.3' S, 179°27.56' E, 565–599 m, 15/11/1993, f.r.v. *Tangaroa* Stn 9310/03; NMNZ M.117985, M, ML 31 mm, 48°52.80' S, 171°41.66' E, Pukaki Rise, 575–594 m, 21/11/1993, f.r.v. *Tangaroa* Stn 9310/15; NMNZ M.95249, M, ML *c.* 50 mm, Pukaki Rise, *c.* 48°52.80' S, 171°41.66' E, f.r.v. *James Cook*, 1980; NMNZ M.131722, F, ML 52 mm, 49°01.00' S, 167°37.00–40.00' E, 668–683 m, 01/04/1982, BT 7.0°C, f.v. *Shinkai Maru* net 110; NMNZ M.117873, F, ML 61 mm, 49°09.2' S, 172°37.92' E, 484–489 m, 21/11/1992, f.r.v. *Tangaroa* Stn 9310/17; NMNZ M.67855, F, ML *c.* 37 mm, 49°19.8' S, 171°07.0' E, 447 m, f.r.v. *Wesermunde* Stn W3/107/79; NMNZ M.117878, M, ML 65 mm, FPT, 49°34.02' S, 167°03.53' E, 402–407 m, 07/12/1993, f.r.v. *Tangaroa* Stn 9310/81; NMNZ M.67854, M, ML 54 mm, 49°40' S, 172°47' E, depNR, 23/07/1979, f.r.v. *Wesermunde* Stn 103/179/79; NZOI Stn D87 TAM, M, ML 29 mm, 49°56.0' S, 171°50.0' E, 483 m, 14/05/1963; NMNZ M.118242, 3M, 45, 41, 28 mm, FPT, 50°40' S, 167°06' E, -/02/1994, f.v. *Peterson*; NMNZ M.118741, 4M, ML 85, 45(2), 37 mm, 8F, ML 107, 63, 60, 38, 37, 35, 31, 25 mm, FPT, 50°48' S, 166°47' E, 400–410 m, 07/10/1994, f.v. *Peterson*, coll.

[1] And possible synonym *O. japonica* Taki, 1963.

M. Marinovich; NMNZ M.118715, 6M, ML 76, 72, 71, 50, 42, 33 mm, 5F, ML 63, 61, 55, 54, 44 mm, FPT, 50°50' S, 166°56' E, 390–400m, 12/11/1994, f.v. *Peterson*, coll. M. Marinovich; NMNZ M.118811, 9M, ML 79, 54, 49, 47, 37, 36, 32, 30, 27 mm, 8F, ML 61, 53, 41(3), 34, 31, 25 mm, FPT, 51°10' S, 166°37' E, 400–410 m, 10/10/1994, f.v. *Peterson*, coll. M. Marinovich; NMNZ M.95296, F, ML 54 mm, 51°11' S, 167°08' E, 558 m, 21/02/1972, f.r.v. *James Cook* Stn J03/014; NMNZ M.131723, F, ML 46 mm, 51°11' S, 167°08' E, 558 m, 21/02/1972, f.r.v. *James Cook* Stn J03/015/72.

REFERENCE MATERIAL: SAM S2339, *Opisthoteuthis* sp. indet., ML *c.* 8 mm, 32°26.6' S, 16°15.04' E, 825 m, 15/08/1989; SAM S2394, *Opisthoteuthis vossi*, det. M.C. Roeleveld, M, ML *c.* 51 mm, 27°20.7' S, 14°03.3' E, 864 m, 19/02/1988; SAM S2502, *Opisthoteuthis agassizii*, det. M.C. Roeleveld, M, ML 54 mm, 33°48.4' S, 17°22.2' E, 900 m, 05/03/1988; SAM A8974, *Opisthoteuthis* cf. *agassizii*, det. O'Shea, F, ML 24 mm, Cape Pt, E 1/2 N, N 36 mile, 700–800 fthm, 28/08/1903, PF 17662; NZOI Stn Z8441, *Opisthoteuthis persephone* Berry, F, ML *c.* 101 mm, 33°22–33°40' S, 151°53–152°09' E, 458 m, 12–20/09/1972, f.r.v. *Kapala*, ex. AMS C.308973, pres. I. Loch.

RECOGNISED DISTRIBUTION (Fig. 8, p. 20): New Zealand, North and South Islands, east and west coasts, Chatham Rise, Campbell Plateau, 35°23–51°11' S, 167°08–175°06' E, 360–1000 m.

DIAGNOSIS: A moderate-sized species with pronounced anteroposterior compression of cephalopedal mass (disc-shaped). Fins small, flaplike; mantle and nuchal constrictions absent; arms long, deeply invested in web; web deep; male abrupt sucker enlargement strong in proximal and weak in distal field. Suckers many, ASC to 71.

DESCRIPTION (Fig. 9A–B): Adult animal of moderate size, ML to 121 mm, TL to 340 mm; mantle, head and web extensively gelatinous; arms semi-gelatinous; cephalopedal mass disc-shaped. Eyes large, bulbous, oriented laterally. Areolar spots extending over dorsal surfaces of mantle, head and along arm bases 1–4; mature specimens with 6–11 areolar spots over head and along arm pairs 1, 6–12 spots over head and along arm pairs 2, and 6–9 along arm pairs 3 and 4; areolar spots in juveniles are larger in size and fewer in number (Table 5).

Fins deeply invested in mantle tissues; free portion oriented laterally, paddlelike, length short to moderate (FLI out. 27–64) and, at least in preserved state, often retracted into pouchlike invaginated pockets in mantle; inner and outer fin margins parallel-sided to weakly convex, FWI 55–78; fin distally truncated to weakly rounded, margins delicate; basal constriction poorly developed; muscular portion of exposed fin about half fin length (Table 6).

Mantle aperture reduced, enveloping base of funnel; mantle attached to base of arm pair 4 at level equivalent to 18th adoral sucker; funnel length moderate to long (37–78% ML), attached to ventral arm bases 4 similarly at position of 18th adoral sucker; funnel attached ventrally to arm bases 4 to level of mantle attachment to arms, free portion short. Funnel organ V-shaped.

Arm formula variable, arms 1–3 frequently longest, 4 shortest; arms long, thick; longest arm length 70–85% TL, shortest arm length 58.3–72.8% TL. Web deep, thick, extensively gelatinous; deepest web sector 63–78% longest arm length, 74–96% shortest arm length; shallowest web sector 42–55% longest arm length, 49–66% shortest arm length. Cirrus length short to moderate, about 4–10% ML or 0.6–1.2 times as long as greatest sucker diameter; cirri apparent between suckers 1 and 2 on all arms, attaining greatest length between suckers 8 and 11 along each arm, and present to arm tips. Suckers slightly larger in male (male, 4.3–8.6 % ML; female, 4.6–7.5% ML), abruptly enlarged in proximal field, weakly in distal field; first 3 suckers of moderate size, next 5–8 abruptly enlarged and bulbous, thereafter suckers gradually and slightly decrease to a point where the dorsolateral surface of each arm and web intersect, after which the terminal 15–25 suckers on each arm tip rapidly reduce in diameter. Suckers with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, and small, simple sucker aperture (Fig. 10C). Suckers well spaced within web sectors, invested into oral surface of arms; suckers crowded along distal half of each arm, bases touching; to 71 uniserial suckers along each arm; suckers extend to arm tips. Indices, formulas, and counts for male and female *O. mero*, in Tables 7 and 8; raw measures, Table 9.

Dorsal and ventral surfaces of mantle, head and arms 1–4 deep red to light purple; margin of eye, outer margin of fins and cirri, pale white. Adoral surface of arms and web darker, purplish-red; outer adoral surface fades slightly to pink; suckers and sucker apertures pale yellow.

Gills with 6 or 7 tightly compacted lamellae (almost invariably 7); innermost and outermost reduced in size, lamellae 3 or 4 with common arterial base, slightly reduced in size relative to adjacent lamellae.

Optic lobe large, kidney-shaped (Fig. 10D). Optic nerve branching pattern asymmetric, with 3 right and 5 left nerves, all with multiple terminal branching into back of eyeball. White bodies well separated across dorsal mid-line of head.

Shell simple (Fig. 10E), solid (non-vacuolate), light-honey coloured, translucent and flexible but easily fragmented, surface texture polished. Saddle well developed, thickened relative to wings, with single pronounced excavation; outer surface concave, inner surface convex; muscle insertion points marked by 2 well-developed prominences. Lateral wings laminar;

Table 5. Areolar spot distribution for *Opisthoteuthis mero* sp. nov. (* denotes damage).

	NMNZ M.118811	NMNZ M.118811	NMNZ M.118810	NZOI H-673	NMNZ M.118810	NMNZ M.118811	NZOI P-1108	NMNZ M.118811	NMNZ M.118810
BL1R	10	9	10	6	9	11	8	9	3
BL2R	7	7	8	8	6	12	10	10	9
BL3R	5	5	6	*	6	9	5	6	6
BL4R	8	7	8	*	8	9	9	6	3

Table 6. Fin dimension indices for *Opisthoteuthis mero* sp. nov.

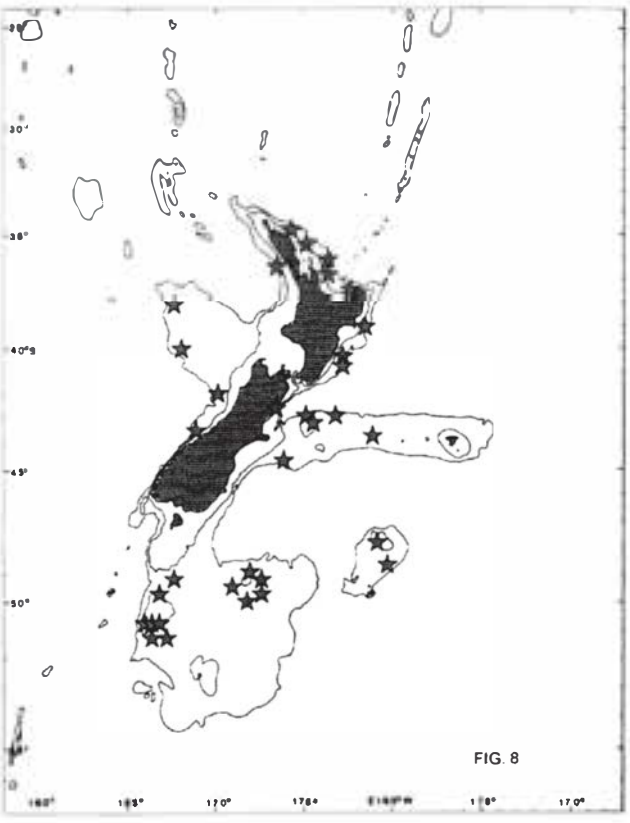
	NMNZ M.118811	NMNZ M.118811	NMNZ M.118810	NZOI H-673	NMNZ M.118810	NMNZ M.118811	NZOI P-1108	NMNZ M.118811	NMNZ M.118810
FLI Out	47.7	43.0	40.5	44.6	27.3	37.5	45.4	64.1	52.8
FLI In	45.0	39.8	36.1	38.6	24.0	30.1	41.4	55.6	47.2
FWI	55.8	67.3	67.2	69.2	78.0	71.4	67.2	54.9	73.7

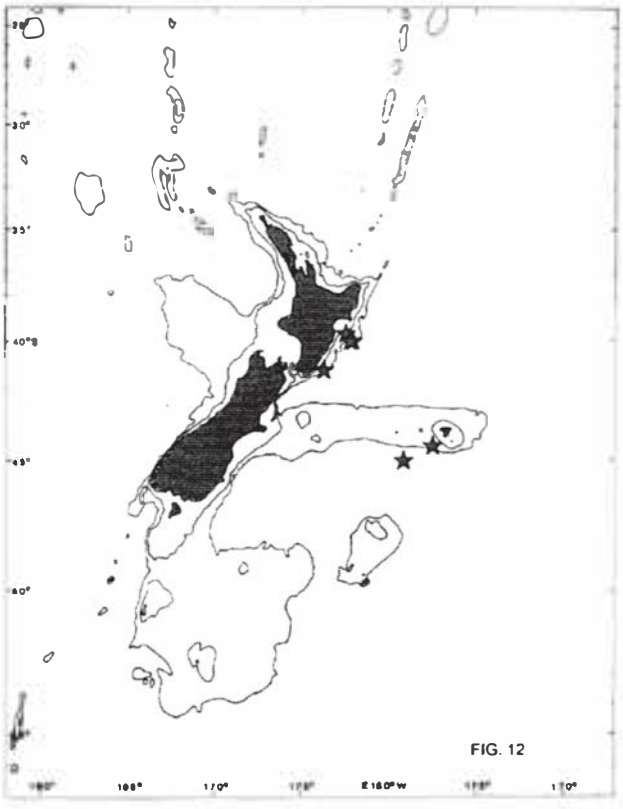
Table 7. Indices, formulas, and counts for male *Opisthoteuthis mero* sp. nov. (* denotes damage).

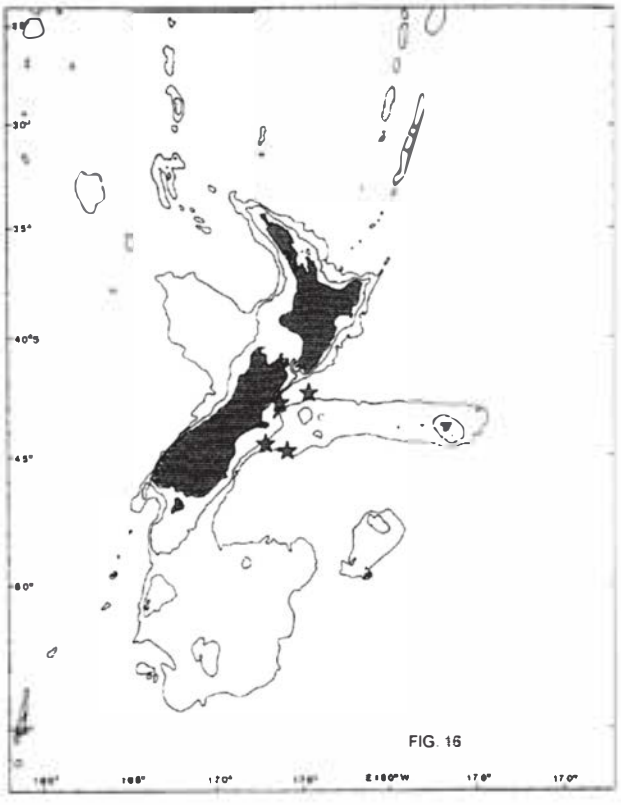
	NMNZ M.118811	NMNZ M.118811	NMNZ M.118810	NZOI H-673	NMNZ M.118810
AL1–4R	67.0–80.3	74.7–85.7	79.2–83.4	69.0–79.0	68.1–71.5
ALFR	1.4.3.2	1.3.2.4	2.1.3.4	1.2.4.3	1.2.3=4
ALFL	3.1.4.2	1.2.3.4	*	1.4.3.2	1.4.2.3
WDIA–E	51.3–63.0	43.8–62.9	52.8–78.3	48.6–71.0	58.3–77.4
WFR	B.C.A.E.D	*	A.B.D.E.C	A.B.C.E.D	A.B.C.D.E
WFL	B=A.D.C=E	A.D.B.C.E	A.B.E.D.C	A.E.D.B.C	A.B.D.E.C
ASC1–4	62–71	57–71	64–71	62–67	56–61
CiLI1–4	3.3–4.4	7.8–10.9	3.8–5.9	2.9–5.7	2.6–3.9
ASIn1–4	4.4–6.8	7.8–8.6	5.3–6.3	5.7–6.4	4.3–5.5

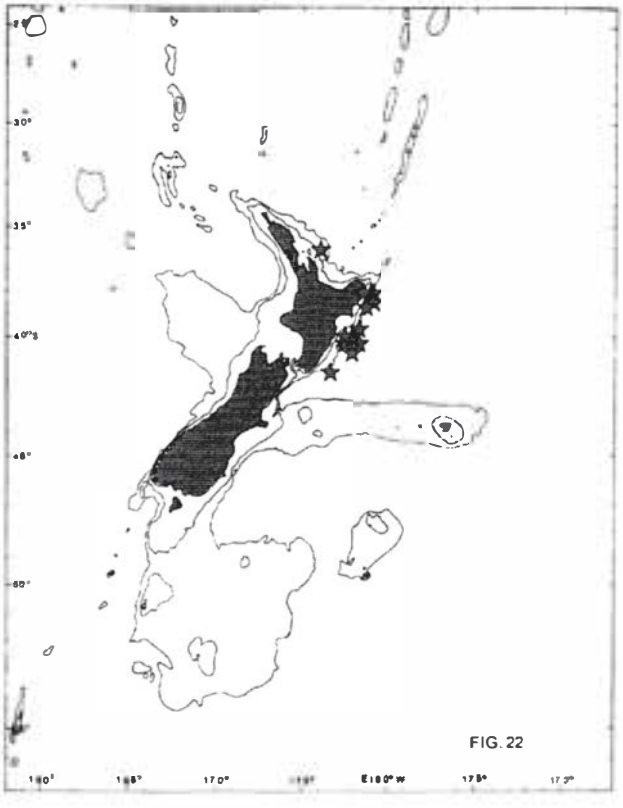
Table 8. Indices, formulas, and counts for female *Opisthoteuthis mero* sp. nov. (* denotes damage).

	NMNZ M.118811	NZOI P-1108	NMNZ M.118811	NMNZ M.118810
AL1–4R	72.6–83.5	70.4–78.8	61.7–70.6	71.5–81.9
ALFR	3.1.2.4	1=2.3.4	3.1.2.4	3.4.2=1
ALFL	1.2.4.3	2=3.1.4	2.3.1.4	*
WDIA–E	50.7–65.7	47.8–66.8	47.0–70.5	42.4–63.6
WFR	C.D.B.A.E	B.A.C.E.D	B.A.C.D.E	A.D.C.B.E
WFL	C.A=D.B=E	C.A=B.D.E	C=A.B.D.E	B.A.C.D.E
ASC1–4	61–67	64–70	58–64	54–57
CiLI1–4	4.4–5.9	4.7–6.2	4.2–5.6	4.2–6.9
ASIn1–4	6.6–7.4	5.1–5.3	4.6–5.9	6.7–7.5









Recognised distribution. **Fig. 8**, *Opisthoteuthis mero* sp. nov. **Fig. 12**, *Opisthoteuthis chathamensis* sp. nov. **Fig. 16**, *Opisthoteuthis robsoni* sp. nov. **Fig. 22**, *Cirroctopus hochbergi* sp. nov.

Table 9. Raw measures for *Opisthoteuthis mero* sp. nov. (* denotes damage).

	NMNZ M.118811	NMNZ M.118811	NMNZ M.118810	NZOI H-673	NMNZ M.118810	NMNZ M.118811	NZOI P-1108	NMNZ M.118811	NMNZ M.118810
SEX	M	M	M	M	M	F	F	F	F
TL	340	328	265	271	235	248	260	235	144
ML	90	64	79	70	75	68	76	71	36
MW	93.5	67	73	90	50	81	106	71	53
PA	28.5	20	23.5	29.2	15	21	31.5	25	12.5
FunL	33	50	41.0	38.0	34.5	37	39.5	34	22.0
FL Out	43	27.5	32.0	31.2	20.5	25.5	34.5	45.5	19.0
FL In	40.5	25.5	28.5	27.0	18.0	20.5	31.5	39.5	17.0
FW	24	18.5	21.5	21.6	16.0	18.2	23.2	25	14.0
EO	15	10.2	10.0	10.0	10.0	11	11.5	*	8.0
AL1R/L	273/260	281/258	221/221	214/208	168/165	200/202	205/195	165/149	103/100*
AL2R/L	228/240	259/254	220*/195*	210/158	164/148	195/192	205/203	162/160	104/110
AL3R/L	260/267	271/248	216/200	187/200	160/146	207/170	187/202	166/150	118/115
AL4R/L	261/242	245/239	210/205	191/204	160/150	180/175	183/193	145/137	108/110
WDA	157	170	173	152	130	108	135	111	75
WDBR/L	172/158	177/162	160/153	137/118	120/118	122/104	137/135	117/108	60/81
WDCR/L	163/145	*/160	130/120	135/105	110/92	136/115	113/140	108/112	62/70
WDDR/L	140/154	123/165	140/124	104/120	101/105	128/107	98/130	92/98	71/66
WDE	145	128	135	123	98	105	100	78	50
ASC1R	66/64	57/65	66/64	64/62	57/56	67/68	66/64	58/58	55/45*
ASC2R	62/66	64/67	57*/53*	64/44*	56/57	65/62	66/64	60/54*	54/54
ASC3R	68/69	71/67	65/66	66/66	60/58	67/61	65/65	64/43*	57/43*
ASC4R	71/66	63/71	70/71	67/66	61/61	58*/66	70/68	56*/41*	44*/57
CIL1R	3.0	7.0	4.5	4.0	2.5	4.0	4.7	3.2	1.5
CL2R	4.0	6.0	3.0	3.0	2.0	4.0	4.0	3.0	1.5
CL3R	4.0	5.0	4.0	2.0	2.9	3.5	4.0	3.2	2.5
CL4R	3.9	6.5	4.7	3.0	2.5	3.0	3.6	4.0	2.5
ASn1R/L	5.1/4.0	5.0/5.8	4.5/5.0	4.0/4.0	3.2/3.4	4.5/4.5	3.9/4.0	4.2/4.1	2.7/2.0
ASn2R/L	4.0/5.5	5.5/5.5	4.2/5.0	4.0/4.0	3.5/3.5	4.6/4.0	4.0/4.0	4.0/4.0	2.5/2.0
ASn3R/L	6.1/5.5	5.5/5.0	5.0/5.5	4.1/4.0	4.0/4.0	5.0/5.0	3.9/3.2	3.3/3.9	2.4/2.3
ASn4R/L	6.0/5.6	5.0/5.2	4.9/5.5	4.5/4.0	4.1/3.9	5.0/5.0	3.9/4.1	3.8/3.5	2.5/2.8
GiLC	7	7	7	7	6	7	7	7	7

margins not inrolled; wings diverge from saddle at angle about 45° and taper to acute points.

Male reproductive system (Fig. 10F) with massive development of seminal vesicles 1–3 and accessory glands 1–3; complex of accessory glands almost equivalent in size to seminal vesicle complex; accessory gland 3 dominates accessory gland complex; penis poorly developed, triangular, lappet-like. Female reproductive system (Fig. 10G) with massive ovary sac, about twice diameter of oviducal ball and containing about 100 similar-sized eggs (7.2 x 4.9 mm) and a similar number of variably developed smaller eggs (6.5–2.5 mm length); eggs with 15–18 longitudinal striations. Similar-sized eggs in proximal oviduct, distal oviducal chamber, and distal oviduct and frequently free in mantle cavity. Proximal oviduct about three times longer than distal duct, thin walled, with numerous (to 9) eggs disposed in single file. Oviducal gland with 2 unequal-sized, non-striate chambers, the second of greater size and diameter than the first; single egg frequently present in lumen of second chamber. Distal oviduct short, thick, muscular, frequently containing single egg.

Alimentary canal (Fig. 10H) with moderate-sized buccal bulb; anterior salivary glands large; radular and palatine teeth absent; crop well developed, attaining greatest dilation about mid-oesophagus length, diverticulum absent. Stomach large, without external demarcation; caecum poorly developed, without spiral coiling. Intestine long, about twice oesophagus length, thin walled, distended for greatest length; anal flaps absent. Hepatic ducts two; digestive gland large, bilobed; pancreas well developed.

Upper beak (Fig. 10I) tall (height 74% length), with dark-pigmented hood with delicate translucent wall margins; hood moderately deep (depth 67% beak

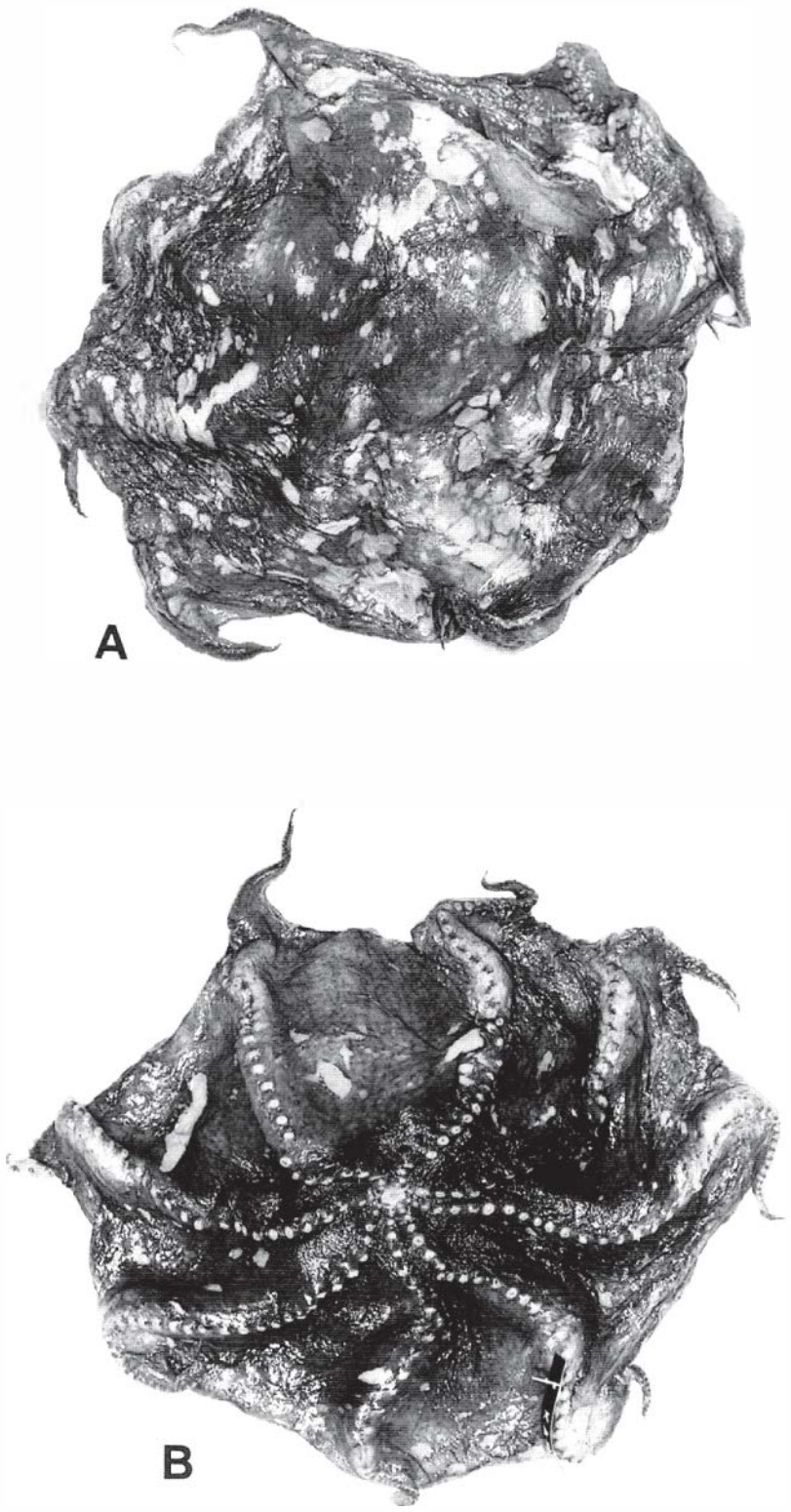


Figure 9. ***Opisthoteuthis mero*** sp. nov.: Holotype, aboral (A) and oral (B) perspectives, NZOI H-673, male, ML 70 mm.

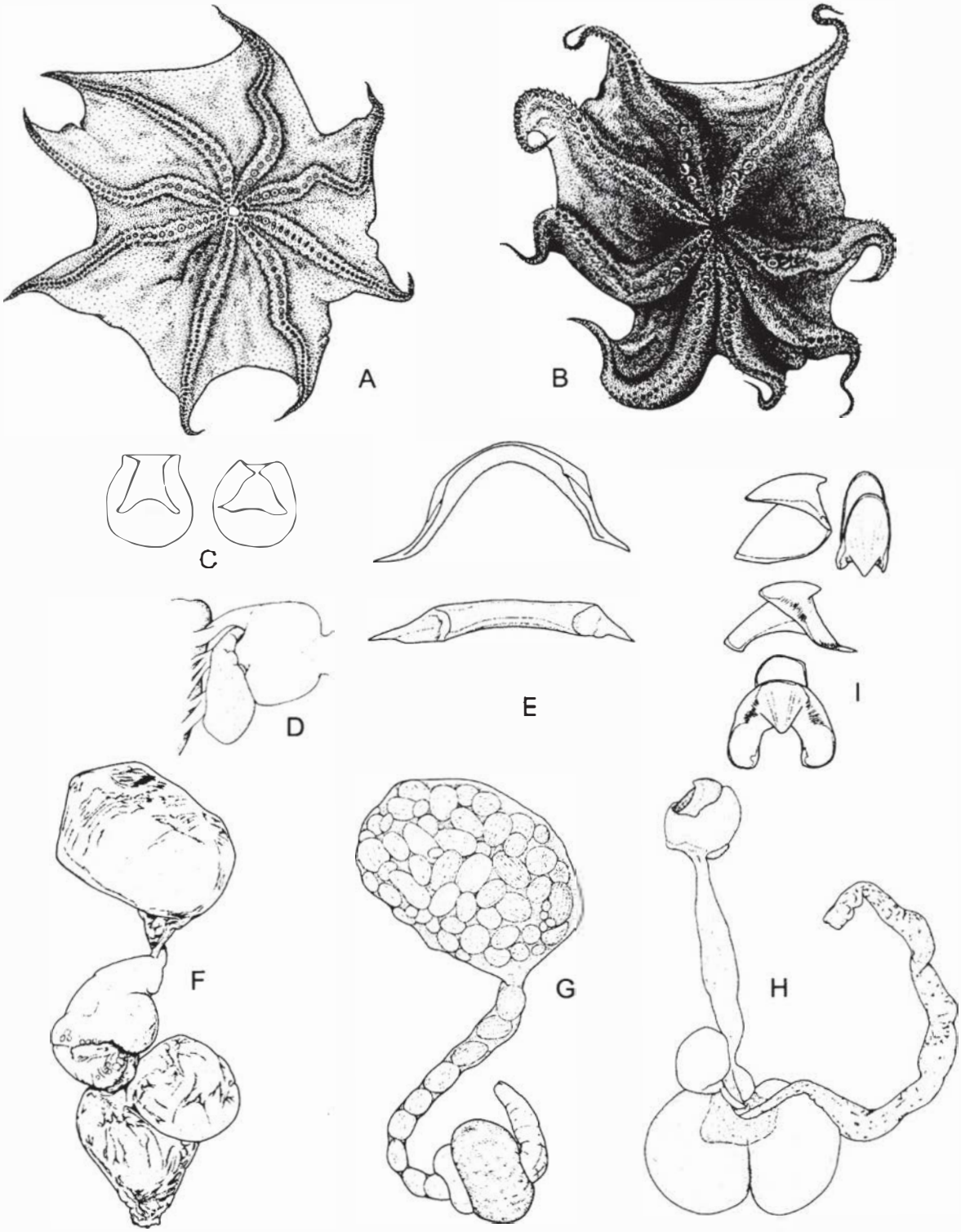


Figure 10. *Opisthoteuthis mero* sp. nov.: Anatomy: **A**, NMNZ M.67854, M, ML 54 mm. **B**, NMNZ M.95258, female, ML 57 mm. **C**, sucker morphology (sections), left, proximal field, right, distal field, NMNZ M.67854. **D**, optic lobe, NMNZ M.67855, female, ML about 37 mm. **E**, shell, dorsal and posterior views, NMNZ M.95288. **F**, male reproductive system, NMNZ M.118242, M, ML 45 mm. **G**, female reproductive system, NZOI P-1108, ML 76 mm. **H**, alimentary canal, NMNZ M.118242, male, ML 45 mm. **I**, beaks, NMNZ M.118242, M, ML 45 mm.

length); jaw without teeth; rostrum acute, sharp, slightly deflected down. Lateral walls almost parallel sided, with rounded crest and weak lateral wall fold. Lower beak (Fig. 10I) tall (height 73% width), dark pigmented, with translucent lateral wing and wall margins; hood moderately deep (depth 50% beak length) projecting forward; rostrum pointed; lateral wall with moderate notch and broadly convex crest; lateral wings moderately long (length 93% beak length), with 2 weak folds.

ETYMOLOGY: Named for Mero Marinovich who collected the holotype and much additional material.

REMARKS: Four species are similar to *Opisthoteuthis mero* sp. nov: *O. agassizii*, *O. vossi*, *O. persephone*, and *O. phillipi*. *Opisthoteuthis agassizii* (SAM S2502) can be distinguished from *O. mero* in having 4 enlarged proximal field suckers (numbers 5–9), 8 gill lamellae, and an ASIn (male) to at least 11.2% ML (respective figures for *O. mero*: 5–8, 6 or 7 and to 8.6). The Southeast Atlantic *O. vossi* has smaller suckers (male and female combined ASIn 4.4–6), and more suckers (79 [Paratype IIPV]–93 [Paratypes ICMB, 2 specimens]); enlarged suckers also occur proximally (3 adoral) and distally (involving 7 or 8 suckers at the web margin along arms 2–4) (Sanchez & Guerra 1989: 1162–1163). A redescription of *O. vossi* is required to determine whether mainland Namibian specimens are conspecific with those from the type locality. Although not described by Sanchez and Guerra (1989), the digestive gland of specimens attributed to *O. vossi* from coastal Namibian waters is typical of the genus *Opisthoteuthis* as now diagnosed (pers. obs.), being bilobate. The South Australian *O. persephone* almost invariably has 6 lamellae per gill (*O. mero* almost invariably has 7 lamellae per gill), and an ASC to 93 (similar to the Indian Ocean *O. phillipi* and *O. vossi*).

Opisthoteuthis Group 2

DIAGNOSIS: With characters of the family; animal bell-shaped. Cirri commence between adoral suckers 2–4; male with gross sucker enlargement in both proximal and distal fields. Shell solid, muscle insertion points well developed; lateral wings short. Accessory gland 1 dominates accessory gland complex; penis well developed. Digestive gland bilobed.

The recognition of this Group follows direct examination of specimens of *Opisthoteuthis pluto* Berry, 1918 and *O. chathamensis* sp. nov., and literature accounts of morphology and anatomy for *O. albatrossi* Sasaki, 1920. This morphological group is represented in all major world oceans, albeit sporadically, although it is absent from polar regions.

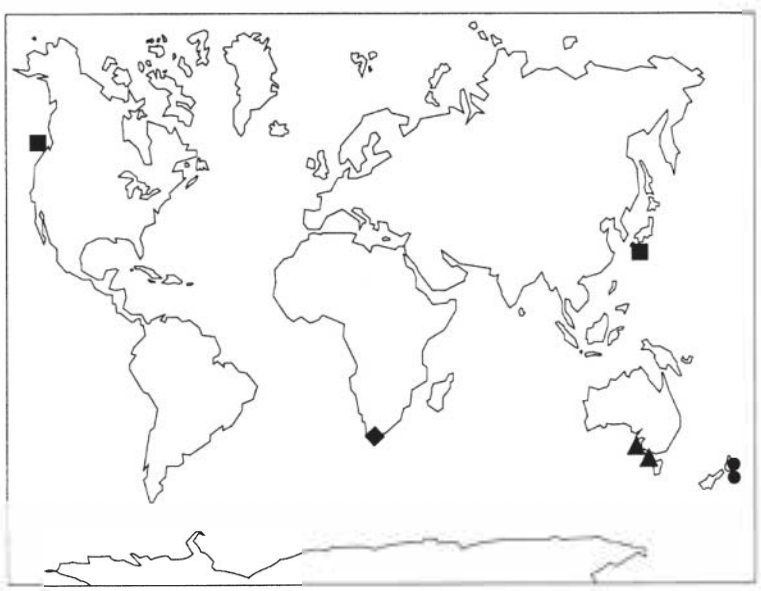


Figure 11. Recognised distribution of *Opisthoteuthis* Group 2. ■ *Opisthoteuthis albatrossi* (Sasaki, 1920)[1]; ▲ *O. pluto* Berry, 1918; ● *O. chathamensis* sp. nov.; ♦ *Opisthoteuthis* sp. nov.

[1] And probable synonym *O. californiana* Berry (Hochberg, pers. comm.).

Opisthoteuthis chathamensis sp. nov. (Figs 13, 14) (Tables 10–12)

TYPE MATERIAL (6 specimens, 2 male [M], 4 female [F]): Holotype: NZOI H-664, M, ML 47 mm, FPT, 44°43.80–44.15' S, 177°15.78–13.01' W, 1174–1195 m, BT 4.3°C, 17/10/1995, f.r.v. *Tangaroa* Stn TAN9511/78, NZOI Stn Z8442. Paratype: NZOI P-1106, F, ML 51 mm, FPT, 39°50' S, 177°39' E, 1000–1100 m, 10/08/1995, f.v. *Peterson*, NZOI Stn Z8371; NZOI P-1107, F, ML 49 mm, FPT, 40°03–05' S, 178°09–06' E, 850–1544 m, 24/09/1995, f.v. *San Torshavn*, NZOI Stn Z8376.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.118299, F, ML 34.5 mm, FPT, 39°58.55' S, 178°14.80' E, 900 m, datNR, f.v. *San Manukau*; NMNZ M.95287, M, ML 42 mm, 41°10.5' S, 176°34.8' E, 1195–1200 m, 06/04/1984, f.r.v. *James Cook* Stn J06/030/84; NZOI Stn Z8420, F, ML 30 mm, FPT, 44°47.79–48.33' S, 179°06.57–09.29' W, 1417–1438 m, BT 3.1°C, 14/10/1995, f.r.v. *Tangaroa* Stn TAN9511/57.

REFERENCE MATERIAL: *Opisthoteuthis pluto* Berry, 1918, det. C.C. Lu, NMV F78356, 3M, ML 42, 36, 21 mm, 38°37.12' S, 141°00.68' E, 1080–1110 m, 08/02/1988, f.r.v. *Soela* Stn S01/88/86; SAM S3052, *Opisthoteuthis medusoides*, det. M.C. Roeleveld, M, ML *c.* 31 mm, 25°38.0' S, 33°54.0' E, 420 m, 25/06/1994.

RECOGNISED DISTRIBUTION (Fig. 12, p. 20): New Zealand, south of East Cape, off the east coast of North Island to the Chatham Rise, 39°50–44°48.33'S, 177°39'E–179°06.57'W, 900–1438 m (excluding NZOI Stn Z8376). Known bottom temperature range (two stations) 3.1–4.3°C.

DIAGNOSIS: Small-bodied species with moderate anteroposterior compression of cephalopedal mass (bell-shaped); with areolar spots across mantle, head, and aboral surface of arms. Fins long, flaplike; mantle and nuchal constrictions poorly developed; arms long, deeply invested in web; web deep; male with abnormal sucker enlargement in proximal and distal fields; suckers in both sexes few, ASC to 55.

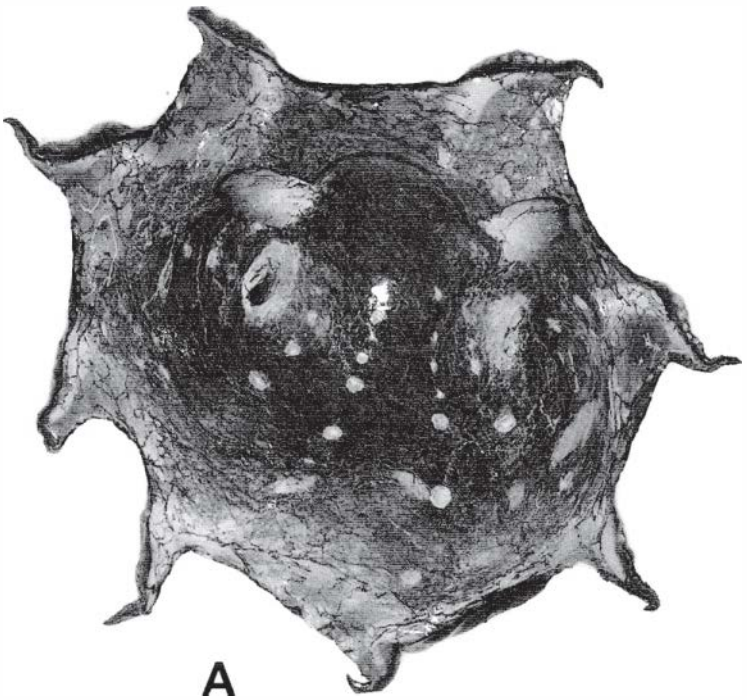
DESCRIPTION (external facies, Fig. 13A–B). Small-bodied species, ML to 54 mm, TL to 180 mm. Mantle, head, and web extensively gelatinous; arms semi-gelatinous; cephalopedal mass moderately compressed along anteroposterior axis, bell-shaped. Head wider than mantle; eyes large, bulbous, oriented laterally. Areolar spots extending over dorsal surfaces of mantle, head, and arm bases 1–4; mature specimens with 7–10 areolar spots over head and along arm pairs 1, 5–7 spots over head and along arm pairs 2, 3–5 along arm pairs 3, and 1–5 along arm pairs 4.

Fins long (53–64% ML), slender to moderately broad (fin width 38–53% outer fin length), laterally oriented, deeply invested in mantle tissues; inner and outer margin of fins parallel sided to weakly convex; fin distal margin rounded; fin margins delicate; basal constriction poorly developed; muscular portion of exposed fin extending about half fin length.

Mantle aperture reduced, enveloping base of funnel; mantle attached to ventral arm bases 4 at level equivalent to 10th adoral sucker; funnel length moderate to long (35–67% ML), attached to ventral arm bases 4 at position equivalent to 10th adoral sucker, free portion short. Funnel organ V-shaped. Interpallial septum long, thin, attached to viscera adjacent to genital aperture, fused to ventral surface of mantle. Anus on raised portion of rectum.

Arm formula variable, no consistent disparity in length or continuity between right and left arm pairs apparent; arms long, thick; longest arm length 65–88% TL or 235–338% ML, shortest arm length 60–69% TL. Web formula variable, no consistent disparity in depth or continuity between right and left sectors apparent; nodules at junction of web and arm sectors absent. Web deep, thick, extensively gelatinous; deepest web sector 59–70% longest arm length, 66–86% shortest arm length; shallowest web sector 38–44% longest arm length, 43–55% shortest arm length. Cirrus length short to moderate, about 6–10% ML or about 0.5–2 times as long as greatest sucker diameter; cirri apparent between suckers 2 and 3 or 3 and 4 on all arms, abruptly increasing in length between suckers 5 and 6 along each arm; cirri present to at least terminal 3 or 4 suckers from arm tip. Sucker size sexually dimorphic, abruptly enlarged in male (ASIe 10.6–11.9% ML), enlargement to lesser extent in female (ASIn 4.7–7.0% ML); abrupt sucker enlargement in male occurs on all arms in both proximal and distal fields; first 3 or 4 suckers of moderate size, 5–7 abruptly enlarged bulbous suckers follow, then 8–10 suckers of slightly reduced diameter extend to web margin, thereafter 6–8 suckers secondarily and abruptly enlarge, after which the terminal 14–16 suckers on each arm tip rapidly decrease in diameter. Suckers (Fig. 14A) with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, and small, simple aperture. Mature specimen arm sucker counts low in both sexes, slightly higher in female (male: 41–49, female: 45–55). Suckers sunk into oral surface of arms, closely spaced within web sectors, packed at web margin; suckers extend to arm tips. Indices, formulas, and counts in Table 10; raw measures in Table 11.

Gills with 6–8 tightly compacted lamellae; innermost and outermost reduced in size, with lamellae 3–5 from the outer surface with common arterial base, slightly reduced in size relative to adjacent lamellae. Funnel organ not preserved in any material.



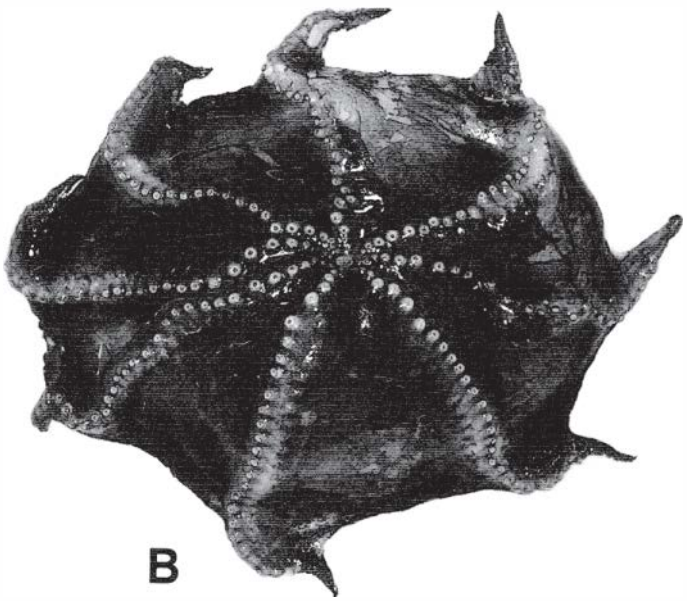


Figure 13. *Opistioteuthis chathamensis* sp. nov.: Holotype, NZ●I H-664, male, ML 47 mm.

Table 10. Indices, formulas, and counts for *Opisthoteuthis chathamensis* sp. nov. (* denotes damage).

	NMNZ M.95287	NZOI P-1106	NZOI H-664	NZOI P-1107	NZOI Stn Z8420
MWI	102.4	80.0	110.6	88.9	123.3
PAI	52.4	35.2	38.7	35.6	38.0
FunLI	66.7	49.1	34.9	48.4	66.7
FLI Out	60.7	55.6	63.8	53.3	64.3
FLI In	57.1	42.6	56.6	42.2	63.3
FWI	53.3	38.7	50.0	37.5	49.7
ALI1-4[1]	66.7–78.9	67.8–76.7	69.4–87.5	60.8–69.3	59.7–65.3
AFR	1.4.2.3	4.3.2.1	4.3.1.2	1.2=4.3	1=4.3.2
AFL	3.2.1.4	4.3.2.1	4.3.1.2	1.2=3.4	1.3.2.4
BL1R/L	*	8/10	8/8	7/7	7/8
BL2R/L	*	5/7	5/7	5/6	5/5
BL3R/L	*	3/4	3/3	3/3	3/5
BL4R/L	*	3/3	1/2	2/3	4/5
WFR	B.A.E.C.D	D=E.C.B.A	D.E.B.C.A	B.A.C.D.E	*
WFL	A=B.D.E.C	D.E.B.C.A	E.D.C.B.A	A.B.E=C.D	B.C.D.E.A
ASC1-4	45–49	45–55	41–46	48–55	*
CiLI1–4	5.5–6.0	5.6–6.7	6.0–8.5	8.2–8.6	8.3–10.0
ASiN1–4	10.7–11.9	3.9–5.2	10.4–10.6	4.4–4.7	6.7–7.0

[1] As a percentage of total length.

Table 11. Raw measures for *Opisthoteuthis chathamensis* sp. nov. (* denotes damage).

	NMNZ M.95287	NZOI P-1106	NZOI H-664	NZOI P-1107	NZOI Stn Z8420
SEX	M	F	M	F	F
TL	180	180	160	153	124
ML	42	54	47	45	30
MW	43	43.2	52	40	37
PA	22	19	18.2	16	11.4
FunL	28	26.5	16.4	21.8	20
FL outer	25.5	30	30	24	19.3
FL Inner	24	23	26.6	19	19
FW	13.6	11.6	15	9	9.6
EO	6.9	10	10	6.5	8
AL1R/L	137/128	122/123	120/127	99/106	76/81
AL2R/L	123/131	127/125	111/121	96/98	68/76
AL3R/L	120/142	128/129	128/137	89*/98	74/77
AL4R/L	130/127	131/138	124*/140	96/93	76/61*
WDA	90	58	61	69	38
WDBR/L	95/90	61/73	67/67	74/62	36/49
WDCR/L	75/77	71/68	81/83	63/48	?/47
WDDR/L	57/80	80/81	95/85	62/40	42/44
WDE	78	80	90	48	39
ASC1R/L	36*/45	50/54	44/41	51/48	*
ASC2R/L	33*/46	51/45	43/44	51/52	*
ASC3R/L	46/47	49/55	46/45	38*/53	*
ASC4R/L	49/49	45/52	33*/44	55/52	*
CL1R	2.4	3.6	3.2	3.7	3.0
CL2R	2.4	3.0	4.0	3.7	3.0
CL3R	2.5	3.2	3.2	3.9	3.0
CL4R	2.3	3.0	2.8	3.8	2.5
ASn1R/L	4.5/5	2.1/2.7	5/5	2/2	2/2
ASn2R/L	5/5	2.7/2.6	4.9/5	2/2	2.1/2.1
ASn3R/L	5/5	2.5/2.8	5/5	2.1/2	2.1/2.1
ASn4R/L	5/5	2.7/2.8	5/5	2.1/2.1	2.1/2.1
GiLC	7	6	7	8	7

Shell simple U-shape (Fig. 14B), solid (non-vacuolate), amber coloured, easily fragmented, surface smooth. Saddle well developed, thickened relative to wings, with single outer groove, and convex inner margins; lateral wings short, tapering to acute points. Lateral wings well developed, laminar, without inrolled margins, wings diverge from saddle at about 40° angle; muscle insertion points marked by two small prominences.

Adoral surface of arms and web maroon; suckers and sucker apertures paler, cream coloured. Dorsal surface of mantle, head and arms, purplish-red. Ventral surface of mantle, dorsal surface of fins, orbit, web margin, and portion of arm free from web, paler, translucent to cream coloured.

Optic lobe (Fig. 14C) large, kidney-shaped. Right and left optic nerve branching pattern asymmetric, right with 2–4, left with 2–5 large nerves, each undergoing minor branching into rear of eyeball. White bodies disc-shaped, dark brown to purple, well separated across dorsal midline of head.

Male reproductive system (Fig. 14D) with massive development of seminal vesicles 1–3 and accessory glands 1–3; complex of accessory gland structures appreciably larger than seminal vesicle complex; accessory gland 1 dominates accessory gland complex; penis well developed. Female reproductive system (Fig. 14E) with large ovary sac; proximal oviduct short, containing few (to 3) eggs. Oviducal gland 2-chambered; proximal chamber striate, about half the size of distal chamber; distal chamber with weak striations, thick walled, with well-developed inner lining and frequently single egg in process of egg capsule secretion; capsule deposited around egg in spiral formation. Distal oviduct short, frequently containing several eggs with complete capsules. One egg, 8.3 x 5.6 mm, free in mantle cavity has complete capsule and sculpture comprising dense pimplelike processes, longitudinal furrows, and weak circular lines (Fig. 14F, left); egg in distal oviducal ball (Fig. 14F, centre) and eggs in proximal oviduct (Fig. 14F, right) smaller, to 7.9 x 4.0 mm, smooth.

Alimentary canal (Fig. 14G) with moderate-sized buccal bulb; anterior salivary glands, radular and palatine teeth absent; crop diverticulum absent but crop well developed, attaining greatest dilation at anterior third oesophagus length. Stomach without external demarcation. Caecum poorly developed, spiral coiling absent. Intestine moderately long, about 1.5 times oesophageal length, thin walled, distended in two parts, proximally and distally with weak central constriction; anal flaps absent. Digestive gland large, bilobed; pancreas well developed.

Upper beak (Figs 14H) tall (height 77% length), darkly pigmented; hood and lateral wall margins translucent; hood moderately deep (67% beak length); jaw with single broad tooth; rostrum strongly deflected down, acutely angled, with sharp point. Lateral walls parallel-sided, with rounded crest and strong lateral wall fold. Lower beak (Figs 14H) darkly pigmented; lateral wing, hood, and wall margins translucent. Lateral wall with weak basal notch and broad convex crest. Hood deep (62% beak length), projecting forward; rostrum slightly rounded; lateral wings moderately long (length 94% beak length), with two weak folds. Lower beak tall (height 70% width).

ETYMOLOGY: Named after the Chatham Rise, where most of the specimens have been obtained.

REMARKS: *Opisthoteuthis chathamensis*, *O. pluto*, and *O. californiana* all possess grossly enlarged proximal field suckers. Male specimens of each species, however, are readily distinguished by the different patterns of enlarged distal sucker distribution along the arms: *O. chathamensis* on all arm pairs (1–4), *O. pluto* on arms 2–4, and *O. californiana* on arm pair 1 only. *Opisthoteuthis medusoides* has 1 or 2 abnormally, abruptly enlarged suckers on the male ventral arm pair only — although this species may not be referable to *Opisthoteuthis* Group 2.

Opisthoteuthis Group 3

DIAGNOSIS: With characters of the family. Cirri commence between suckers 2 and 4 along all arm pairs. Shell vacuolate (not solid); digestive gland entire (not bilobed); penis well developed.

Opisthoteuthis robsoni sp. nov. (Figs 17, 18) (Tables 12–14)

TYPE MATERIAL (4 specimens, all male [M]): Holotype: NMNZ M.95255, M, ML 58 mm, BS 660, 42°41.7' S, 174°28.0' E, NW Mernoo Slope, 1723–1549 m, 13/01/1979, f.r.v. *Tangaroa* (NZOI Stn R18), substratum mud. Paratypes: NMNZ M.134147, M, ML 31 mm, FPT, 42°35' S, 175°29' E, 1440 m, 15/12/1996, coll. D. Pollock (956/152); NMNZ M.131724, M, ML 62 mm, 44°49.80–49.20' S, 172°48.50–50.10' E, 1180–1184 m, BT 3.3°C, 09/06/1984; NMNZ M.131725, M, ML 65 mm, 44°59.20–58.10' S, 174°00.90–01.50' E, 1178–1190 m, 04/10/1984, f.r.v. *James Cook* Stn J17/23/84.

RECOGNISED DISTRIBUTION (Fig. 16, p. 20): Off the east coast of South Island and the southern Chatham Rise (42°35–44°59.20' S, 172°48.50'–174°28.0' E), 1178–1723 m.

DIAGNOSIS: Size moderate, with weak anteroposterior

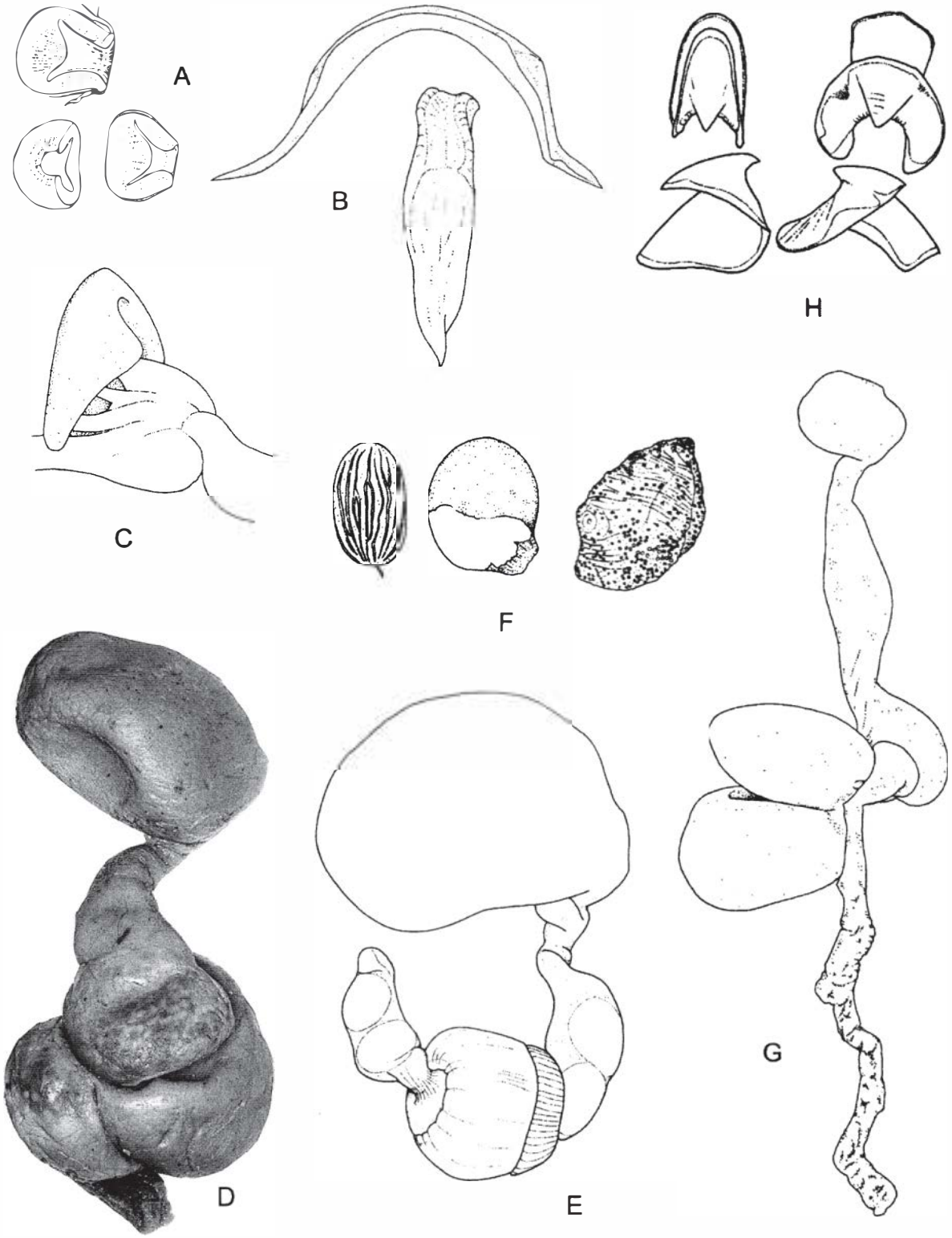


Figure 14. *Opisthoteuthis chathamensis* sp. nov.: **A**, NMNZ M.95287, sucker morphology (sections), upper, sucker # 6, lower, sucker # 26. **B**, NMNZ M.95287, male, ML 42 mm, shell. **C**, NMNZ M.95287, right optic lobe. **D**, NMNZ M.95287, male reproductive system. **E**, NZOI Stn Z8420, female, ML 30 mm, female reproductive system. **F**, NZOI Stn Z8420, eggs recovered from ovary sac (left), oviducal ball (centre), mantle cavity (right). **G**, NMNZ M.95287, alimentary canal. **H**, NZOI Stn Z8420, beaks.

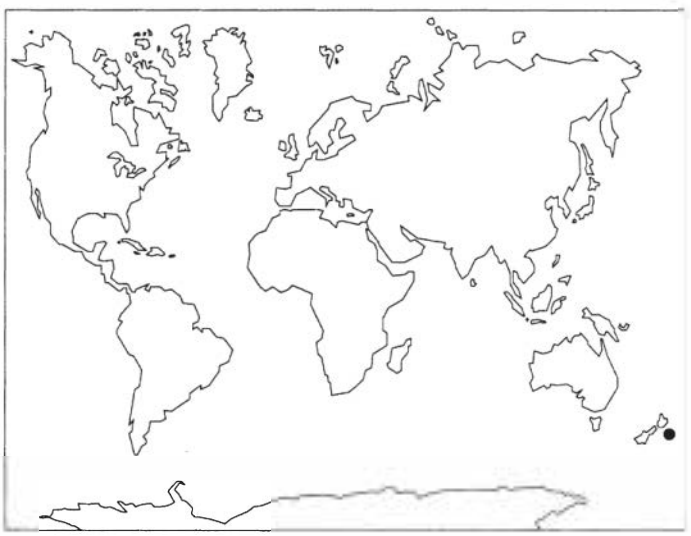


Figure 15. Recognised distribution of *Opisthoteuthis* Group 3. ● *Opisthoteuthis robsoni* sp. nov.

elongation of cephalopedal mass (bell-shaped). Fins of short to moderate length, triangular; radular and palatine teeth absent; mantle and nuchal constrictions absent; arms long, deeply invested in web; web deep, thin; male proximal field suckers enlarged, distal field sucker enlargement weak; cirri commence on all four arm pairs between suckers 2 and 3 or 3 and 4. Digestive gland entire (not bilobed). Penis well developed.

DESCRIPTION (external facies, Fig. 17A–B): Animal to moderate size, ML to 65 mm, TL to 362 mm; mantle, head, arms, and web semi-gelatinous. Cephalopedal mass with weak anteroposterior axis elongation (bell-shaped). Head wider than mantle; eyes large, lateral in orientation, bulbous. Areolar spots extending over dorsal surfaces of mantle, head and along arms 1–4 apparent in one specimen only (all others with skin abrasion or surface wrinkling), with 7 areolar spots over head and along arm pair 1, 6 over head and along arm pair 2, 4 along arm pair 3, and 3 along arm pair 4.

Fin length short to moderate (length 48.3–87.7% ML), deeply invested in mantle tissues; free portion oriented laterally, broadly triangular; free-fin width 56.8–71.9% outer fin length; fins with delicate membranous margins; basal constriction well developed; muscular portion of exposed fin about half fin length. Fin indices, Table 12.

Mantle aperture reduced, enveloping base of funnel; mantle attached to ventral arm bases 4 at level equivalent to 11th or 12th adoral suckers; funnel length moderate to long (41.7–78.2% ML), attached to ventral arm bases 4 at position equivalent to 14th or 15th suckers; funnel attached to arm bases 4 past level of mantle attachment to arms, free portion very short. Funnel organ broadly V-shaped.

Table 12. Fin indices for *Opisthoteuthis robsoni* sp. nov.

	NMNZ M.131725	NMNZ M.131724	NMNZ M.95255	NMNZ M.134147
FLI Out	87.7	71.0	48.3	51.6
FLI In	87.7	83.9	51.7	43.5
FWI	68.4	56.8	62.5	71.9

Arm formula variable, no consistent disparity in length or continuity between right and left arm pairs apparent; arms long; longest arm length 80.1–87.4% TL, shortest arm length 68.8–82.0% TL. Web deep, thick, moderately gelatinous; deepest web sector 48.6–65.7% longest arm length, 51.8–75.5% shortest arm length; shallowest web sector 32.9–47.9% longest arm length, 35.0–52.5% shortest arm length. Cirri length short, about 3–8% ML or 0.3–0.6 times as long as enlarged sucker diameter; cirri apparent between suckers 2 and 3 or 3 and 4 on all arms, subject to individual variation, attaining greatest length between 10 and 15th suckers along each arm, and present as vestiges to arm tips. Suckers grossly enlarged in male proximal field (ASIe 8.8–15.5% ML), weakly enlarged in distal field at web margin; first 2 and 3 suckers of moderate size, next 7 or 8 abruptly enlarged and bulbous, suckers 6–8 grossly so, thereafter 30–35 similar-sized suckers of reduced diameter are spaced to a point where the dorsolateral surface of each arm and web intersect, after which the terminal 35–40 suckers gradually decrease in diameter to arm tip.

Suckers (Fig. 18A) with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, and small, simple sucker aperture. Grossly enlarged suckers sometimes assume biserial arrangement, other suckers well spaced within web sectors,

invested into oral surface of arms; suckers secondarily crowd at web margin, sometimes assuming biserial arrangement, raised from arm surface, bases touching; ASC to 89; suckers extend to arm tips. Indices, formulas, and counts in Table 13; raw measures in Table 14.

Dorsal and ventral surfaces of mantle, head, and arms 1-4 maroon; margin of eye, outer margin of fins and cirri, off-white. Adoral surface of arms and web darker, deep maroon to nearly black; suckers and sucker apertures off-white to pale yellow.

Gills with 6–8 tightly compacted lamellae; innermost and outermost reduced in size, lamellae 3 and 4 with common arterial base, slightly reduced in size relative to adjacent lamellae.

Shell simple (Fig. 18B), vacuolate, light-amber-coloured, flexible; surface texture irregular. Saddle well developed, thickened relative to wings, with single deep excavation; outer surface concave, inner surface convex; muscle insertion points marked by 2 well-developed prominences. Lateral wings laminar; margins not inrolled; wings diverge from saddle at about 45° angle and taper to acute points.

Optic lobe (Figs 18C, D) large, kidney-shaped. Optic nerve branching pattern asymmetric, with 3 or 4 right and 2 or 3 left nerves, all with multiple terminal branching into back of eyeball. White bodies dark brown to purple, well separated across dorsal mid-line of head.

Male reproductive system (Fig. 18E) with moderate development of seminal vesicles 1–3 and accessory glands 1–3; complex of accessory glands 1–3 greater in size than seminal vesicle complex; accessory glands 2 and 3 dominate gland complex; penis well developed, short, tubular. Female unknown.

Alimentary canal (Fig. 18F) with large buccal bulb; anterior salivary glands, radula, and palatine teeth, and crop diverticulum absent; crop dilation greatest at posterior third of oesophagus. Stomach large, without external demarcation; caecum poorly developed, without spiral coiling. Intestine moderately long, about 1.7 times oesophagus length, thin walled, distended for greatest length; anal flaps absent. Hepatic ducts two; digestive gland large, ovoid, without lobes; pancreas well developed.

Upper beak (Fig. 18G) tall (height 74% length), with dark-pigmented hood with translucent wall margins; hood moderately deep (depth 66% beak length), with weak posterior notch; jaw with single broad-based tooth; rostrum acute, sharp, slightly deflected downwards; lateral margins of rostrum strongly chiselled. Lateral walls almost parallel sided, with rounded crest and strong lateral wall fold. Lower beak (Fig. 18G) depressed (height 66% width); darkly pigmented, with translucent lateral wing and wall margins; hood deep (depth 61% beak length), projecting forward; rostrum pointed; lateral wall with shallow notch and broadly convex crest; lateral wings long (length 98% beak length), with two weak folds.

ETYMOLOGY: Named in honour of G.C. Robson for his much valued contributions to octopod systematics.

REMARKS: Stomach contents of NMNZ M.1311725 comprise densely compacted masses of well-macerated large-bodied amphipods.

Table 13. Indices, formulas, and counts for *Opisthoteuthis robsoni* sp. nov. (* denotes damage).

	NMNZ M.131725	NMNZ M.131724	NMNZ M.95255	NMNZ M.134147
AL1–4R	68.8–84.6	73.2–80.1	74.4–82.9	82.0–87.4
ALFR	?1.2.3.4	?2.1.4.3	1.2=3.4	?4.3.1.2
ALFL	*	2.1=3.4	*	*
WDIA–E	39.9–61.5	47.9–61.7	45.7–65.7	32.9–48.6
WFR	A.B.D.C=E	C.B.A=D.E	A.D=C.B.E	A.B.D.C.E
WFL	A.B.C.E.D	B.A.D.C.E	A.B.C.E.D	*
ASC1–4	74–88	79–89	71–73	> 56– > 66
CiLI1–4	4.6–5.4	4.8–8.1	3.4	6.5–7.1
ASIn1–4	12.8–13.8	14.4–15.5	8.8–9.5	11.9–12.6

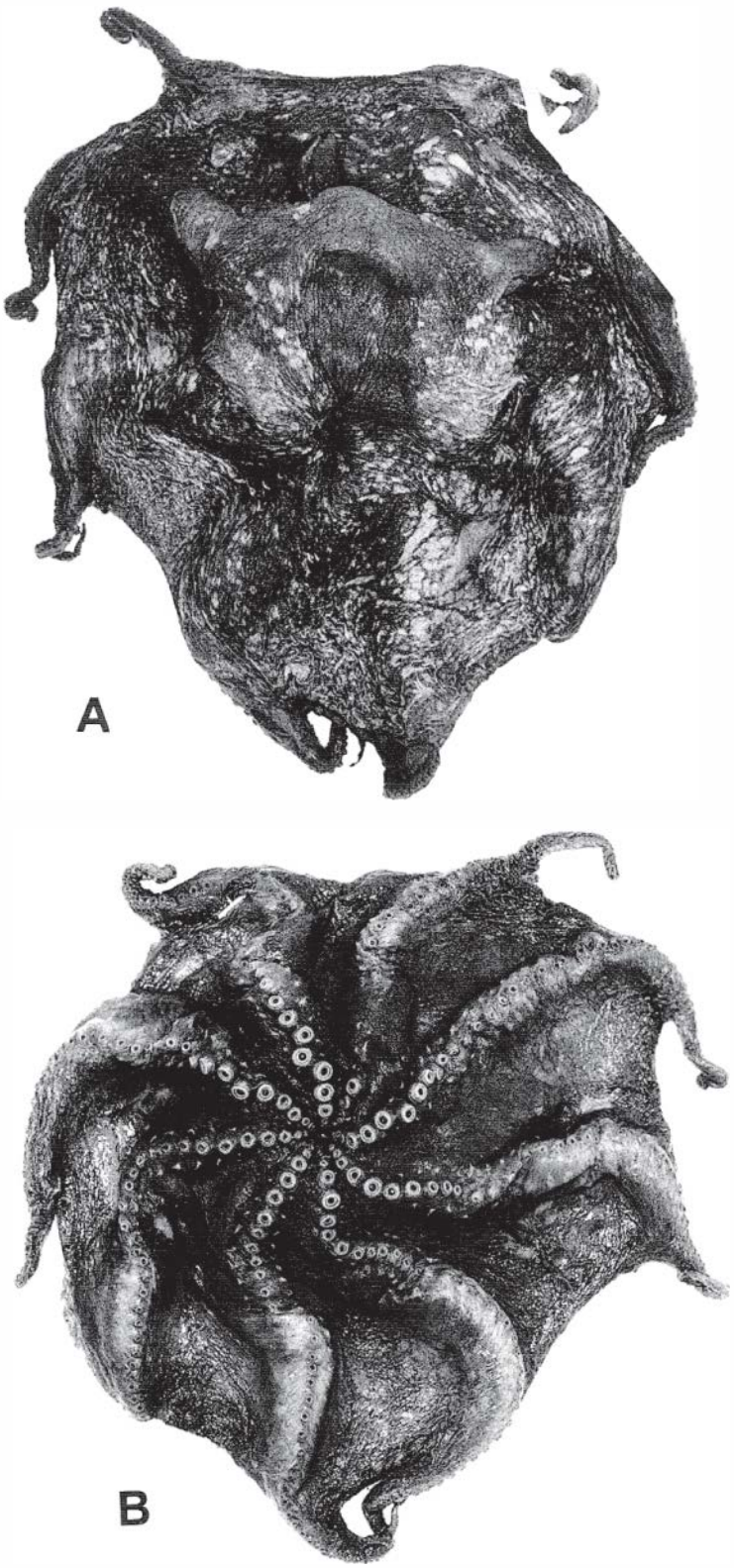


Figure 17. *Opisthoteuthis robsoni* sp. nov.: Holotype, NMNZ M.95255, male, ML 58 mm.

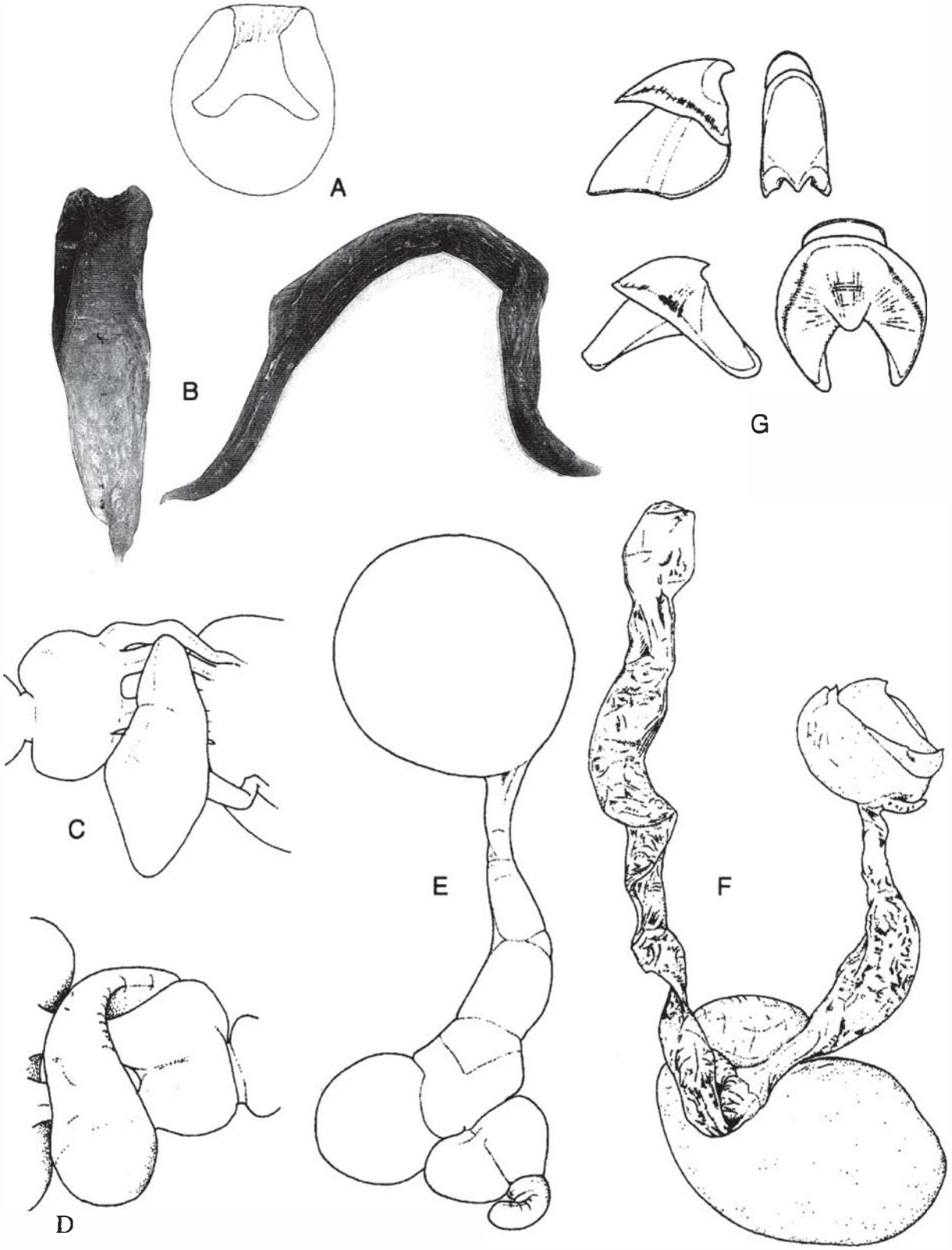


Figure 18. *Opisthoteuthis robsoni* sp. nov.: **A**, sucker morphology (section). **B**, shell, NMNZ M.131724, male, ML 62 mm. **C, D**, NMNZ M.134147, male, ML 31 mm, optic lobes, **B**, left, **C**, right. **E**, male reproductive system, NMNZ M.131724. **F**, alimentary canal, NMNZ M. M.131724. **G**, beaks, NMNZ M.131724.

Table 14. Raw measures for *Opisthoteuthis robsoni* sp. nov. (* denotes damage).

	NMNZ M.131725	NMNZ M.131724	NMNZ M.95255	NMNZ M.134147
TL	356	362	211	167
ML	65	62	58	31
MW	84.5	101	75	55
PA	24	26	17.6	20
FunL	50	48.5	24.2	24
FL Out	57	44	28	16
FL In	57	52	30	13.5
FW	39	25	17.5	11.5
EO	17	13.5	9.8	22.2
AL1R/L	295/301	282/286	175/162	126/146
AL2R/L	250*/269*	290/290	171/115*	97*/143
AL3R/L	255/260	254*/287	171/146*	140/112*
AL4R/L	245/257*	271/265	157/164	137/93*
WDA	185	160	115	66
WDBR/L	165/171	171/165	97/104	55/71
WDCR/L	125/135	179/154	104/86	48/49
WDDR/L	130/120	160/156	105/80	49/34*
WDE	125	139	84	47
ASC1R/L	74/75	69*/79	63*/70*	60*/66*
ASC2R/L	68*/81	84/80	71/*	*/57*
ASC3R/L	86/87	62*/89	73/*	56*/*
ASC4R/L	88/75*	87/88	67*/59*	56*/*
CL1R	3.5	5.0	2.0	2.0
CL2R	3.0	3.5	2.0	2.2
CL3R	3.0	3.5	2.0	2.2
CL4R	3.2	3.0	2.0	2.0
ASn1R/L	8.9/8.9	9.3/9.5	5.4/5.5	3.7/3.8
ASn2R/L	8.9/8.9	9.3/8.9	5.5/5.5	3.9/3.8
ASn3R/L	9.0/8.9	8.9/9.5	5.5/5.5	3.8/3.9
ASn4R/L	8.3/8.3	9.4/9.6	5.1/5.5	3.8/3.8
GiLC	8	8	6	7

Cirroctopus Naef, 1923

TYPE SPECIES: *Stauroteuthis mawsoni* Berry, 1917.

Cirroctopus mawsoni (Berry): Naef, 1923.
Grimpoteuthis mawsoni (Berry): Robson 1932.

DIAGNOSIS: Large robust-bodied cirrates. Fins terminal, massive, paddlelike. Four (or ?six) areolar spots present, one super- and one suborbital pair, positioned at base of either fin and on dorsal surface of head below either eye. Cirri commence between suckers 1 and 2 on all arms; cirrus length equivalent to greatest sucker diameter. Mantle not tightly enveloping funnel. Interpallial septum membranous, oriented along anteroposterior axis of mantle cavity, extending entire mantle cavity length without perforation. Shell robust, vacuolate; surface texture irregular; saddle short, thick; wings spikelike; muscle insertion points poorly developed. Digestive gland entire (not bilobed); intestine about 2.5 times longer than oesophagus. Male accessory gland 3 dominates accessory gland complex. White bodies meet across dorsal midline of head, enveloping cerebral ganglion. Optic nerve branching pattern symmetric, optic nerves numerous (8 or 9).

REMARKS: The general facies of this animal, presence of areolar spots over mantle and head, numerous optic nerves, kidney-shaped optic lobe, length of intestine relative to oesophagus, antero-posterior compression of the cephalopedal mass, and the comparatively shallow-water distribution of this genus are all characters and character states shared with *Opisthoteuthis*. For these reasons *Cirroctopus* is removed from synonymy under *Grimpoteuthis* and coupled with *Opisthoteuthis* in the rediagnosed Opisthoteuthididae.

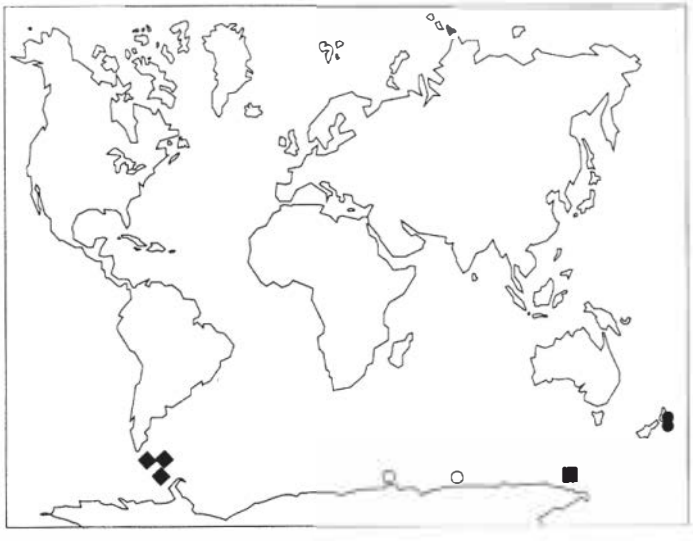


Figure 19. Recognised distribution of genus *Cirroctopus*. ● *C. hochbergi* sp. nov.; ○ *C.* cf. *mawsoni* (Berry) (NMV F.74329); ■ *C. mawsoni* (Berry), holotype; ◆ *C. glacialis* (Robson) holotype (distribution includes junior synonym *C. antarctica* (Kubodera & Okutani): holotype and paratype).

Although not apparent on the type specimen, 6 areolar spots over the head and ventral surface of the mantle are apparent in fresh-collected specimens of *Cirroctopus glacialis* Robson (M. Vechionne pers. comm.).

New Zealand records of this genus appear somewhat anomalous given it is otherwise circum-Antarctic in distribution. Two additional records would provide further distributional data for this genus, although as material has not personally been sighted these records have not been included in Figure 19: Hochberg and Short (1983), 60°30' S, 47°34' W, 616–662m (*Eltanin* cruise 7, Stn 538), and Clarke (1986), 78°23' S, 173°06' W.

Representative material of the following species has been examined to facilitate the description of the New Zealand species. All are referable to the genus *Cirroctopus* as here rediagnosed, with indices, formulas, and raw measures presented in Tables 15 and 16.

Cirroctopus cf. *mawsoni* (Berry), NMV F.65707, M, ML 51.0 mm, ?F, ML 46.5 mm, 66°03.0' S, 49°50.0' E, 690–911 m, 29/11/1985, r.v. *Nella Dan* Stn HRD013, coll. M. Norman, Accn # 86/01; NMV F.74329, *Cirroctopus* cf. *mawsoni* (Berry), F, ML 137.5 mm, 68°33.1–32.9' S, 76°58.1–77.0' E, 729–733 m, 18/02/1987, r.v. *Nella Dan* Stn 6 (Figs 20A–E).

Stauroteuthis mawsoni Berry, 1917, holotype, AMS C40886, sex indet., ML 12.1 mm, 66°55' S, 145°21' E, 526–548 m, 28/12/1913 (Fig. 20F).

Cirroteuthis glacialis Robson, 1930, holotype, BMNH 1951.4.26.1, M, ML 66.0 mm, 64°21.00' S, 62°58.00' W, 508–914 m, 14/03/1927 (Fig. 21A–B).

Grimpoteuthis antarctica Kubodera & Okutani, 1986, holotype, NSMT Mo-63958, M, ML 94.2 mm, 62°59' S, 62°09' W, 803–804 m, 30/01/1982 (Fig. 21C–D).

Cirroctopus hochbergi sp. nov. (Figs 23, 24, 25) (Tables 17–19)

TYPE MATERIAL (48 specimens, 27 male [M], 20 female [F]). Holotype: NZOI H-674, M, ML 90.0 mm, FPT, 39°58–54' S, 178°14–16' E, 800–1070 m, 09/09/1995, f.v. *San Torshavn*, NZOI Stn Z8321. Paratypes: NZOI P-1105, M, ML 92.5 mm, FPT, 39°57–40°00' S, 178°16–15' E, 1020–1250 m, 25/09/1995, f.v. *San Torshavn*, NZOI Stn Z8375; NZOI P-1104, F, ML 104.5 mm, FPT, 39°59–55' S, 178°13–16' E, 750–1130 m, 14/09/1995, f.v. *San Torshavn*, NZOI Stn Z8323; NZOI P-1103, Stn Z8371, F, ML 66.5 mm, FPT, 39°50' S, 177°39' E, 1000–1100 m, 10/08/1995, f.v. *Peterson*; SBMNH 143066, M, FPT, 39°54' S, 178°16' E, 1187 m, 20/09/1995, ex. NZOI Stn Z8380; SBMNH 143065, F, ML 98.0 mm, FPT, 39°58.55' S, 178°14.80' E, 900 m, datNR, f.v. *San Manukau*.

ADDITIONAL MATERIAL EXAMINED: NZOI Stn Z8483, M, ML 136.0 mm, FPT, 35°57–58' S, 176°30–49' E, 700–750 m, 29/04/1996, f.v. *Peterson*; NMNZ M.118245, M, ML 103.0 mm, FPT, *c.* 37°41.91' S, 179°21.99' E, 900 m, -/06/1994, f.v. *Peterson*; NMNZ M.119955, 2M, ML 135.0, 123.0 mm, FPT, 37°47' S, 179°24' E, 1050–1020 m, 17/04/1995; NZOI Stn Z8634, M, ML 107.5 mm, *c.* 37°48' S, 179°00' E, 800 m, -/01/1997, f.r.v. *Tangaroa*; NMNZ M.119888, F, ML 151.0 mm, FPT, 37°50' S, 179°10' E, 1150 m, 12/04/1995; NZOI Stn Z8481, 2F, ML 160.0, 126.5 mm, FPT, 37°54' S, 179°13–14' E, 1050–1100 m, -/05/1996, f.v. *Peterson*; NMNZ M.100327, F, ML 80.0 mm, 38°37.2' S, 178°44.2' E, 929–1067 m, 25/09/1989, f.r.v. *James Cook* Stn J9/41/89; NZOI Stn Z8545, M, ML 115.5 mm, FPT, 38°47' S, 178°47–46' E, 750–830 m, 26/08/1996, f.v. *San Torshavn*; NZOI Stn Z8546, M, ML 101.5 mm, FPT, 38°47.3' S, 178°48.6' E, 750 m, -/01/1996, f.v. *Peterson*; NMNZ M.90433, F, ML 66.0 mm, 39°24.5' S, 178°19.9' E, 921–967 m, 26/06/1987; NMNZ M.117879, M, ML 93.0 mm, FPT, 39°29.20' S, 178°23.82' E, 926 m, 16/06/1993, f.r.v. *Tangaroa* Stn 9306/26; NMNZ M.118289, M, ML 86.0 mm, FPT, *c.* 39°35.0' S, 178°24' E, 1000 m, -/04/1994, f.v. *Peterson*; NMNZ M.100353, F, ML 103.0 mm, 39°45.8' S, 178°19.0' E, 850–740 m, 18/09/1989, f.r.v. *James Cook* Stn J9/28/89; NZOI Stn Z8371, 2M, ML 120.5, 111.0 mm, FPT, 39°50' S, 177°39' E, 1000–1100 m, 10/08/1995, f.v. *Peterson*; NZOI Stn Z8380, M, ML 88.0 mm, FPT, 39°54' S, 178°16' E, 1187 m, 20/09/1995, f.v. *San Torshavn*; NZOI Stn Z8319, M, ML 58.0 mm, 39°55–54' S, 178°10–11' E, 1100 m, 11/09/1995, f.v. *San Torshavn*; NZOI Stn Z8326, M, ML 89.0 mm, FPT, 39°56–54' S, 178°14.55–16' E, 960–1130 m, 08/09/1995, f.v. *San Torshavn*; NZOI Stn Z8542, M, ML 126.5 mm, FPT, 39°57–40°01' S, 177°39–35' E, 990–1350 m, 02/09/1996, f.v. *San Torshavn*; NZOI Stn Z8328, F, ML 116.5 mm, FPT, 39°58–54' S, 178°14–16' E, 800–1140 m, 09/09/1995, f.v. *San Torshavn*; NMNZ M.118295, M, ML 90.0 mm, FPT, *c.* 39°58.55' S, 178°14.8' E, 1000 m, -/02/1994, f.v. *San Manukau*; NMNZ M.118244, 5M, ML 106.0, 103.5, 101.0, 72.5, 65.0 mm, 5F, ML 124.0, 119.0, 103.0, 80.5, 64.5 mm, FPT, *c.* 39°59.0' S, 178°13' E, 900 m, -/06/1994, f.v. *Peterson*; NMNZ M.118326, F, ML 124.0 mm, FPT, 39°59' S, 178°13' E, 940–1070 m, -/04/1994, f.v. *Peterson*; NZOI Stn Z8320, M, ML 112.0 mm, FPT, 39°59–40°03' S, 178°07–04' E, 600–950 m, 21/08/1995, f.v. *San Torshavn*; NZOI Stn Z8322, F, ML 160.0 mm, FPT, 40°00–04' S, 178°06–02' E, 550–1000 m, 28/08/1995, f.v. *San Torshavn*; NZOI Stn Z8327, F, ML 111.0 mm, FPT, 40°00–39°55' S, 178°13–16' E, 750–1137 m, 15/09/1995, f.v. *San Torshavn*; NZOI Stn Z8379, 2M, ML 105.0, 99.0 mm, FPT, 40°01–39°58' S, 178°14–16' E, 750–1230 m, 22/09/1995, f.v. *San Torshavn*; NMNZ M.118176, M, ML 108.0 mm, FPT, 40°03.80' S, 178°12.68' E, 760 m, 27/03/1994, f.r.v. *Tangaroa* Stn TAN 9403/86; NZOI Stn Z8329, F, ML 150.0 mm, FPT, 40°06–09' S, 178°10–09' E, 750–1220 m, 21/08/1995, f.v. *San Torshavn*; NMNZ M.100350, F, ML 141.5 mm, 41°14.2' S, 176°30.4' E, 1150–1120 m, 11/09/1989, f.r.v. *James Cook* Stn J9/1/89.

RECOGNISED DISTRIBUTION (Fig. 22, p. 20): 35°57–58' S to 40°06–09' S, 700–1350 m — excluding the shallowest records of NZOI Stn Z8322 (550–1000 m) and NZOI Stn Z8320 (600–950 m) in which specimens were most likely captured towards the deeper end of the trawl range.

DIAGNOSIS: Adult animal large and, robust, with weak anteroposterior elongation of cephalopedal mass (bell-shaped); arms moderately long, deeply invested

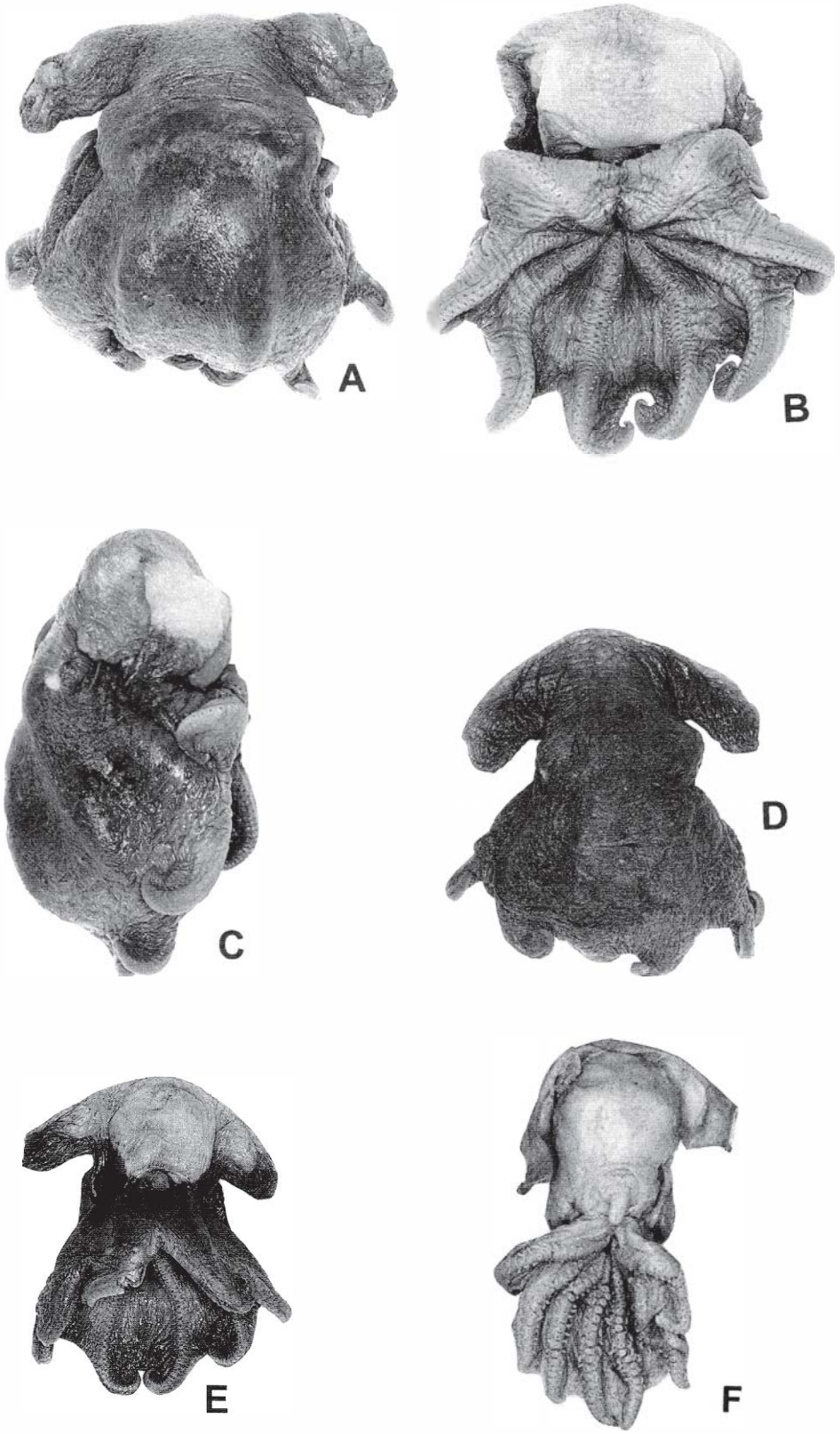


Figure 20. *Cirroctopus* spp.: A–C, *C.* cf. ***mawsoni*** Berry, NMV F65707, ?female, ML 46.5 mm. D, E, *C.* cf. ***mawsoni*** Berry, NMV F65707, male, ML 51 mm. F, holotype *C. mawsoni* (Berry), AM C40886.

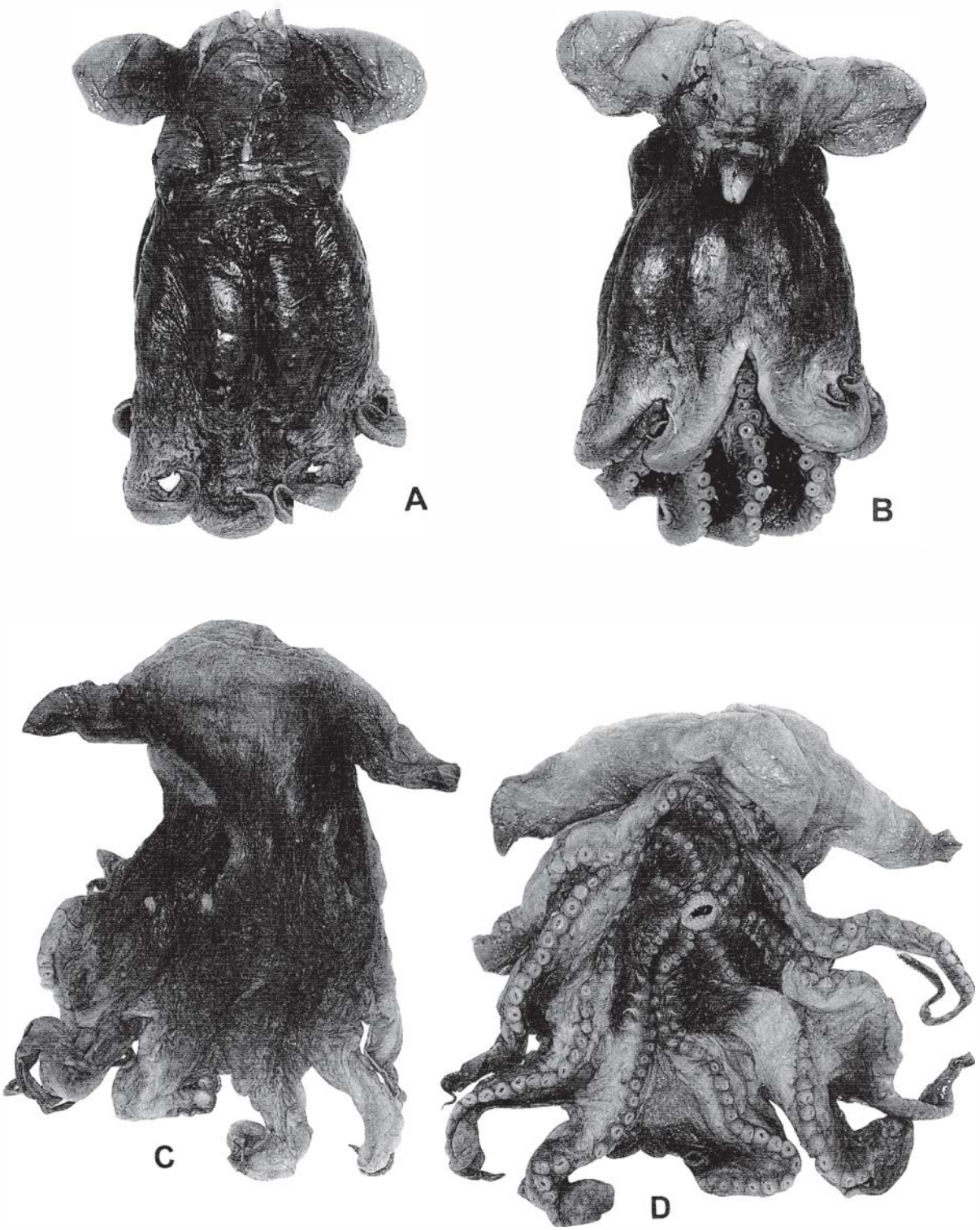


Figure 21. *Cirroctopus* spp.: **A,** B, *C. glacialis* (Robson, 1930), holotype, male, ML 66.0 mm, BMNH 1951.4.26.1. **C,** D, *C. antarctica* (Kubodera & Okutani, 1986), holotype, male, ML 94.2 mm, NSMT Mo-63958.

Table 15. Indices and formulas for *Cirroctopus* spp. († denotes character not measured / enumerated).

	Cirroctopus sp. NMV F.74329	*C. antarctica* Holotype	*C. glacialis* Holotype	*Cirroctopus* sp. NMV F.65707	*Stauroteuthis mawsoni* Holotype
MWI	81.5	73.2	87.1	89.2	65.3
FLI Out	149.1	71.1	109.4	117.6	99.2
FLI In	94.5	64.2	85.0	57.6	†
FWI	39.8	44.0	51.2	42.5	41.7
AFR	2.1.3.4	2.1.4.3	1?.2.3.4	2.3.1=4	†
AFL	†	2.4.3.1	1.2.3.4	3.2.1=4	1.2=3=4
WDIA–E	28.9–57.7	22.0–51.0	34.1–60.2	45.2–65.6	43.5–80.6
WFR	A.B.C.D=E	A=C.B.D.E	A.B.C.D.E	A.C.BD.E	A.B.C.D.E
WFL	†	C.D=A=B.E	A.B.C.D.E	†	†
ASC1–4	66–74	55–66	67–72	54–59	27–31
CiLI1–4	5.1–10.9	5.3–9.0	5.3–7.6	2.9–4.1	4.1–8.3
ASIn1–4	5.8–6.2	6.4–7.4	8.9–9.1	6.1	5.0

Table 16. Raw measures for *Cirroctopus* spp. (*denotes damage; † character not measured/enumerated).

	Cirroctopus sp. NMV F.74329	*C. antarctica* Holotype	*C. glacialis* Holotype	*Cirroctopus* sp. NMV F.65707	*Stauroteuthis mawsoni* Holotype
ML	137.5	94.2	66	51	12.1
MW	112	69	57.5	45.5	7.9
FunL	†	18.5	26.1	†	†
FL outer	205	67	72.2	60	12.0
FL Inner	130	60.5	56.1	29.4	†
FW	81.5	29.5	37	25.5	5.0
AL1R/L	355/†	245/232	160*/164	87/87	12.2/12.4
AL2R/L	381/†	255/253*	176/162	93/90	11.7/10
AL3R/L	295/†	231/235	173/161	88/91	*/10
AL4R/L	268/†	230*/236	150/147	8787	*/10
WDA	220	115	106	61	11
WDBR/L	205/†	101/112	99/97	54/†	10/†
WDCR/L	185/†	116/130	95/88	58/†	9.4/†
WDDR/L	110/†	85/115	79/76	51/†	6.6/†
WDE	110	56	60	42	5.4
ASC1R/L	R 71/†	66/55	58*/72	59/†	28/28
ASC2R/L	R 74/†	64/64	72/69	54/†	27/27
ASC3R/L	†/L 66	65/58	69/69	*/†	27/31
ASC4R/L	†/L 71	63/55	70/67	*/†	29/27
CL1R	R 15	8.5	5.0	2.1	1.0
CL2R	R 13.5	8.0	4.0	2.1	0.8
CL3R	R 10.0	7.5	3.5	2.0	0.5
CL4R	L 7.0	5.0	3.9	1.5	0.5
ASn1R/L	8.5/†	7.0/6.9	6.0/6.0	3.1/†	0.6/†
ASn2R/L	8.0/†	6.6/6.0	5.9/6.0	3.1/†	0.6/†
ASn3R/L	8.0/†	6.3/6.5	6.0/6.0	3.1/†	0.6/†
ASn4R/L	8.0/†	6.9/7.0	6.0/5.9	3.1/†	0.6/†
GiLC	†	5?	6	7	?4

in web; web deep; shell V-shaped; body mauve to purple; with four areolar spots.

DESCRIPTION (external facies, Fig. 23A, B): Adult animal of moderate size, ML to 160 mm, TL to 493 mm, robust; cephalopedal mass extensively gelatinous, bell-shaped. Eyes large, lateral in orientation (between arm bases 2 and 3), bulbous; eye apertures well developed. Areolar spots 4, one at the base of either fin, one below each eye. Head width variable, slightly narrower than to exceeding mantle length. Fins massive, muscular, paddlelike and long, deflected downwards, meeting across anteriormost margin of mantle (length 86–173% ML; width 36–43% length); outer fin margin weakly convex, inner margin strongly convex; fins with thick membranous margins, distal margin of fins rounded; constriction at base of fin well developed; muscular portion of exposed fin extending about 60% fin length.

Mantle aperture reduced, slightly more extensive than funnel; mantle attached to base of arm pair 3 at level equivalent to 4th or 5th adoral sucker; funnel broad, with moderate taper and wide funnel aperture, of moderate length (30–50% ML), points of attachment almost free of arm pair 4; funnel organ indistinct in all available material. Mantle cavity (Fig. 24A) with half-orange-type gills, each with 7 or 8 tightly compacted lamellae, the innermost and outermost reduced in size, with lamellae 3 and 4 from the outer surface with common arterial base (minimally reduced in size relative to adjacent lamellae). Ventral pallial musculature very thin; interpallial septum extends as a continuous, membranous nonperforated sheet extending along anteroposterior axis of mantle cavity, completely dividing mantle cavity into separate compartments.

Arms thick; arm length moderate to long (65–78% TL, 206–376% ML), longest arm length 65–78% TL, shortest arm length 46–71% TL; arm formula variable, frequently 1.2.3.4 or 2.1.3.4, with arms 4 usually the shortest, arms 1 and 2 usually longest. Abrupt sucker enlargement absent in both sexes; suckers small (ASIn: male 3.5–5.3%; female 3.5–6.3); enlargement affects suckers within web to web margin; first 3 and 4 suckers of small size, followed by 30–35 similar-sized, slightly enlarged bulbous suckers to margin of web, thereafter 30–35 suckers rapidly decrease in diameter to arm tips. Suckers (Fig. 24B) with small suction chamber, large sucker aperture, well-developed muscular suction pad, parallel sided wall ring, and moderately well-developed grasping pad; sucker aperture simple. Suckers closely spaced and sunk into arm surface; ASC to 88, increasing with mantle length and more numerous in similar-sized females than males; suckers extend to arm tips. Cirri short, about 3–6% ML or 0.7–1.2 times as long as greatest sucker diameter; cirri commence between suckers 1 and 2 on all arms, gradually increasing in length to 9th or 10th sucker, thereafter gradually decreasing in length to arm tip; cirri present to arm tip. Web moderately deep, deepest web sector 45–66% longest arm length, 65–91% shortest arm length; shallowest web sector 18–31% longest arm length, 19–37% shortest arm length; web formula variable, generally A.B.C.D.E, sectors A and B consistently deepest and sector E shallowest; nodules at junction of web and arm absent.

Dorsal surface of mantle, head, and arms mauve to purple. Margin of orbits white to pale mauve. Ventral surface of mantle and dorsal and ventral surfaces of fins slightly paler, reddish; adoral surface of web sectors A, B, and C (to 16–18th sucker) and D and E (to 12–13th sucker) deep mauve to purple; outer adoral web surfaces of sectors A–E to margin of web and oral surfaces of arms 1–4 and suckers, white to pale mauve. Indices and formulas, Table 17.

Shell (Figs 24C–E) simple V-shape, robust, highly vacuolate, opaque to translucent, with an irregular pitted and folded surface texture. Saddle thick, very short and well developed; ventral-projecting basal shelf poorly developed; lateral wings well developed, thickened, lacking inrolled margins, spikelike, tapering to acute points at about 20° angle from saddle; muscle insertion points poorly developed.

Optic lobe (Fig. 24F) kidney-shaped, massive, heavily invested within massive disc-shaped, violet-coloured white body; left and right white bodies envelop cerebral ganglion, confluent along midline of head. Optic nerve branching pattern symmetric; optic nerves numerous (8 or 9), slender, with little terminal branching into back of eyeball.

Male reproductive system (Fig. 25A) with moderate development of seminal vesicles 1–3 and accessory glands 1–3; complex of accessory glands considerably larger than seminal vesicle complex; accessory gland 3 dominates gland complex; penis poorly developed, flimsy, triangular and lappet-like. Female reproductive system (Fig. 25B) with ovary sac about twice diameter of oviducal ball; proximal oviduct distended with numerous eggs (to 14) with 16–18 very faint longitudinal striations; proximal oviduct about five times length of distal duct. Oviducal gland massive, comprising two unequal-sized and contrasting pigmented striate chambers; distal chamber pinkish-brown, lumen frequently with single egg in process of capsule deposition, chamber about 1.5 times larger than cream-coloured proximal chamber. Distal oviduct short, muscular, frequently containing single egg with secreted capsule, linked to egg in second oviducal gland chamber by long, thin stalk. Single

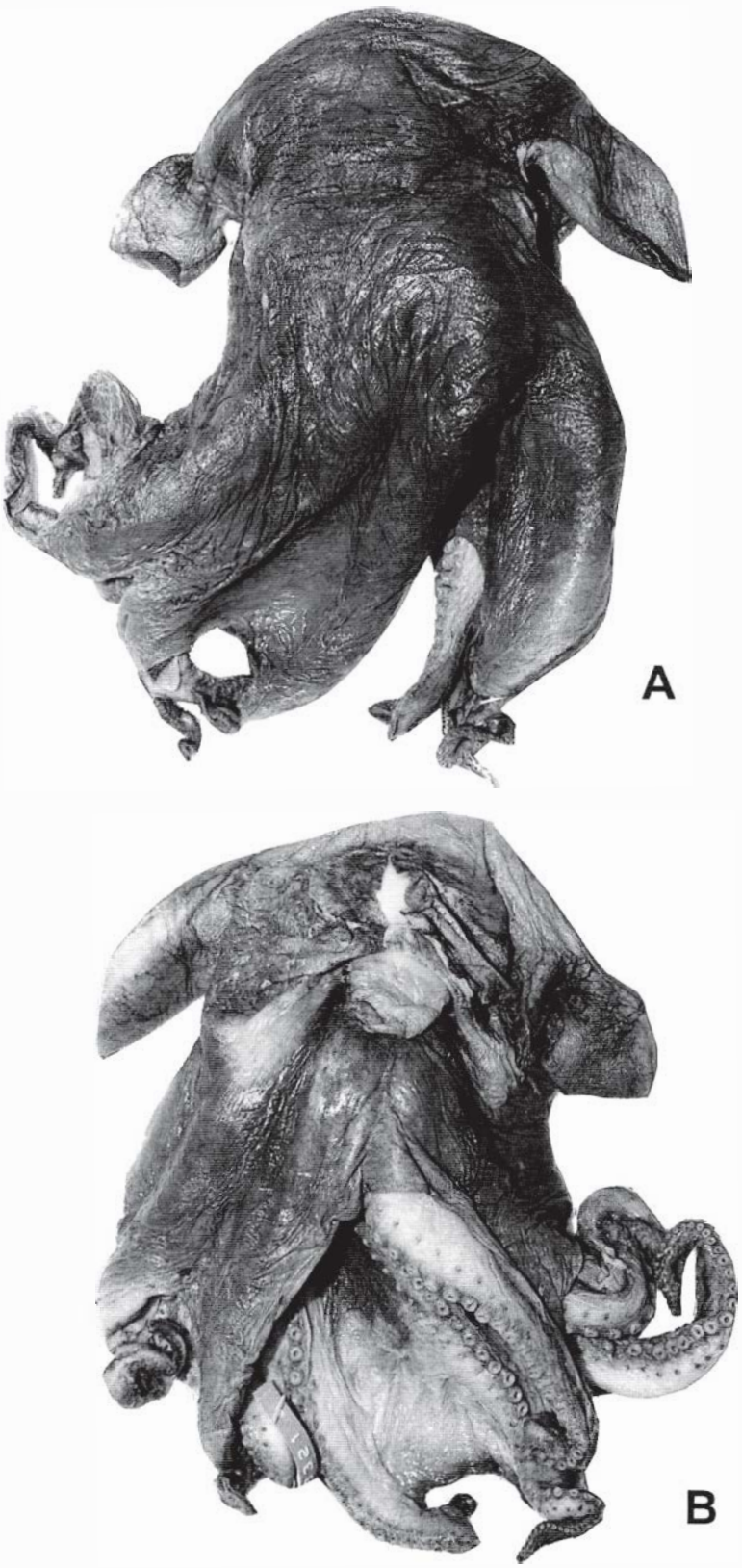
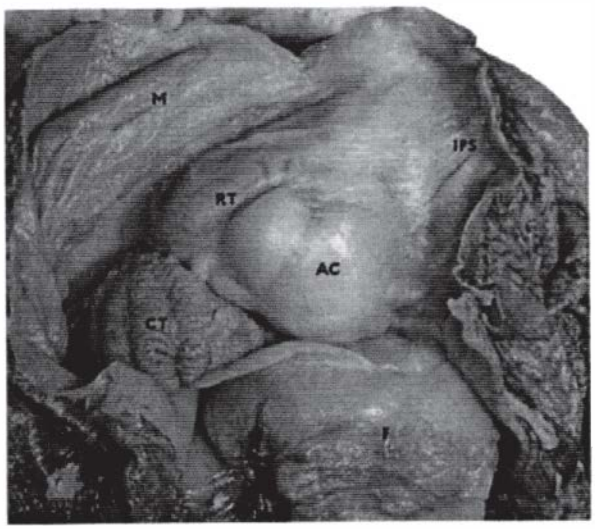
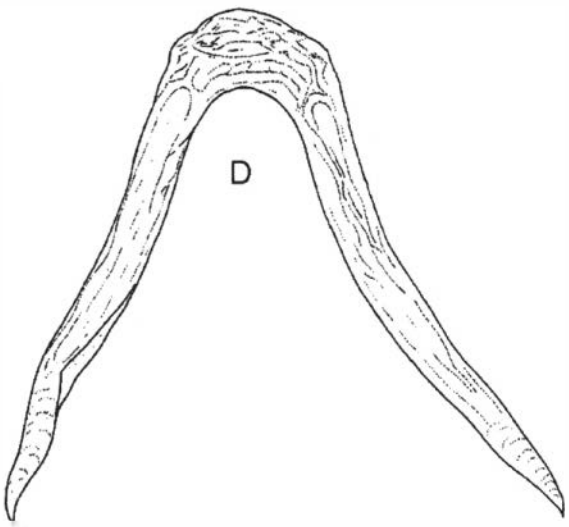
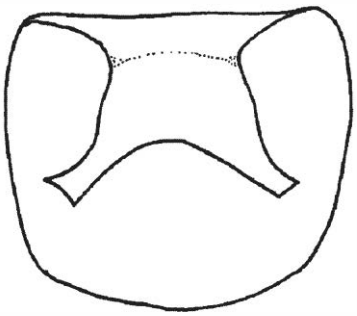


Figure 23. *Cirroctopus hochbergi* sp. nov.: **A, B**, holotype, NZOI H-674, male, ML 90.0 mm.

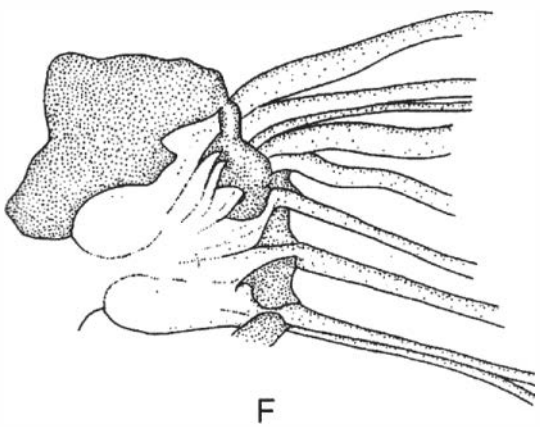


C





B



F

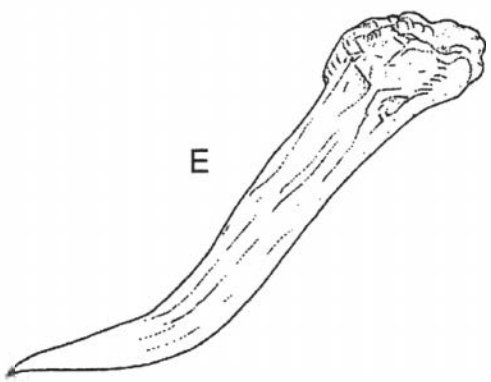


Figure 24. ***Cirroctopus hochbergi*** sp. nov.: **A**, mantle cavity, holotype, NZOI H-674, male, ML 90.0 mm. **B**, sucker morphology (section), NZOI H-674. **C–E**, shell structure, posterior, dorsal and lateral perspectives. **F**, optic lobe, NMNZ M.118289, male, ML 86 mm. Legend: AC, accessory gland; CT, gill; F, funnel; IPS, interpallial septum; M, mantle (reflected); RT, renal tissue.

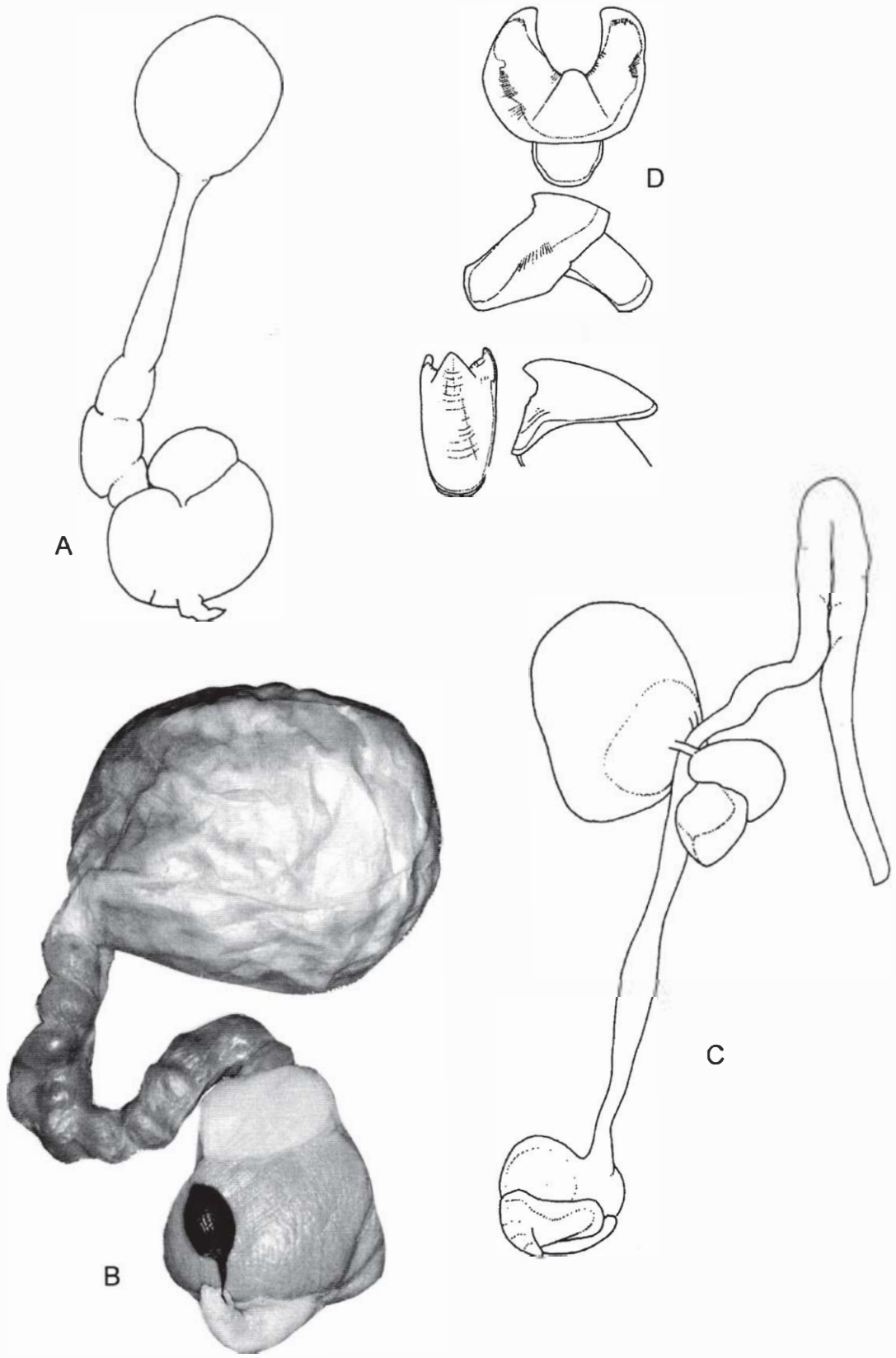


Figure 25. *Cirroctopus hochbergi* sp. nov.: **A, C, D**, NMNZ M.118289, male, ML 86 mm. **B**, NMNZ M.118244, female, ML 124 mm. **A**, male reproductive system. **B**, female reproductive system. **C**, alimentary canal. **D**, beaks.

Table 17. Indices and formulas for *Cirroctopus hochbergi* sp. nov.

	NMNZ M.119888	NZOI Stn Z8379	NMNZ M.118244	NZOI Stn Z8326	NZOI Stn Z8380	NMNZ M.118244	NZOI Stn Z8319
MWI	87.4	83.3	104.8	147.8	103.4	106.2	98.3
PAI	43.7	33.3	58.9	67.4	44.3	45.0	44.0
FunLI	31.9	35.1	38.3	50.0	29.5	38.8	48.3
FLI Out	104.6	85.7	123.0	173.0	92.0	114.3	134.5
FLI In	65.6	68.7	83.1	109.2	63.1	66.7	87.9
FWI	29.8	43.1	36.4	41.6	38.9	45.0	50.0
ALI1–4[1]	57.4–70.2	58.1–65.3	70.9–78.3	60.5–76.1	51.9–70.2	46.3–66.7	63.3–70.6
AFR	1.2.4.3	3.2.1.4?	1.2.3.4?	2.3.1.4	1.2.3.4	1.3.2.4	3.2.1.4
AFL	3.1.2.4	2.1.3.4	1.2.3.4?	2.1.3.4	2.1.3.4	1.2.3.4	3.1.2.4
WFR	A.B.C.D.E	B.A.C.D.E	A.D.B.C.E	C.B.A.D.E	A.B.C.D.E	A.B.C.D.E	B.C.A.D.E
WFL	A.B.C.D.E	B.A.C.D.E	A.C.B.D.E	B.C.A.D.E	B.A.C.D.E	A.B.C.D.E	A.B.C.D.E
ASC1–4	84–88	74–81	81–88	71–78	70–75	69–75	73–79
CiLI1–4	2.5–4.6	1.7–4.0	3.6–4.8	4.5–5.6	2.3–3.0	2.2–3.1	3.5–5.2
ASIn1–4	3.6–4.0	4.1–4.8	4.8–6.4	6.7–7.9	3.4–3.5	3.1–3.9	4.3–5.2

[1] As a percentage of total length.

Table 18. Variation in egg characters from female mantle cavities of *Cirroctopus hochbergi* sp. nov.

	NZOI Stn Z8329	NMNZ M.118244	NMNZ M.118244	NZOI Stn Z8328	NZOI Stn Z8327
ML (mm)	150.0	124.0	119.0	116.5	111.0
Egg length	13.2	14.3	15.8	8.5	14.0
Egg width	8.9	8.9	10.0	5.4	8.2
Surface texture	circular ridges	longitudinal ridges and circular lines	smooth	irregular	irregular
Colour	khaki	tan	tan	khaki	khaki
Anterior peak	absent	present	absent	absent	absent
Posterior spike	present	present	present	present	present

egg frequently free in mantle cavity; eggs elliptical; egg size, shape, colour and surface texture variable. Egg characteristics in Table 18.

Alimentary canal (Fig. 25C) with moderate-sized buccal bulb; anterior and posterior salivary glands, radular and palatine teeth absent. Oesophagus long, without crop diverticulum; oesophageal dilation great-est about one-third along oesophagus. Stomach large,with external demarcation marking thick muscular and thin cuticular sections, lumen continuous, without chambers. Caecum large, thin walled, of equivalent size to stomach, without spiral coiling. Intestine long, about 2.5 times oesophagus length, thin walled, distended for greatest length, particularly proximal half and distal third; anal flaps absent. Hepatic ducts two; digestive gland large, entire; pancreas well developed. Gut contents of all specimens examined contain unidentifiable soft tissue.

Upper beak (Fig. 25D) tall (height 75% length), with dark-pigmented hood with fine translucent hood and lateral wall margins; hood very deep (depth 80% beak length), with square crest; jaw minutely serrate (2 or 3 teeth); rostrum sharp, slightly deflected down. Lateral walls parallel sided, with broad crest and weak lateral-wall fold. Lower beak (Fig. 25D) depressed (height 61% width); hood, lateral wings, and wall darkly pigmented, with broad, translucent, lateral wing margins. Lateral wall with moderate notch and acutely convex crest. Hood moderately long (depth 50% beak length), projecting forward; rostrum with blunt tip; lateral wings very long (length 110% beak length), with strong basal and weak central fold.

ETYMOLOGY: Named for F.G. Hochberg in recognition of his assistance in this study and valued discussions on cirrate systematics.

REMARKS: Solitary eggs recovered from mantle cavities of female *Cirroctopus hochbergi* are so variable in size, colour, and gross surface texture that they cannot be shown to be different from solitary eggs described from 36°31' S, 178°38' W, 4520 m, *Galathea* Stn 663, and 36°34' S, 178°57' W, 4625 m, *Galathea* Stn 664 (Boletzky 1982). Boletzky (*l.c.*) considered differences in egg colour and sculpture may enable differentiation of taxa, particularly among eggs of similar size. However, in light of egg variation in *C. hochbergi* differentiating eggs of different taxa may prove more difficult than anticipated.

The most significant difference between the classification proposed here and those of Voss (1988a, 1988b) is the removal of *Cirroctopus* from synonymy with *Grimpoteuthis* and recognition of a closer relationship between both *Opisthoteuthis* and *Cirroctopus* than between either genus and *Grimpoteuthis*. In doing so, and in recognising three discrete types of *Opisthoteuthis* anatomy, there may be a need for additional generic recognition. For this reason *Grimpoteuthis* is removed from the family Opisthoteuthididae to form a new family, the Grimpoteuthididae.

Cirroctopus hochbergi is most similar to *C. mawsoni* (Berry), and it is not without reservation that this species is described as distinct. However, as the distributions of these two species are strongly allopatric, and because they differ in the degree of ventral mantle pigmentation (similar to dorsal pigmentation in *C. hochbergi* but markedly paler in *C.* cf. *mawsoni*) and lower arm-sucker counts in apparent mature specimens, the two species are treated as distinct. From *C. glacialis* and its probable junior synonym *C. antarctica*, *C. hochbergi* differs in having four areolar spots only, in having more and smaller suckers relative to mantle length, and higher gill lamellae counts. Sufficient differences are apparent between

Table 19. Raw measures for *Cirroctopus hochbergi* sp. nov. (* denotes damage).

	NMNZ M.119888	NZOI Stn Z8379	NMNZ M.118244	NZOI Stn Z8326	NZOI Stn Z8380	NMNZ M.118244	NZOI Stn Z8319
TL	493	432	437	440	258	216	218
ML	151	126	124	89	88	64.5	58
MW	132	105	130	131.5	91	68.5	57
PA	66	42	73	60	39	29	25.5
FunL	48.2	44.2	47.5	44.5	26	25	28
FL Out	158	108	152.5	154	81	73.7	78
FL In	99.0	86.5	103.0	97.2	55.5	43.0	51.0
FW	47.0	46.6	55.5	64.0	31.5	29.0	29.0
AL1R/L	320/328	258*/274	225*/211*	296/285	161/180	129/144	145/144
AL2R/L	315317	276/282	325/316*	335/324	160/181	118/122	153/143
AL3R/L	283346	280/263	342/320	333/277	150/175	122/108	154/153
AL4R/L	295305	260/251	310/205*	295/266	134/160	117/100	138/142
WDA	194	150	155	120	117	91	90
WDBR/L	178/170	163/158	140/123	168/155	116/119	79/87	95/79
WDCR/L	147/166	142/140*	130/128	186/141	81/108	75/65	91/73
WDDR/L	100/162	124/122	143/110	109/92	61/99	55/54	76/63
WDE	81	67	60	78	50	35	48
ASC1R/L	86/86	63*/78	*/*	74/71	71/74	74/75	76/78
ASC2R/L	88/88	74/81	88/*	76/78	74/75	72/72	79/75
ASC3R/L	86/87	77/80	87/81	73/72	73/72	69/73	73/73
ASC4R/L	?/84	79/75*	83/*	74/73	70/70	69/69	73/76
CL1R	7.0	4.1	6.0	4.8	2.6	2.0	3.0
CL2R	5.0	5.0	5.5	4.5	2.1	1.4	2.0
CL3R	3.8	4.0	5.5	4.0	2.3	1.7	2.5
CL4R	6.3	2.2	4.5	5.0	2.0	1.7	2.2
ASn1R/L	5.8/5.5	5.5/5.9	7/7	6.5/7.0	3.0/3.1	2.4/2.5	3.0/3.0
ASn2R/L	5.5/5.6	5.2/6.1	7.0/6.5	6.5/6.0	3.1/3.1	2.2/2.0	3.0/2.9
ASn3R/L	6.0/5.5	6.0/6.0	6.0/7.0	6.0/6.0	3.0/3.0	2.1/2.0	2.8/3.0
ASn4R/L	6.0/5.9	5.4/6.0	7.0/7.9	6.3/6.0	3.0/3.0	2.1/2.4	3.0/2.5
GiLC	7	7	7	7	7	7	8

the New Zealand species, *C. glacialis* and *C. mawsoni* to recognise it as novel, although additional material of *C. mawsoni* and *C. glacialis* is required before the systematic status of this species complex can more fully be resolved.

Family **GRIMPOTEUTHIDIDAE** new family

Extensively gelatinous cirrates; cephalopedal mass anteroposteriorly elongate; web single, web-nodules present. Cirrus length variable, about 5–10% ML, equal to 2.5 times longer than greatest sucker diameter; cirri commence between suckers 4 and 6 on all arms, present to arm tips. Suckers small, cylindrical, not abruptly enlarged in males; sucker aperture simple. Interpallial septum short, oriented along anteroposterior axis of body, with communication between mantle chambers extensive. Gills sepioid or seemingly transitional between 'half orange' condition and sepioid condition (semi-sepioid, possibly attributable to post-mortem fixation artifact in one species). Shell simple, broadly U-shaped; lateral wings lobelike, distally expanding in width, with rounded distal margin with or without short off-centre prolongation; muscle insertion points poorly developed. Radular and palatine teeth absent; anterior and posterior salivary glands absent. Intestine short, of equivalent length to oesophagus; digestive gland entire (not bilobed). Optic lobe small, spherical; optic nerve branching pattern symmetric, optic nerve single.

Grimpoteuthis Robson, 1932

TYPE SPECIES: *Cirroteuthis umbellata* Fischer, 1883 (by designation, Robson 1932: 136).

DIAGNOSIS (new): With characters of the family. Mantle and head tissues translucent, adoral and aboral surfaces of arms and web darkly pigmented, not translucent. Arm formula 1.2.3.4; cirri about 10% ML or 2.5 times longer than greatest sucker diameter; cirri commence between suckers 4 and 6 on all arms, present to arm tips. Inter-pallial septum thick, short, oriented along antero-posterior axis of body. Gills with two well-developed rows of lamellae. Shell solid, with inner and outer saddle and wing surfaces convex; lateral wings lobe-like, distally expanding, terminally rounded; basal shelf absent, features characterising the type species [interpretation of figures of Ebersbach (1915)].

REMARKS: Despite *Grimpoteuthis umbellata* (Fischer) being the type species of *Grimpoteuthis*, no detailed description of this species exists. For this reason the *Grimpoteuthis* (*sensu stricto*) morphology is identified primarily on the basis of the characteristic shell shape, and secondarily upon the recurring morphological characters such as arm length, arm formula, sucker size, and cirrus length, present in species with the most simple U-shaped shell.

Although gill type in *Grimpoteuthis* (*sensu stricto*) has conventionally been referred to as 'half-orange' *Opisthoteuthis*-type (Robson 1932; Voss 1988a, 1988b; Voss & Pearcy 1990), Robson (1932: 138, footnote), described the gills of *G. umbellata* as not greatly similar to those of *Opisthoteuthis*. Ebersbach (1915: 124) described gill structure in *G. umbellata* as *Octopus*-like "zweireihige Anordnung" (inferring two rows or series of filaments). This gill type is consistent with that of the single specimen from Lord Howe Rise, west of New Zealand, taken to represent the *Grimpoteuthis* (*sensu stricto*) morphology.

The female attributed to *G. umbellata* (Fischer) (Voss 1955) from off Guantanamo, Cuba, 2431–3016 m, was overlooked by Voss (1988b) in his biogeographic assessment of deep-sea octopod distribution. The shell of this specimen was described as "horse shoe-shaped, the ends lying parallel, the posterior curve forming part of the arc of the circle", and figured with rounded terminal wing extremities, weak lateral muscle insertion points, a smooth non-excavate outer saddle surface, and no basal shelf. Additional characters for this specimen included: very few and large eggs (6 of about 12.5 x 7.0 mm, and about 12 smaller eggs within the ovary sac.), an arm formula of 1.2.3.4, with arms 74% TL, small suckers (4% ML) extending to arm tips, and cirri about 2.5 times sucker diameter, also extending to the arm tips. This specimen is referable to *Grimpoteuthis* (s.s.) as rediagnosed herein. A similar species represented by a single immature male captured at 27°37.6–38.5' S, 0°50.8–51.3' E, 4660 m, 09/01/1979, Angola Basin (SAM S765), is also extremely similar in morphology and anatomy to *Grimpoteuthis umbellata* (Fischer). Finally, although considered a *nomen dubium* (Voss 1988b), *Grimpoteuthis plena* (Verrill, 1885) is also referable to *Grimpoteuthis* (s.s.), based on examination of recently collected material proximal to the type locality of this species.

Four characters described for *Chunioteuthis gilchristi* (Robson, 1924a: 204–205, as *Cirrhoteuthis gilchristi*) preclude generic placement in this new schema: cirri commence at the first sucker and are of exceptional length, the digestive gland is entire, and the intestine is of equivalent length to the oesophagus (Robson 1924a, 1924b, 1926, 1932). Although Robson (1924a: 205) refers to "abrupt sucker enlargement in

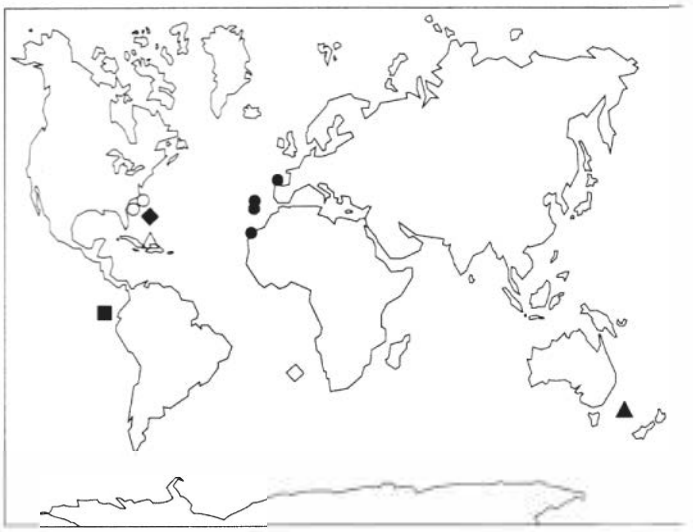


Figure 26. Recognised distribution of ***Grimpoteuthis*** (s.s.). ● *G. umbellata;* ■ *G. hippocrepium;* o *G. megaptera;* ◆ *G. plena;* ◊ *G.* sp. (SAM S 765); Δ *G.* aff. *umbellata (Voss 1955);* ▲ *G. abyssicola* sp. nov.

the proximal field", the same specimen is also described "with no definite trace of sucker enlargement" (Robson 1932: 160). On the basis of this character combination this species should be treated as incertae sedis in the suborder Cirrata (although somewhere around the Grimpoteuthididae n. fam.).

Grimpoteuthis abyssicola sp. nov. (Figs 28, 29) (Table 20)

TYPE MATERIAL (1 specimen, female [F]). Holotype: NZOI H-661, F, ML 75.0 mm, 35°35.1' S, 160°57.1' E, 3180–3154 m, 27/09/1982, NZOI Stn U200 TAM.

REFERENCE MATERIAL (1 specimen, male [M]): SAM S765, *Grimpoteuthis* (*s.s.*) sp., M, ML 49.5 mm, 27°37.6' S, 0°50.8' E, Angola Basin, 4660 m, 09/01/1979.

RECOGNISED DISTRIBUTION (Fig. 27, p. 52): Known only from the type locality, west of New Zealand off Lord Howe Rise.

DIAGNOSIS: A moderate-sized species; cephalopedal mass bell-shaped. Mantle and head tissues translucent, gelatinous; arm and web tissues deep purple, not translucent, gelatinous. Fins small, subterminal; radula absent; arms long, deeply invested in web; web deep; cirri moderately long.

DESCRIPTION (external facies, Fig. 28A–B): Adult animal of moderate size, ML to 75 mm, TL to 305 mm; mantle, head, and web extensively gelatinous; arms semi-gelatinous; cephalopedal mass antero-posteriorly elongate, bell-shaped; mantle and nuchal constrictions poorly developed. Eyes large, lateral. Fins subterminal, of moderate length (FLI 84% ML), slender (FWI 38%), lateral, paddlelike. Outer fin margin straight, inner margin weakly convex, fin margins delicate, constriction at junction with mantle poorly developed; muscular portion of exposed fin extending about half fin length.

Mantle aperture reduced, enveloping base of funnel; funnel of moderate length, 44% ML, attached to base of ventral arms at level of 4th and 5th sucker. Mantle cavity disproportionately small (Fig. 28C); interpallial septum well developed, thick, short, oriented along anteroposterior axis of body, with communication between right and left chambers of mantle cavity extensive. Gills with 4 inner and 4 outer lamellae, neither demibranch demonstrably reduced; 4th inner and outer, and terminal lamella with common arterial base, slightly reduced in size relative to adjacent lamellae. Funnel organ V-shaped, limbs thick.

Arm formula 1.2.3.4; arms long, slender; longest arm length about 70% TL, shortest arm length about 50% TL. Web single, deep, delicate; formula A.B.C. D.E, with web sector E about half depth of sector A; dorsal web depth 67% of dorsal arm length, distal third free; ventral web depth 40% of ventral arm length, 60% arm length free (deepest web sector 67% longest arm length, 90% shortest arm length; shallowest web sector 30% longest arm length, 40% shortest arm length). Web extends almost to arm tip along dorsal face of arm, to suckers 32–34, proximal to fleshy web nodule on ventrolateral surface of each arm. Cirri of moderate length, about 10% ML, 2.5 times longer than greatest sucker diameter; cirri commence between suckers 4 and 5 on arms 1 and 2, and 5 and 6 on arms 3 and 4, attaining greatest length between suckers 10–30; suckers and cirri extend to arm tip. Suckers numerous, ASC to 77, evenly spaced within web sectors; small, ASIn 4% ML; first 6–8 suckers similar sized, following 30–35 suckers slightly

enlarged; terminal 30–35 suckers on free portion of arm outside web sector decrease rapidly in diameter. Suckers (Fig. 29A) cylindrical, with small to medium-sized suction chamber, well-developed muscular suction pad and wall ring, and simple sucker aperture.

Dorsal and ventral surfaces of mantle, head, and fins translucent; aboral and adoral surfaces of arms and web deep purple, not translucent. Sucker apertures orange-brown.

Shell simple (Fig. 29B), solid, light honey-coloured, translucent, flexible but easily fragmented, surface smooth. Saddle with convex outer and inner margins; lateral wings lobelike, with broadly rounded tips, without inrolled margins; wings expanding, distally broader than saddle; muscle insertion points poorly developed.

Optic lobe (Fig. 29C) small, spherical; optic nerve branching pattern symmetric, with single right and left optic nerve branching considerably into rear of eyeball; white body small, heart-shaped, brown, well separated across dorsal midline of head.

Female reproductive system (Fig. 29D–E) with small ovary sac; eggs very large, to 17.8 x 7.0 mm, with 19 or 20 longitudinal striations; proximal oviduct thin walled, twice the length of distal oviduct, containing two eggs. Oviducal gland with two well-developed chambers, distal two times larger than proximal, both radially striate, with single egg in second chamber; distal oviduct short. Male anatomy unknown.

Alimentary canal (Fig. 29F) with large buccal bulb; radular and palatine teeth, anterior and posterior salivary glands, absent. Anterior oesophagus short, about 10% total oesophagus length; crop without diverticulum. Stomach large, muscular, without chamber demarcation. Spiral caecum large, volution incomplete; hepatic ducts two. Intestine thin walled, length equivalent to oesophagus and crop, without marked regional distension; terminal portion of rectum freely projecting in mantle cavity, muscular; anal flaps absent. Digestive gland ovoid, entire; pancreas well developed.

Upper beak (Fig. 29G) tall (height 78% length), with dark-pigmented hood with translucent hood and lateral wall margins; hood moderately deep (depth 65% beak length); rostrum sharp, slightly deflected down; lateral walls weakly convex, with rounded crest and weak lateral wall fold. Lower beak (Fig. 29G) moderately tall (height 60% width); darkly pigmented, with translucent lateral wing and wall margins; lateral wall with weak basal notch and broadly convex crest. Hood deep (depth 50% beak length), projecting for-ward, pointed; lateral wings long (length 100% beak length), with two weak folds.

Table 20. Raw measures for *Grimpoteuthis abyssicola* sp. nov. (* denotes damage).

	NZOI Stn U200
TL	305
ML	75
MW	72
PA	27
FunL	33
FL outer	63
FL Inner	54
FW	24
AL1R/L	200/215
AL2R/L	190/189
AL3R/L	172/173
AL4R/L	161/115*
ALFR	1.2.3.4
ALFL	1.2.3.4
WDA	145
WDBR/L	131/130
WDCR/L	95/106
WDDR/L	75/87
WDE	65
WFR	A.B.C.D.E
WFL	A.B.C.D.E
ASC1R/L	77/74
ASC2R/L	75/72
ASC3R/L	74/70
ASC4R/L	70/37*
CL1R	7.4
CL2R	6.0
CL3R	6.0
CL4R	6.0
ASn1R/L	3.0/2.8
ASn2R/L	2.8/2.5
ASn3R/L	2.8/2.5
ASn4R/L	2.8/2.5
GiLC	4/4

ETYMOLOGY: From the abyssal habit of this species.

REMARKS: Gut contents comprised densely packed small amphipods.

Enigmatiteuthis gen. nov.

TYPE SPECIES: *Enigmatiteuthis innominata* gen. et sp. nov.

DIAGNOSIS (new): With characters of the family. Mantle and head tissues gelatinous, not translucent; aboral and adoral surface of arms and web darkly pigmented, not translucent. Cirri commence between

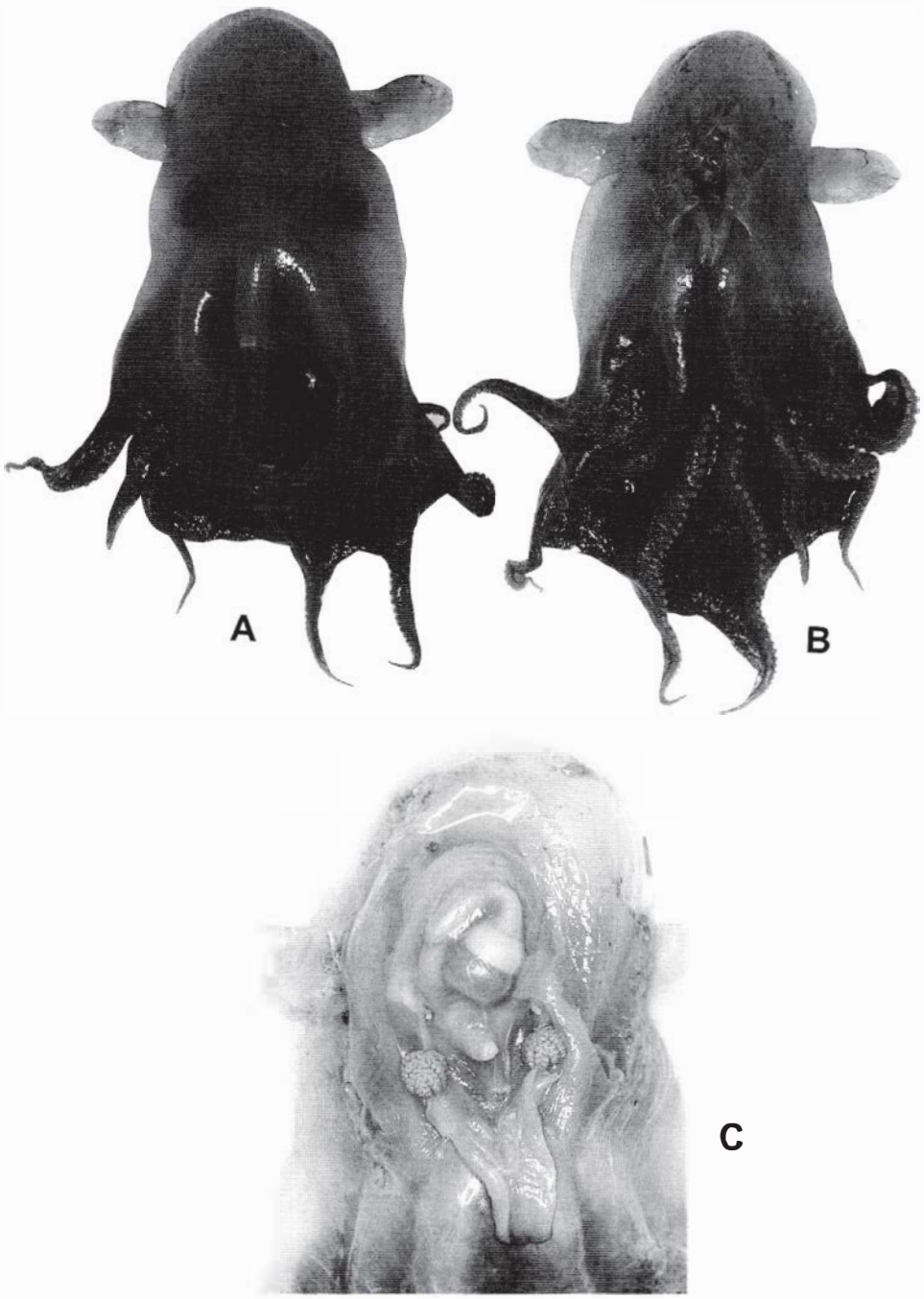


Figure 28. *Grimpoteuthis abyssicola* sp. nov.: Holotype, female, ML 75.0 mm. **A, B**, whole-animal perspectives. **C**, mantle cavity.

suckers 4 and 6; cirrus length equivalent to greatest sucker diameter; cirri present to arm tips. Suckers small to moderate sized, slightly enlarged in male proximal field. Interpallial septum thin, long. Shell simple, vacuolate; saddle with single shallow excavation; basal shelf weakly developed; muscle-insertion points weakly developed; lateral wings flay out into broadly rounded paddles, with offset-centre terminal prolongation to acute point.

Enigmatiteuthis innominata gen. et sp. nov.
(Figs 32, 33)
(Tables 21, 22)

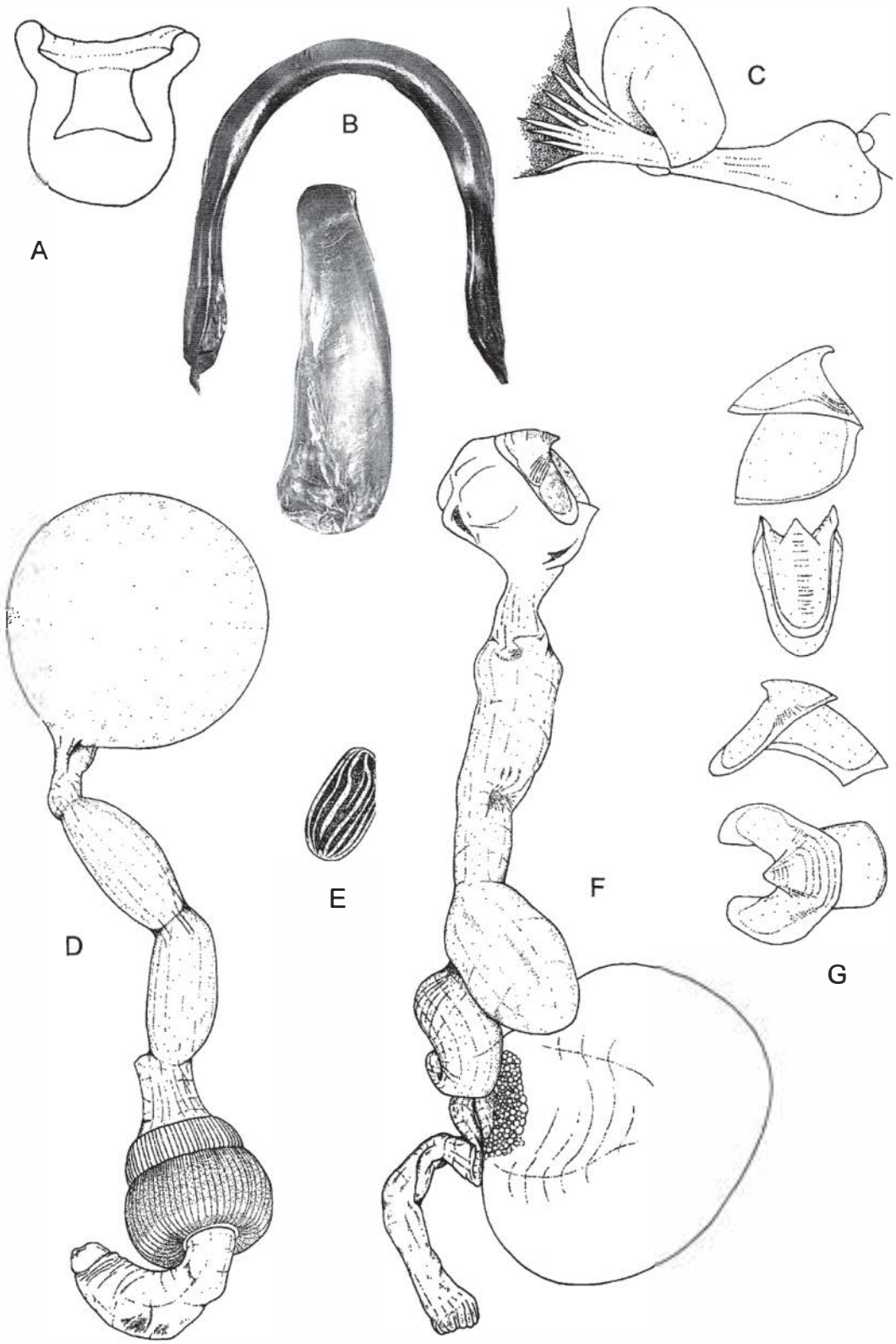


Figure 29. ***Grimpoteuthis abyssicola*** sp. nov.: Anatomy of holotype. **A**, sucker morphology. **B**, shell, dorsal and lateral perspectives. **C**, right optic lobe. **D**, female reproductive system. **E**, inset egg from proximal oviduct. **F**, alimentary canal. **G**, beaks.

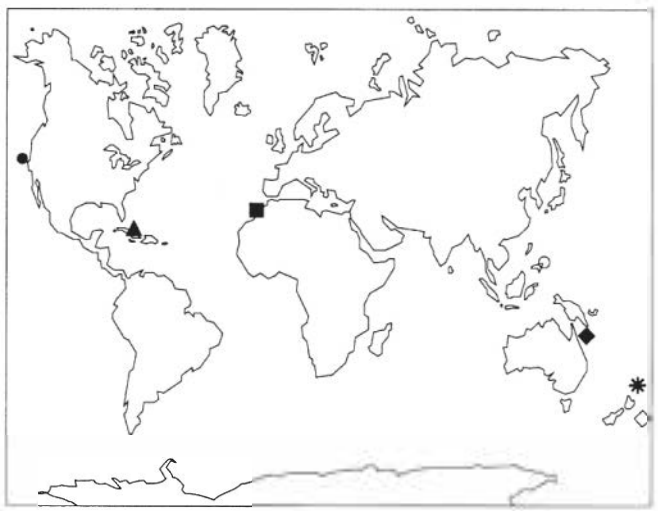


Figure 30. Recognised distribution of ***Enigmatiteuthis*** gen. nov.: ● *E. bathynectes* (Voss & Pearcy); ◊ *E. innominata* sp. nov.; ✳ ?*E. meangensis* (Hoyle, partim: small Kermadec Island syntype); ○?*E. meangensis* (Hoyle, partim: large Meangis Island Type); ▲ *E.* sp. (=?*Grimpoteuthis meangensis* Voss 1955 [not Hoyle, 1885]); ◆ *E. pacifica* (Hoyle); ■ *E. wulkeri* (Grimpe).

?*Cirroteuthis meangensis* Hoyle, 1885 (*partim*: small Kermadec Island syntype)
?*Stauroteuthis meangensis* (Hoyle, 1885): Hoyle 1909 (*partim*: small Kermadec Island syntype)

TYPE MATERIAL (2 specimens, 1 male [M], 1 female [F]): Holotype: NMNZ M.109381, M, ML 35.0 mm, FPT, 42°36.79' S, 176°09.81' W, 1999–2002 m, 02/03/1992, f.r.v. *Tangaroa*. Paratype: NZOI P-1117, F, ML 43.2 mm, FPT, 42°36.79' S, 176°09.81' W, 1999–2002 m, 02/03/1992, f.r.v. *Tangaroa* (ex NMNZ M.109381).

REFERENCE MATERIAL: SAMS221, *Chunioteuthis* cf. *ebersbachi* Grimpe, det. O'Shea, F, ML *c.* 61 mm., 31°0.0' S, 30°27.2' E, 900 m, 12/05/1977.

RECOGNISED DISTRIBUTION (Fig. 31, p. 52): Known only from the Chatham Rise, 1705–2002 m, possibly extending to Kermadec Islands if synonymy is correct.

DIAGNOSIS: Small-bodied, anteroposteriorly elongate (bell-shaped) animals. Fins large, paddlelike; radula absent; arms long, deeply invested in web; web deep; suckers with slight enlargement in male proximal field. Shell vacuolate, amber coloured, translucent, flexible, surface texture irregular; basic U-shape. Gills semi-sepioid, with 7 loosely compacted lamellae. Body counter-pigmented, ventral surfaces of mantle, head, arms 3 and 4, and aboral surface of web and arms darker than dorsal and adoral surfaces of same; dorsal surfaces pinkish-red; ventral surfaces dark red; adoral surfaces of arms and web deep maroon. Cirrus length equivalent to greatest sucker diameter, cirri commence between suckers 4 and 6. Suckers small to moderately large, without abrupt enlargement; ASC 50–60.

DESCRIPTION (external facies, Fig. 32A, B): All available specimens immature, ML to 43.2 mm, TL to 156.0 mm; mantle, head, and arms with substantial subgelatinous deposits; web thin, non-gelatinous (in preserved state). Cephalopedal mass anteroposteriorly elongate, bell-shaped. Eyes large, lateral in orientation (between arm bases 2 and 3), bulbous. Head large, wide; mantle and nuchal constrictions poorly developed; orbits large, aperture laterally oriented. Fins long, slender (FLI 106–145, FWI 31–40), muscular portion of exposed fin about half fin length; fins subterminal, orientated 90° from axis of mantle; outer margin convex, inner margin straight-sided; fins with distal margin broadly rounded, membranous; basal constriction poorly developed.

Mantle aperture moderately wide; mantle and funnel attached to ventral surface of arm bases 4 at level of 8 or 9th sucker. Funnel long, FLI 30–40%, slender; distal two-thirds of funnel free of arm bases 4. Mantle cavity (Fig. 33A) with semi-sepioid gills, each with 7 loosely compacted lamellae, innermost and outermost slightly reduced in size, lamellae 3–5 with common arterial base, reduced in size relative to adjacent lamellae. Interpallial septum thin, belt-like, attached to viscera lateral to genital aperture, extending directly to inner, ventral surface of mantle musculature.

Arm formula variable, with no consistent disparity between right and left sectors of male and female; longest arm length 76–77% TL, shortest arm length 59–61% TL; arms slender, rapidly attenuating to laterally compressed tips. Suckers small to moderate sized, none abruptly enlarged; ASC 50–60 per arm; suckers sexually dimorphic, larger in male (ASln 8.3% male, 4.6% female); first 25–35 suckers of similar size, slightly enlarged in male proximal to web margin; terminal or so 25 suckers comparatively small; individual suckers cylindrical, elevated from arm surface, with moderate-sized suction pad,

Table 21. Formulas of *Enigmatiteuthis innominata* gen. et sp. nov.

	NMNZ M.109381	NZOI P-1117
AFR	1.4.2.3	1.3.4.2.
AFL	1.2.3.4	2.1.4.3
WFR	A.B.E.D.C	A.E.C.D=E
WFL	A.E.B.D.C	B.A.E.D.C

chamber, well-developed muscular suction pad, weakly convex wall ring, simple sucker aperture, and well-developed grasping pad (Fig. 33B). Cirrus length short to moderate (CiL male 8.6% ML, female 5.1% ML); length equivalent to greatest sucker diameter in both sexes; cirri commence between suckers 4 and 5 or 5 and 6, gradually increasing in length towards web margin, thereafter length rapidly decreases to arm tips; cirri and suckers present to arm tip. Web formula asymmetric, variable between male and female, sectors A and B deepest, D and C shallowest; secondary web absent. Web shallow to moderately deep, thin; about 40% of each arm free of web; well-developed crescentic nodule present at intersection of web sector with ventrolateral surface of each arm at level of 22–24th sucker. Deepest web sector 53–59% longest arm length, 70–74% shortest arm length, shallowest web sector 21–40% longest arm length, 26–52% shortest arm length.

Body counter-pigmented, ventral surfaces of mantle, head, arms 3 and 4, and oral surface of web and arms darker than dorsal surfaces of same. Dorsal surfaces of mantle, fins, head, and arms 1 and 2 pinkish-red; ventral surfaces of mantle, head, arms 3 and 4, and distal margin of fins, darker red; adoral surfaces of web and arms maroon, apparent in transparency through aboral surface of web sectors A–E; sucker apertures orange-brown.

Shell (Fig. 33C) vacuolate, amber coloured, translucent, flexible, surface texture irregular. Saddle well developed, with single shallow excavation on outer surface and convex inner surface; muscle insertion points well developed; basal shelf imperfectly developed; lateral wings nearly parallel-sided, diverging from saddle at about 10° angle; wings lobelike, laminar, without inrolled margins; with short offset-centre terminal prolongation into acute point.

Optic lobe (Fig. 33D–E) large, spherical; right and left branching pattern symmetric, optic nerve single, or secondarily finely divided, undergoing considerable branching into rear of eyeball. White bodies green-brown, well separated across dorsal midline of head.

Male reproductive system (Fig. 33F) with moderate development of seminal vesicles 1–3 and accessory glands 1–3; complex of accessory glands larger than seminal vesicle complex; accessory gland 3 dominates accessory gland complex; penis well developed. Female (immature) reproductive system (Fig. 33G) with ovary sac about 1.5 times diameter of oviducal ball; eggs numerous, 3.0 x 1.7 mm; proximal oviduct thin walled, slender, about 1.5 times longer than distal duct; oviducal gland comprising 2 similar-sized striate chambers; distal oviduct short, thick; genital aperture with 6 finger-like projections.

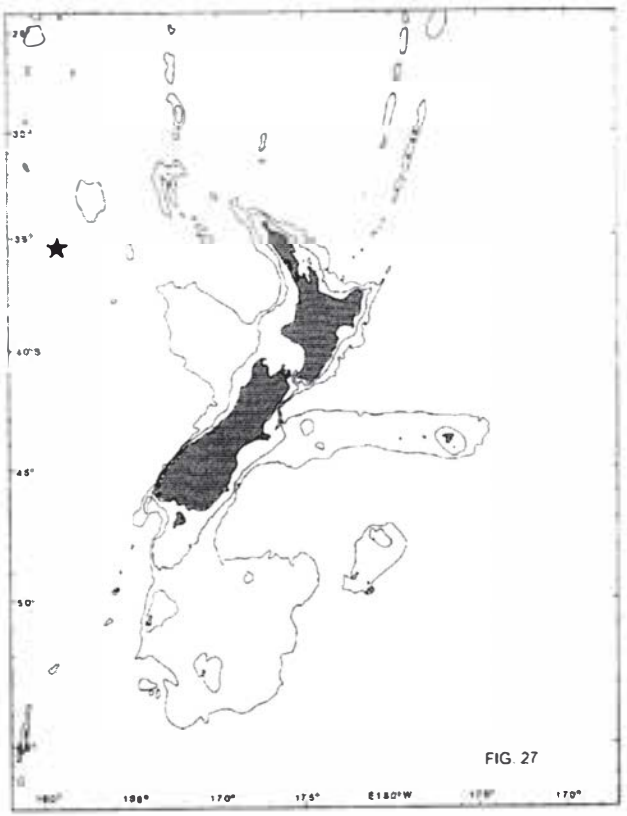
Alimentary canal (Fig. 33H) with moderate-sized buccal bulb; anterior and posterior salivary glands, radular and palatine teeth absent. Anterior oesophagus long, about one-third oesophagus length; crop diverticulum absent; stomach large, with single lumen but external demarcation delimiting thick muscular basal section and thin-walled outer section; caecum poorly developed, spiral coiling weak, of equivalent size to stomach. Intestine short, length equivalent to oesophagus, thin walled, distended; anal flaps absent. Hepatic ducts 2; digestive gland ovoid, entire; pancreas well developed.

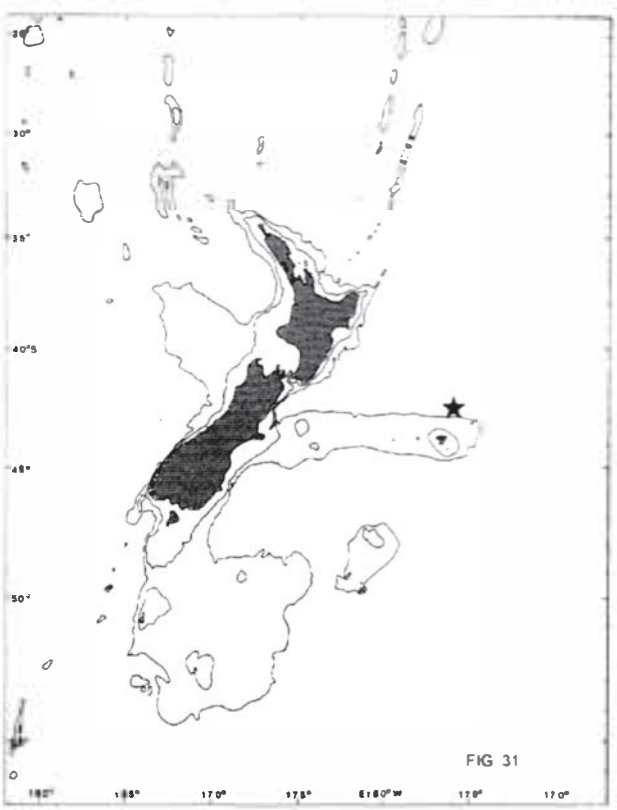
Upper beak (Fig. 33I) tall (height 70% length); rostrum darkly pigmented, with well-developed lateral fold and square crest; lateral wall and rostrum margins weakly pigmented; rostrum moderately deep (depth 68% beak length); jaw without teeth; rostrum tip sharp, slightly deflected down; lateral walls parallel sided; crest rounded, lateral wall fold weak. Lower beak (Fig. 33I) slightly depressed (height 66% width), dark-pigmented, with exception of lateral wing and wall margins. Lateral wall with weak basal notch and broadly convex crest. Rostrum moderately long (depth 53% beak length), projecting forward, pointed; hood posterior notch broadly concave; lateral wings long (length 100% beak length), with two weak folds.

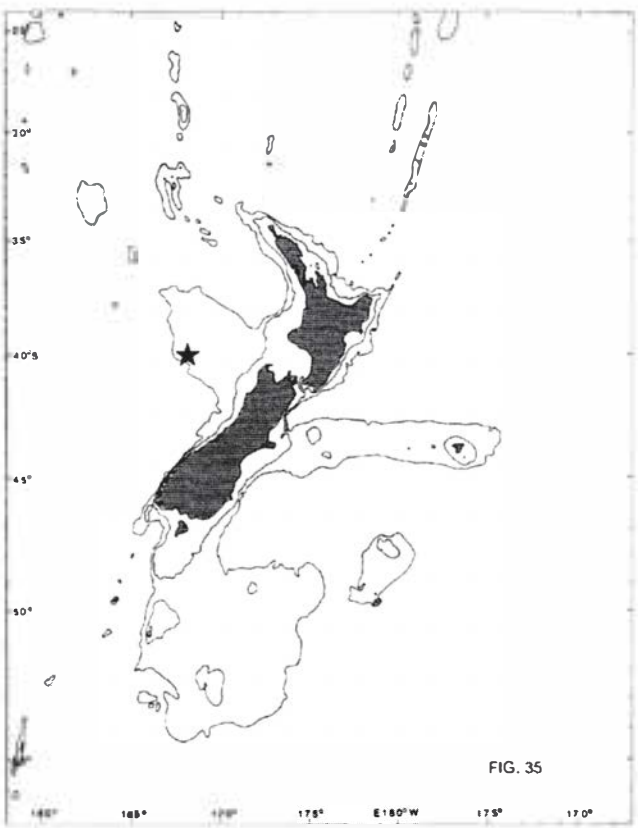
ETYMOLOGY: From the Latin 'innominatus', meaning no name.

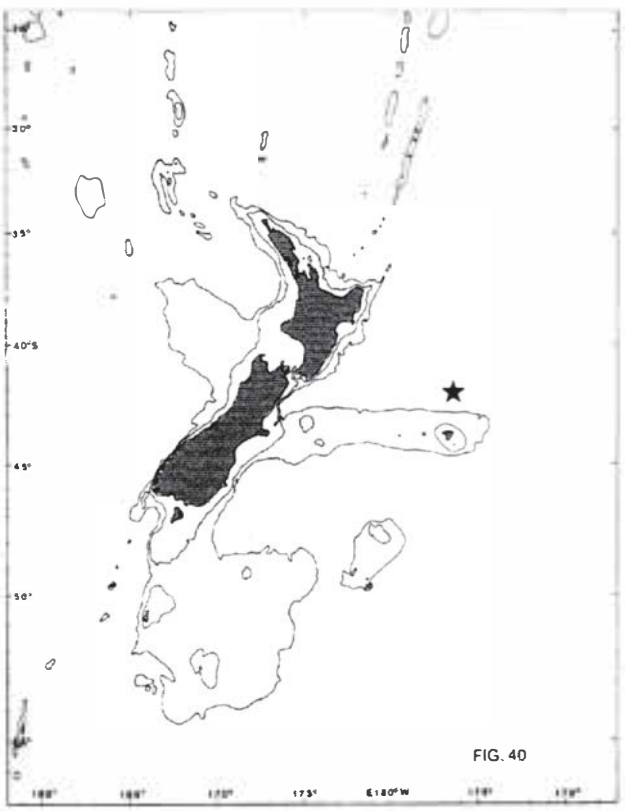
REMARKS: Hoyle (1885) attributed a juvenile cirrate collected off the Kermadec Islands (28°33' S, 177°50' W, about 1100 m) to *Cirroteuthis meangensis* Hoyle, 1885, because it shared with the larger type specimen collected off the Meangis Islands (04°33' N, 127°6' E, about 914 m) similarities in dorsal cartilage shape, and presence of papillae at the junction of the web and ventrolateral surface of the arms.

The shell described for this juvenile is similar to that of *Enigmatiteuthis*; however, given the specimen is no longer extant (Robson 1932; Naggs 1995 pers. comm.) its systematic status is uncertain.









Recognised distribution. **Fig. 27**, *Grimpoteuthis abyssicola* sp. nov. **Fig. 31**, *Enigmatiteuthis innominata* gen. sp. nov. **Fig. 35**, *Luteuthis dentatus* gen. et sp. nov. **Fig. 40**, *Cirroteuthis* sp. cf. *muelleri* Eschricht, 1836.

Two damaged specimens referred to by Voss (1955) as ?*Grimpoteuthis meangensis* (Hoyle) have a shell similar to both *Enigmatiteuthis* (*s.s.*) and *Opisthoteuthis* in possessing well-developed muscle insertion points, and wings 'probably' terminating in acute points (although no lateral illustration is presented: Voss, 1955: 106, Fig 2E [not fig. 2C, see text]). Collected in comparatively shallow water (603 m), these two specimens were excluded by Voss (1988b) in his biogeographic assessment of deep-sea octopod distribution. These specimens require re-examination to ascertain their systematic status.

Cirroteuthis pacifica Hoyle, 1885, may also be referable to *Enigmatiteuthis* based on:

1) absence of a secondary web;
2) presence of fleshy web nodules at junction of ventrolateral surfaces of arms and web;
3) cirri commence between suckers 6 and 8, with cirrus length about twice sucker diameter, and the cirri continue to arm tips;
4) arm sucker counts are low (50), and the suckers are small; and
5) the exposed proximal end of the cartilage as described by Hoyle (1885: 63) "presented a long grooved articular surface" — not smooth or polished.

Albeit poorly known, sufficient characters are described for this species should specimens subsequently be collected from the type locality. This species is here referred to as *Enigmatiteuthis pacifica* (Hoyle, 1885) new combination. The dubious record of *Cirrhoteuthis pacifica* Hoyle ? [sic] from the Andaman Sea, based on a single mutilated juvenile (Goodrich 1896: 19), was unaccompanied by any description. This record is excluded on both bathymetric and geographic grounds, it being highly unlikely that the specimens of Goodrich and Hoyle are conspecific.

The cirrate identified as *Opisthoteuthis* sp. from off New Caledonia by Roux (1994: figs 17 C, D) is similar in external facies to both *Enigmatiteuthis* and *Chunioteuthis*. Voss (1988a: 265) considered *Chunioteuthis* a synonym of *Stauroteuthis*, or at least belonging to the family Stauroteuthididae, and both *Chunioteuthis* and *Enigmatiteuthis* are similar in gross external facies with no way presently known to differentiate live-animal morphologies from an aboral perspective (both *Chunioteuthis* and *Stauroteuthis* diagnosed with a secondary web, albeit only between the 1st and the 8th or 9th suckers in *Chunioteuthis* [Grimpe 1916: 358, fig. 3]). Nevertheless, this species is not referable to *Opisthoteuthis*.

Table 22. Raw measures for *Enigmatiteuthis innominata* sp. nov.

	NMNZ M.109381	NZOI P-1117
TL	156.0	134.0
ML	35.0	43.2
MW	26.5	28.0
HdW	26.5	28.0
HdL	19.5	15.5
FiL Out	50.8	46.0
FiW	11.0	17.5
ALIR/L	117/118	100/97
AL2R/L	108/113	79/103
AL3R/L	95/107	91/92
AL4R/L	109/104	82/96
CiL1R	3.5	2.0
CiL2R	3.0	2.0
CiL3R	2.0	2.2
CiL4R	2.8	2.0
GiLC	7	7
ASC1R/L	52/56	51/52
ASC2R/L	50/58	55/52
ASC3R/L	62/60	54/55
ASC4R/L	59/55	55/54
ASn1R	2.9	2.0
ASn2R	2.6	2.0
ASn3R	2.6	1.9
ASn4R	2.2	2.0
ED17.5	13.9	
EO7.0	3.0	
FuL	14.0	12.8
WDA	70	54
WDBR/L	48/43	41/55
WDCR/L	25/38	43/47
WDDR/L	38/41	41/48
WDE	46	49

Family **LUTEUTHIDIDAE** new family

TYPE GENUS: *Luteuthis* gen. nov.

DIAGNOSIS (new): Cephalopedal mass with pronounced anteroposterior elongation; areolar spots absent; web simple; web nodules absent; cirri commence between suckers 1 and 2; cirri very short, length about 2% ML or 50% greatest sucker diameter, and present to each arm tip; sucker aperture crenulate. Interpallial septum thick, short, a membranous band oriented along anteroposterior axis of mantle; gills of 'half orange' type; shell complex, W-shaped, lateral wings with inrolled margins, tapering to acute points; basal shelf deflected beneath saddle. Radular and palatine teeth present; radular ribbon long, with about 70 transverse rows of well-developed teeth; palatine teeth large.

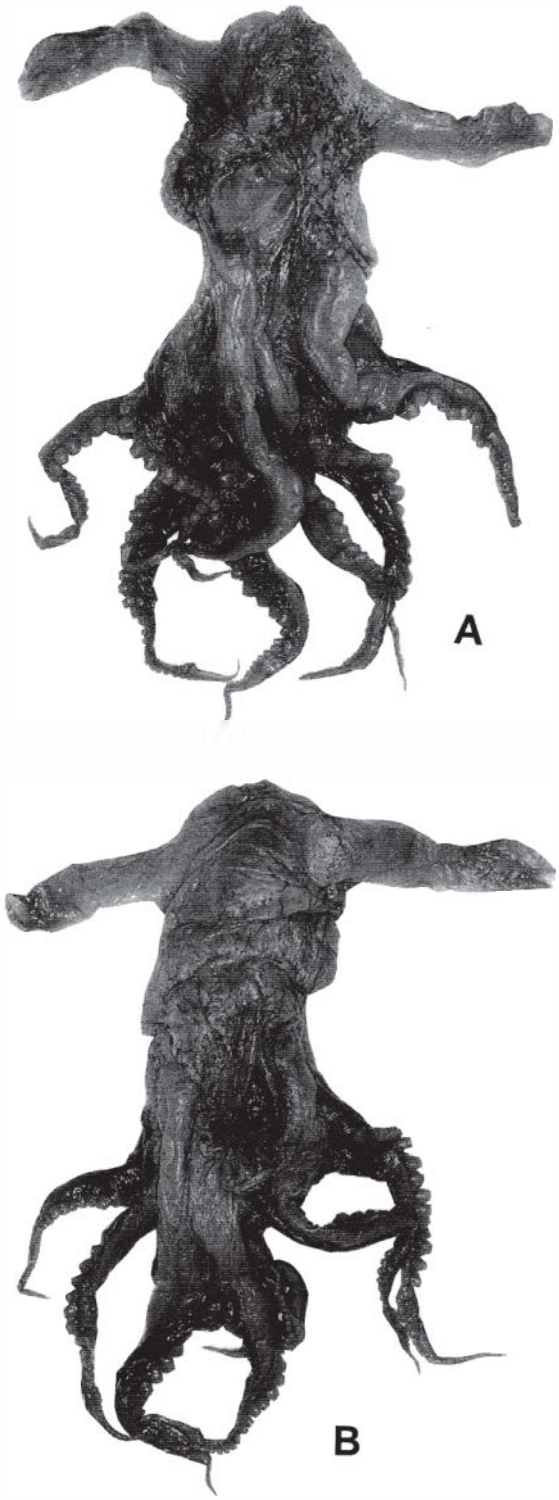


Figure 32. ***Enigmatiteuthis innominata*** gen. et sp. nov.: A, paratype, NZOI P-1117, female, ML 43.2 mm. **B**, holotype, NMNZ M.109381, male, ML 35.0 mm.

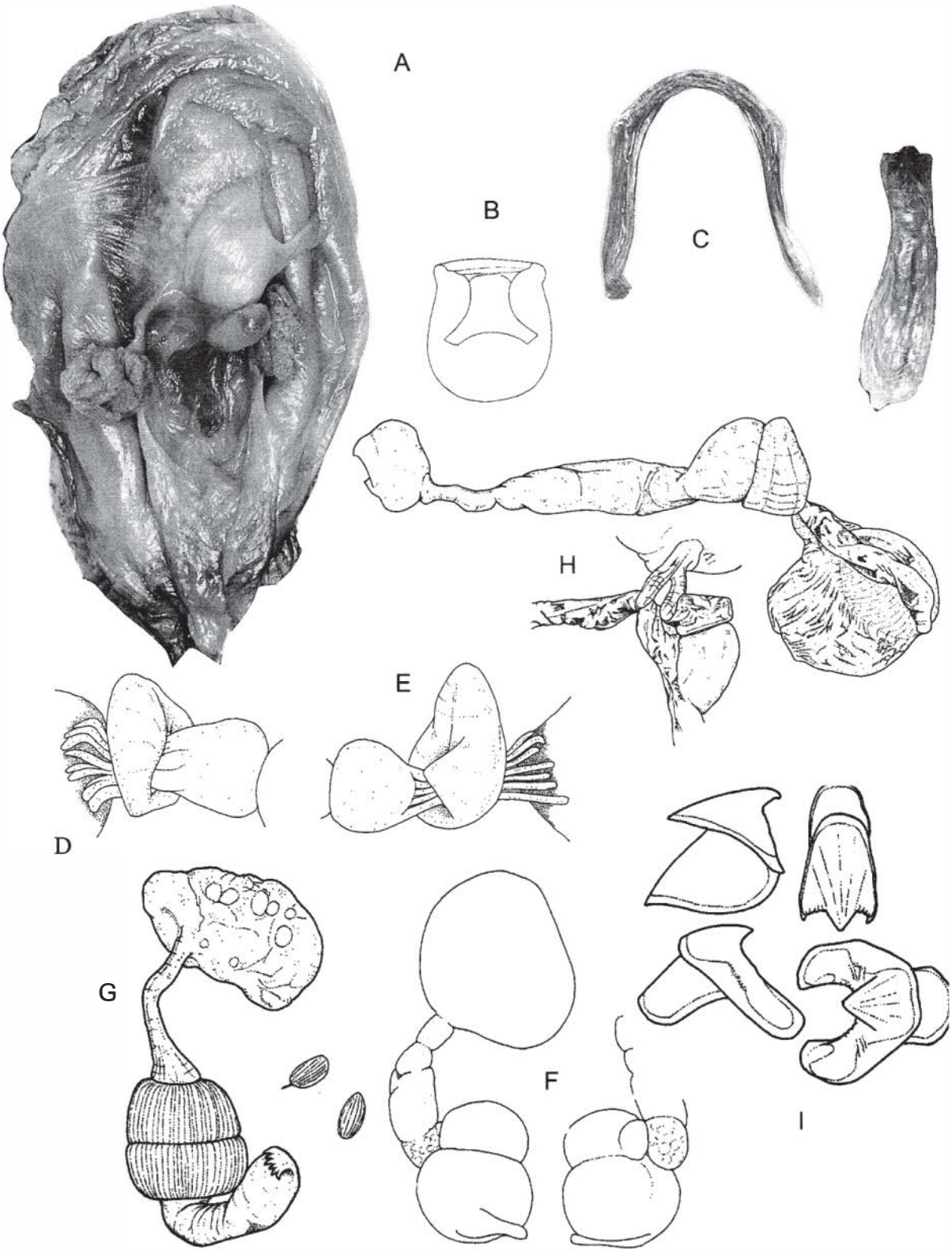


Figure 33. ***Enigmatiteuthis innominata*** gen. et sp. nov.: Anatomy (A–E, G–I, female paratype; F, male holotype). **A**, female mantle cavity. **B**, sucker. **C**, shell; **D, E**, optic lobe, **D**, right, E, left; **F**, male reproductive system. **G**, female reproductive system. **H**, alimentary canal. **I**, beaks.

Digestive gland bilobed; intestine length appreciably shorter than oesophagus length. Optic lobe ovoid; branching pattern between right and left lobes symmetric; optic nerve single. Male accessory glands 2 and 3 dominate accessory gland structural complex, accessory glands 1–3 disposed in linear sequence; penis well developed.

Luteuthis n. gen.

DIAGNOSIS: With characters of the family.

ETYMOLOGY: Both family and genus have been named after C.C. Lu who first brought the existence of a similar Australian specimen to my attention.

REMARKS: Shared between *Luteuthis* and *Opisthoteuthis* (*s.s.*) are the characters of bilobed digestive gland, short cirri commencing between adoral suckers 1 and 2, gill type, and lateral wings of the shell that taper to acute points. *Luteuthis* also shares characters similar to those of species in the families Grimpoteuthididae n. fam., and Cirroteuthididae — notably the intestine being of comparable length to oesophagus, a single optic nerve, and the presence of a basal shelf to the shell. What differentiates the Luteuthididae from the Opisthoteuthididae, Grimpoteuthididae and Cirroteuthididae is the possession of well-developed radular and palatine teeth, the peculiar 'W'-shaped shell, the male reproductive system with accessory glands disposed in linear sequence, and sucker morphology. For these reasons the family Luteuthididae n. fam. and genus *Luteuthis* n. gen. are created to accommodate the distinctive morphology of one new species.

The anatomy of female *Luteuthis* species is unknown (the single female NMV specimen not dissected), although the female of ?*Grimpoteuthis tuftsi* Voss & Pearcy, which appears very closely related, perhaps congeneric, is most peculiar in having the proximal oviducal ball chamber, although of reduced diameter, of greater length than the distal chamber, a secondarily modified genital aperture with a terminal liplike structure, and both proximal and distal oviducts of similar length. The male anatomy of both species is similar. The 'W' shape of the shell is less pronounced in ?*G. tuftsi*, although a small central prominence is apparent in the U-bend of the shell as depicted by Voss and Pearcy (1990: 64, fig. k). The alimentary canal of *Luteuthis dentatus* is remarkable in that the digestive gland is bilobed, a feature characteristic of some species of *Opisthoteuthis*. The digestive gland in ?*Grimpoteuthis tuftsi* is without lobes. Given the similarity between ?*Grimpoteuthis tuftsi* and *Luteuthis dentatus*, *Grimpoteuthis tuftsi* may ultimately prove to be a species of *Luteuthis*.

A peculiar sucker morphology similar to that diagnostic for *Luteuthis* has previously been described for *Cirroteuthopsis massayae* Grimpe, 1920. The crenulate sucker aperture described for *C. massayae* has some 23 radiating ridges that resemble shallow pointed teeth (as *Cirroteuthis umbellata* Massy, 1909: 4–5 [not Fischer, 1883]; Robson 1932: 160). The corresponding figure for *Luteuthis dentatus* is appreciably less (10), although it is possible that the "radiating ridges and shallow pointed teeth" recorded by Massy (*loc. cit.*) are not homologous with the teeth-like structures in *Luteuthis*. Additional characters

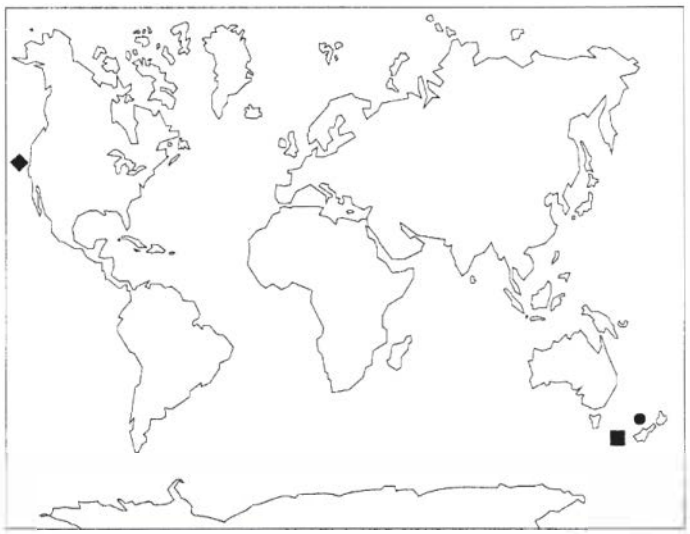


Figure 34. Recognised distribution of the genus *Luteuthis* (*sensu lato*).[1] ◆ *Grimpoteuthis tuftsi* Voss & Pearcy; ■ *Luteuthis* sp., gen. nov. (NMV F.74468); ● *Luteuthis dentatus* gen. et sp. nov (NMNZ M.131564).

[1] Inclusion of *Grimpoteuthis tuftsi* Voss & Pearcy, 1990.

described for *Cirroteuthopsis massayae* include about 80 suckers on the longest arms and cirri which do not exceed the diameter of the largest suckers (Massy *loc. cit.*); otherwise the inadequate description of this species precludes further evaluation of family placement.

Luteuthis dentatus sp. nov (Figs 36–38) (Table 23)

TYPE MATERIAL (1 specimen, male [M]): Holotype: NMNZ M.131564, M, ML *c.* 98 mm, 40°01.3' S, 167°49.9' E, 991 m, 29/07/1989, BT 6.9°C, f.v. *Oyang 86*, Trip 375, tow 16, coll. B. Connel.

REFERENCE MATERIAL: USNM 730714, Holotype, *Grimpoteuthis tuftsi* Voss & Pearcy, 1990, M, ML 101 mm, 45°05.2' N, 134°43.4' W, 3900 m, 09/10/1972, r.v. *Yaquina*; NMV F74468, *Luteuthis* sp., F, ML 400 mm (pre-fix), 54°48.0–38.0' S, 158 41.1–43.6' E, 979–870 m, f.v. *Austral Leader*, Haul 34, Voyage 1.

RECOGNISED DISTRIBUTION (Fig. 35, p. 52): Known only from type locality, 40°01.3' S, 167°49.9' E, 991 m.

DIAGNOSIS: Adult animal attaining moderate size, with pronounced anteroposterior elongation of cephalopedal mass. Fins large, broad, subterminal; mantle and nuchal constrictions poorly developed. Arms long; radular and palatine teeth present; digestive gland bilobed.

DESCRIPTION (external facies, Fig. 36): Animal of moderate size, ML to 98 mm, TL to 524 mm. Mantle saccular, width approximately two-thirds length (MWI 77%), anterior margin broadly rounded; head narrower than mantle, mantle and nuchal constrictions not apparent; eyes small, apertures large, laterally oriented, non-bulbous. One anterior and 5 interorbital to suborbital asymmetrically arranged knobs (resembling hardened wartlike blisters) present on dorsal surface of mantle. Pronounced surface wrinkling and large folds of skin over mantle, head, arms, and web indicate severe preservation shrinkage has occurred. Fins large, broad, subterminal, with inner and outer margins weakly convex; fin margins delicate; fin constricted basally proximal to attachment with head; muscular portion of fin extending about half fin length.

Mantle aperture reduced, fitting around base of funnel; mantle attached entirely to ventral surface of head. Funnel short, weak, attached entirely to ventral surface of head, little protruding through mantle aperture; funnel aperture barely reaching bases of arms 3 and 4. Funnel organ indistinct, scar indicates V-shaped single pad. Mantle cavity (Fig. 37A) with large 'halforange' gills, each with 7 large, loosely compacted, similar-sized lamellae. Penis freely projecting in mantle; interpallial septum thick, short, a membranous band attached lateral to accessory gland 2 and extending to ventral pallial musculature. Anus on erect portion of rectum.

Dorsal arms long, slender, arm length 75% TL; ventral arms short, arm length 38% TL; arm formula 1.2.3.4 or 1.2.4.3 (RHS, LHS respectively). Web single, damage precludes web depth or formula calculation. Cirri short, about 2% ML or 50% greatest sucker diameter; pimplelike vestiges of cirri apparent at level of 1st sucker on all arms, enlarged cirri first apparent at level of 4th, between suckers 4 and 5, 5 and 6, and 4 and 5 on arm pairs 1, 2, 3, and 4 respectively, attaining greatest length between suckers 9 and 10 on each arm; cirri present to the last sucker present on each arm; arm tips devoid of suckers (arm tips damaged?). First 3 suckers of moderate size, thereafter sucker diameter gradually increases, with similar-sized suckers present to midpoint of arms, thereafter suckers gradually decrease in diameter to arm tips. Suckers small, about 5% ML, with small suction chamber, well-developed muscular suction pad and wall ring, and sucker aperture with 10 well-developed, hardened, radiating processes (Fig. 37B). Suckers well spaced within remnant sections of web, invested into oral face of arms; along distal half of each arm suckers crowded with touching bases, and proud of arm surface; up to 58 suckers present along each arm, (arm tips damaged).

Dorsal and ventral surfaces of mantle, head, and arms 1–4 ground colour pale pinkish-red, with faint traces of darker red maculations; margin of eye, outer margin of fins and cirri, wine-red. Oral surface of arms and web slightly darker, purplish-red; suckers and sucker apertures pale yellow.

Shell (Figs 37C–D) light-honey coloured, translucent, flexible, surface texture highly irregular. Lateral wings well developed, with inrolled margins, distally tapering to fine tips. Saddle comprises thickened central portion and basal shelf; lateral wing margin expansions extending over saddle, meeting midpoint as small downward deflected prominence. Basal shelf platelike, deflected downward; wings diverge from basal shelf at about 35°.

Optic lobe large (Fig. 37E), spherical; optic nerve branching pattern symmetric; optic nerve single, thick, with multiple branches into back of eyeball; white body dark brown, doughnut-shaped, well separated across dorsal midline of head.

Male reproductive system (Fig. 38A) with moderate development of seminal vesicles 1–3 and accessory glands 1–3; accessory gland complex larger than seminal vesicle complex; accessory glands 2 and 3

dominate accessory complex, accessory gland 2 spherical, accessory gland 3 rectangular; seminal vesicle 3 and accessory gland 1 of similar granular consistency; accessory gland complex disposed in linear series 1–3. Penis well developed.

Alimentary canal (Fig. 38B) with disproportionately large buccal bulb; anterior and posterior salivary glands absent. Radula well developed (Fig. 38C); ribbon long, with about 70 transverse rows of well-developed teeth; across one transverse row 7 rows of homodont teeth positionally homologous to the central tooth, 2 lateral teeth, marginal tooth and marginal plate; individual teeth tall, narrow, with single cusp; teeth honey coloured and brittle; palatine teeth large, thorn-shaped, concentrated along inner margin of palp. Crop large, diverticulum absent; stomach and spiral caecum large, of similar size; stomach with single muscular chamber; spiral caecum well developed, volution incomplete; hepatic ducts two. Digestive gland bilobed; pancreas well developed. Intestine appreciably shorter than oesophagus; anal flaps absent.

Upper beak (Fig. 38D) tall (height 75% length); hood darkly pigmented, hood and lateral wall margins translucent; hood short (depth 59.7% beak length); jaw with single pronounced tooth; rostrum slightly deflected down, with rounded tip. Lateral walls almost parallel-sided, with square crest and weakly developed lateral wall fold. Lower beak (Fig. 38D) tall (height 75% width), darkly pigmented, with hood, lateral wall, and wing margins translucent; lateral wall with moderate notch and weakly convex crest; hood short (depth 32% beak length) weakly forward projecting; rostrum blunt; lateral wings very long (length 110% beak length), with 2 weak folds. Raw measures in Table 23.

ETYMOLOGY: Refers to the well-developed radular and palatine teeth.

REMARKS: Should *Grimpoteuthis tuftsi* Voss & Pearcy, be shown to be a species of *Luteuthis*, then the New Zealand form is distinguished from it by the shape of the beaks, radular dentition (possibly influenced by KOH dissolution, Voss & Pearcy 1990: 65), in having the cirri commence at the level of the suckers 1 and 2 (5–7 in *tuftsi*), general colouration of the body, arm length, and total arm sucker count.

The possession of palatine teeth on the inner surface of the labial palps, seven well-developed rows of teeth, and a bilobed digestive gland distinguish *Luteuthis dentatus* from all known cirrate octopus species.

Table 23. Raw measures of *Luteuthis dentatus* gen. et sp. nov. (* denotes damage).

	NMNZ M.131564
TL	524.0
ML	98.0
MW	76.0
PA	18.0
FunL	28.0
FL Out	80.0
FLIn	85.0
FW	42.8
EO	13.2
AL1R/L	392/360*
AL2R/L	334/385
AL3R/L	300/340
AL4R/L	201/362
ALFR	1.2.3.4
ALFL	1.2.4.3?
WDA	60
WDBR/L	*/60
WDCR/L	*/60
WDDR/L	40/69
WDE	34
WFR	*
WFL	D.A=B=C.E
ASC1R/L	58*/ 48*
ASC2R/L	54*/53*
ASC3R/L	42*/27*
ASC4R/L	45*/46*
CL1R	2.0
CL2R	2.1
CL3R	2.0
CL4R	1.9
ASn1R/L	5.0/4.1
ASn2R/L	4.0/4.1
ASn3R/L	4.0/4.1
ASn4R/L	4.0/4.0
GiLC	7

Family **CIRROTEUTHIDIDAE** Keferstein, 1866

Fins long, subterminal; anteroposterior elongation of cephalopedal mass pronounced; tissues gelatinous; arms long and slender; web deep; secondary web present. Cirri commence between suckers 3 and 5, extending to or almost to arm tip; cirri extremely long, length about 25–60% ML or ten times that of enlarged sucker diameter; suckers modified in central portion of each arm. Shell complex, with two lobe-like, deeply excavate flared wings. Anterior salivary glands present; radular and palatine teeth absent; intestine of equivalent length to oesophagus; digestive gland entire (not bilobed). Optic lobe large,

Figure 36. ***Luteuthis dentatus*** gen. et sp. nov.: Holotype, NMNZ M.131564, male, ML about 98 mm.

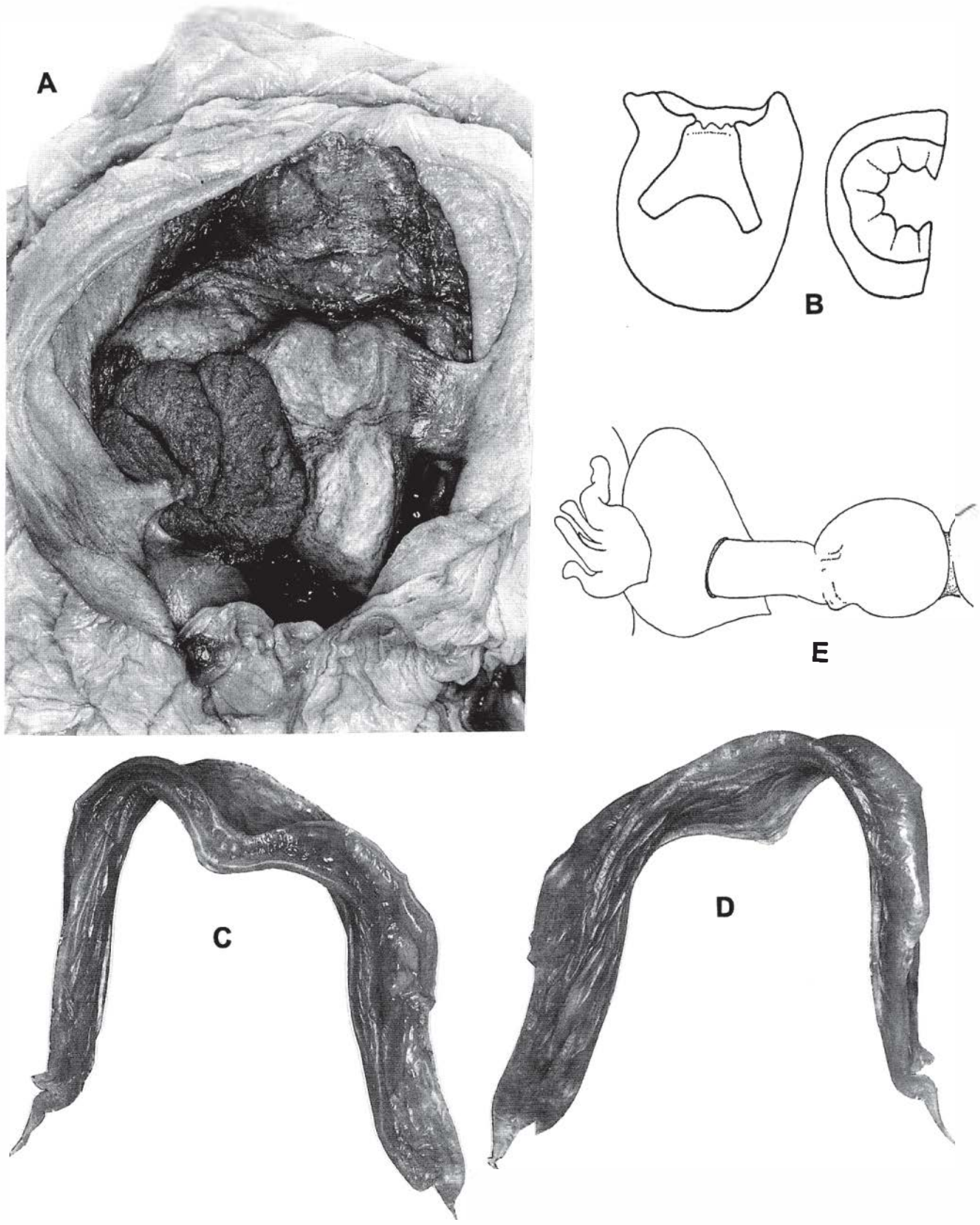


Figure 37. ***Luteuthis dentatus*** gen. et sp. nov.: Holotype, NMNZ M.131564, male, ML about 98 mm. **A**, mantle cavity; **B**, sucker morphology (section). **C, D**, shell, dorsal and ventral perspectives. **E**, left optic lobe.

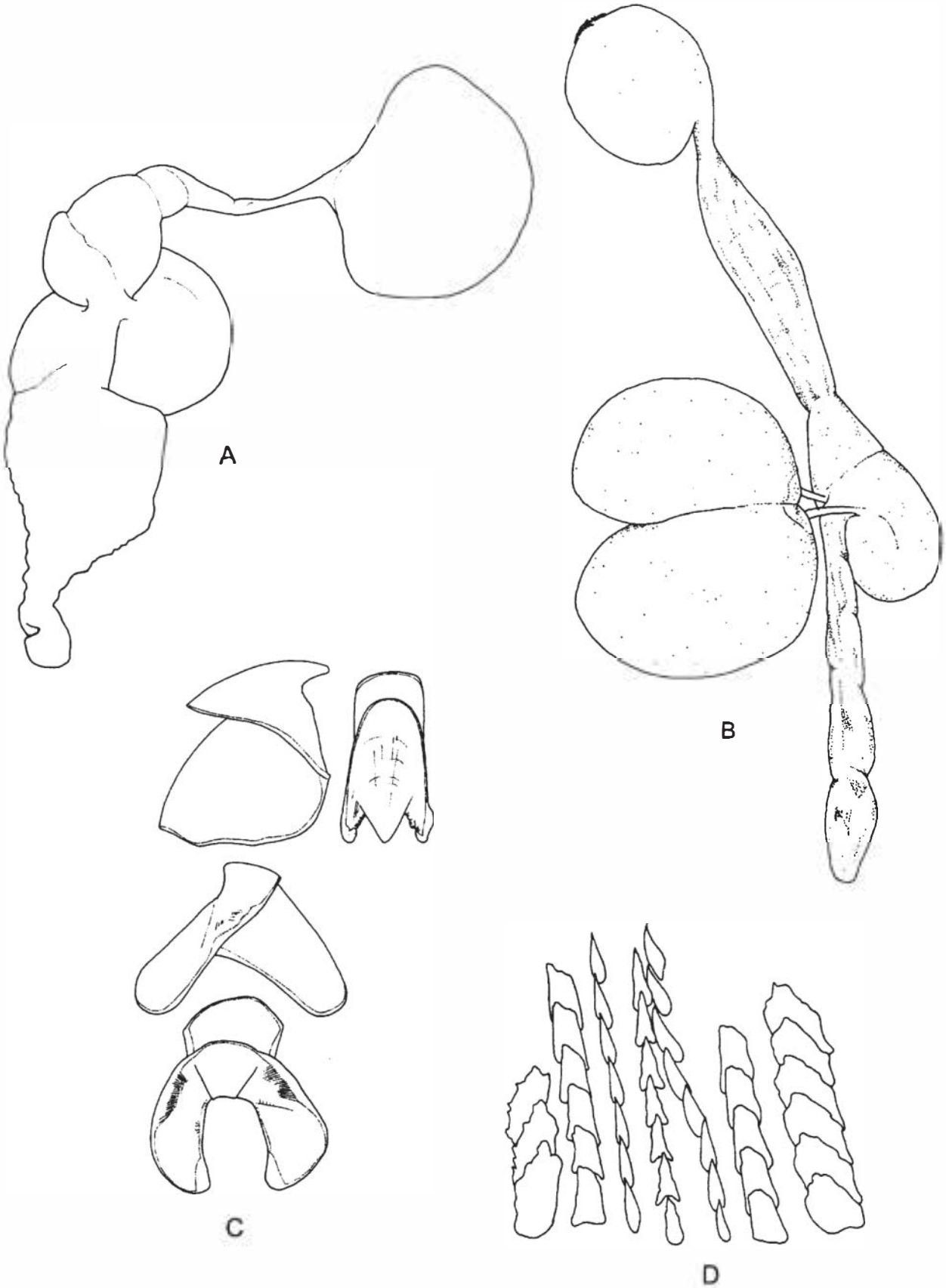


Figure 38. ***Luteuthis dentatus*** gen. et sp. nov. Holotype, NMNZ M.131564, male, ML about 98 mm. **A**, male reproductive system. **B**, alimentary canal. **C**, beaks. **D**, radula.

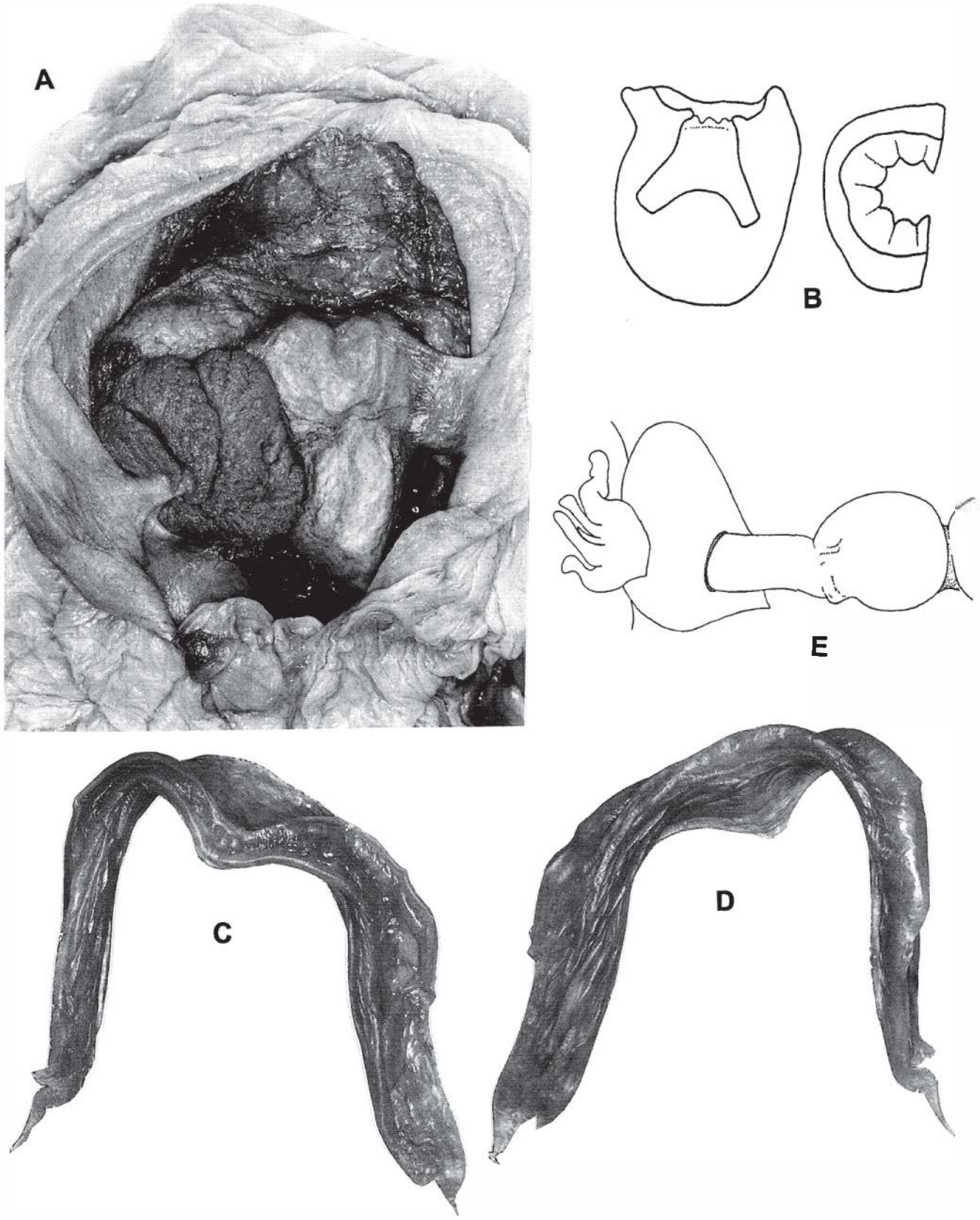


Figure 37. ***Luteuthis dentatus*** gen. et sp. nov.: Holotype, NMNZ M.131564, male, ML about 98 mm. **A**, mantle cavity; **B**, sucker morphology (section). **C, D**, shell, dorsal and ventral perspectives. **E**, left optic lobe.

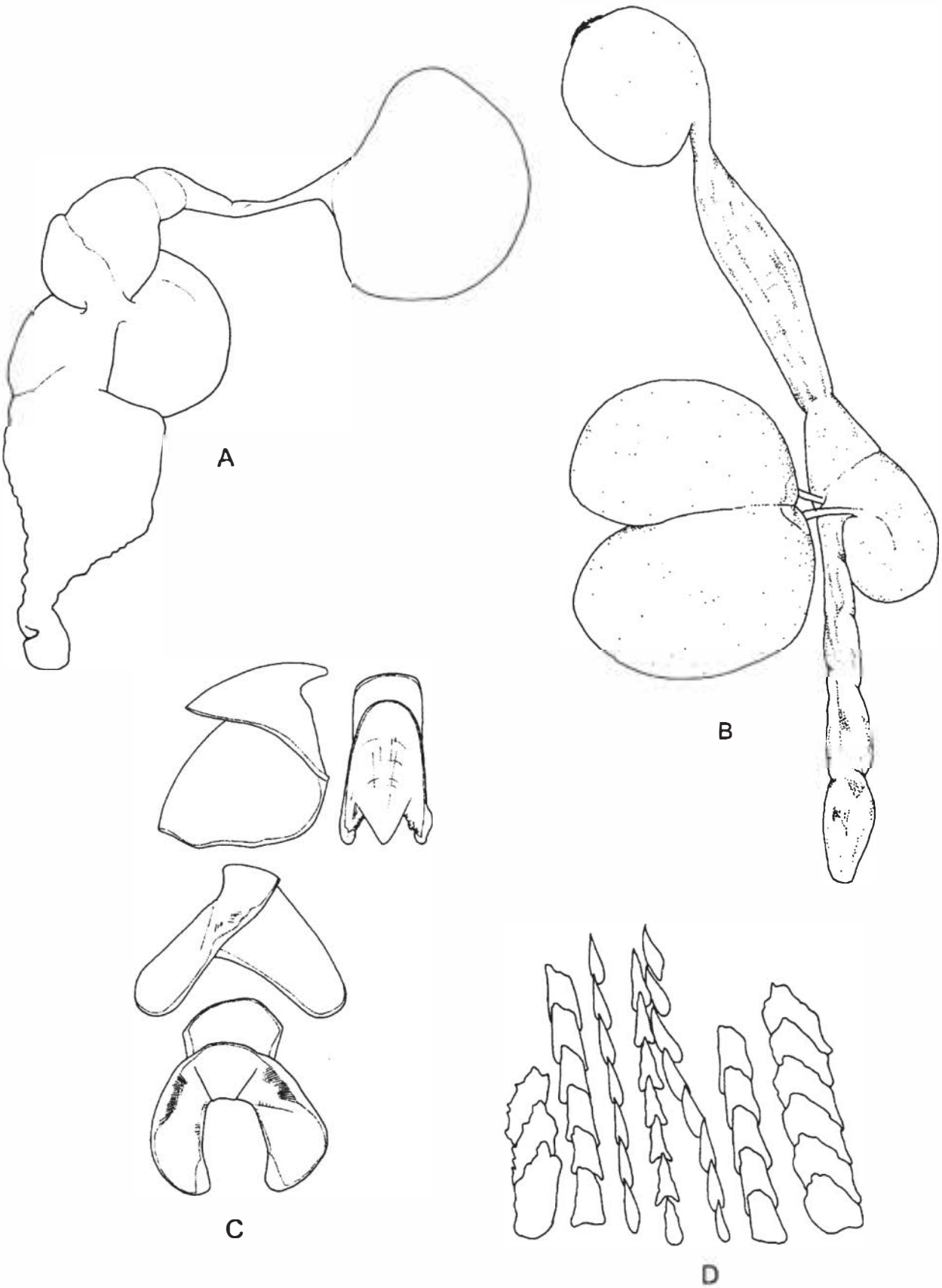


Figure 38. ***Luteuthis dentatus*** gen. et sp. nov. Holotype, NMNZ M.131564, male, ML about 98 mm. **A**, male reproductive system. **B**, alimentary canal. **C**, beaks. **D**, radula.

spherical; branching pattern between right and left orbits symmetric; optic nerve single. Male accessory glands 2 and 3 dominate accessory gland complex, gland 2 spherical, with many lobes; penis poorly developed.

REMARKS: The family Cirroteuthididae (of Voss 1988a) contains two recognised genera, *Cirroteuthis* Eschricht, 1836, and *Cirrothauma* Chun, 1913, both previously considered monotypic. Evidentally North Atlantic specimens attributed to *Cirroteuthis muelleri* Eschricht (Voss 1988b; Voss & Pearcy 1991) lack an intermediate web (Nesis pers. comm.), while the North Pacific and New Zealand specimens have one. Obviously two or more species exist in this group, but given the northernmost Atlantic (off Greenland) type locality of *Cirroteuthis muelleri*, doubt is cast on identifications of both North and South Pacific *Cirroteuthis*.

Cirroteuthis Eschricht, 1836

TYPE SPECIES: *Cirroteuthis muelleri* Eschricht, 1836.

DIAGNOSIS: With characters of the family: shell with narrow longitudinally oriented saddle and ovoid, rapidly expanding lateral wings.

Cirroteuthis cf. *muelleri* Eschricht, 1836.

(Figs 41, 42)
(Table 24)

MATERIAL EXAMINED (1 specimen, female [F]): NMNZ M.109379, F, ML 36.0 mm, FPT, 42°36.79' S, 176°09.81' W, 1999–2002 m, 02/03/1992, f.r.v. *Tangaroa*.

Figure 39. Recognised distribution of genus *Cirroteuthis* (*sensu stricto*). ● *Cirroteuthis muelleri* Eschricht (*fide* Voss 1988b); o *Cirroteuthis* cf. *muelleri* Eschricht.

RECOGNISED DISTRIBUTION (Fig. 40, p. 52): Off the Chatham Rise, New Zealand, 1999–2002 m.

DIAGNOSIS: A specimen of small size (immature), with pronounced anteroposterior elongation of cephalopedal mass (bell-shaped). Fins large, paddlelike; radula absent; mantle and nuchal constrictions absent; arms long, deeply invested in web; web deep; intermediate web present. Shell saddle-shaped; cirri very long; suckers in central portion of arms appear borne on stalks.

DESCRIPTION (external facies, Fig. 41): Specimen of small size (immature), ML 36 mm, TL 147 mm. Mantle, head, arms and web gelatinous; cephalopedal mass anteroposteriorly elongate, slender, bell-shaped. Mantle and head distinct from brachial region. Head narrower than mantle; eyes small, projecting forward (possibly collection damage or preservation artefact), lateral in orientation (between arm bases 2 and 3). Fins massive, highly muscular, long (FLI 150), narrow (FWI 27), paddlelike; outer fin margin straight, inner margin weakly convex, distal margin of fin membranous, broadly rounded; basal constriction at junction with mantle not apparent; muscular portion of exposed fin extending about 60% fin length.

Mantle aperture reduced, enveloping base of funnel; mantle attached entirely to ventral surface of head; funnel long (50% ML), attached entirely to ventral surface of head, free portion very long, tubular (FFI 86% funnel length), extending to base of arms 4 to level equivalent to 5th adoral sucker, though barely reaching web sector D between bases of arms 3 and 4. Funnel organ indistinct; olfactory organ minute, ovoid, positioned either side of funnel at corners of mantle aperture. Mantle cavity (Fig. 42A) with long, thin interpallial septum attached to viscera lateral to genital aperture, extending directly to ventral, inner surface of pallial musculature. Gills sepioid, with 7 outer and 7 inner lamellae; innermost and outermost reduced in size, with terminal 3 filaments on either side with common arterial base, slightly reduced in size relative to adjacent lamellae.

Arm formula 1.2 = 3.4 (RHS), 3.1.2.4 (LHS); arms long, slender, longest arm length 80% TL or 325% ML. Intermediate web present. Primary web delicate, extends almost to arm tips in both dorsal and ventral sectors; web formula D.C.E.A.B (RHS), E.C.A.D.B (LHS); web moderately deep, deepest web sector 41% longest arm length, 63% shortest arm length; shallowest web sector 15% longest arm length, 22% shortest arm length; web nodules not apparent. Cirri exceedingly long, about 25% ML or 9 times longer than the greatest sucker diameter; small but well-developed cirri commence on all arms between suckers 2 and 3, with length gradually increasing to suckers 7 and 8, thereafter length abruptly increases to at least the 22nd sucker along each arm, then decrease to arm tip; cirri extend almost to arm tip as extremely small vestiges. Suckers small (ASIn 2.7% ML); ASC low, 33–39; suckers not extending to distal filamentous extremities of arm; first 7 suckers of similar small size, with normal sucker pad, sucker aperture and urnlike structure; following 4 suckers (suckers 8–11) almost vestigial, without apparent sucker pore or suction chamber; thereafter 12 or 13 suckers appear borne on short pedestals, with both suctorial chamber and sucker aperture poorly developed; 8 normal urnlike suckers follow, the proximal 6 the largest, with sucker pore and very small suction chamber, well-developed muscular suction pad and poorly developed wall ring and sucker aperture, the latter lacking a grasping ring (Fig. 42B). First 4 to 5 suckers well spaced, about 2 sucker diameters between adjacent suckers; suckers 6–22 well separated along the arm, with about 5 sucker diameters between adjacent suckers, the distal 8 urnlike suckers are closely spaced, their bases touching.

Dorsal and ventral surfaces of mantle and head and ventral surface of fins rose pink; skin over dorsal surfaces of fins abraded. Lateral surfaces of arms 1–4 translucent yellowish, oral surface of arms, cirri, adoral and aboral surfaces of primary web, and intermediate web maroon to purple; sucker apertures pale yellow.

Optic lobe (Fig. 42C) large, spherical; optic nerve branching pattern symmetric, optic nerve single. White body spherical, tan coloured; bodies well separated across dorsal midline of head; white body of equivalent size to eyeball.

Shell (Figs 42D–E) with very narrow longitudinal (rather than transverse) saddle with deep, narrow longitudinal excavation, 2 rapidly expanding laterally oriented wings with broadly rounded extremities, and a wide, thick basal shelf. Muscle insertion points difficult to interpret. The wings diverge from saddle at an angle about 30°; the overall shell vacuolated, of a yellowish hue, quite translucent and flexible, not easily fragmented; the overall surface texture is irregular.

Alimentary canal (Fig. 42F) with large buccal bulb; anterior salivary glands large; radular and palatine teeth absent. Anterior oesophagus short (23% total crop length). Crop large, thin walled, diverticulum absent, reaching greatest dilatation about midoesophagus. Stomach with external demarcation, divided into thick muscular basal and thin walled outer section, with continuous lumen. Caecum large, of equivalent size to stomach, without spiral coiling. Intestine short, of equivalent length to oesophagus, thin walled, distended for distal half; anal flaps absent; digestive gland ovoid, entire; pancreas well developed.

Upper beak (Figs 42G) tall (height 86% length), with darkly pigmented hood; lateral wall, hood and wing margins translucent; hood moderately deep (depth 68% beak length); jaw without teeth; rostrum weakly deflected down, sharp pointed. Lateral walls broadly convex, with broadly rounded crest; lateral wall fold weak. Lower beak (Figs 42G) moderately tall (height 64% width); hood proximal to rostrum and lateral margins dark pigmented; outer wings and rear wall margins light pigmented; hood posterior notch deep. Lateral wall with pronounced broadly concave basal notch; crest broadly rounded. Hood shallow (50% lower beak length) forward projecting; rostrum acutely pointed; lateral wings long (100% lower beak length), with 2 weak folds.

Raw measures in Table 24.

REMARKS: The shell is most similar to that described and illustrated for *Cirroteuthis muelleri* (*fide* Voss & Pearcy 1990: 54, figs 2d–h). Arm sucker counts (33–39) for the New Zealand female are considerably higher than those of *C. muelleri* Eschricht, (about 28, *fide* Voss & Pearcy 1990). Of those specimens described by Voss and Pearcy (*loc. cit.*), ML varied between 40 and 79 mm — larger than the New Zealand female (ML 36.0 mm). Moreover, the specimen described by Voss and Pearcy (1990: 53, ref. Fig 3A and text) appears to have been the largest specimen available, a male of ML 79 mm. Since arm sucker counts as a rule increase with mantle length, the small New Zealand female might be expected to have a lower ASC than the mature specimens described by Voss and Pearcy. This is not the case. Although the New Zealand species is most likely distinct from *C. muelleri*, description of it should await the collection of additional comparative material.

The female reproductive system of this species is quite immature, indicating the animal probably attains a size far greater than that presently recorded.

Figure 41. ***Cirroteuthis*** cf. ***muelleri*** Eschricht, 1836. NMNZ M.109379, female, ML 36.0 mm.

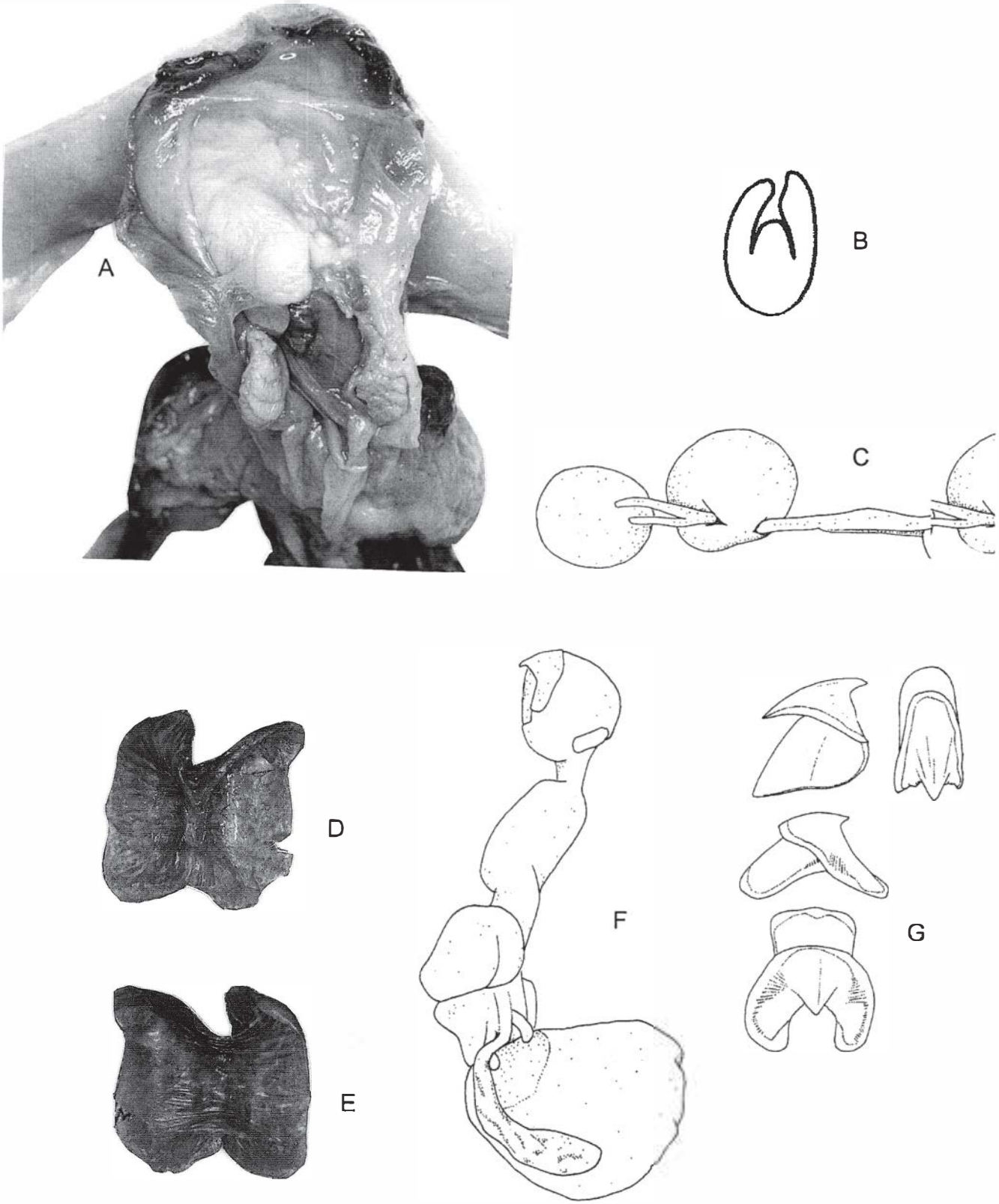


Figure 42. ***Cirroteuthis*** cf. ***muelleri***. NMNZ M.109379, female, ML 36.0 mm. **A**, mantle cavity. **B**, sucker morphology, distal urn-shaped sucker (section). **C**, optic lobe. **D**, **E**, shell, dorsal and ventral perspectives. **F**, alimentary canal. **G**, beaks.

Table 24. Raw measures for *Cirroteuthis* cf. *muelleri*.

	NMNZ M.109379
TL	147
ML	36
MW	21.5
HdW	19.6
HdL	8.5
ED	6.5
FunL	18.5
FFl	16.0
FiL Out	54.5
FiW	14.8
ALIR/L	85/112
AL2R/L	76/93
AL3R/L	103/100
AL4R/L	117/85
AFR	1.2=3.4
AFL	3.1.2.4
CiL1R	7.0
CiL2R	9.0
CiL3R	8.0
CiL4R	9.0
ASC1L	38
ASC2L	39
ASC3L	33
ASC4L	33
ASn1R	1.0
ASn2R	1.0
ASn3R	1.0
ASn4R	1.0
WDA	28
WDBR/L	17/21
WDCR/L	46/32
WDDR/L	48/27
WDE	35
WFR	D.C.E.A.B
WFL	E.C.A.D.B
GiIL	7/7

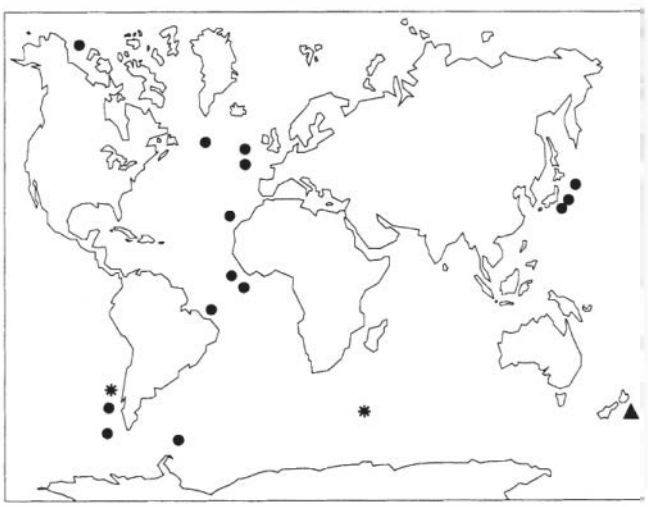


Figure 43. Recognised distribution of *Cirothauma* (s.l.) (modified from Voss 1988b). ● *Cirrothauma murrayi*; ✳ *'Cirroteuthis' magna* Hoyle; ▲*Cirrothauma* cf. *magna* Hoyle.

Cirrothauma Chun, 1911

TYPE SPECIES: *Cirrothauma murrayi* Chun, 1911

DIAGNOSIS: With characters of the family: shell with wide transverse-oriented saddle and rapidly expanding triangular-shaped lateral wings.

REMARKS: The genus *Cirrothauma* was previously considered monotypic, the sole recognised species being *Cirrothauma murrayi* Chun. As the shell of the New Zealand species differs in no substantial way from that depicted for *C. murrayi* (*fide* Aldred *et al.* 1983: 11, figs 9a–d), the New Zealand form is placed in this genus. *Cirrothauma murrayi* possesses vestigial eyes and total arm-sucker counts of 36 (*fide* Chun 1913; *c.* 36, Aldred *et al.* 1983: specimen A). The New Zealand species attributed to this genus differs, however, by possessing large eyes and in having an ASC to 99, characters similar to those described for *Cirroteuthis magna* Hoyle, 1885 (also with similar sucker type, count and distribution along the arms, body facies, and shell). Accordingly, the poorly known *Cirroteuthis magna* Hoyle is provisionally transferred to the genus *Cirrothauma*, although neither *Cirrothauma magna* (Hoyle), nor *Cirrothauma* cf. *Cirroteuthis magna* Hoyle in fact may be *Cirrothauma sensu stricto*. Despite the extensive geographic distribution attributed to *Cirrothauma murrayi* (*fide* Voss 1988b), few specimens have been critically examined and the systematic status of the majority of them is uncertain.

Cirrothauma cf. *magna* (Hoyle, 1885)

(Figs 44-46)

MATERIAL EXAMINED (1 specimen, male [M]): NMNZ M.102591, M, ML 118.0 mm, 39°58.27' S, 178°01.81' E, 1450–1468 m, 05/10/1990, f.v. *Cordella* Stn C02 9003/86.

RECOGNISED DISTRIBUTION (Fig. 44, p. 69): Off the Wairarapa coast, North Island, New Zealand.

DIAGNOSIS: Adult animal attaining large size, with pronounced anteroposterior elongation of cephalopedal mass (bell-shaped). Fins large, paddlelike; radula absent; mantle and nuchal constrictions poorly developed; arms long; web unknown; suckers in male enlarged in both proximal and distal fields, cirri of great length. Shell saddle-shaped.

DESCRIPTION (external facies, Fig. 45): Large-bodied species, ML to 118 mm, TL to 884 mm. Mantle, head and web extensively gelatinous; arms semi-gelatinous; cephalopedal mass anteroposteriorly elongate. Mantle and head distinct from brachial region; head wider than mantle; eyes very large, lateral (between arm bases 2 and 3), bulbous. Fins long, 80% ML, broad, fin width 71% of outer fin length, subterminal, laterally oriented, deeply invested in mantle tissues, paddlelike; inner and outer fin margins with parallel to weakly convex sides, tapering to broadly rounded points, margins membranous; basal constriction at junction with mantle poorly developed; muscular portion of exposed fin extending about half fin length.

Mantle aperture reduced, enveloping base of funnel; mantle attached entirely to ventral surface of head; funnel of moderate length, 45% ML, almost entirely attached to ventral surface of head, with short free-funnel portion; funnel aperture not reaching base of arms 3 or 4. Funnel organ indistinct. Interpallial septum appears to have been a long, thin riblet of tissue attached lateral to male genital aperture and extending directly to ventral mantle musculature. Gills semi-sepioid, with 10 loosely compacted lamellae; inner-most and outermost reduced in size, with lamellae 4–7 with common arterial base, slightly reduced in size relative to adjacent lamellae.

Arm formula cannot be calculated owing to incompleteness of specimen; arms long, slender, longest arm length 82% TL or 614% ML. No strengthening web nodules detected along ventral face of arms in remnant web sectors. Web appears to have been extremely deep and thin, extending to arm tip along ventral surface of arms; web depth at midweb sector cannot be calculated for any sector. Cirri extremely long, about 58% ML, or about 10 times longer than the greatest enlarged sucker width; first apparent cirri commence between suckers 4 and 5 on arm pair 4, suckers 3 and 4 on arms 3, 2, and 1, gradually increasing in length to suckers 18–20, thereafter abruptly increasing in length to suckers 30–32, then becoming vestigial, extending to or almost to arm tips. Suckers extend to each arm tip, intact ASC to 99. First 11 suckers of small size, gradually increasing in diameter to 11–13th sucker; thereafter about 20 suckers abruptly enlarge on all arms, suckers small (ASIn 5.9% ML), with poor muscular development, wide sucker aperture, minute sucker pore and no apparent sucker chamber; similar large sized but different sucker type commences at level of 30–32nd sucker along each arm, suckers secondarily assume muscular vase-shaped structure, becoming closely spaced with crowded bases; thereafter sucker size gradually decreases towards arm tips. Secondarily modified suckers (Fig. 46A) with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, large grasping ring, and moderately wide simple sucker aperture. First 11 or 12 suckers closely spaced, not crowded; subsequently about 20 suckers are well separated along each arm, in some instances with distances of about 2 cm between successive suckers; thereafter about 70 suckers are closely spaced to the arm tip.

Dorsal and ventral surfaces of mantle, head, fins and outer surface of arms rose pink; posterior margin of fins dark red. Adoral surface of arms 1–4 and web sectors A–E maroon to purple; cirri dark red; modified suckers and sucker apertures within web, pale yellow; distal enlarged suckers light pink to white, with dark red sucker rims.

Shell (Fig. 46B) complex, vacuolated, dirty honey coloured, translucent and flexible, not easily fragmented; surface texture irregular, with numerous pits, folds, and bumps. Saddle well developed; lateral wings enormously developed, widely flaring, lateral profile triangular; basal shelf thick; muscle insertion points poorly defined, probably marked by deep cavernlike recess in wing bases; lateral wings diverge from saddle at about 60° angle.

Optic lobe (Fig. 46C) large, spherical; optic nerve branching pattern symmetric; optic nerve single, undergoing considerable branching into rear of eyeball; white body small, disc-shaped, well separated across dorsal midline of head, light brown to purple.

Male seemingly immature; reproductive system (Fig. 46D) with large testis sac, poorly differentiated seminal vesicle complex, and 2 large accessory gland structures. Accessory gland complex dissimilar to all other cirrates thus far examined, with 2 glands folded over on themselves; penis massively developed. Complex of accessory gland structures appreciably larger than seminal vesicle complex; accessory gland complex size about 33% that of testis sac.

Alimentary canal (Fig. 46E) with large buccal bulb and anterior salivary glands; radular and palatine teeth absent. Anterior oesophagus long (32% total crop and oesophagus length), narrow. Crop large, diverticulum absent, reaching greatest dilation at midoesophagus; stomach with single external demarcation, divided into thick muscular basal and thin-walled outer section, its lumen continuous. Caecum massive, about 30% larger than stomach, without

spiral coiling. Intestine short, length that of oesophagus, thin walled, distended for entire length, particularly distal half; anal flaps absent. Digestive gland kidney-shaped, entire; pancreas well developed.

Upper beak (Fig. 46F) tall (height 74% length), with dark pigmented hood, with fine translucent hood, lateral wall, and wing margins; hood moderately deep (depth 62% beak length), with single broad pronounced tooth in jaw; rostrum weakly deflected down, acute angled and sharp pointed. Lateral walls narrow, parallel sided, with rounded crest and moderate lateral wall fold. Lower beak (Fig. 46F) moderately tall (height 63% width), darkly pigmented, with translucent hood, lateral wall, and wing margins. Lateral wall without basal notch but with acute convex crest. Hood short (depth 44% beak length) projecting forward; rostrum pointed; hood with well developed broadly concave posterior notch; lateral wings long (length 100% beak length), with 2 weak folds.

Raw measures in Table 25.

REMARKS: The shell is most similar to that of *Cirrothauma murrayi* in the position of the muscle insertion points, its narrow transversely oriented saddle with concave outer channel, and broad, thickened basal shelf. The shell is not typical of *Cirroteuthis*, although shell shape for both is conventionally referred to as 'saddle-shaped' (Voss 1988a, b). The shell of *Cirrothauma* seems to be derived from some V- or U-shaped structure in which the lateral wings have become inordinately large and flared outwards, and in which a deep cavernlike recess has developed at the base of the saddle — quite unlike that of *Cirroteuthis* with its longitudinally oriented saddle.

Although both *Cirroteuthis* and *Cirrothauma* species have similar crop morphology, oesophagus, and intestine relative lengths, these characters are shared also with *Grimpoteuthis* and *Luteuthis*. The comparable size of the spiral caecum and stomach, and presence of anterior salivary glands (or their positional homologue) are the two most obvious characters shared between *Cirroteuthis* and *Cirrothauma* that are not present in either of the other genera. The systematic position of *Cirrothauma* (if the New Zealand species really belongs there) is problematic. Restraint is exercised in describing the single damaged specimen as a new species since its condition precludes description of web depth, formula, presence or absence of web nodules, arm formula, and female reproductive system.

Although the arms appear exceedingly long in *Cirrothauma* sp., at about 80% they are no longer than those described for the three species of *Opisthoteuthis* herein (to about 87% TL) — for which the arms appear exceedingly short. It is the pronounced anteroposterior elongation of the cephalopedal mass in *Cirrothauma*, as in *Luteuthis*, which gives the appear-ance of the arms being longer relative to the mantle length than actually is the case.

Table 25. Raw measures *Cirrothauma* sp. (* denotes damage).

	NMNZ M.102591
TL	884
ML	118
MW	95
FunL	53
FL outer	95
FL Inner	96
FW	57
ED	46
AL1R/L	33*/75*
AL2R/L	400*/52*
AL3R/L/	724/617*
AL4R/L	525*/705
ASC2R	30*
ASC3R/L	95/49*
ASC4L	99
CL2R	68
CL3R	69
CL4L	65
ASn2R	7.0
ASn3R/L	6.0/7.0
ASn3L	7.0
ASn4L	7.0
GiLC	10

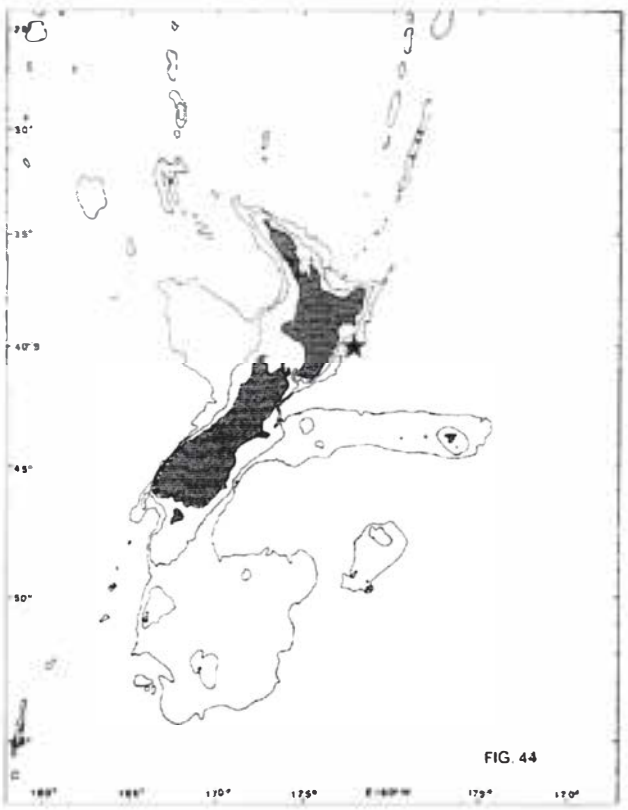
Suborder INCIRRATA Grimpe, 1916

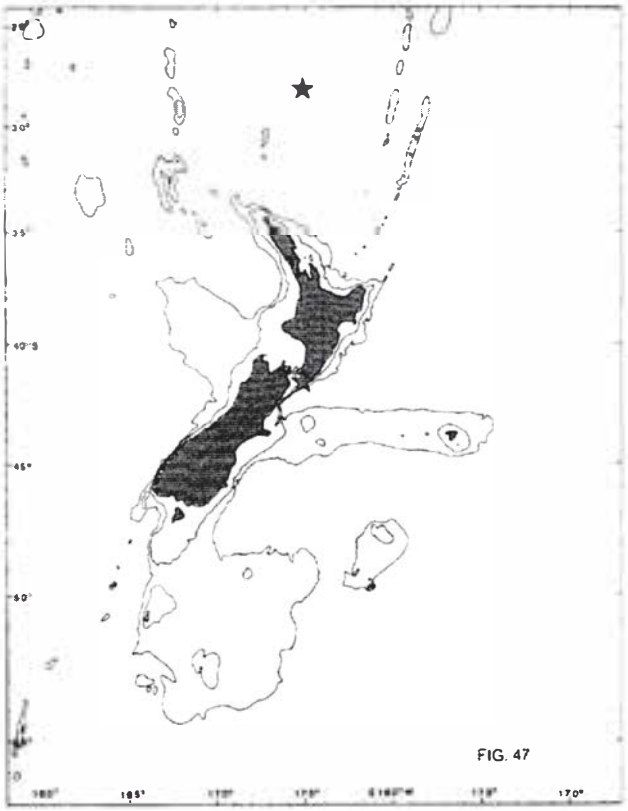
Family **BOLITAENIDAE** Chun, 1911

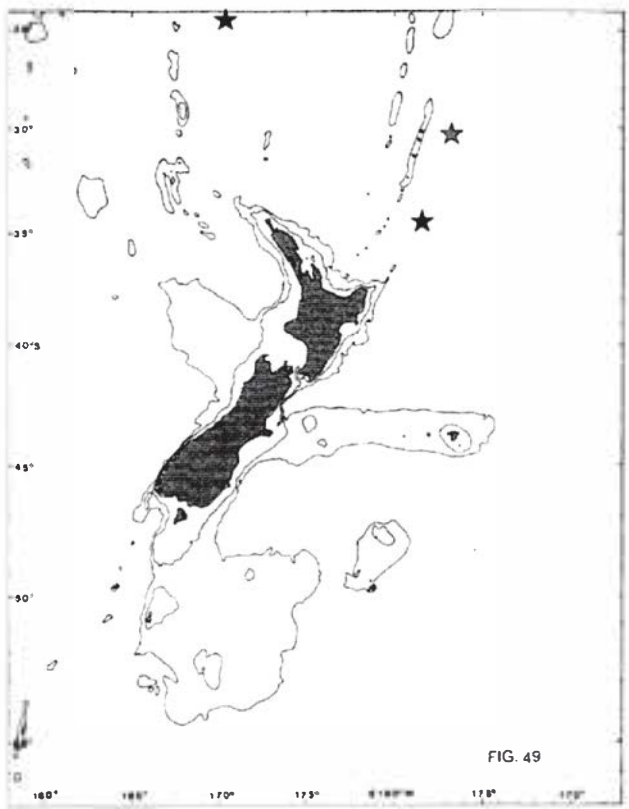
Mantle gelatinous, often with thick, jelly-like outer coating; mantle aperture single, wide; web deep on all arms; digestive gland large, elongate-ovoid; eyes medium sized, elliptical, directed laterally; hectocotylisation involves enlargement of suckers on 3rd right or left arm, arm not detachable; shell vestige absent; funnel organ inverted V; circumoral light organ present in mature females (after Hochberg *et al.* 1992: 289).

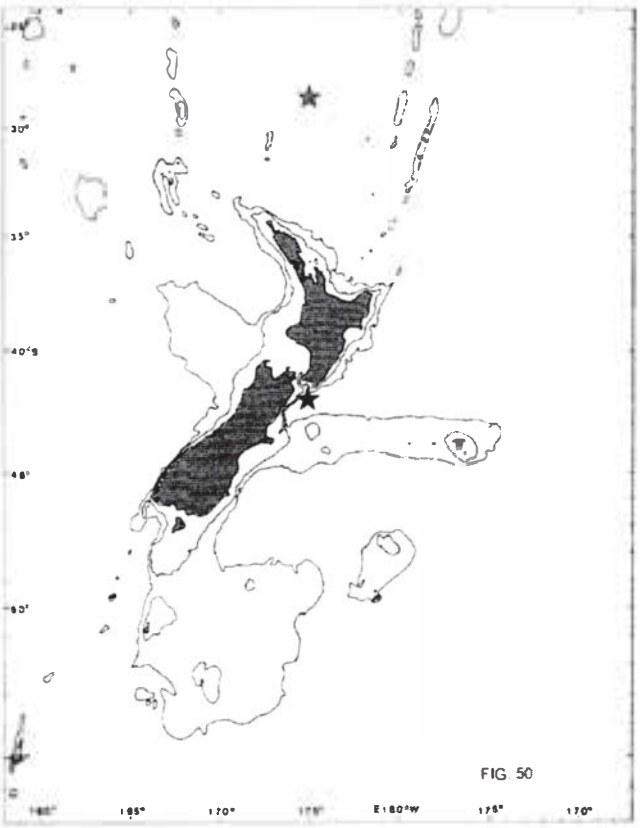
Bolitaena Steenstrup, 1859

TYPE SPECIES: *Bolitaena microtyla* Steenstrup, 1859









Recognised distribution. **Fig. 44**, *Cirrothauma* cf. *Cirroteuthis magna* Hoyle, 1885. **Fig. 47**, *Bolitaena microtyla* Steenstrup, 1859: * new records. **Fig. 49,** *Japetella diaphana* Hoyle, 1885: ⋆ new records; * after Thore (1949). **Fig. 50,** *Eledonella pygmaea* Verrill, 1884: ⋆ new records; * after Thore (1949).

Figure 45. ***Cirrothauma*** cf. ***Cirroteuthis magna*** Hoyle, 1885: NMNZ M.102591, male, ML 118.0 mm.

DIAGNOSIS: Gelatinous animals with long optic nerve, with peduncular ganglion close to optic ganglion.

Bolitaena microtyla Steenstrup *in* Hoyle, 1886
(Fig. 48)
(Tables 26, 27)

Given uncertainty in the systematic status of this

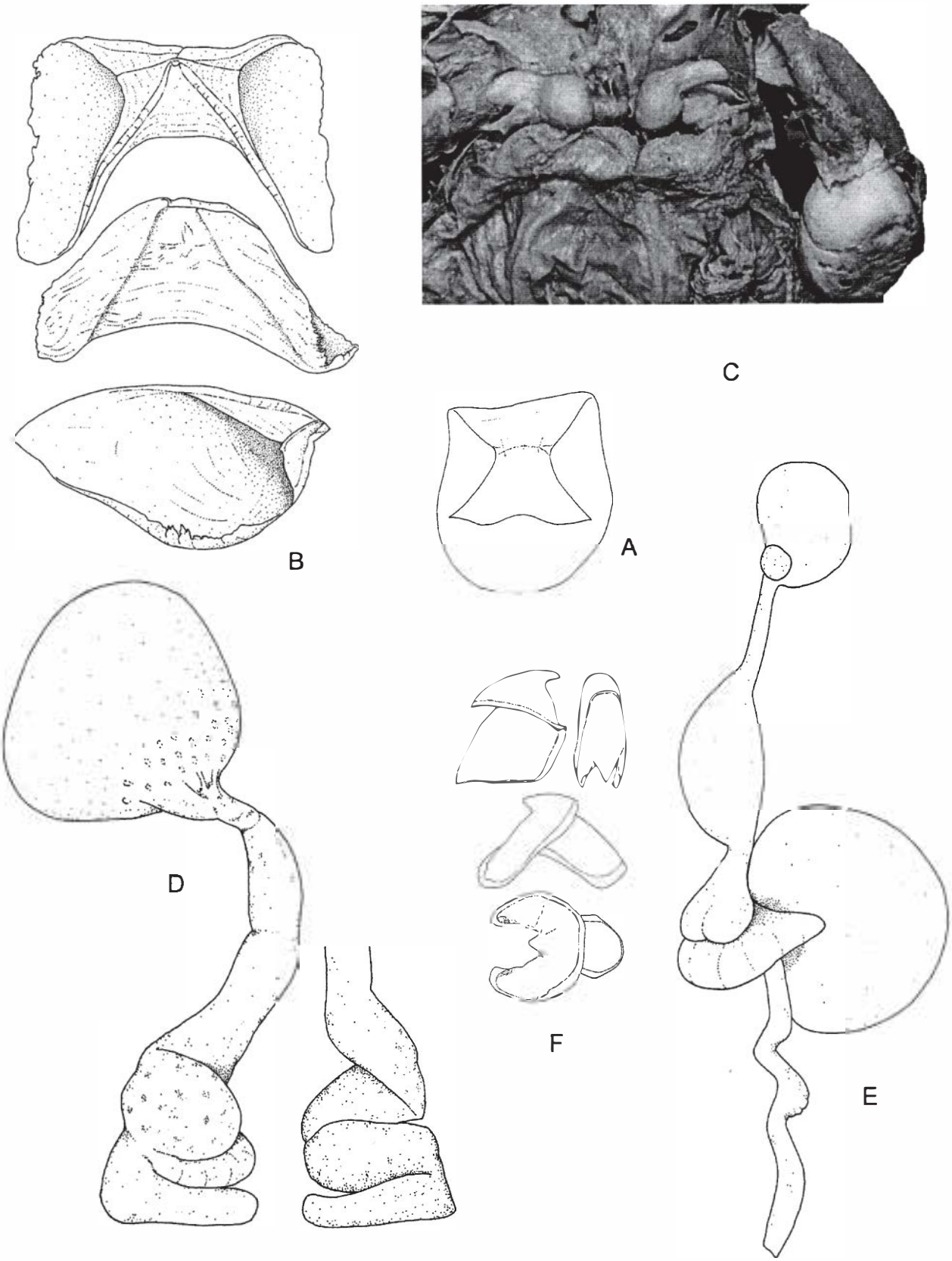


Figure 46. ***Cirrothauma*** cf. ***magna***, Hoyle, 1885. NMNZ M.102591, male, ML 118.0 mm: **A**, sucker morphology (section). **B**, shell, dorsal, posterior and lateral perspectives. **C**, optic lobes. **D**, male reproductive system. **E**, alimentary canal. **F**, beaks.

species, a New Zealand synonymy only is provided:

Eledonella pygmaea (not Verrill, 1884): Dell 1959b: 2; Spencer & Willan 1995: 52 (*partim, fide* Dell).

MATERIAL EXAMINED (5 specimens, 1 male [M], 4 female [F]): NMNZ M.120135, M, ML 27.0 mm, F, ML 16.8 mm, 22°41.5' S, 175°02.0' W, 944 m, 12/12/1979, f.r.v. *James Cook* Stn J17/57/76; NMNZ M.120115, F, ML 17.0 mm, 28°13.2' S, 174°56' E, 1064 m over depths to 5000 m, 14/12/1976, f.r.v. *James Cook* Stn J17/70/76; NMNZ M.74193, F, ML 18.5 mm, AUZ 47 07 (exact co-ordinates not available); NMNZ M.12953, F, ML 14.0 mm, 41°47' S, 175°02' E, VUZ 85, South of Cape Palliser, 1200 m over depths to *c.* 1600 m, 19/04/1957.

RECOGNISED DISTRIBUTION (Fig. 47, p. 69): 22°41.5–41°47' S, 174°56' E–175°02.0' W, 0–822 m to 1200 m (New Zealand) over up to 5000 m. Otherwise tropical–subtropical cosmopolitan bathypelagic species, juveniles also found in epipelagic and mesopelagic zones (Nesis 1987: 289).

DIAGNOSIS: With characters of the genus.

DESCRIPTION (Fig. 48 A–B): Mantle ovoid, thin walled, gelatinous. Large female tan coloured over dorsal, ventral, and oral surfaces of mantle, head, and arms. Head narrow, separated from mantle by weak constriction; dorsal head musculature weakly developed. Mantle aperture single, extensive; mantle attached to head superior to eyes. Funnel long, fused for greatest length to ventral surface of head and arm bases 4, free portion short; funnel organ large, thick limbed, V-shaped, with limbs diverging at 90° angle. Eyes large, spherical, well separated across dorsal midline of head, ventrolaterally oriented, with well-developed lens.

Arms very short, longest arm length about 34–38% TL, shortest arm length about 23–31% TL; arms thick, tubelike, tapering rapidly to blunt points; arm formula 3.4.2.1, with arms 1, 2 and 4 of subequal length, and arm pair 3 much elongated. Web deep, sectors subequal, deepest sector about 43–46% longest arm, about 51–73% shortest arm, shallowest web sector 29–38% longest arm, 45–49% shortest arm; web thin, translucent and delicate, not extending along dorso- or ventrolateral surfaces of arms; web formula variable. Suckers uniserial, ASC low (to 14); suckers present to arm tips, suckers regularly and closely spaced within web sectors, proud of arm surface; with 3 or 4 suckers from base of each arm to web margin. First 4 or 5 suckers on all arms of similar size (ASIn 5.5–5.7% ML), thereafter suckers gradually decrease in diameter to arm tips; no suckers abruptly enlarged. Suckers (Fig. 48C) with large suction chamber, weak muscular suction pad, and with sucker base narrower than aperture; wall ring and sucker aperture simple; with marked constriction between sucker chamber and grasping ring.

Optic nerve long, with peduncular ganglion close to optic ganglion.

Beaks damaged during extraction. Upper beak tall, conical (beak height 100% beak length), with dark brown, weakly pronounced, rounded rostrum; hood and lateral wall margins light brown, opaque to translucent, posterior lateral wall pigmentation same as that of wall margin, without V-shaped notch. Hood very short (depth 33% beak length), with bluntly rounded rostrum with 2 lateral prominences either side. Lateral wall profile rounded, with broadly rounded crest and no apparent wall fold. Lower beak with dark pigmented hood and proximal half of lateral wings; distal half of lateral wings and wall margins translucent. Lower beak damaged on extraction, total beak length incalculable. Hood appears very short, weakly projecting, with rostral apex deflected slightly up; rostrum trilobed, with deep cleft between lobes, individual lobes finely serrate.

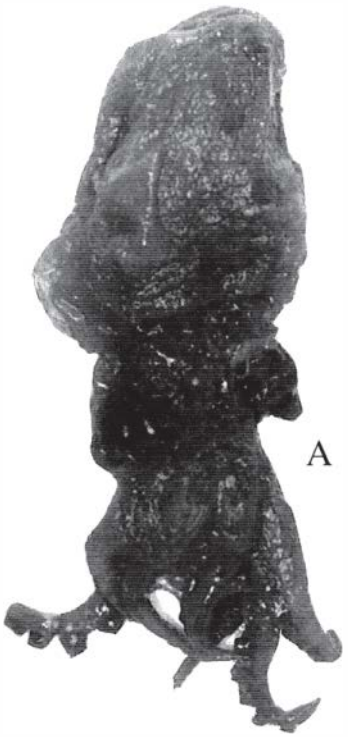
Radula (Fig. 48E) with wide, low-profile rachidian with 6 or 7 cusps; 1st lateral slightly shorter than rachidian, with long base and 4 or 5 tall cusps; 2nd lateral of almost equivalent length to rachidian, with long base and 3 or 4 tall, broad-based cusps; marginal tooth slender; marginal blocks stocky. Radula repeating seriation every 3 to 4 rows.

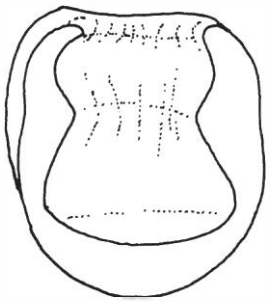
Indices, formulas, and counts in Table 26; raw measures in Table 27.

REMARKS: Cranial dissection of the female attributed to *Eledonella pygmaea* by Dell (1959) reveals a long optic nerve with the peduncular ganglion proximal to the optic ganglion. This specimen is in fact *Bolitaena microtyla* and constitutes the first record from New Zealand waters. This species is very imperfectly known, and it is with some hestitation that the New Zealand specimens are referred to it. Little differentiates species in this genus from those of *Japetella* and *Eledonella.*

Japetella Hoyle, 1885

DIAGNOSIS: Eyes closely spaced; optic nerve short; peduncular ganglion close to cerebral ganglion; 3rd right arm of male hectocotylised (after Hochberg *et al.* 1992: 224–225).





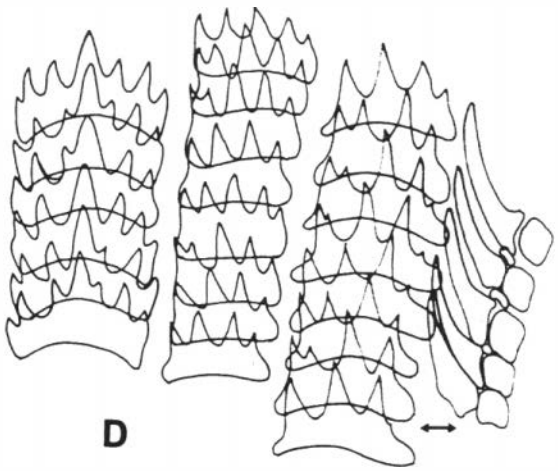


Figure 48. ***Bolitaena microtyla*** (Hoyle, 1885): **A–C**, NMNZ M.120135, female, ML 33 mm. **A, B**, whole animal. **C**, sucker (section). **D**, NMNZ M.74193, radula.

Table 26. Indices, formulas, and counts for *Bolitaena microtyla* (* denotes damage).

	NMNZ M.120135	NMNZ M.120135	NMNZ M.74193
sex	M	F	F
MWI	66.7	69.2	68.6
HdLI	22.3	27.5	22.9
HdWI	59.3	65.9	54.3
EDI	22.2	25.3	22.9
ALI1–4	27.0–45.0	24.2–36.4	30.8–36.9
AFR	3.4=2.1	3.1=2=4	3.1=2=4
AFL	3.2.4.1	3.4.2.1	3.1=2=4
WDIA–E	28.8–44.0	34.2–45.8	37.5–42.5
WFR	B.A=D.C.E	D.C=E.B.A	*
WFL	C.A=B.D.E	D=C=E.B.A	*
ASC1–4	11–14	9–14	10–11
ASIn1–4	5.2–8.3	5.5	5.7
PAI	44.4	49.5	41.7

Table 27. Raw measures for *Bolitaena microtyla* (* denotes damage).

	NMNZ M.120135	NMNZ M.120135	NMNZ M.74193
sex	M	F	F
TL	55.5	33.0	32.5
ML	27.0	18.2	17.5
MW	18.0	12.6	12.0
HdL	6.0	5.0	4.0
HdW	16.0	12.0	9.5
ED	6.0	4.6	4.0
AL1R/L	16/15	9/8	10/10
AL2R/L	17/19	9/9	10/10
AL3R/L	18.6*/25	10/12	12/11
AL4R/L	17/17	9/9	10/10
WDA	8.0	3.7	5.1
WDBR/L	9.5/8.0	4.8/4.1	5.0/*
WDCR/L	7.5/11.0	5.0/5.0	4.5/*
WDDR/L	8.0/7.5	5.5/5.1	4.5/*
WDE	7.2	4.9	*
ASC1R/L	11/14	9/12	10/11
ASC2R/L	14/12	13/10	11/10
ASC3R/L	9*/12	14/12	11/10
ASC4R/L	12/11	14/12	11/11
ASe1R	1.4	1.0	1.0
ASe2R	1.5	1.0	1.0
ASe3R	1.5	1.0	1.0
ASe4R	1.4	1.0	1.0
GiLC	5/5	5/5	5/5

Japetella diaphana (Hoyle, 1885)

Eledonella diaphana Hoyle, 1885a: 232; 1885b: 108; 1886: 107–108, pl. 9, figs 3–6.
Japetella diaphana: Thore 1949: 4–36, figs 1–18, 22; Dell 1951: 96; 1952: 74; Powell 1957: 125; 1962: 126; 1976: 133; Roeleveld 1977: 131–132; Powell 1979: 444; Hess & Toll 1981: 167, fig. 10; Nesis 1987: 289, figs 77A–C; Hochberg *et al.* 1992: 225, figs 241a–g; Spencer & Willan 1995: 52.
Bolitaena diaphana: Chun 1911: 15–20; Thiele 1915: 493; Chun 1915: 494, pls 82, 83, figs 1, 4, 6–9, pls 87–89.
Chunella diaphana: Sasaki 1920: 171; 1929: 14–15, pl. 8, figs 1–4.

MATERIAL EXAMINED (1 specimen, sex indet.): NMNZ M.74188, sex indet., ML 5.0 mm, *c.* 30°14' S, 176°42' W, 0–822 m over 3107–3742 m, 29/07/1962.

RECOGNISED DISTRIBUTION (New Zealand, Fig. 49, p. 69): North Island east coast, offshore; Kermadec Islands.

REMARKS: The only specimen available is juvenile and is with some hesitation referred to this species.

Eledonella Verrill, 1884

TYPE SPECIES: *Eledonella pygmaea* Verrill, 1884

DIAGNOSIS: Eyes widely separated; optic nerve long; peduncular and optic ganglia well separated; 3rd right arm of male hectocotylised.

Eledonella pygmaea Verrill, 1884 (Fig 51) (Table 28)

Eledonella pygmaea Verrill, 1884: Robson 1932: 332–335, figs 76–78; Thore 1949: 49; Dell 1951: 96; 1952: 76; Powell 1957: 125; 1962: 126; 1976: 133; 1979: 444; Nesis 1987: 289, fig. 77D; Hochberg *et al.* 1992: figs 242a–b; Spencer & Willan 1995: 52 [*partim*, exclude Dell (1959) citation *in* Powell (1979)].
Japetella prismatica Hoyle, 1885: 231; Hoyle 1886: 109–110, pl. IX, figs 1–2; Robson 1932: 331–332.
Eledonella massayae Robson, 1924a: 202.
Eledonella ijimae Sasaki 1929: 13–14, pl. 7, figs 1 0–15.
Bolitaena massayae: Robson 1932: 328–329.
Bolitaena massayae purpurea Robson, 1932: 328.
Bolitaena ijimai : Robson 1932: 329–330.
? *Eledonella sheardi* Allan, 1945: 345–347, pl. 26, figs 22–27.

MATERIAL EXAMINED (1 specimen, female [F]): NMNZ M.90316, F, ML 62.5 mm, 28°13.2' S, 174°56' E, 1064 m over 5000 m, 14/12/1976, f.r.v. *James Cook* Stn J17/70/76.

RECOGNISED DISTRIBUTION (Fig. 50, p. 69): Represented by single New Zealand female; Thore (1949) cites one additional specimen from east of Cook Strait (42°32' S, 174°50' E) — New Zealand distribution is therefore

28°13.2–42°32' S. Otherwise tropical–subtropical, bathypelagic, with juveniles found in the epipelagic and mesopelagic zones (Nesis 1987: 289).

DIAGNOSIS: With characters of the genus.

DESCRIPTION: Adult animal small bodied (Fig. 51A–B). Mantle oblong-ovate, thin walled, gelatinous, translucent; tan over dorsal, ventral, and oral surfaces of mantle, head, and arms. Head narrow, separated from mantle by weak constriction; dorsal head musculature weakly developed. Mantle aperture single, extensive, attached to head superior to eyes. Funnel long, almost entirely fused to ventral surface of head and arm bases 4; free portion short; funnel organ large, V-shaped, with thick limbs separated by about 90° angle. Eyes large, spherical, laterally oriented, not meeting across dorsal midline of head, with well-developed lens.

Arms short, thick, tubelike, longest arm 48% TL, shortest arm 29.5% TL; arm formula 3.4.1.2 or 3.2.4.1, with arms 1, 2, and 4 of subequal length, with arm pair 3 greatly enlarged and elongated. Web deep, deepest sector 30% longest arm, 50% shortest arm, shallowest web sector 24% longest arm, 40% shortest arm; web thin, translucent, delicate, not extending along dorso- or ventrolateral surface of any arm.

Suckers uniserial, ASC low (to 21), suckers at arm tips either damaged or absent; suckers regularly and closely spaced within web sectors, proud of arm surface. First 4 suckers on arm pairs 1, 2, and 4 of similar size (ASIn 5.3% ML), followed by gradual decrease in diameter to arm tips; with 5 suckers from base of arm to web margin. First 2 suckers on arm pair 3 small, followed by 6 enlarged suckers (ASIn 6.2% ML), thereafter 6 suckers gradually decrease in size to arm tip; no suckers abruptly enlarged. Sucker base wider than aperture; suction chamber large, suction pad weakly muscular; wall ring and sucker aperture simple; grasping ring poorly developed (Fig. 51C).

Optic nerve long, peduncular ganglion well separated from optic ganglion. Gills with 7 lamellae per outer demibranch.

Female immature; ovary sac with numerous small eggs; oviducal ball very small, scarcely differentiated from proximal or distal oviduct.

Upper beak (Fig. 51D) tall, conical (height 108% beak length), with dark brown, weakly pronounced, rounded rostrum; hood and lateral wall margins translucent; hood short (depth 42% beak length). Lateral walls rounded, with broadly rounded crest and no apparent wall fold. Lower beak (Fig. 51D) depressed (height 60% length), hood and proximal half of lateral wings darkly pigmented; distal half of lateral wings and wall margins translucent. Lateral wall with well-developed basal notch, weakly keeled crest, 2 lateral wall folds, and free corners of lateral wall widely spread apart. Hood very short (depth 41% beak length); rostrum slightly deflected up; rostral margin serrate, with 8 sharp-pointed teeth; lateral wings short (length 66% beak length), without apparent folds.

Radula (Fig. 51E) with wide, low-profile rachidian with 5–7 asymmetric cusps, (2 or 3 lateral cusps aside central cusp); 1st lateral of similar length to rachidian, with long base and 3–5 tall cusps, with pronounced heel adjacent to rachidian; 2nd lateral as wide as or wider than rachidian, with long base and 3 or 4 tall, broad-based cusps, the inner 1st and 3rd cusp of similar size; marginal tooth slender; marginal blocks stocky. Radula with repeat seriation every 5 or 6 rows.

Table 28. Raw measures for *Eledonella pygmaea* (* denotes damage).

	NMNZ M.90316
sex	F
TL	129
ML	56.5
MW	25
HdL	13
HdW	22.5
ED	11
EO	4
AL1R/L	42/42
AL2R/L	38/44
AL3R/L	61/62
AL4R/L	44/47
AFR	3.4.1.2
AFL	3.4.2.1
WDA	18
WDBR/L	16/17
WDCR/L	17/15
WDDR/L	19/19
WDE	15
WFR	D.A.C.B.E
WFL	D.A.B.C=E
ASC1R/L	19*/19*
ASC2R/L	14*/19*
ASC3R/L	14*/14*
ASC4R/L	19*/21*
ASe1R	3
ASe2R	3
ASe3R	3.5
GiLC	7/7
PAI	16.6

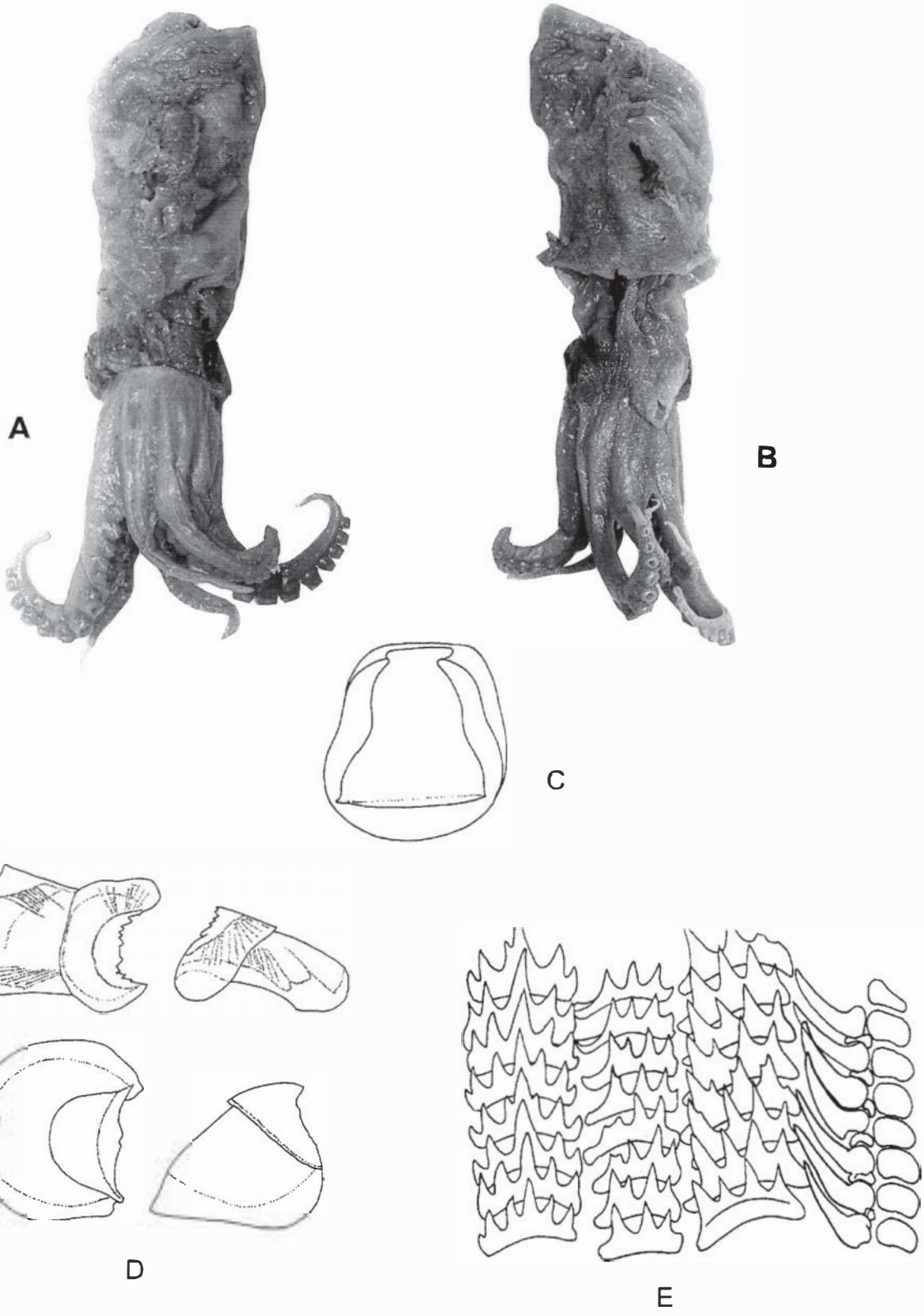


Figure 51. *Eledonella pygmaea* Verrill, 1884. **A–D**, NMNZ M.90316, female, ML 62.5 mm. **A, B**, whole animal, dorsal and ventral. **C**, sucker (section). **D**, beaks. **E**, radula.

REMARKS: The morphology of the largest New Zealand female is consistent with that of the cosmopolitan *Eledonella pygmaea*. The single female available was not dissected, so the anatomical account detailed here is limited largely to characters of external morphology, beak and radula structure.

Family **AMPHITRETIDAE** Hoyle, 1886

DIAGNOSIS: Suckers uniserial; web deep between all arms; body saclike, gelatinous; mantle opening comprises two separate apertures, one either side of funnel; funnel fused to ventral surface of mantle and head; third right arm of male hectocotylised; eyes telescopic, directed dorsally; shell vestige absent; radula ctenodont; digestive gland large, ovoid, posterior to stomach; funnel organ W-shaped (Hochberg *et al.* 1992).

Amphitretus Hoyle, 1885

TYPE SPECIES: *Amphitretus pelagicus* Hoyle, 1885

DIAGNOSIS: With characters of the family.

Amphitretus pelagicus Hoyle, 1885 (Figs 53, 54) (Tables 29, 30)

Amphitretus pelagicus Hoyle, 1885a: 235; 1885b: 113; 1885c: 271, fig. 106; 1886: 4, 67–68, pl. 9, figs 7–9; 1888: 212; Ijima & Ikida 1902: 85, pl. 2, figs 1–3; Chun 1903: 88; Hoyle 1909: 257; 1910: 407; Berry 1912: 397; Sasaki 1917: 361, figs 1–2; Sasaki 1929: 16, pl. 3, figs 1, 2, pl. 7, fig. 5; Thore 1949: 51–57, figs 42–51, table 3; Nesis 1987: 291, fig. 77H, I; Hochberg *et al.* 1992 (*partim*): 219–222, figs 240a–c (not D, = *A. thielei* Robson).
Idioctopus gracilipes Taki, 1964 (*fide* Hochberg *et al.* 1992).
Not *Amphitretus pelagicus*: Allan 1945.

MATERIAL EXAMINED (6 specimens, 1 male[M], 5 female[F]): NMNZ M.90331, M, ML *c.* 30 mm, 2F, ML *c.* 42.0, 31.5 mm, 28°22' S, 175°56' W, 387 m, 14/12/1976, f.r.v. *James Cook* Stn J17/73/76; NMNZ M.118439, F, ML 17.0 mm, 28°13.2' S, 174°56' E, 1064 m ov. 5000 m, 14/12/1976, f.r.v. *James Cook* Stn J17/70/76; NMNZ M.95262, F, ML *c.* 32 mm, 31°08' S, 175°11' W, 377 m, 15/12/1976, f.r.v. *James Cook* Stn J17/79/76; NMNZ M.131726, F, ML 7.0 mm, 31°24' S, 179°00' E, 1500–1700 m, 25/07/1962, AUZ Stn 95 17, *Tui* Cruise.

RECOGNISED DISTRIBUTION (Fig. 52, p. 82): New Zealand, North of Subtropical Convergence, 28°13.2–31°24' S, 174°56–179°00' E, 377–1700 m over depths to 5000 m; Indo-Pacific (Thore 1949). Type locality: Off Kermadec Islands, 950 m.

DIAGNOSIS: With characters of family. Small-bodied; arm sucker counts to 32, hectocotylised arm sucker count 27 or 28; with 10 lamellae per outer demibranch of gill.

DESCRIPTION (Figs 53A–C): Available material small-bodied, ML to 42 mm, TL to 153 mm. Mantle large (ML about 28–35% TL), saccular, in all available specimens with gelatinous sheath abraded. Digestive gland projecting forward, apparent externally due to mantle transparency; head narrow, dorsal head musculature not apparent. Eyes large (diameter about 25–27% ML), dorsally oriented, with large base, hardened central ring and protruding dome-shaped lens. Mantle apertures paired, large, oval, located either side of funnel lateral and superior to eyes. Funnel large, entirely fused to ventral surface of mantle, head and arm bases 4; funnel organ large, W-shaped, with thick outer limbs.

Arms long (AL about 60–80% TL), of subequal length, thick, tubelike, extensively gelatinous; arm formula 2.3.4.1 or 2.3.1.4. Web moderately deep, about 25–50% longest arm, 35–60% shortest arm, shallowest web sector 20–22% longest arm, 23–25% shortest arm; web thin, translucent, delicate, with muscle fibres apparent in transparency. Third right arm of male hectocotylised; calamus short, 7% ligula length, resembling enlarged sucker divided across midline; ligula very long, 17.5% arm length, flagellumlike; ligula with 2 rows of papillae, the basal 9 pairs largest (Fig. 54A).

Non-hectocotylised arm sucker counts low (ASC 22–32). Suckers uniserial, not deeply embedded within arm tissues, widely spaced within web sectors, with 7–9 suckers within web margin set 2 to 3 sucker diameters apart. First 12–14 suckers on non-hectocotylised arms of male and females of similar size, thereafter suckers gradually decrease in diameter to arm tip, showing a tendency to become biserial; suckers present to arm tips. Hectocotylised arm with 28 suckers, none grossly enlarged; suckers 1–9 of similar size, suckers 10–28 slightly decrease in diameter; web nodule present on ventrolateral surface of arm 3R adjacent to suckers 21 and 22. Suckers (Fig. 54B) with base wider than aperture; suction chamber large; suction pad and wall ring weakly muscular; sucker aperture large, simple; grasping ring poorly developed, deep. Indices, formulas, and counts in Table 29.

Female immature; ovary sac (Fig. 54C) very small, ovoid; common oviduct well developed; proximal oviduct narrow, of equivalent length to distal duct; oviducal ball with 2 chambers; distal oviduct stout, bent in pronounced U-shape. Male anatomy unknown.

Alimentary canal (Fig. 54D) with small buccal bulb (length about 4% ML), with ventral radula sac prominent; anterior salivary glands large, loosely applied

Figure 53. ***Amphitretus pelagicus*** Hoyle, 1885. NMNZ M.90331, female, ML 42 mm.

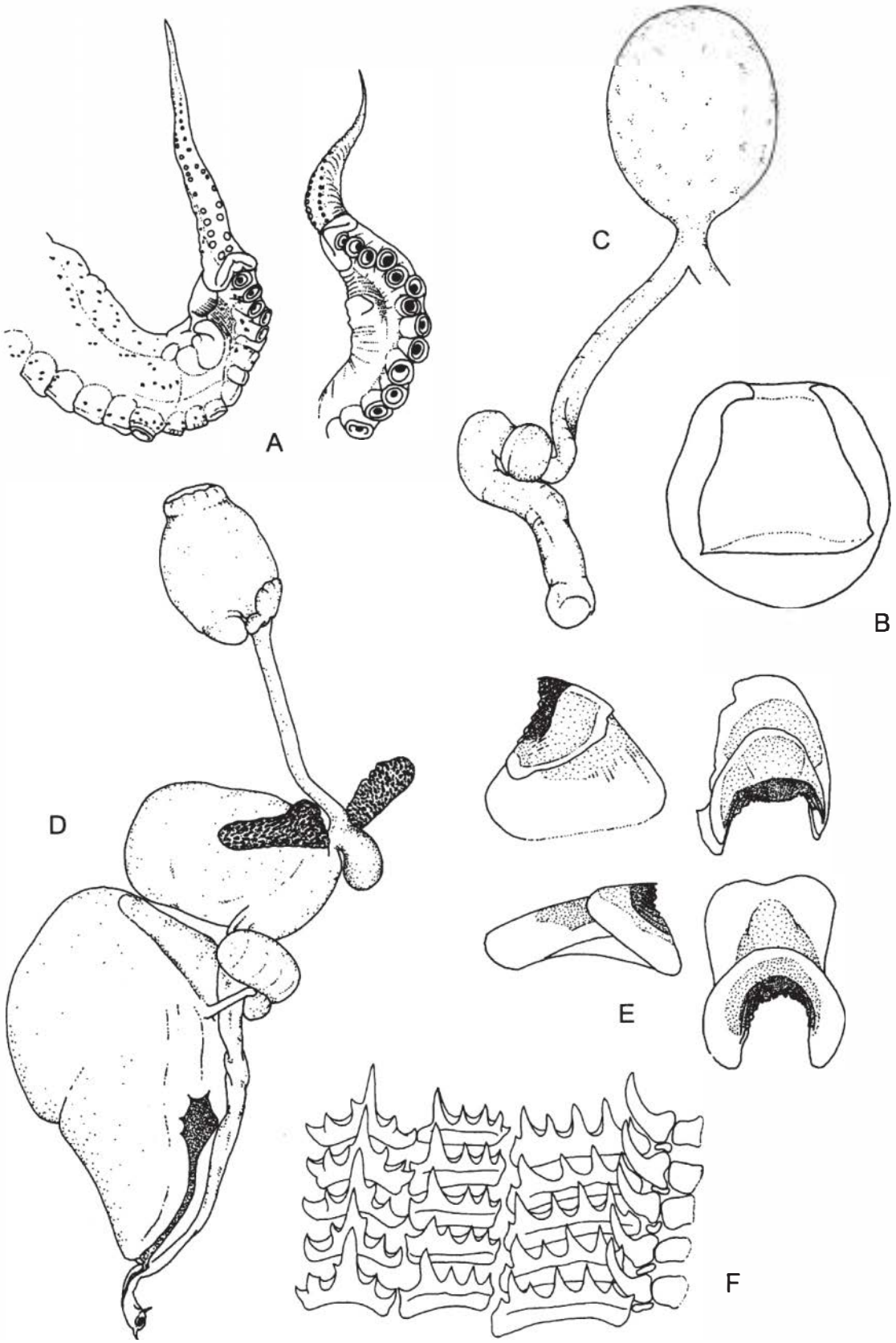


Figure 54. ***Amphitretus pelagicus*** Hoyle, 1885: **A**, hectocotylus NMNZ M.90331, male. **B–F**, NMNZ M.90331, female, ML 42 mm. **B**, sucker (section). **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

to posterior margin of buccal bulb. Anterior oesophagus narrow, of great length (about 85% oesophagus and crop length); posterior salivary glands paired, of equivalent length to buccal bulb, elongate (width about 33% length). Crop with well-developed anterior diverticulum; stomach massive (about 1.5 times diameter of buccal bulb), with 3 external sections delimiting thick, muscular central section and thin-walled outer sections, lumen continuous; spiral caecum small, volution single, complete; intestine slightly longer than anterior alimentary canal, dilated centrally, constricted proximal to caecum and anus. Hepatic ducts paired; digestive gland of metallic green-gold lustre, disproportionately large, widest proximal to hepatic ducts, constricted proximal to ink duct; pancreas well developed (about 25% digestive gland length), cream coloured; ink sac long (length about 50% digestive gland length), cylindrical, not deeply embedded in digestive gland tissues; ink duct short, opening at anus.

Upper beak (Fig. 54E) conical, very tall (height 106% beak length), with dark-brown-pigmented rostrum; lateral wall and hood margins translucent; hood shallow (depth 44% beak length); rostrum with 7 or 8 well-developed teeth; rostral tip not deflected downwards. Lateral wall with rounded profile, crest broadly rounded; lateral wall folds not apparent. Lower beak (Fig. 54E) depressed (height 60% width); hood and proximal half of lateral wings dark pigmented; distal half of lateral wings and wall margins translucent; lateral wings without apparent folds. Lateral wall with acute-angled basal notch and weakly keeled crest. Hood very short (depth 40% beak length), forward projecting; rostrum slightly deflected upwards, with 3 lobes, each lateral with 8 well-developed teeth and incised dark pigmented streaklike ridges extending posteriorly over hood; lateral wings short, beak anteroposteriorly elongate (wing length 60% beak length).

Radula (Fig. 54F) with low-profile, wide-based rachidian with 6 or 7 asymmetric cusps, arranged 2 or 3 either side of the tall, narrow central cusp; 1st lateral of equivalent width to rachidian, with long base and 5 tall cusps, and single poorly developed cusp adjacent to rachidian; 2nd cusp tallest, other cusps of subequal height; 2nd lateral considerably wider than rachidian, with long base and 5–7 tall, slender cusps, the 2nd inner cusp most prominent; marginal tooth robust; marginal blocks stocky. Radula with repeat seriation every 4th row.

REMARKS: A single incomplete New Zealand male is available in which both digestive and reproductive systems were destroyed during capture. Combining known male and female anatomies it is apparent this species possesses up to 28 suckers on the hectocotylised arm and 10 inner and outer lamellae per gill.

Table 29. Indices, formulas, and counts for *Amphitretus pelagicus* (* denotes damage).

	NMNZ M.90331	NMNZ M.90331	NMNZ M.90331
sex	F	F	M
MWI	47.0	54.8	*
HdLI	25.4	21.4	30.0
HdWI	44.4	39.3	*
EDI	25.0	25.0	26.7
ALI1–4	61.5–70.0	61.4–72.5	69.8–80.2
AFR	2=3.4.1	2.3.4.1	*
AFL	2.3.1.4	*	*
WDIA–E	*	30.0–45.0	21.7-49.3
WFR	*	?C.A.D.B.E	*
WFL	*	*	*
ASC1–4	22–29	28–32	25–29
ASIn1–4	6.3–8.3	8.3–9.5	6.7–7.0
PAI	25.4	19.0	*

Table 30. Raw measures for *Amphitretus pelagicus* (* denotes damage).

	NMNZ M.90331	NMNZ M.90331	NMNZ M.90331
sex	F	F	M
TL	96	153	86
ML	31.5	42	*c.* 30
MW	14.8	23	*
HdL	8	9	9
HdW	14	16.5	*
ED	7.9	10.5	8
AL1R/L	59/59	94/98	*/30*
AL2R/L	63/67	111/*	67/29*
AL3R/L	63/61	103/*	60/66
AL4R/L	61/58	96/102	67/69
WDA	*	40	*c.* 30
WDBR/L	*/*	22/*	24/20
WDCR/L	*/*	50/*	19/15
WDDR/L	*/*	33/*	34/28
WDE	*	15*	*
ASC1R/L	23/27	30/31	*/*
ASC2R/L	25/22	31/*	29/*
ASC3R/L	26/29	32/*	28/28
ASC4R/L	26/27	28/32	28/25
ASn1R	2.6	4	*
Asn2R	2	4	2
ASn3R	2.5	3.5	2.1
ASn4R	2.6	3.5	2
GiLC	10	10	*
PAI	8	8	*
CaL	F	F	0.75
LL	F	F	10.5

Sasaki (1929) described a Japanese specimen attributed to *A. pelagicus* with 27 suckers on the 3rd right hectocotylised arm, having the terminal part of the arm with the flattened oval surface beset with two series of minute rounded protuberances, and 20 lamellae per gill (in total = 10 lamellae per demibranch). These characters are consistent with New Zealand material collected near the type locality of this species. Although I have not seen Japanese specimens attributed to *A. pelagicus*, Sasaki's specimen is considered conspecific with New Zealand material given it is clearly not referable to the next species, *A. thielei* Robson, 1930. Moreover, only two species are presently recognised in this genus. Insufficient data are presented by Rancurel (1970) or Roper and Young (1975) to evaluate critically those specimens attributed to *A. pelagicus* from the South Pacific (northwest of New Zealand) or the South Atlantic respectively.

Amphitretus thielei Robson, 1930 (Figs 56, 57) (Tables 31, 32)

? *Cirroteuthis* sp. Hoyle, 1886: 66, pl. 9, figs 10, 11.
Amphitretus pelagicus (not Hoyle 1885): Thiele 1915, 415–416, pl. 41, figs 6–10; ?Allan 1945: 347, pl. 27, figs 1 2–14.
Amphitretus thielei Robson, 1930: 383–386, figs 11–13, pl. III, fig. 2; Robson 1932: 337–338.
? *Grimpoteuthis* sp. (Hoyle, 1886): Robson 1932: 153, fig. 25.
Amphitretus pelagicus thielei: Nesis 1987: 291.

MATERIAL EXAMINED (34 specimens, 8 male [M], 22 female [F], 4 sex indet. & fragments): NZOI Stn Z8819, F, ML *c.* 135 mm, 41°42' S, 164°19' W, 1000 m, -/12/1975, f.v. *Peterson*; NZOI Stn Z8411, F, ML 57.0 mm, 44°10.64–10.18' S, 177°22.31–25.03' E, 906–909 m, 05/11/1995, BT 4.8°C, f.r.v. *Tangaroa* Stn TAN9511/168; NZOI Stn Z8391, F, ML 103.0 mm, 44°21.72–21.52' S, 177°52.90–55.69' E, 1143–1145 m, BT 3.1°C, 10/10/1995, f.r.v. *Tangaroa* Stn TAN9511/037; NZOI Stn Z8412, M, ML 57.0 mm, 44°26.84' S, 179°15.19–15.00' W, 883–914 m, 06/11/1995, f.r.v. *Tangaroa* Stn TAN9511/174; NZOI Stn Z8410, M, ML 51 mm, F, ML 53 mm, FPT, 44°32. 7–32.88' S, 177°50.34–51.85' W, 913–920 m, BT 4.7°C, f.r.v. *Tangaroa* Stn TAN9511/071; NZOI Stn Z8685, F, ML 20.3 mm, 44°37.37' S, 174°33.25' E, 50–300 m, FMMWT, 13/02/1992, f.r.v. *Tangaroa* Stn TAN9202/06; NZOI Stn Z8745, M, ML 13.0 mm, 44°37.65' S, 179°48.78' E, 0–1010 m, FMMWT, 21/02/1992, f.r.v. *Tangaroa* Stn TAN9202/66; NZOI Stn Z8413, M, ML 73.5 mm, 44°42.51–42.52' S, 177°04.62–04.83' W, 730–780 m, 28/10/1995, BT 5.9°C, f.r.v. *Tangaroa* Stn TAN9511/148; NMNZ M.90325, 3F, ML 18.5, 16.5, 15.0 mm, 44°44.6' S, 172°50.4' E, 840–868 m, 15/04/1984, f.r.v. *James Cook* Stn's J07/023/84, J07/024/84, J07/025/84 (combined); NMNZ M.102176, sex indet, ML 4.0 mm, 44°45.3' S, 167°01.1' E, 205 m over 2520 m, 29/08/1985, f.v. *Kaiyo Maru* Stn 230B, Bongo 0.335; NMNZ M.100380, M, ML 22.0 mm, 44°46.2' S, 173°06.9' E, 952 m over 967 m, 08/02/1982, f.r.v. *James Cook* Stn J3/7/82; NMNZ M.95247, 3F, ML 31.0, 26.5, 23.5 mm, 44°46.3' S, 173°22.7' E, 982 m, 11/06/1984, f.r.v. *James Cook* Stn J10/24/84; NZOI Stn Z8688, 2F, ML 16.7, 11.0 mm, 44°59.19' S, 174°36.35' E, 50–300 m, FMMWT, 13/02/1992, f.r.v. *Tangaroa* Stn TAN-9202/09; NZOI Stn Z8691, F, ML *c.* 63 mm, 45°24.23' S, 174°35.39' E, 50–316 m, FMMWT, 14/02/1992, f.r.v. *Tangaroa* Stn TAN9202/12; NMNZM.102162, sex indet., ML 12.5 mm, 45°25–22.5' S, 171°33.6–35.1' E, 500–190 m over 916–960 m, 14/09/1985, f.v. *Kaiyo Maru 3* Stn 216C, FMMWT; NZOI Stn Z8370, 2M, ML 30.0, 23.5 mm, 2F, ML 50.0, 26.0 mm, sex indet., ML 22.0 mm, 45°34' S, 156°40' W, 870–900 m, -/09/1995, f.v. *Peterson*; NZOI Stn Z8694, 2F, ML 14.0, 11.4 mm, 45°47.85' S, 174°34.29' E, 50–300 m, FMMWT, 14/02/1992, f.r.v. *Tangaroa* Stn TAN9202/15; NMNZ M.118400, M, ML *c.* 51 mm, 2F, ML 109.0, 64.5 mm, 2F fragments, 46°57.64' S, 165°25.21' E, 950–970 m, -/09/1994, f.v. *San Hauraki*; NZOI Stn Z8820, F (fragments), 49°34.02' S, 167°03.53' E, 402–407 m, f.r.v. *Tangaroa* Stn TAN9310/81; NMNZ M.118438, F (fragment), sex indet. (fragments), 50°40' S, 167°06' E, 367–410 m, datNR, f.v. *Peterson*.

RECOGNISED DISTRIBUTION (New Zealand, Fig. 55, p. 82): 44°10.64–50°40' S, 167°06–179°48.78' E, South of the Subtropical Convergence, recognised depth range 0 (–300*)–1145 m; adults evidentally bathypelagic, juveniles in shallower water. Otherwise known from Tasmania (*?fide* Allan 1945; Stranks pers. comm.), and southern subtropical and notalian Atlantic (*fide* Nesis 1987: 291).

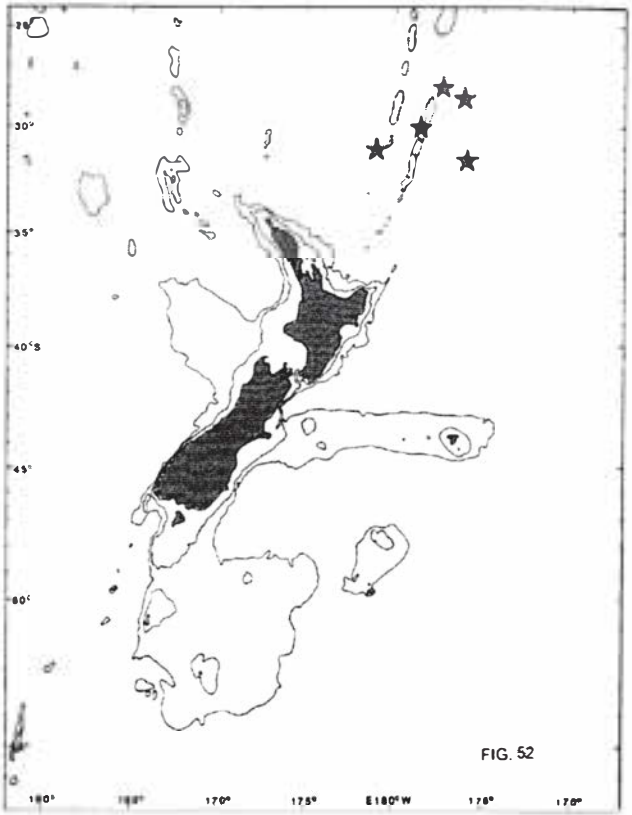
TYPE LOCALITY: 33°50–34°13' S, 16°04–15°49' E, 0–399 m.

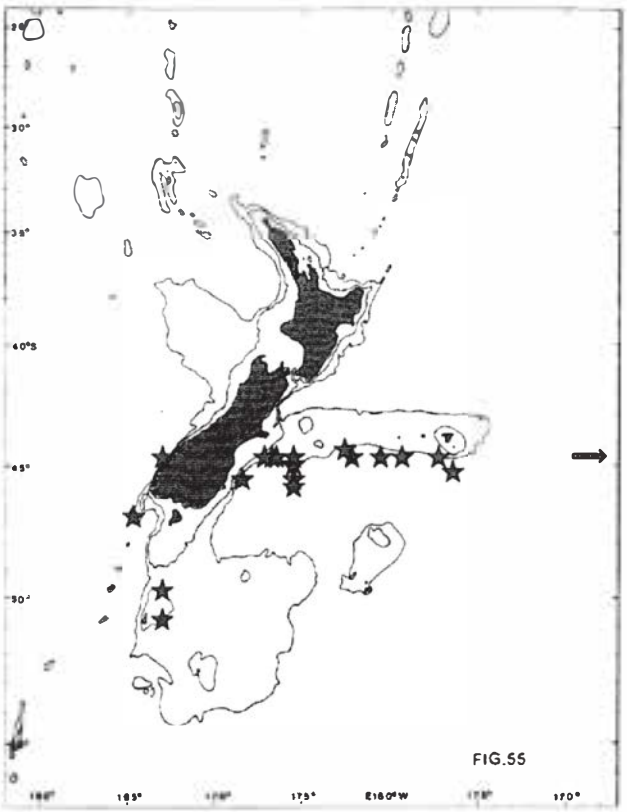
DIAGNOSIS: With characters of the family. Male with 21–24 suckers on hectocotylised arm. Gills with 8 outer lamellae per demibranch.

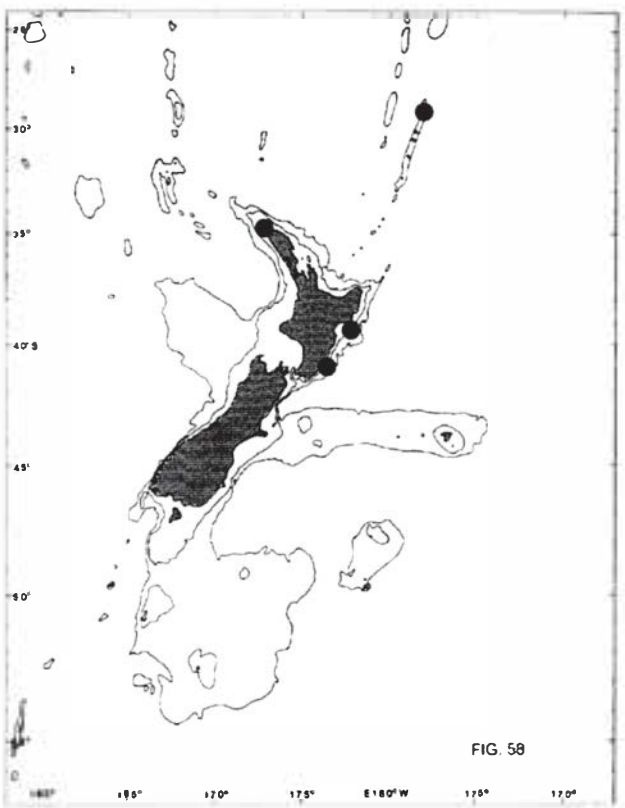
DESCRIPTION (Figs 56A–D): Sexually dimorphic: female ML to about 135 mm (head only), largest females mutilated, TL incalculable; male ML to 73.5 mm, TL 197 mm. Mantle large, saccular, with well-developed translucent gelatinous sheath. Digestive gland projecting forward, apparent in transparency through mantle superior to eyes; head narrow, comprising 2 dorsally to dorsolaterally oriented eyes; dorsal head musculature poorly developed. Mantle apertures paired, large, ovoid, lateral and superior to eyes. Funnel large, entirely fused to ventral surface of mantle, head, and arm bases 4; funnel organ large, W-shaped, with thick outer limbs. Eyes large, with large basal region, hardened central ring, and protruding dome-shaped lens.

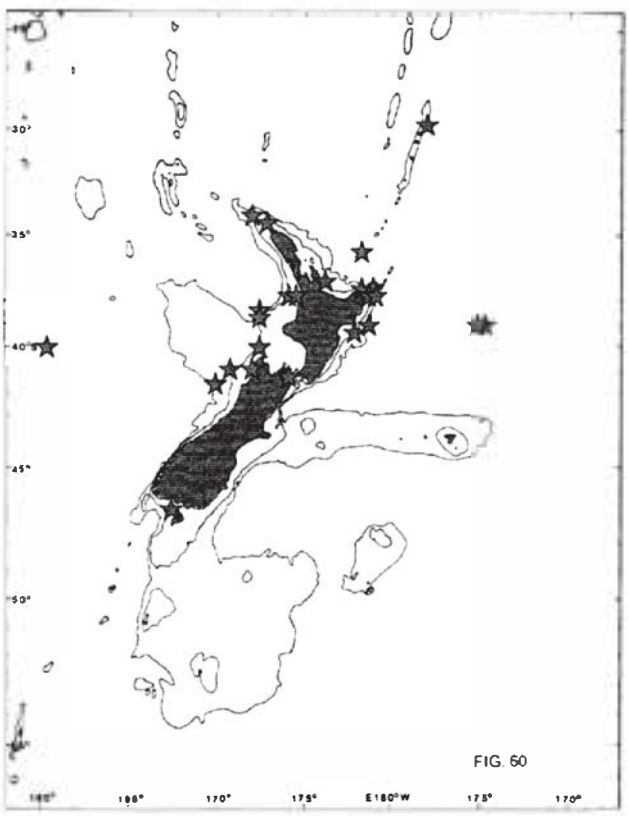
Arm length moderate to long (AL 57–82% TL); arms thick, tubelike, extensively gelatinous; arm formula variable, no consistent disparity between right and left sides or specimens apparent. Web moderately deep, 44–54% longest arm, 58–78% shortest arm, most shallow web sector 25–38% longest arm, 37–56% shortest arm; web thin, translucent and delicate, with thin muscle fibres apparent in transparency between

* Non-closing nets









Recognised distribution. **Fig. 52**, *Amphitretus pelagicus* (Hoyle, 1885). * new records; ⋆ type locality. **Fig. 55**, *Amphitretus thielei* Robson, 1930. **Fig. 58**, *Argonauta argo* Linnaeus, 1758: shells. **Fig. 60**, *Argonauta nodosa* Solander, 1786: animals.

Third right arm of male hectocotylised (Fig. 57A), ASC 21–24; mature specimens with constriction in arm proximal to 8th sucker from arm base; calamus and ligula appear to be enclosed in a pouch formed from membranes connecting outer surfaces of web sector C with inner dorsolateral surface of arm 3R (independent of web sector D). Calamus short (CaLI 5.9–8), basal, resembling single sucker divided across centre line; ligula very long (LLI 32.5-41.8), flagellum-like, without groove or papillae.

Non-hectocotylised arm sucker counts low, ASC to 41. Suckers widely spaced within web, not deeply embedded within arm tissues, often appearing borne on short gelatinous stalks (possibly preservation artefact); distance between suckers within web about 3 to 4 sucker diameters; suckers 9–14 at web margin closely spaced; distal suckers to arm tips well spaced. Female with first 7 suckers on arms 1–4 of similar size, sucker 8 of increased diameter, suckers 9–14 at web margin abruptly increased in diameter (suckers 11 and 12 the largest); thereafter sucker size gradually decreases to arm tip. Male sucker enlargement moderate on arm pairs 1, 2, 3L and 4, upon which suckers 12–14 at web margin are slightly enlarged. Hectocotylised arm with pronounced constriction proximal to suckers 7 and 8; suckers 10–21 on expanded and hardened section of arm; suckers 11–15 from arm base abruptly enlarged; web nodule present on ventrolateral arm surface between suckers 15 and 16. Suckers of mature male and female (Fig. 57B) with moderate-sized suction chamber, well-developed muscular suction pad and wall ring, and large, simple sucker aperture; grasping ring deep but inconceivably suctorial; sucker base wider than aperture.

Male reproductive system (Fig. 57C) with elongate testis sac; funnel-shaped structure joins testis sac with long, thin spermatophoral gland; accessory gland disproportionately large; spermatophoric sac slender, elongate; proximal duct to penis long, thin walled; penis diverticulum large, flask-shaped; penis long, cylindrical; spermatophores unknown. Female (Fig. 57D) with large ovary sac; ovarian eggs small (3.5 x 1.0 mm); proximal oviducts long, narrow; oviducal ball with 2 chambers, anterior small, yellow, distal large, black, striate; distal oviducts of equivalent length to proximal ducts, stout, bent in pronounced U-shape; distal oviduct with swelling proximal to genital aperture.

Alimentary canal (Fig. 57E) with large buccal bulb; ventral radula sac prominent; anterior salivary glands large, ovoid, loosely applied to posterior margin of buccal bulb. Anterior oesophagus extensive (about 75% total oesophagus and crop length); posterior salivary glands elongate (about twice buccal bulb length); crop with well-developed anterior diverticulum; stomach large, of greater size than buccal bulb, with thick-walled basal and thin-walled distal sections, its lumen is continuous; spiral caecum small, thin walled, volution incomplete; intestine slightly longer than oesophagus, dilated proximal to caecum, distally constricted and cylindrical for about 80% intestine length. Hepatic ducts 2; digestive gland disproportionately large, slender, of metallic green-gold lustre; pancreas well developed (about 33% digestive gland length); ink sac long (about 50% digestive gland length), cylindrical, lying subsurface in digestive gland; ink duct short, opening at anus.

Upper beak (Fig. 57F) conical, tall (height 71% length), with darkly pigmented hood with transparent hood and lateral wall margins; hood shallow (depth 42% beak length); rostrum with 7 or 8 well-developed teeth; rostrum not deflected down. Lateral walls of rounded profile, with broadly rounded crest; lateral wall fold not apparent. Lower beak (Fig. 57F) depressed (height 40% width), with darkly pigmented hood and proximal half of lateral wings; distal half of lateral wings and wall margins translucent; lateral wall with acute-angled basal notch and sharp-keeled crest. Hood very short (depth 39% beak length), forward projecting; rostrum slightly deflected up, with 12 or 13 sharp-pointed teeth; lateral wings long (length 94% beak length), without apparent folds.

Radula (Fig. 57G) with wide, tall-profile central rachidian with 6–8 asymmetric cusps (with 2–4 shorter cusps beside central); 1st lateral of equivalent width to rachidian, with long base and 3 tall cusps, and pronounced uncusped heel facing rachidian; 2nd lateral of greater width than rachidian, with long base and 4 or 5 tall, broad-based cusps, the 2nd inner cusp most prominent; marginal tooth slender; marginal blocks stocky. Radula with repeat seriation every 3 or 4 rows.

Indices, formulas, and counts in Table 31; raw measures in Table 32.

REMARKS: Thore (1949: 52) synonymised *A. thielei* with *A. pelagicus* Hoyle on grounds that the single specimen described by Robson was damaged, and on the assumption that Robson had incorrectly counted the number of gill leaflets in *A. thielei*. The redescription of the anatomy, morphological characters, and indices presented in this report shows that, while these two species are similar, they differ appreciably in geographic distribution, outer gill lamellae count, and hectocotylised and non-hectocotylised arm sucker counts. On this basis, *A. thielei* is recognised as distinct from *A. pelagicus*, a distinction in part recognised by Nesis (1987: 291) who treated *A. thielei* as a subspecies of *A. pelagicus*. The character of mantle shape, cited by Nesis (*loc. cit.*) to differentiate

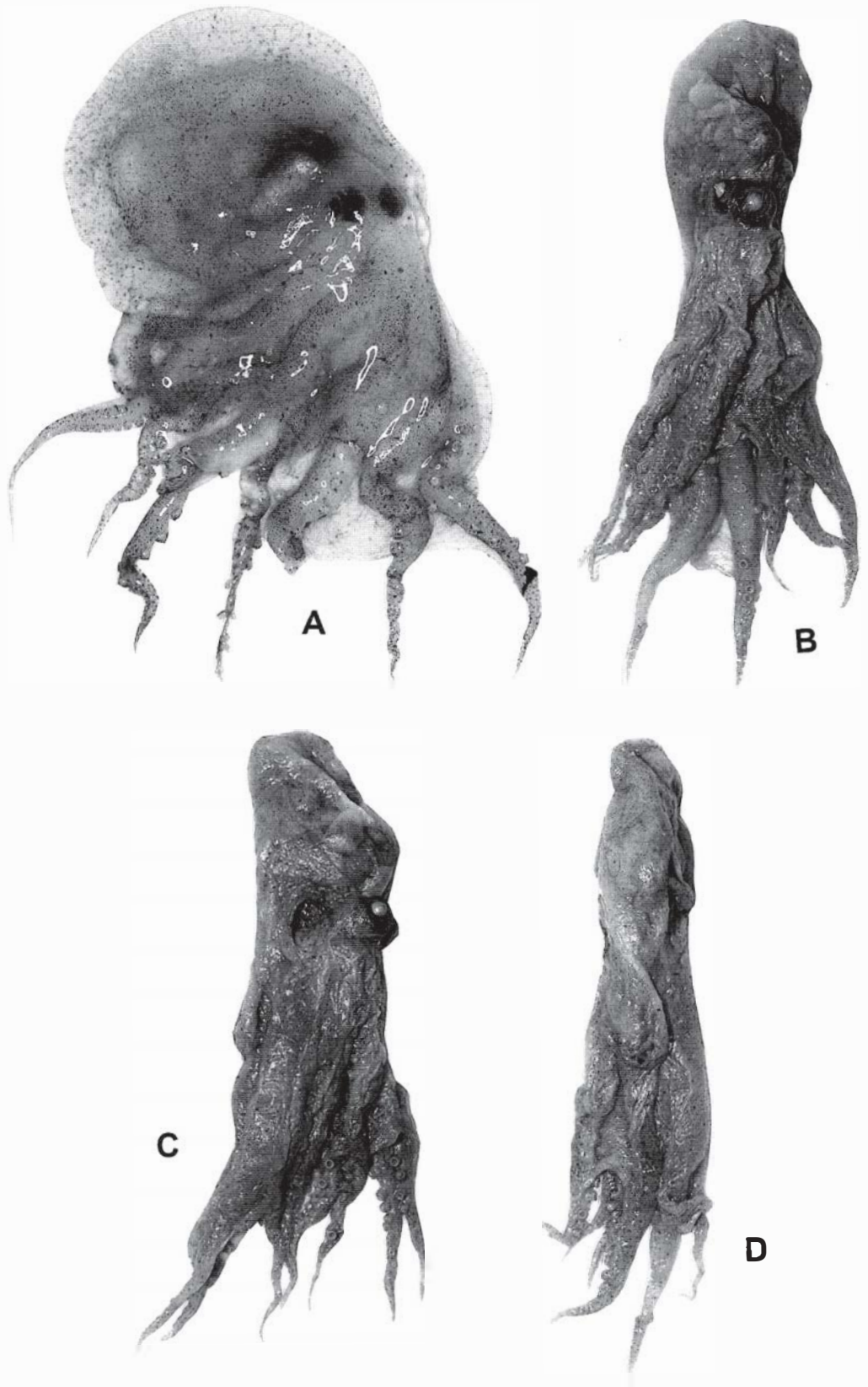


Figure 56. *Amphitretus thielei* Robson, 1930: A, NZOI Stn Z8410, male, ML 51 mm. **B–D**, NZOI Stn Z8411, female, ML 57.0mm.

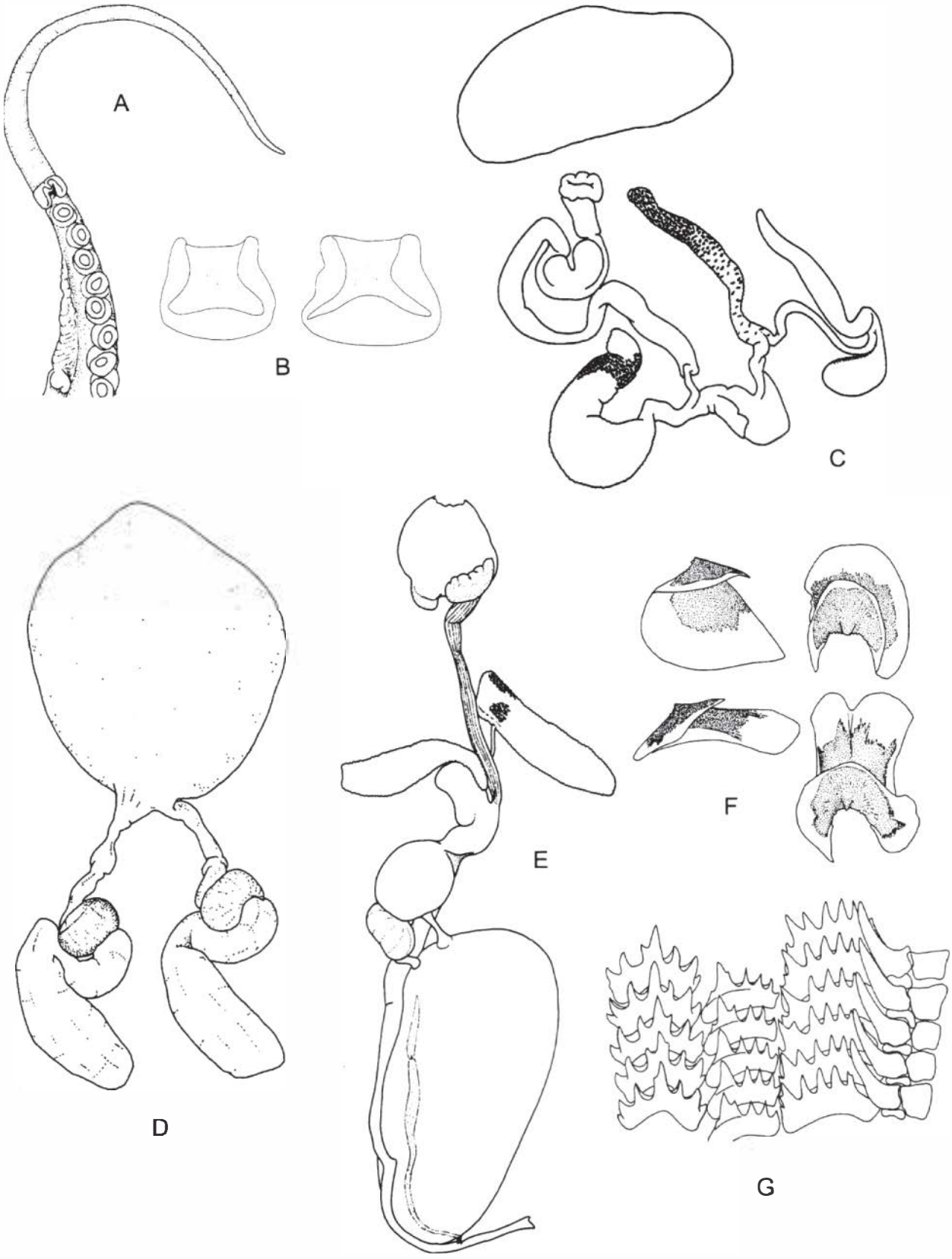


Figure 57. ***Amphitretus thielei*** Robson, 1930: **A**, NZOI Stn Z8410, male, ML 51 mm. **B**, **D**, **F**, NZOI Stn Z8820, female, fragments. **C**, **E**, NZOI Stn Z8413, male, ML 73.5 mm. **F**, NMNZ M.118438, female (fragments). **A**, hectocotylus. **B**, sucker (section). **C**, male reproductive system. **D**, female reproductive system. **E**, alimentary canal. **F**, beaks. **G**, radula.

these subspecies, is considered of dubious systematic value given the high degree of morphological plasticity in these gelatinous animals. All presently known southern Australian *Amphitretus* specimens (off Tasmania, about 41°S–47°S, 142°E–148°E) are immature (specimens exceeding 70 mm ML unknown, Stranks 1996 pers. comm.). Gill lamellae counts on these specimens do not exceed 8, and males have about 21 suckers on the hectocotylised arm. Therefore, the juvenile South Australian specimen identified as *A. pelagicus* by Allan (1945: 42°35' S, 148°37' E) is likely to be *A. thielei*. Furthermore, if *A. thielei* proves to be a cosmopolitan southern ocean species, *Cirroteuthis* sp. Hoyle, 1886 (= ? *Grimpoteuthis* sp. (Hoyle, 1886); Robson 1932) is most likely *A. thielei*. Described on the basis of a single arm fragment with three suckers, the sucker-type of this specimen (Robson 1932: 153, fig. 25) is quite inconsistent with that of any cirrate.

Table 31. Indices, formulas, and counts for *Amphitretus thielei* (* denotes damage; # denotes third right arm enclosed in pouch, length not calculated to avoid specimen damage).

	NZOI Stn Z8413	NMNZ M.118400	NZOI Stn Z8475	NZOI Stn Z8412	NMNZ M.118400	NMNZ M.95247
	M	F	F	M	M	F
MWI	57.8	62.0	51.8	72.8	66.7	80.6
HdLI	18.4	23.6	17.5	20.6	22.3	
HdWI	30.6	60.5	31.9	67.5	42.2	84.5
EDI	12.2	17.8	15.8	14.0	20.6	19.4
ALI1–4[1]	39.1–56.9	52.5–73.4	42.2–51.5	63.9–79.8	-	65.3–81.6
AFR	1.2.3.4	2.3.4.1	3.4.2.1	#	3.1.2.4	*
AFL	4.3.2.1	3.2.4.1?	4.1.3.2	3.1.2.4	1=2.3.4	3=4.2.1
WDIA–E	38.4–50.4	35.8–43.5	24.8–51.5	25.8–49.5	-	32.5–46.3
WFR	?E.D.A.C.B	*	C.E.A.D.B	B.E.C.A.D	*	D.C=A.B.E
WFL	?E.D=C=B.A	*	E.D.A.C.B	B.C.E.D.A	*	B.C.D.A.E
ASC1–4	27–30	33–39	28–35	36–41	36–39	28–37
ASIn1–4	2.9–3.9	8.5–10.9	3.7–4.0	3.5	6.5–9.8	7.1–7.7
PAI	17.1	27.4	19.3	13.2	-	-
CaLI	8	F	F	#	5.9	F
LLI	32.5	F	F	#	41.8	F

[1] Excludes hectocotylised third right arm.

Family **ARGONAUTIDAE** Tryon, 1879

Suckers biserial, borne on marginal membranes; water pores absent; web very shallow; body firm, mantle thin and muscular; tips of female dorsal arms with broad, membranous, glandular flaps that secrete and hold secondary shell; sexual dimorphism pronounced, males dwarf; entire third right or left arm (almost invariably left) hectocotylised, arm developing in pouch beneath eye, autotomised when mature; radula heterodont; mantle-locking apparatus well developed; funnel organ W-shaped; shell vestige absent (after Hochberg *et al.* 1992: 232–234). Family monogeneric for *Argonauta* Linnaeus, 1758.

REMARKS: Hochberg *et al.* (1992) provide a synopsis of information on *Argonauta* species that includes several apparent errors. Consequently, to facilitate comparison of the New Zealand species with foreign species, specimens of *A. boettgeri* Maltzan and *A. hians* Solander have had to be examined (measures in Tables 33 and 34). Amended characters (in parenthesis) include: *A. hians* is described with 20 lamellae per outer demibranch of each gill, a figure probably misquoted and meant to read 10 lamellae per outer demibranch (one specimen detailed below possessed 12 outer lamellae); *A. boettgeri* cited with arm pair 4 shorter than arm pairs 2 and 3 (the single specimen for which data is provided has arm pairs 2–4 of subequal length).

Argonauta Linnaeus, 1758

DIAGNOSIS: With characters of the family.

TYPE SPECIES: *Argonauta argo* Linnaeus, 1758.

Table 32. Raw measures for *Amphitretus thielei* (* denotes damage; # denotes third right arm enclosed in pouch, measures not calculated to prevent damage).

	NZOI Stn Z8413	NMNZ M.118400	NZOI Stn Z8475	NZOI Stn Z8412	NMNZ M.118400	NMNZ M.95247
sex	M	F	F	M	M	F
TL	197	253.5	161	119	181	98
ML	73.5	64.5	57	57	*c.* 51	31
MW	42.5	40	29.5	41.5	34	25
HdL	13.5	15	10	10	10.5	6.9
HdW	22.5	39	18.2	38.5	21.5	26.2
ED	9	11.5	9	8	10.5	6
EO	1.9	2.3	*	2	*	*
AL1R/L	102/90	133/112*	77/72	76/89	104/96	*/77
AL2R/L	87/96	186/151	82/68	82/78	94/96	64/79
AL3R/L	77/105	172/160	101/71	#/95	141/94	75/80
AL4R/L	67*/112	159/138	90/74	76/77	88/ *c.* 90	75/80
WDA	50.5*	66.5	41.0	31.0	55.5	30.0
WDBR/L	43.0/54.5	81.0/78.0	25.0/32.0	43.0/47.0	*/*	27.0/37.0
WDCR/L	47.5/54.0	78.0/78.5	52.0/37.0	33.0/45.0	*/*	30.0/34.0
WDDR/L	56.5/54.5	73.0/66.5	27.5/45.0	24.5/37.0	*/*	31.0/33.0
WDE	60.5	47*	47.0	41.0	*	26.0
ASC1R/L	*/27	38/19*	23*/25*	38/38	36/37	*/34
ASC2R/L	30/21*	29*/38	21*/30	36/38	38/38	36/36
ASC3R/L	24/30	20*/39	32/35	#/38	21/37	33/34
ASC4R/L	13*/29	20*/33	31/28	36/41	36/39	28/37
ASn1R	2.9	7	2.1	2	3.3	2.2
ASn2R	2.9	6.3	2.3	2	3.3	2.4
ASn3R	2.1	5.5	2.3	2	5	2.3
ASn4R	2.6	6.2	2.1	2	3.3	2.3
GiLC	8	8	8	8	8	8
PAI	12.6	17.7	11	7.5	*	*
CaL	2	F	F	#	3.5	F
LL	25	F	F	#	59	F

Argonauta argo Linnaeus, 1758 (Fig. 59) (Tables 35, 36)

Argonautam Argon [*sic*]: Forster 1844.

Argonauta argo: Suter 1913: 1066–1067, pl. 72; Powell 1937: 95; 1946; Dell 1951: 97; 1952: 48, pl. 10–11: 100; Powell 1957: 125; 1962: 125;1976: 133; 1979: 444, pl. 80, figs 3–4; Nesis 1987: 327, figs 88A–C; Hochberg *et al.* 1992: 234, figs 251a–b; Smale *et al.* 1993: 282–283, figs a–b; Spencer & Willan 1995: 53.

Argonauta bulleri Kirk, 1885: 138–139, pl. 4; Hoyle 1897: 365.

MATERIAL EXAMINED (No New Zealand animals known; shells number 8): NMNZ M.5298, 3, ø 111, 62, 45 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. T. Iredale, 1908; NMNZ M.11316, 1, ø 104 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. R.S. Bell, ex. Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. Mrs Gelderd; NMNZ M.75276, 1, ø 155 mm, Ninety Mile Beach, *c.* 34°50' S, 173°00' E, coll. I. McMillan, pres. P. Jamieson; NMNZ M.4160, 1, ø 147 mm, Portland Island, *c.* 39°17' S, 177°52' E, coll. M. Anderson, 1897; NMNZ M.32950, 1, ø 153 mm, Riversdale Beach, Wairarapa, *c.* 41°05' S, 176°04' E, coll. P. Barton, 10/03/1974.

FOREIGN MATERIAL EXAMINED (2 females [F]): BMNH 1898.5.21.362, F, ML 49.8 mm, Nice, France, Gal Frères, 1840, ex. Norman coln; BMNH 1958.12.30.90, F, ML 37.7 mm, Madeira, ex. G.E. Maul colln (no. 3489).

REFERENCE MATERIAL: *Argonauta boettgeri* Maltzan, det. G.C. Robson, BMNH 1995156, Arcturus Expedition 1925 Stn ?258 [*sic.*], 51F (+ tube of hectocotylii); *Argonauta hians*, BMNH 1897.1.13.1–3, 3F, ML 52.7, 44.5, 29.3 mm, Muscat, Arabia, col. Dr Jayakar.

RECOGNISED DISTRIBUTION (New Zealand, Fig. 58, p. 82): *c.* 29°16–41°05' S, 173°00'E–177°54' W, all records based on beach-cast shells. Otherwise tropical-subtropical cosmopolitan (Nesis 1987: 327).

Table 33. Indices, formulas and counts for *Argonauta* spp. (* denotes damage; # denotes distortion of dorsal arm tips making accurate length measurement difficult; † denotes distal arm tip suckers difficult to count).

	A. boettgeri BMNH 1995156	*A. hians* BMNH 1897.1.13.1–3
MWI	62.8	63.6
HdLI	27.2	29.4
HdWI	61.1	56.9
EDI	27.8	28.3
EOI	6.7	6.1
ALI1	119.5#	86.0#
ALI2–4	51.2–56.1	40.4–73.0
AFR	1.3.2.1	1.2.3.4
AFL	1.2.4.3	1.2.3.4
WDIA–E	10.4–14.3	7.9–14.4
WFR	A.B=D.E.C	A.C.D.B.E
WFL	A.D.B.E.C	A.B.D.C.E
ASC1R	150†	-
ASC2–4	48–83†	-
ASIn1–4	8.3–9.4	9.7–12.7
FuLI	52.2	51.2
FFuI	27.8	25.0

Table 34. Raw measures for female *Argonauta* spp. (* denotes damage; # denotes distortion of dorsal arm tips making accurate length measurement difficult; † denotes distal arm tip suckers difficult to count).

	A. boettgeri BMNH 1995156	*A. hians* BMNH 1897.1.13.1–3
ML	18.0	52.7
TL	41	178
MW	11.3	33.5
HW	11.0	30.0
HdL	4.9	15.5
AL1R/L	49#/-	134#/153#
AL2R/L	22/23.0	122/130
AL3R/L	22.5/21	91/90
AL4R/L	21/21.5	70*/72
WDA	7	22.1
WDBR/L	6.0/5.9	14.0/17.0
WDCR/L	5.1/5.1	15.5/16.0
WDDR/L	6.0/6.2	15.0/16.5
WDE	5.6	12.1
ASC1R	150†	*
ASC2R	83†	*
ASC3R	74†	*
ASC4R	48†	*
ASn1R	1.7	6.1
ASn2R	1.5	5.4
ASn3L	1.5	5.1
ASn4R	1.5	6.0
GiLC	13	12
FuL	9.4	27.0
FFL	5.0	13.2
ED	5.0	14.9
EO	1.2	3.2

DESCRIPTION: New Zealand shells attaining moderate size (shell to 155 mm greatest diameter). The following account of female morphology is based on non-New Zealand specimens. Mantle elongate, conical, laterally compressed, with anterior third strongly reflected upwards; pallial aperture very wide, points of mantle attachment superior to eyes, mantle attached directly to base of arm pair 1. Head indistinct, dorsal head musculature absent; head partially retracted into mantle, neither head nor mantle constrictions distinct. Orbits large (EDI 22.1–24.4), bulbous, laterally oriented; orbits situated on base of arm pairs 2 and 3; eye aperture small. Funnel long (FuLI 56.2–58.1), free distal portion short to moderately long (FFLI 23.1–28.1), attached to base of arm pair 4 at level of 3rd sucker by lateral membrane continued along aboral surface of arm pair 4.

Female brachial crown and arms slender. Arms laminar, short to very long (about 44–96% TL), tapering to laminar tips; arm formula 1.4.2.3, with arm pair 4 about two times longer than arm pairs 2 and 3; dorsal arm pair 1 develops a wide membranous extension along arms at level of 13 or 14th adoral sucker; membranes (in preserved specimens) throw arms into convoluted folds. Web shallow (WDI 5.9–11.5% longest arm length), without web extension down arm pairs 2–4; web formula variable, with sector A deepest and C shallowest in both specimens.

Female whole-arm sucker count high, to 250 (ASC: arm pair 1, 232–250; 2, 138–143; 3, 58–149; 4, 137–147); suckers extend almost to tip of each arm, terminally indistinct. Suckers biserial, positioned along lateral margins of arms, small (ASIn 5.6–8.0); suckers on distal third of arm minute. Suckers widely spaced along entire arm length, distance between suckers about 1 sucker diameter; first 13 or 14 suckers along arm pair 1 largest, thereafter suckers abruptly decrease in size, size gradually decreasing to arm tips; first 12 suckers on arm pair 2, and 10 on arms 3 and 4, largest, thereafter suckers gradually decrease in diameter to each arm tip.

Shell well described and illustrated throughout conchological literature; it is pearly white, with a narrow keel, laterally compressed, with knobs on narrow keel sepia-stained (Fig. 59).

Indices, formulas, and counts for *A. argo* in Table 35; raw measures in Table 36.

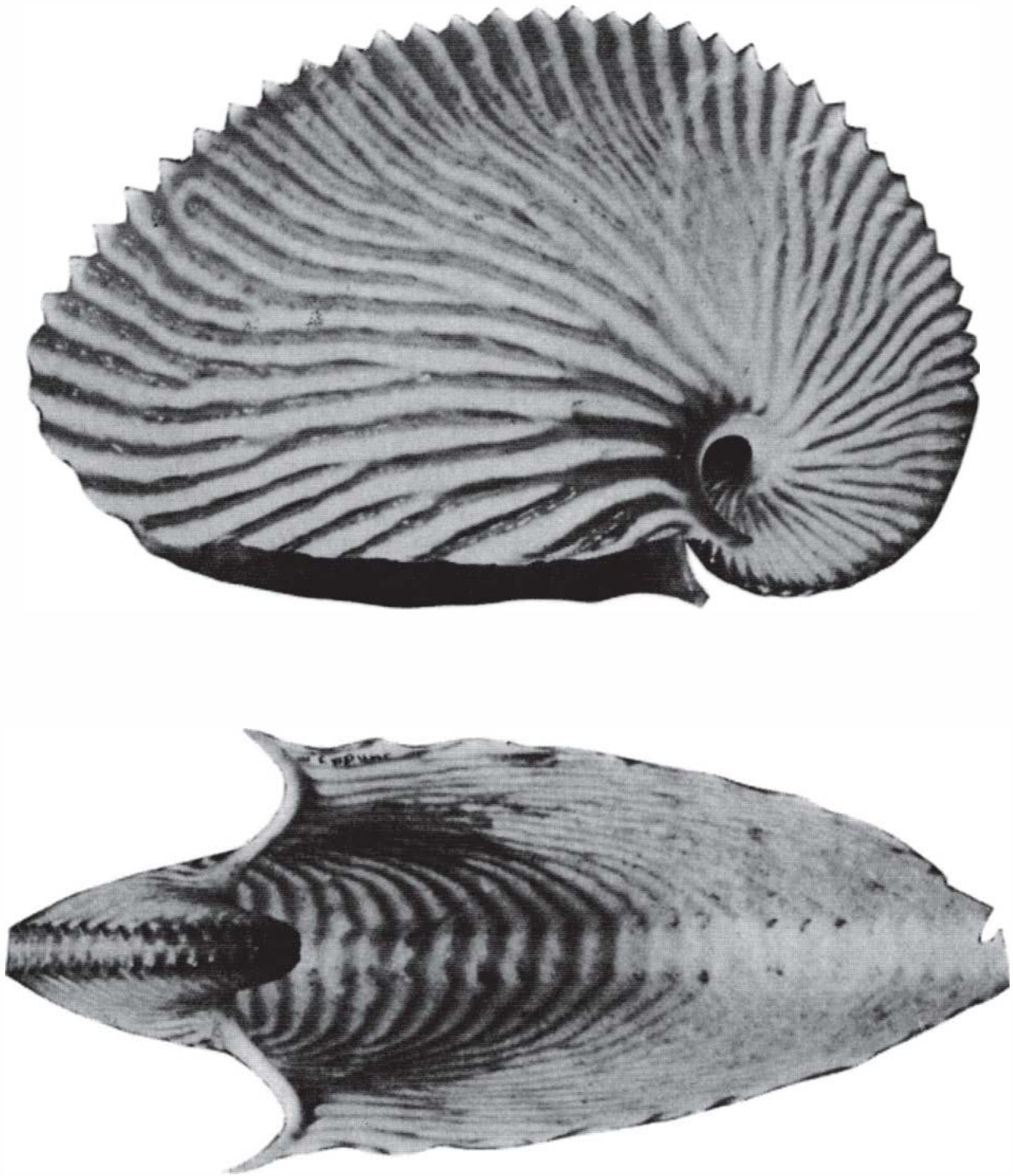


Figure 59. ***Argonauta argo*** Linnaeus, 1758 Shells NMNZ M.5298.

Table 35. Indices, formulas, and counts for female *Argonauta argo* (* denotes damage; # denotes distortion of dorsal arm tips making accurate length measurement difficult; † denotes distal arm tip suckers difficult to count).

	BMNH 1898.5.21.362	BMNH 1958.12.30.90
MWI	40.6	39.8
HdLI	21.1	25.2
HdWI	40.0	37.1
EDI	22.1	24.4
EOI	6.6	7.2
ALI1	84.2–89.5#	89.1–94.6#
ALI2–4	44.7–74.7	44.2–73.6
AFR	1.?4.2.3	1.4.2.3
AFL	1.4.?2.3	1.4.2.3
WDIA–E	5.9–10.3	6.6–11.5
WFR	A.E.B=D.C	A.D.B.E.C
WFL	A.E.B=D.C	A.B.D.E.C
ASC1	232†	250†
ASC2–4	58–147†	137–149†
ASIn1–4	5.6–7.0	6.1–8.0
FuLI	56.2	58.1
FFuI	23.1	28.1

Table 36. Raw measures female *Argonauta argo* (* denotes damage; # denotes distortion of dorsal arms makes length measurement difficult; † denotes distal arm-tip suckers difficult to count).

	BMNH 1898.5.21.362	BMNH 1958.12.30.90
ML	49.8	37.7
TL	190.0	129.0
MW	20.2	15.0
HW	19.9	14.0
HdL	10.5	9.5
AL1R/L	170#/160#	122#/115#
AL2R/L	11856*	67/75
AL3R/L	85/94	62/57
AL4R/L	109*/142	95/86
WDA	17.5	14.0
WDBR/L	13.0/13.0	10.0/12.0
WDCR/L	10.0/10.5	8.5/8.0
WDDR/L	13.0/13.0	11.0/10.0
WDE	13.5	9.0
ASC1R	L 232†	250†
ASC2R	L 138†	143†
ASC3R	58†	149†
ASC4R	L 147†	137†
ASn1R	3.5	3.0
ASn2R	3.0	2.3
ASn3L	2.8	2.3
ASn4R	3.1	2.9
GiLC	13	12
FuL	28.0	21.9
FFL	11.5	10.6
ED	11.0	9.2
EO	3.3	2.7

Neither female available was dissected to examine reproductive system and alimentary canal; nor were there any detached hectocotyli in the mantle cavity, although both specimens appear mature and possess eggs in the distal oviducts. There are 12 or 13 gill lamellae per outer demibranch.

REMARKS: Hochberg *et al.* (1992) gave the following characteristics for *A. argo* (with amended details in parentheses): females with arm pair 4 longer than pairs 2 and 3 (arm pair 4 about twice arm lengths 2 and 3), with arm pair 1 with 150 suckers (ASC to 250), and gills with 28 lamellae per outer demibranch (with 12 or 13 lamellae per outer demibranch). *Argonauta argo* differs markedly from *A. nodosa*, *A. boettgeri*, and *A. hians* in the relative length of arm pair 4, the three latter species having arms 4 shorter than or of subequal length to arm pairs 2 and 3. An excellent account of comparative beak structure for *A. argo*, *A. nodosa*, and *A. hians* is presented by Smale *et al.* (1993: 282–283, figs 12a–d).

Argonauta nodosa Solander, 1786 (Figs 62-65) (Tables 37, 38, 40, 41)

New Zealand synonymy:

Argonauta nodosa Solander, 1786: Gray 1843: 244; 1849: 33; Powell 1937: 95, pl. 17, fig. 7; 1946: 100, pl. 17, fig. 7; Dell 1951: 97, figs 23–24; 1952: 56, pl. 12, 13, 15, 16; Powell 1957: 125, pl. 17, figs 6–7; 1962: 125, pl 17, figs 6–7; 1976: 133, pl. 24, figs 6–7; 1979: 445, pl. 80, figs 3–4; Imber 1975: 30; 1976: 124; Nesis 1987: 327, fig. 88D; Imber 1992: 248; Smale *et al.* 1993: 283, figs c, e; Spencer & Willan 1995: 53.

Argonauta tuberculata Shaw, 1791: Hutton 1880: 2; Hoyle, 1885; Kirk 1885: 58–59, pl. 13; Suter 1913: 1067, pl. 71; Powell 1937: 95, pl. 17, fig. 6; 1946: 100, pl. 17, fig. 6.

Argonauta gracilis Kirk, 1885: 58–59, pl. 13; Hoyle 1885; 1886a: 5; 1886b: 213.

?*Argonauta hians* (not Solander): Suter 1913: 1067, pl. 69, fig. 4; Powell 1937: 95; 1946: 100; Dell 1951: 97; 1952: 53; Powell 1962: 125; 1976: 133; 1979: 445.

Argonauta boettgeri (not Maltzan): Massy 1916a: 143–144, figs 1–2; Powell 1937: 95; 1946: 100; Dell 1951: 97; 1952: 50; Powell 1962: 125; 1976: 133.

MATERIAL EXAMINED (32 animals, 7 male [M], 23 female [F], 2 sex indet.; 86 shells): NMNZ M. 2056371, F, ML 87.0 mm, Raoul Island, Kermadec Islands, *c.* 29°16'S, 177°54'W, coll.

R.S. Bell, 1913; NMNZ M.2056379, hectocotyl, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. K. Bell, 1913; NMNZ M.56365, 2F, ML 68.2, 44.1 mm, Kermadec Islands, *c.* 29°16' S, 177°54' W, R.S. Bell, 1910, ex. Oliver colln.; BMNH 1919.12.30.80, F, ML 8.0 mm, off Three Kings Islands, *c.* 34°10' S, 172°05' E, surface, plankton, 27/08/1911, *Terra Nova* Stn 130; NMNZ M.67329, F, ML 4.0 mm, sex indet., ML 3.0 mm, 34°25' S, 173°04' E, off North Cape, 4–35 m, 02/07/1977, f.r.v. *Ikatere*; NMNZ M.90360, F, ML c. 79 mm, *c.* 35°30' S, 174°45' E, 12/12/1971, ex. stomach contents Kingfish; NMNZ M.90285, F, ML 73.5 mm, 35°37' S, 178°13' E, depNR, 8/12/1981, f.v. *Island Princess*, set 9; NZOI Stn Z8575, F, ML 47.0 mm, FFN (+ shell, ø 76.5 mm), 37°00.38–36°54.34' S, 176°16.58–17.58' E, 417–421 m, 20/10/1996, f.v. *Drysdale* Stn DRY9602/09; NMNZ M.90334, F, ML 90.0 mm, 37°28.4' S, 178°17.2' E, 67–108 m over 450–800 m, 07/03/1976, f.r.v. *James Cook* Stn J4/63/76; NMNZ M.90303, F, ML 76.0 mm, 37°34.75' S, 178°22.25' E, surface over 42 m, 19/11/1976, f.r.v. *James Cook* Stn J16/71/76; NMNZ M. 131728, M, ML 5.1 mm, F, ML 4.0 mm, 37°48' S, 178°45' E, *c.* 35 m, f.r.v. *James Cook*, 19/10/1969; NMNZ M.102214, M, ML 2.5 mm, 37°49.0' S, 174°06.5' E, 151–155 m, 19/07/1985, f.v. *Kaiyo Maru* Stn 101A, Bongo 0.335; NZOI Stn Z8588, F, ML 57.5 mm (+ shell [damaged] ø 64.5 mm), FFN, 37°49.12–47.55' S, 174°33.77–34.23' E, 63–61 m, BT 13.9°C, f.r.v. *Kaharoa* Stn KAH9615/069; NMNZ M.67235, F, ML 53.0 mm, 37°51.6' S, 179°19.9' E, 30 m, 30/09/1979, f.r.v. *James Cook* Stn J13/006/79; NMNZ M.102126, M, ML 3.5 mm, 2F, ML 4.0, 3.4 mm, 38°30.0' S, 172°42.4' E, 190 m over 802 m, 20/08/1985, f.v. *Kaiyo Maru* Stn KM2/85/202C, Bongo; NMNZ M.102219, F, ML 4.0 mm, 38°49.2' S, 172°45.5' E, 146–147 m, 19/07/1985, f.v. *Kaiyo Maru* Stn 102A, Bongo; NMNZ M.126436, F, ML 29.6 mm, 39°00.22' S, 174°55.52' W, 15–100 m over 5500 m, 20/03/1995, f.r.v. *Tangaroa* Stn TAN9503/07; NMNZ M.126437, M, ML 10.1 mm, 39°00.76' S, 175°09.70' W, 15–93 m over 4850 m, 20/03/1995, f.r.v. *Tangaroa* Stn TAN9503/06; NMNZ M.67872, F, ML 63.0 mm, 39°09.15' S, 178°50.72' E, surface, 12/10/1979, f.r.v. *James Cook* Stn J13/25/79; NMNZ M.6725, eggs, Portland Island, Hawke Bay, *c.* 39°17' S, 177°52' E, coll. R. Morrisey, 1954; NMNZ M.102130, M, ML 3.0 mm, 39°53.6' S, 172°25.6' E, 220 m over 236 m, 24/08/1985, f.v. *Kaiyo Maru* Stn KM2/203B, Bongo 0.335; NMNZ M.95260, M, ML 13.5 mm, 3F, ML 24.0, 12.5, 9.3 mm, 40°08.3–05.6' S, 160°14.9–16.6' E, FMMWT, 45–35 m over 4700+ m, 16/10/1985, f.r.v. *James Cook* Stn J16/08/85; NMNZ M.67892, F, ML 7.0 mm, 40°55.6' S, 172°01.2' E, 30 m, 13/10/1979, f.r.v. *James Cook* Stn J14/5/79; NMNZ M.102225, 2F, ML 3.8, 3.4 mm, 40°58.0' S, 170°57.3' E, 485–478 m, 23/07/1985, f.v. *Kaiyo Maru* Stn 105B, Bongo; NMNZ M.11215, F, ML 65.2 mm (+ shell), Kopea Bay, Tory Channel, *c.* 41°14' S, 174°14' E, coll. I. Kirk, -/-/1957; NMNZ M.102258, F, ML 3.0 mm, 41°34.6–34.0' S, 169°55.5–56.2' E, 450 m over 925 m, 23/07/1985, f.v. *Kaiyo Maru* Stn 106C, FMMWT; NMNZ M.102189, M, ML 4.5 mm, *c.* 46°38' S, 167°20' E, 50–0 m, 01/09/1985, f.v. *Kaiyo Maru* Stn 228B, Bongo 0.335.

ADDITIONAL MATERIAL EXAMINED (Shells): NMNZ M.211318, 3, ø 163, *c.* 144, 130 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. T. Iredale, -/-/1908, ex. Oliver colln; NMNZ M.205301, 3, ø 75, 49, 24 mm, Raoul Island Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. R.S. Bell, -/-/1910; NMNZ M.211313, 3, ø 84, 59, 48 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. R.S. Bell, 1910, ex. Oliver colln; NMNZ M.5294, 3, ø 200, 196, 76 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, pres. Mrs Gelderd, datNR; NMNZ M.5300, 13, ø 57, 54(2), 41(2), 40(2), 26, 20, 19, 3 damaged, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, pres. Mrs Gelderd, -/-/1945; NZOI Stn F909, fragment, 35°06.4' S, 175°11' E, 1027 m, 10/10/1968; NMNZ M.23915, 2, ø 99, 87 mm, Middle Arch, 10–13 m, Poor Knights Islands, *c.* 35°30' S, 174°45' E, coll. A.N. Baker, 05/01/1970; NZOI Stn I6, 1, ø 51.5 mm, 35°47.2' S, 175°36.8–39.2' E, 263–287 m, 03/05/1975; NMNZ M.5682, 1, ø 98 mm, Great Barrier Island, *c.* 36°10' S, 175°25' E, datNR, ex. C.A. Fleming colln; NMNZ M.95204, 1, ø *c.*35 mm, 36°28.6' S, 177°43.5' E, E. off Cuvier Island, 30 m, datNR, f.r.v. *James Cook* Stn J15/1/87; NMNZ M.9636, 2, ø 248, 242 mm, Kaipara, *c.* 36°30' S, 174°20' E, datNR; NMNZ M.5683, 11, ø 63, 46, 39, 32, 30, 28, 23, 22(2), 19, 18, Mayor Island, *c.* 37°18' S, 176°16' E, coll. C.A. Fleming, -/12/1936; NMNZ M.21732, 3, ø 170, 83, 73 mm, Mayor Island, *c.* 37°18' S, 176°16' E, coll. E.J. Booth, 26/10/1960; NMNZ M.23908, 1, ø 23 mm, Southeast Bay, Mayor Island, *c.* 37°18' S, 176°16'' E, coll. A.N. Baker, 27/10/1969; NMNZ M.75282, 3, ø 126, 94, 86 mm, Mayor Island, *c.* 37°18' S, 176°16' E, datNR, coll. E.Y. Wolf; NMNZ M.67864, 2, ø 76, 75 mm, Mayor Island, *c.* 37°18' S, 176°16' E, coll. N.J. Peterson, -/-/1972; NMNZ M.17987, 4, ø 138, 99, 89, 88 mm, washed ashore, White Island, *c.* 37°31' S, 177°11' E, coll. S. Sampson, 17/11/1964; NMNZ M.4161, 1, ø 148 mm, Portland Island, *c.* 39°17' S, 177°52' E, coll. M. Anderson, -/-/1897; NMNZ M.9635, 1, ø 105 mm, Portland Island, *c.* 39°17' S, 177°52' E, datNR; NMNZ M.6725, 1, ø 109 mm, Portland Island, *c.* 39°17' S, 177°52' E, coll. R. Morrisey, -/-/1954; NMNZ M.11844, 1, ø 115 mm, Portland Island, *c.* 39°17' S, 177°52' E, coll. D. Neilson, -/-/1957; NMNZ M.11208, 1, ø 121 mm, Makara, *c.* 39°24' S, 175°17' E, coll. A. Christie, 08/06/1957; NMNZ M.14973, 1, ø 38 mm, Makara Beach, *c.* 39°24' S, 175°17' E, 21/01/1961; NMNZ M.9634, 2, ø 56, 50 mm, Kapiti Island, *c.* 40°5' S, 174°54' E, datNR; NMNZ M.9637, 1, ø 181 mm, Kapiti Island, *c.* 40°52' S, 174°54' E, datNR; NMNZ M.10928, 1, ø 118 mm, Kapiti Island, *c.* 40°52' S, 174°54' E, coll. Mrs Fox, -/01/1957; NMNZ M.83601, 1, ø 116 mm, Kapiti Island, *c.* 40°52' S, 174°54' E, coll. P.R. Jamieson, -/02/1982; NMNZ M.11873, 1, ø, damaged, Waikanae Beach, Wellington, *c.* 40°53' S, 175°04' E, 25/12/1956; NMNZ M.12995, 2, ø 189, 138 mm, Paraparaumu Beach, Wellington, *c.* 40°54' S, 174°59' E, coll. D. Neale, 13/06/1957; NMNZ M.5685, 1, ø 115 mm, d'Urville Island, French Pass, *c.* 40°55' S, 173°51' E, datNR, pres. M.K. Mestayer; NMNZ M. 15143, 1, ø 42 mm, d'Urville Island, *c.* 40°55' S, 173°51' E, datNR, ex Suter colln; NMNZ M.11104, 1, ø 66 mm, Tory Channel, *c.* 41°14' S, 174°14' E, coll. M. Kirk, -/12/1956, -/03/1957; NMNZ M.11105, 4, ø 140, 118, 66, 54 mm, Tory Channel, *c.* 41°14' S, 174°14' E, coll. M.W. Kirk, -/12–03/1957–1958; NMNZ M.17930, 5, ø 60, 55(2), 46, 28, Erie Bay, Tory Channel, *c.* 41°14' S, 174°14' E, coll. E.M. Perano, 1961–1964; NMNZ M.10445, 1, ø 165 mm, Palliser Bay, Wellington, *c.* 41°25' S, 175°05' E, 18/12/1956; NMNZ M.9633, 1, ø 212 mm, Port Hutt, Chatham Islands, *c.* 43°51' S, 176°42' W, coll. R.K. Dell, 09/02/1954; NMNZ M.5684, 1, ø 188 mm, Momoe-a-

toa Beach, Chatham Islands, *c.* 44°00' S, 176°35' W, datNR, coll. R. MacClurg, ex C.A. Fleming colln; NMNZ M.11207, 1, ø 105 mm, Flower Pot, Pitt Island, Chatham Islands, *c.* 44°17' S, 176°13' W, coll. C.J. Lindsay, 30/01 /1957.

REFERENCE MATERIAL: *Argonauta argo*, BMNH 1898.5.21.362, F, ML 49.8 mm, Nice, France, Gal Frères 1840, ex. Norman colln; *Argonauta argo*, BMNH 1958.12.30.90, F, ML 37.7 mm, Madeira, ex. G.E. Maul colln (no. 3489); *Argonauta boettgeri* Maltzan, det. G.C. Robson, BMNH 1995156, Arcturus Expedition 1925 Stn ?258 [*sic.*], 51F + tube hectocotyli.

DISTRIBUTION (New Zealand, Fig. 60, p. 82; Fig. 61, p. 100): North of Subtropical Convergence, about 29°16–46°38' S, 173°51' E –176°13' W; recorded depth range from surface to 485–478 m over bottom depths up to 4850 m. Otherwise recorded from tropical Indo-West Pacific from Red Sea and southern Japan to southern Africa, Australia, Polynesia and ?Chile [*sic*] (Nesis 1987: 327).

DESCRIPTION (Females, Figs 62A–D): New Zealand females attain moderate size (ML to 90 mm, TL to 267 mm, shell to 248 mm greatest diameter). Skin entirely smooth; mantle ovoid, with weak lateral compression, with anterior third weakly reflected upwards; pallial aperture very wide, points of mantle attachment dorsolateral to eyes, free of arm pair 1. Head indistinct, dorsal head musculature absent; head partially retracted into mantle, neither head nor mantle constrictions distinct. Orbits large (EDI about 20–35), bulbous, laterally oriented, situated on base of arm pairs 2 and 3; eye aperture small. Funnel long (FuLI about 51–66), free distal portion short to long (FFLI about 18–44), attached to base of arm pair 4 at level equivalent to 5th sucker by lateral membrane continued along aboral surface of arm 4.

Female brachial crown and arms robust, arms stout, broadly laminar, short to very long (about 44–138% TL); arm formula 1.2.3.4 to 1.2.4.3, with arm pairs 3 and 4 subequal, arm 2 longer and arms 1 usually even longer; dorsal arm pair 1 develops wide membranous extensions down arm from level of 14–20th sucker; membranes (in preserved specimens) distort arms into convoluted folds. Web shallow (WDI 6–15% longest arm length), without web extension down arm pairs 2–4; web formula variable, with sector A usually deepest, sectors C or E shallowest.

Female whole-arm sucker count high, to 292 (ASC: arm pair 1, 248–292; 2, 120–199; 3, 106–178; 4, 80–120); suckers extend almost to tip of each arm, indistinct terminally. Suckers biserial, positioned along lateral margins of arms, small to moderate sized (ASIn 5.9–10.1); suckers on distal third of arm minute. Suckers widely spaced along entire arm length, distance between suckers about 1 to 2 sucker diameters; first 14–16 suckers along arm pair 1 largest, thereafter suckers gradually decrease in size to arm tips; first 14 suckers on arm pair 2, and 12–14 on arms 3 and 4, largest, thereafter suckers gradually decrease in size to arm tips.

Mantle and head (fresh dead) iridescent pinkish-red with numerous small dark red chromatophores; ventral surfaces of mantle iridescent greenish-blue or pink; dorsal arms iridescent bluish-purple, the lateral extensions of web iridescent silver to gold. Arm pairs 2–4 translucent to opaque with patches of gold, blue and green iridescence.

Shell (Fig. 63) inflated, with sepia-stained knobs on keel, the remainder of the shell pearly white; keel wide.

Male (Figs 62E–F, 64A–C) considerably smaller than female, lacking both shell and dorsal arm tip membrane development. New Zealand males small (ML to 13.5, TL to 29.5 mm); skin entirely smooth; mantle ovoid, not laterally compressed nor with mantle anterior third deflected up; pallial aperture very wide, points of mantle attachment dorsolateral to eyes, free of brachial crown. Head indistinct, dorsal head musculature absent; head partially retracted into mantle, neither head nor mantle constrictions distinct. Orbits large (EDI about 39–45), bulbous, laterally oriented; orbits situated at base of arm pairs 2 and 3; eye aperture small. Funnel long (FuLI about 60–66), free distal portion short (FFLI about 18–19), attached to base of arm pair 4 at level equivalent to 1st or 2nd sucker.

Male brachial crown and arms robust; arms stout, tubular, short (about 30–52% TL), rapidly tapering to tips; arm formula 1=4.2.3 or 1=4.3.2, with arm pairs of subequal length. Web deep to very deep (WDI about 33–63% longest arm length), extending to level equivalent to 5–7th suckers; web formula variable, with sectors C and D on left side united into common sector.

Male whole-arm sucker count low (ASC 16–21), without pronounced difference in ASC values between arms; suckers extend almost to tip of each arm. Suckers biserial, small to moderate in size (ASIn 7.4–10.0). Suckers evenly spaced along arms, not deeply embedded within arm tissues, with distance between suckers about 0.5–1 sucker diameters; first 15–17 suckers on all arms of similar size, thereafter suckers abruptly decrease in diameter to arm tip; male without abrupt sucker enlargement on any arm. Third right or left arm hectocotylised; detached hectocotyli (Fig. 64D) recovered from female mantle cavities with 30–39 sucker pairs (Table 39).

Indices, formulas, and counts for female and male *A. nodosa* in Tables 37 and 38. Raw measures for male and female in Tables 40 and 41.

Table 37. Indices, formulas, and counts for female *Argonauta nodosa* (* denotes damage; # denotes difficulty in accurately enumerating distal arm tip suckers; † denotes distal arm tip suckers difficult to count).

	NMNZ M.126436	NMNZ M.256365	NZOI Stn Z8575	NZOI Stn Z8588	NMNZ M.256365	NMNZ M.90285	NMNZ M.90303
MWI	72.0	59.0	69.1	61.6	57.3	76.9	31.6
HdLI	34.8	24.9	25.5	23.7	20.4	24.4	23.7
HdWI	73.3	59.2	68.3	48.9	51.3	53.6	37.9
EDI	29.7	34.9	27.9	24.4	20.5	26.0	28.0
EOI	6.8	5.0	4.9	*	5.4	4.4	1.4
ALI1	87.5#	138.0#	119.1#	64.4#	115.0#	97.4#	90.2#
ALI2–4	52.5–61.3	56.7–71.6	52.6–71.7	51.4–71.8	49.5–68.4	43.8–73.4	56.0–78.7
AFR	1.2.3.4	1.2.3.4	1.2.3.4	2.1.3.4	1.2.3.4	1.2.4.3	1.2.3.4
AFL	1.2.3.4	1.2.4.3	1.2.4.3	2.1.3=4	1.2.3.4?	1.2.4.3	1.2.4.3
WDIA–E	8.6–13.6	9.2–12.5	9.1–13.4	10.6–19.7	7.4–11.2	6.2–11.0	8.4–15.0
WFR	A=D.C.B.E	A.D.E.C.B	A.D.B.C.E	A.D.B.E.C	A=D.B.C.E	D.C.A.B.E	A.D.E.B.C
WFL	D.A.C.B.E	A.D.C.B.E	A.D.B.C.E	A.E.B.C.D	A.B.D.C.E	A.E.B=D.C	A.D.E.B.C
ASC1R	-	-	257†	260†	L 292†	248†	-
ASC2–4	80–133†	88–156†	93–150†	103–160†	120–199†	104–160†	104–164†
ASIn1–4	7.1–10.1	7.9–9.1	7.0–8.5	6.3–7.5	5.9–7.6	6.3–8.2	6.4–8.8
FuLI	57.4	61.2	66.2	53.7	59.1	63.4	51.4
FFuI	17.6	43.8	31.9	29.1	38.1	28.7	25.0

Table 39. Number of hectocotyls and sucker counts recovered from females.

Reg.	NMNZ M. 90334	NMNZ M. 256371	NMNZ M. 90303	NMNZ M. 11844	NMNZ M.256365	NMNZ M. 11215	NMNZ M. 67872	NMNZ M. 67235
ML	90	87	73	68	66	64	63	53
# hects	1	1	1	1	2	3	4	1
# sucker pairs	30	32	39	36	36, 35	33, 34, 33	32, 34, 34, 33	35

Table 38. Indices, formulas, and counts for male *Argonauta nodosa* (* denotes hectocotylised arm distortion precluding calculation).

	NMNZ M.126437	NMNZ M.95260
MWI	71.3	74.8
HdLI	38.6	44.4
HdWI	78.2	81.5
EDI	38.6	45.2
EOI	10.0	8.9
ALI1–4	30.0–40.0	33.9–51.5
AFR	1=4.2.3	1=4.3.2
AFL	*	*
WDIA–E	37.5–62.5	32.9–46.1
WFR	B.A.C.D.E	E.D.C.A=B
WFL	*	*
ASC1–4	16–21	18–21
ASIn1–4	10.0	7.4
FuLI	59.4	65.9
FFuI	17.8	18.5

Male reproductive system (Fig. 65A) with disproportionately large cream-coloured testis sac; funnel-like structure joins testis sac to short, thick, *in situ* weakly convoluted proximal vas deferens; spermatophoral gland long, without pronounced central swelling; spermatophoral gland enters base of slender, granular accessory gland; accessory gland with incomplete terminal volution; common spermatophoral and accessory gland duct to spermatophoric sac without apparent basal appendix; spermatophoric sac vestigial, with incomplete terminal volution; penis and spermatophoric sac separated by constriction; penis about twice length of spermatophoric sac, barrel-shaped, with subterminal genital aperture.

Female with large ovary sac (Fig. 65B) distended with thousands of eggs (to 1.3 x 0.5 mm); proximal oviducts with long, well-developed funnel-like common antrum; basal portion of each oviduct strongly folded on itself, thick walled, almost fused into appendix structure, oviducal ball not located.

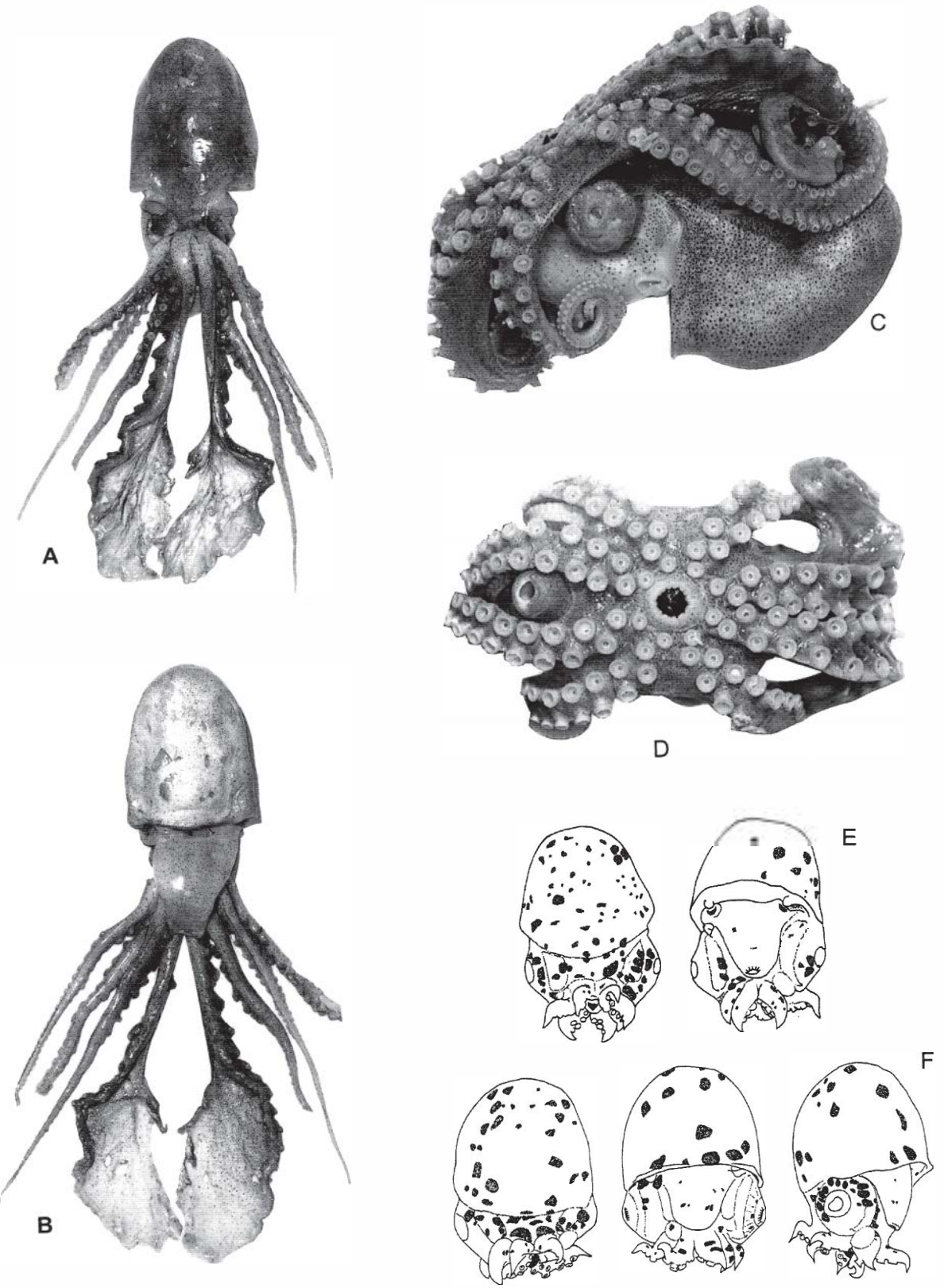


Figure 62. *Argonauta nodosa* Solander, 1786: **A, B**, unlocalised, non-accessioned female, photo post-mortem, post-thaw. **C, D**, NZOI Stn Z8575, female, ML 47 mm, photo post-narcotised-fixed specimen. **E**, NMNZ M.131728, male, ML 5.1 mm, dextral hectocotylus. **F**, NMNZ M.101216, male, ML 3.5 mm.

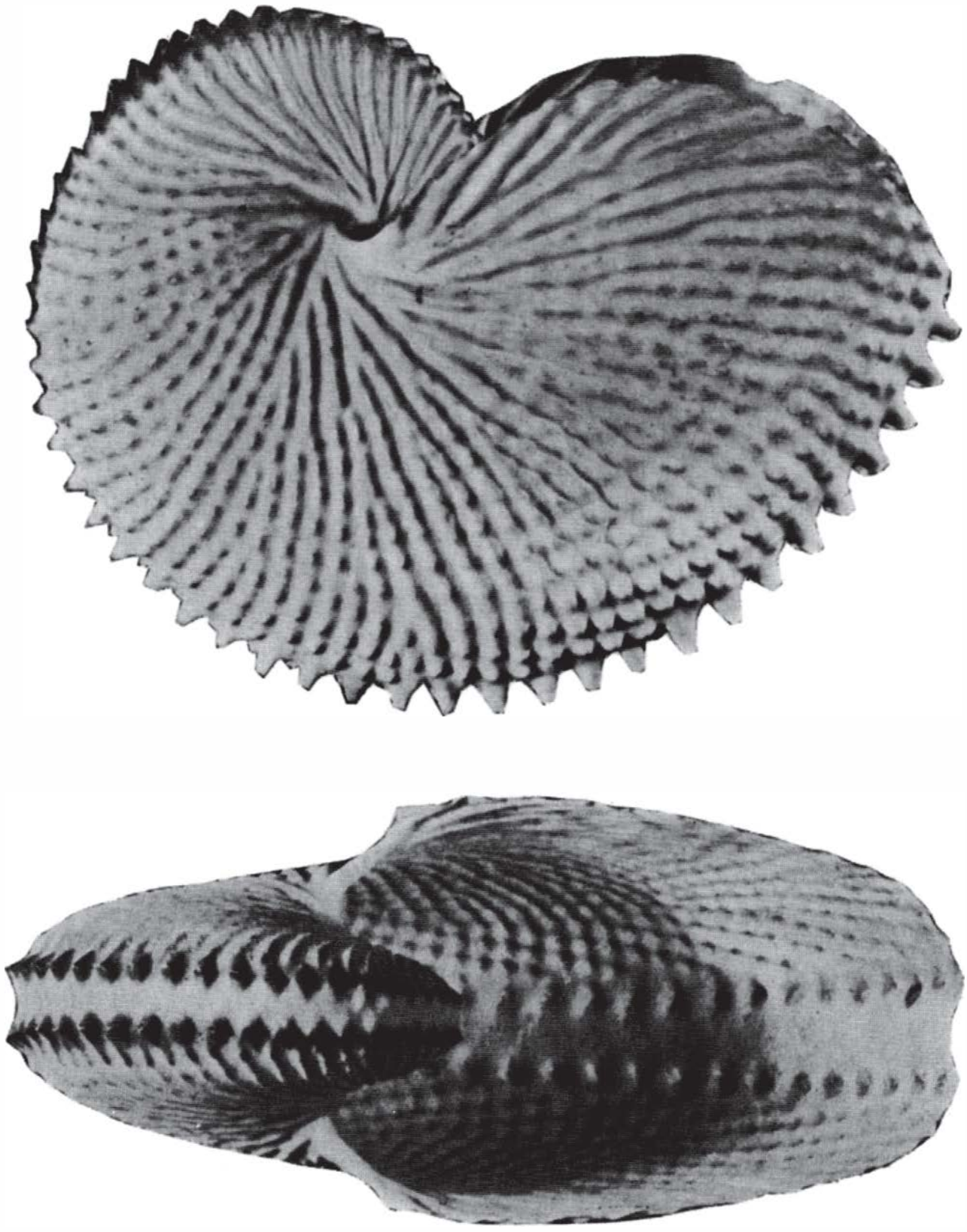


Figure 63. ***Argonauta nodosa*** Solander, 1786: Shells.

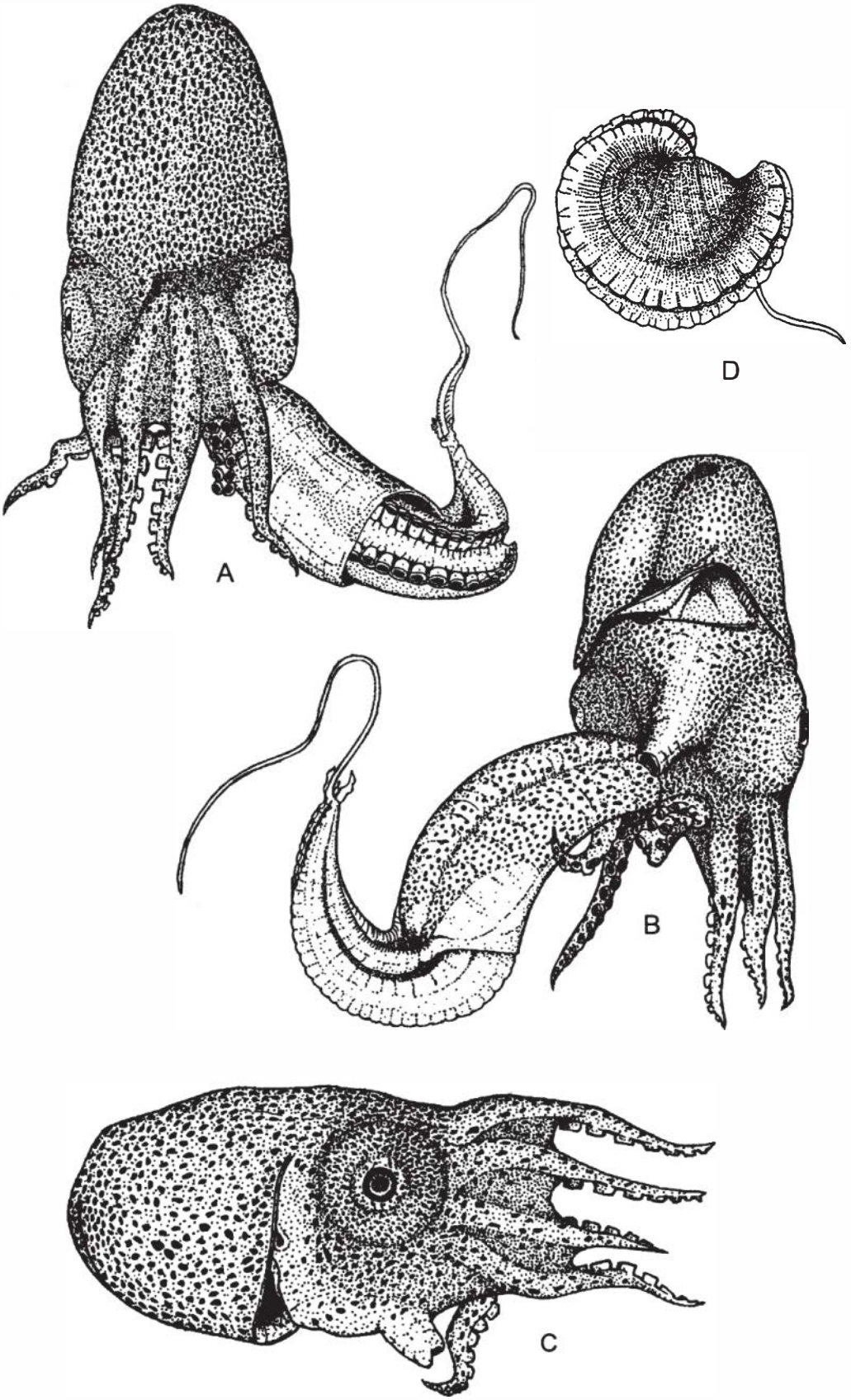


Figure 64. ***Argonauta nodosa*** Solander, 1786: **A–C**, NMNZ M.95260, male, ML 13.5 mm. **D**, hectocotylus removed from female mantle cavity, NMNZ M.67872.

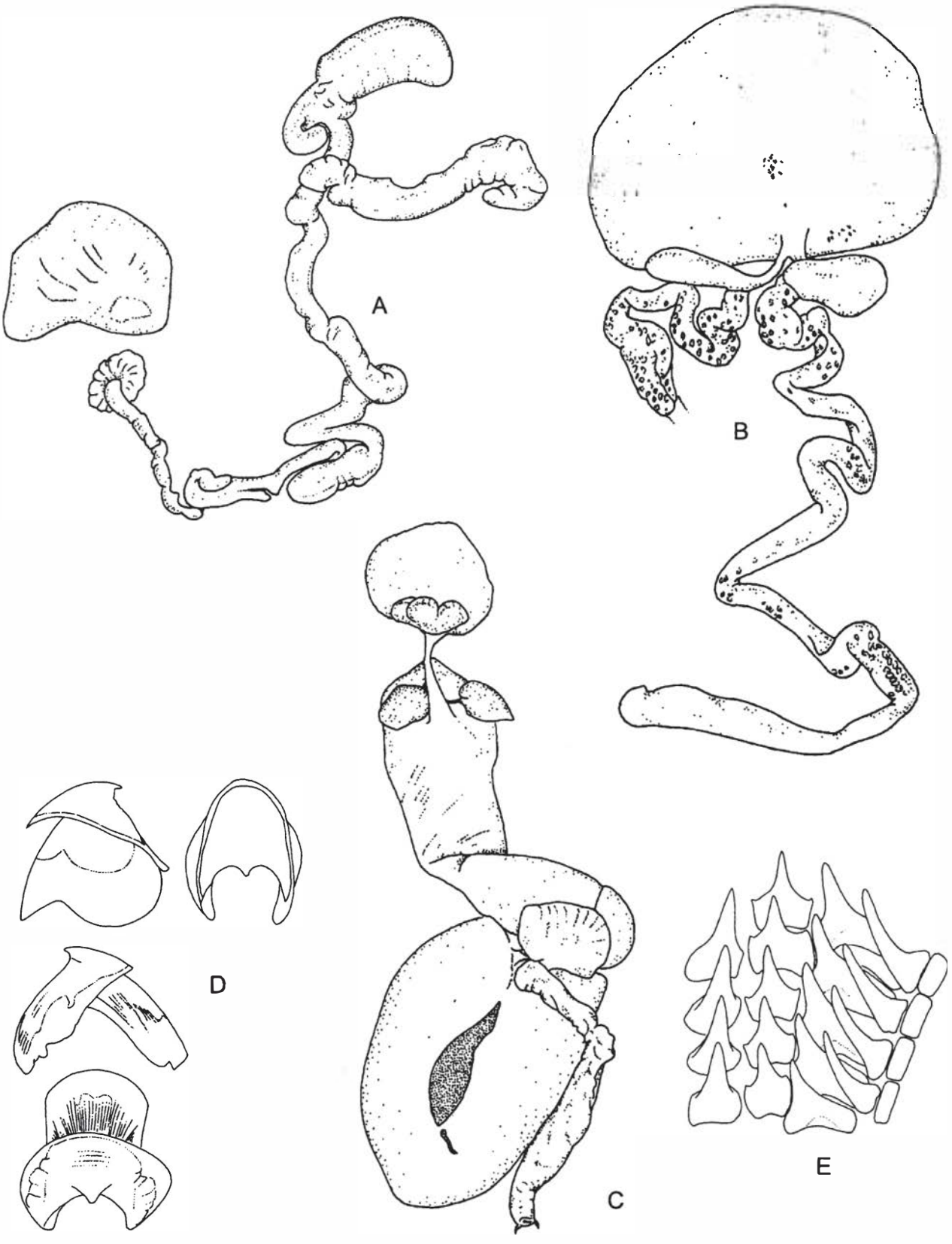


Figure 65. *Argonauta nodosa* Solander, 1786. **A**, NMNZ M.95260, male, ML 13.5 mm; **B–E**, NMNZ M.90360, female, ML about 79 mm. **A**, male reproductive system; **B**, female reproductive system; **C**, alimentary canal; **D**, beaks; **E**, radula.

Table 40. Raw measures for male *Argonauta nodosa* (* denotes damage; ‡ excludes exploded tip of flagellum; † denotes common web sectors D and CL, arms 4L and 2L united by single web sector).

	NMNZ M.126437	NMNZ M.95260
ML	10.1	13.5
TL	20.0	29.5
MW	7.2	10.1
HW	7.9	11.0
HdL	3.9	6.0
AL1R/L	8.0/8.0	13.0/13.5
AL2R/L	7.0/7.0	10.0/13.0
AL3R/L	6.7/-	10.6/37‡
AL4R/L	8.0/6.0	13.0/15.2
WDA	4.8	5.0
WDBR/L	5.0/4.0	5.0/6.5
WDCR/L	4.0/†	5.2/0
WDDR/L	3.5/†	6.8/0
WDE	3.0	7.0
ASC1R	21	20
ASC2R	19	21
ASC3R	16	20
ASC4R	20	18
ASn1R	1.0	1.0
ASn2R	1.0	1.0
ASn3L	1.0	1.0
ASn4R	1.0	1.0
HcL	-	37
GiLC	9	10
FuL	6.0	8.9
FFL	1.8	2.5
ED	3.9	6.1
EO	1.0	1.2

Proximal oviducts of enormous length, tortuously convoluted and distended with numerous eggs, with two regional constrictions, centrally and distally proximal to genital aperture; genital aperture situated on rosette-shaped papilla, with highly convoluted lumen.

Alimentary canal (Fig. 65C) with large buccal bulb higher than long; anterior salivary glands large (length about 50% buccal bulb length), crescentic, loosely applied to posterior margin of buccal bulb. Anterior oesophagus narrow, long (about 33% total oesophagus and crop length); posterior salivary glands paired, small, broadly triangular (length about 50% buccal bulb length); crop with well-developed thin-walled anterior diverticulum; stomach large (about 1.4 times buccal bulb length), with thick-walled, muscular basal section and thin-walled distal section, lumen continuous; spiral caecum thin walled, large (about 75% buccal bulb length), smaller than stomach (about 50% stomach dimension), with single incomplete volution; intestine short, of equivalent length to oesophagus and crop, dilated for greatest length; anal flaps well developed. Hepatic ducts paired; digestive gland large, elongate, of golden lustre; pancreas cream coloured, restricted to region proximal to hepatic ducts; ink sac large, deeply embedded in digestive gland, surface visible throughout length, ink sac cylindrical (length about 50% digestive gland length); ink duct short, opening at base of anus.

Upper beak (Fig. 65D) tall, conical (height 100% length), with dark brown, weakly pronounced, downward-deflected, acutely pointed rostrum; hood and lateral wall margins translucent; lateral wall crest with pronounced W-shaped dark-brown pigmentation. Hood deep (depth 62% beak length), with weakly serrate lateral prominences. Lateral walls rounded in profile, with broadly rounded crest and deep lateral wall concavity; lateral creases or ridges not apparent. Lower beak (Fig. 65D) low in profile (height 68% width), with dark-brown hood and lateral wings; margins of lateral wings and hood translucent. Lateral wall with shallow basal notch, sharp-keeled crest, and single lateral wall thickening; free corners of lateral wall acutely angled, little spread. Hood shallow (depth 43% beak length), broad, low; rostrum slightly pinched in laterally, little projecting, sharp pointed, apex slightly deflected down; lateral wings long (length 97% beak length), without apparent folds.

Radula (Fig. 65E) with wide, tall-profile rachidian with large central cusp and 2 small lateral prominences, one either side of central cusp; 1st lateral almost as wide as rachidian, with single well-developed tall cusp and basal prominence similar to 2nd cusp adjacent to rachidian tooth; 2nd lateral considerably wider than rachidian, with well-developed long cusp of similar size to that of rachidian; marginal teeth whole, robust, with cusp of equivalent proportion to that of 2nd lateral and rachidian teeth; marginal blocks large, longer than wide, stocky.

REMARKS: Female *A. nodosa* are distinguished from females of other *Argonauta* species by higher outer demibranch gill lamellae (14–17) with 14 + lamellae easily counted in specimens of ML 3 mm. Although the 3rd left arm of the male *Argonauta* is typically hectocotylised, forms in which the 3rd right arm is hectocotylised are known (Vecchionne *in* Hochberg *et al.* 1992: 234; one specimen of *A. nodosa* Solander, herein, NMNZ M.131728). This dextrally hectocotylised New Zealand male differs in no obvious respect from normal sinistrally hectocotylised males of *A. nodosa*.

The New Zealand specimen recorded as *Argonauta boettgeri* by Massy (1916a) is referable to *A. nodosa*: the small female specimen (ML 8.0 mm) has 17 outer

gill lamellae per demibranch. The buccal mass of this specimen has been been removed and figured (Massy 1916a: figs 1–2), a figure which led Robson (1932: 196) not surprisingly to remark "certainly the radula figured by Smith (1887) and Massy (*Terra Nova*) [of *A. boettgeri*] do not seem to come from the same species".

Family **OCYTHOIDAE** Gray, 1849

Suckers biserial; web almost absent between arm bases; body muscular; ventral mantle surface of females larger than about 55 mm ML develops reticular cartilaginous sculpture crossing skin ridges and tubercles; ventral surface of mantle in male and immature females with faint pitlike depressions; males with 9–11 lamellae and females with 15–20 lamellae per outer demibranch of gill; sexes dimorphic, male comparatively minute, to 30 mm ML, females large, to 345 mm ML; entire right arm 3 hectocotylised, set on peduncle, autotomous; radula heterodont; funnel long, extending anterior to base of arms; mantle-locking apparatus well developed; arm pairs 1 and 4 about twice the length of arm pairs 2 and 3, with arm pairs 1 and 4, and 2 and 3, of subequal length; single pair of ventral cephalic water pores; shell vestige absent; funnel organ W-shaped (modified from Hochberg *et al.* 1992: 230–231).

Ocythoe Rafinesque, 1814

DIAGNOSIS: With characters of the family; considered monotypic, *Ocythoe tuberculata* Rafinesque, 1814.

Ocythoe tuberculata Rafinesque, 1814

(Figs 67, 68)
(Tables 42–45)

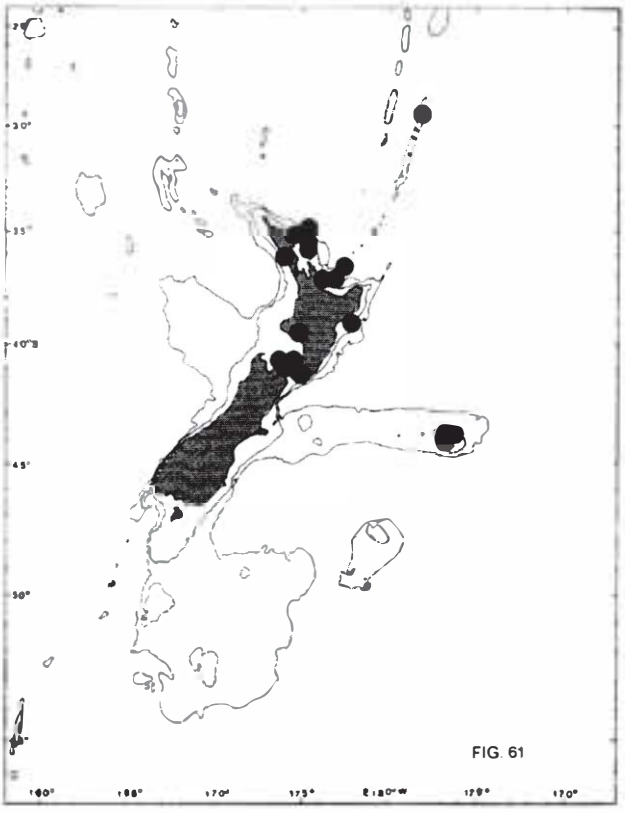
TYPE SPECIES: *Ocythoe tuberculata* Rafinesque, 1814

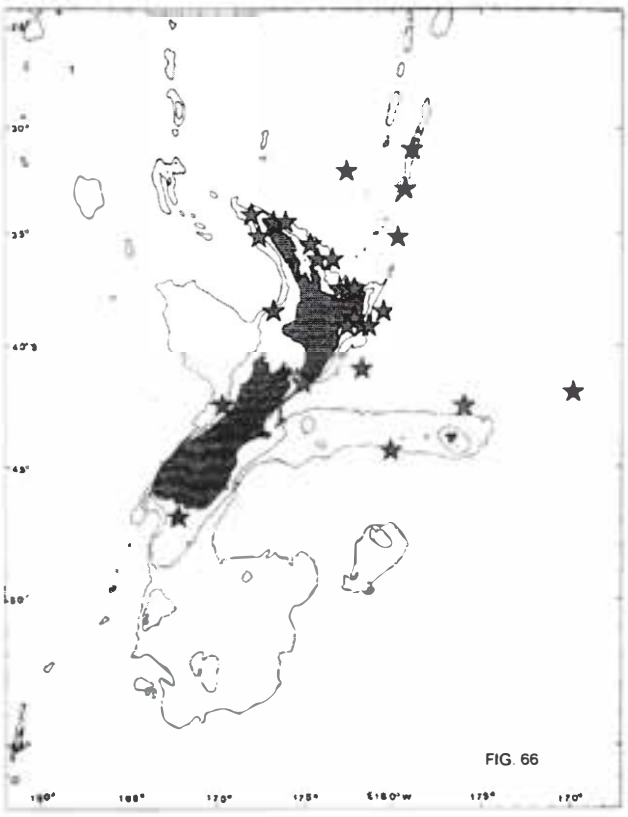
Argonauta ? *argo* [*sic*] (not Linnaeus, 1758): Imber & Russ 1975.

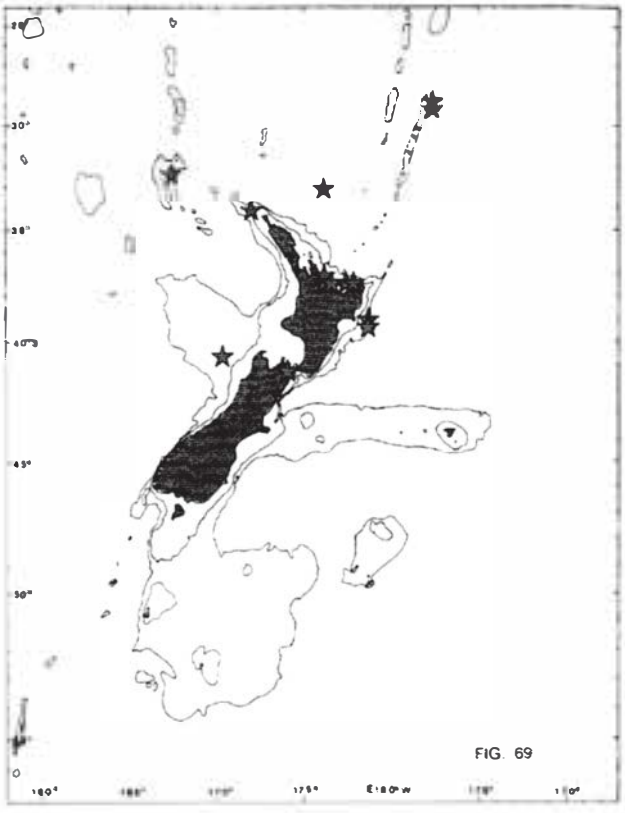
Argonauta argo (not Linnaeus, 1758): Imber 1976: 124.

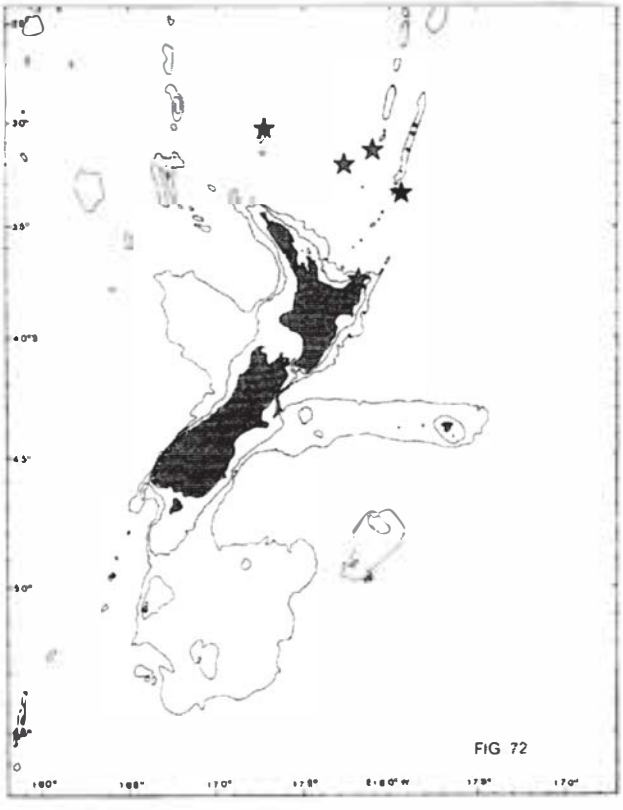
Ocythoe tuberculata Rafinesque: Roper & Sweeney 1976: 21–28; West & Imber 1986; Nesis 1987: 326, figs 87E–G; Hochberg *et al.* 1992: 231–232, figs 250a–h; Imber 1992: 248; Smale *et al.* 1993: 281–282, figs a, b; Spencer & Willan 1995: 53; O'Shea 1997b: 265–266.

MATERIAL EXAMINED (60 specimens, 21 male [M], 39 female [F]): NMNZ M.120109, M, ML 7.2 mm, F, ML 15.9 mm, 31°05.6' S, 178°44.8' W, surface, 14/01/1976, f.r.v. *James Cook* Stn J9/09/76; NMNZ M.74165, F, ML 4.1 mm, AUZ 087 14, 31°57' S, 177°38' E, depth uncertain, 24/07/1962; NMNZ M.74190, F, ML 4.4 mm, AUZ 088/77, 31°57' S, 177°38' E, depth uncertain, 24/07/1962; NMNZ M.90451, M, ML 13.0 mm, 33°15' S, 179°13' W, 695 m over 3000 m, 04/12/1976, f.r.v. *James Cook* Stn J17/09/76; NZOI Stn Z8674, M, ML 13.0 mm (+ host salp), 34°08' S, 172°08' E, surface, 03/03/1997, coll. C. Duffy; NMNZ M.67272, 3F, ML 29.0, 17.8, 16.0 mm, 34°20.0' S, 173°16.8' E, 30 m, 18/11/1978, f.r.v. *James Cook* Stn J18/033/78; NMNZ M.95275, M, ML 14.3 mm, F, ML 12.0 mm, 34°24.5' S, 173°33.8' E, 30 m over 1251–1360 m, 25/10/1985, f.r.v. *James Cook* Stn J16/30/85; NMNZ M.67279, M, ML 12.5 mm, F, ML 16.0 mm, 34°30' S, 173°22.4' E, 250 m, 17/11/1978, f.r.v. *James Cook* Stn J18/008/78; NMNZ M.67328, M, ML 16.5 mm, 34°30' S, 173°08' E, 0–50 m, 05/07/1977, f.r.v. *Ikatere*; NMNZ M.67275, 4M, ML 19.5, 16.0, 11.0, *c.* 10.0 (damaged) mm, 2F, ML 12.2, 10.5 mm, 34°30.6' S, 173°05.5' E, surface, 16/11/1978, f.r.v. *James Cook* Stn J18/004/78; NMNZ M.67276, M, ML 12.0 mm, F, ML 21.5 mm, 34°41.1' S, 173°16.0' E, 40 m, 17/11/1978, f.r.v. *James Cook* Stn J018/031/78; NMNZ M.67325, F, ML 12.5 mm, 34°48' S, 173°15' E, 40 m, 05/07/1977, f.r.v. *Ikatere*; NMNZ M.67299, 2F, ML 15.2, 15.0 mm, 34°59.5' S, 172°33.6' E, 30 m, 19/11/1978, f.r.v. *James Cook* Stn J18/082/78; NMNZ M.90448, M, ML 11.5 mm, 35°00' S, 179°29' W, 338 m over 3000 m, 04/12/1976, f.r.v. *James Cook* Stn J17/06/76; NMNZ M.120122, 2M, ML 18.8, 9.3 mm, 35°07.0' S, 179°22.0' W, 774 m over 3000+ m, 03/12/1976, f.r.v. *James Cook* Stn J17/03/76; NMNZ M.118417, F, ML 240.0 mm, *c.* 35°36' S, 175°20' E, 414 m, f.v. *Linberg*, 8–10/12/1980; NMNZ M.90319, F, ML 64.0 mm, 35°38' S, 175°10' E, 17/12/1980, f.v. *Island Princess* set # 18; NMNZ M.67233, F, ML 82.0 mm, 36°01' S, 175°55' E, depNR, 30/01/1980, f.v. *Island Princess* set # 45; NMNZ M.67244, M, ML 14.0 mm, 36°08.8' S, 176°20.83' E, 30 m, 05/11/1979, f.r.v. *James Cook* Stn J15/023/79; NMNZ M.90438, M, ML 15.5 mm, 37°17.4' S, 176°53.6' E. 337–292 m, 23/01/1981, r.v. *Tanga-roa* (NZOI Stn O588); NMNZ M.90463, M, ML 12.5 mm, 37°30.8' S, 177°17.6' E, 306–320 m over 1298–1372 m, 14/12/1975, f.r.v. *James Cook* Stn J17/60/75; NMNZ M.67240, F, ML 24.2 mm, 37°32' S, 177°56.2' E, 30 m, 19/11/1979, f.r.v. *James Cook* Stn J16/020/79; NMNZ M.91692, F, ML 44.0 mm, 37°34.2–31.2' S, 177°14.5–14.6' E, 108 m over 820–622 m, 13–14/12/1975, f.r.v. *James Cook* Stn J17/54/75; NMNZ M.120120, F, ML 17.5 mm, 37°34.2' S, 177°14.5' E, 108 m over 820–622 m, 13–14/12/1975, f.r.v. *James Cook* Stn J17/54/75; NMNZ M.90297, F, ML 55.5 mm, 37°37' S, 177°12' E, 190 m over 406 m, 02/08/1976, f.r.v. *James Cook* Stn J11/87/76; NMNZ M.90459, M, ML 13.8 mm, 37°39' S, 177°14.6' E, 142 m, 13/12/1975, f.r.v. *James Cook* Stn J17/51/75; NMNZ M.67241, 2F, ML 28.0, 25.2 mm, 37°39.2' S, 177°41.5' E, 30 m, 20/11/1979, f.r.v. *James Cook* Stn J16/022/79; NMNZ M.118432, F, ML 31.7 mm, 37°50' S, 177°49.20' E, 30 m, 20/11/1979, f.r.v. *James Cook* Stn J16/21/79; NMNZ M.90323, M, ML 18.1 mm, 38°21.05' S, 179°16.1' E, 30 m over 1700 m, 05/06/1981, f.r.v. *James Cook* Stn J09/79/81; NMNZ M.90315, 3F, ML 27.0, 22.5, 18.5 mm, 38°21.8' S, 179°16.2' E, 30 m over 1700 m, 05/06/1981; NMNZ M.117696, F, ML 81.0 mm, 38°33' S, 173°32.2' E, 03/03/1989, f.v. *Island Princess* set # 22; NMNZ M.95279, 2F, ML 20.5, 14.0 mm, 38°45.45' S, 178°03.93' E, 31/05/81, 27 m over 28 m, f.r.v. *James Cook* Stn J09/06/81; NMNZ M.67296, M, ML 11.5 mm, 38°57.6' S, 178°16.7' E, 30 m, 19/11/1979, f.r.v. *James Cook* Stn J16/003/79; NMNZ M.67289, F, ML 12.0 mm, 39°01.7' S, 178°28.2' E, surface, 10/01/1980, f.r.v. *James Cook* Stn J01/004/80; NZOI Z8215, M, ML 20.8 mm, stomach contents









Recognised distribution. **Fig. 61**, *Argonauta nodosa* Solander, 1786: shells. **Fig. 66**, *Ocythoe tuberculata* Rafinesque, 1814: animals. **Fig. 69**, *Tremoctopus robsonianus* Kirk, 1883. **Fig. 72**, *Vitreledonella richardi* Joubin, 1918: * new records; ⋆ from Thore (1949).

Table 41. Raw measures for female *Argonauta nodosa* (* denotes damage; # denotes difficulty in accurately enumerating distal arm tip suckers; † denotes distal arm tip suckers difficult to count; TL measured from tip of arm pair 2 (or next longest arm) given distorted arms 1).

	NMNZ M.126436	NMNZ M.256365	NZOI Stn Z8575	NZOI Stn Z8588	NMNZ M.256365	NMNZ M.90285	NMNZ M.90303
ML	29.6	44.1	47.0	57.5	68.2	73.5	76.0
TL	80.0	134.0	152.0	177.0	206.0	267.0	225.0
MW	21.3	26.0	32.5	35.4	39.1	56.5	24.0
HW	21.7	26.1	32.1	28.1	35.0	39.4	28.8
HdL	10.3	11.0	12.0	13.6	13.9	17.9	18.0
AL1R/L	70#/64#	165#/185#	173#/181#	104#/114#	180#/237#	258#/260#	193#/203#
AL2R/L	48/49	95/96	109/105	127/115	137/141	196/166*	160/177
AL3R/L	47/44	78/82	84/83	101/91	106/102	138/117	139/126
AL4R/L	42/43	76/83	80/84	98/91	102/21*	145/131	127/150
WDA	9.0	23.1	24.3	25.0	26.5	20.0	30.5
WDBR/L	8.0/8.0	16.0/19.0	19.0/19.0	17.5/16.5	20.0/22.0	19.5/17.0	21.5/23.0
WDCR/L	8.5/8.7	17.0/19.5	17.0/17.0	16.0/14.0	19.0/19.5	24.5/16.0	17.0/18.4
WDDR/L	9.0/9.5	19.0/21.0	20.0/21.0	19.5/13.5	26.5/21.5	28.5/17.0	29.0/28.0
WDE	6.0	18.0	16.5	17.0	17.5	18.5	26.0
ASC1R	-	-	257†	260†	L 292†	248†	-
ASC2R	120†	156†	150†	160†	199†	160†	144†
ASC3R	133†	144†	142†	106†	178†	160†	164†
ASC4R	80†	88†	93†	103†	120†	104†	104†
ASn1R	3.0	4.0	4.0	4.3	5.2	6.0	6.0
ASn2R	2.7	3.5	3.3	3.9	4.0	5.0	4.9
ASn3L	2.1	3.5	3.3	3.6	4.2	4.6	4.9
ASn4R	3.0	4.0	4.0	4.2	5.0	5.0	6.7
GiLC	14	16	16	15	16	15	15
FuL	17.0	27.0	31.1	33.1	40.3	46.6	39.1
FFL	5.2	19.3	15.0	17.9	26.0	21.1	19.0
ED	8.8	15.4	13.1	15.0	14.0	19.1	21.3
EO	2.0	2.2	2.3	*	3.7	3.2	1.1

beach cast *Alepisaurus ferox*, *c.* 39°06' S, 177°20' E, -/01/1995, coll. C. Duffy; NMNZ M.95274, F, ML 22.6 mm, 39°09.3' S, 178°49.0'E, 30 m over 1700 m, f.r.v. *James Cook* Stn J09/70/81; NMNZ M.95283, F, ML 16.5 mm, 40°55.0' S, 178°09.3' E, 20 m over 2006–2031 m, 15/09/1987, f.r.v. *James Cook* Stn J12/22/87; NMNZ M.118416, F, ML 3450 mm, *c.* 41°25' S, 175°06' E, 01/04/1980; NMNZ M.118415, F, ML 2310 mm, 41°59' S, 169°57' W, 15/01/1987, depNR; NMNZ M.67245, F, ML 21.0 mm, 42°19.68' S, 170°29.75' E, 153 m, 09/12/1978, f.r.v. *James Cook* Stn J19/002/78; NMNZ M.109380, F, ML 37.5 mm, 42°36.79' S, 176°09.81' W, 1999–2002 m, 02/03/1992, f.r.v. *Tangaroa*; NZOI Stn Z8743, F, ML 16.8 mm, 44°16.78' S, 179°52.97' E, 30-400 m, FMMWT, 20/02/1992, f.r.v. *Tangaroa* Stn TAN9202/64; NMNZ M.118418, F, ML 2310 mm, f.v. *Seisho Maru* 28, Stn 43.50, 1980 jigging season, Stewart Island, *c.* 47°00' S, 168°00' E, depNR.

Additional Material Examined (beaks ex. bird stomach contents): *Ocythoe tuberculata* (as *Argonauta ? argo* [*sic*]: Imber & Russ 1975); *Ocythoe tuberculata* (as *Argonauta argo*: Imber 1976); *Ocythoe tuberculata*: West & Imber 1986; Imber 1992.

Foreign Material Examined (*Ocythoe tuberculata*): NZOI Stn Z8347, F, ML 35.0 mm, 31°21.78–20.41' S, 11°41.13–39.30' E, 35–38 m, 22/06/1991, f.r.v. *Tangaroa* Stn TAN-9101/007; BM 1889.2.11.10, F, ML 116.0 mm, Nice, France.

Recognised Distribution (New Zealand, Fig. 66, p. 100): coastal and offshore waters off Chatham and Kermadec Islands, east and west coasts of North Island, and west coast of South Island. All *in situ* records from waters north of Subtropical Convergence. Two beach-cast specimens known; several individuals collected at surface, the majority collected between 30 and 40 m from surface, and several from purported depths of 2000 m. Beaks recorded from long-distance-foraging bird stomachs from Auckland, Chatham, and Great Barrier Islands. Otherwise bi-subtropical cosmopolitan, pelagic species (Nesis 1987: 326).

Description (Figs 67A–C, E): Female ML to 345.0 mm, TL to 830 mm; in females exceeding about 55 mm ML, ventral and ventrolateral surfaces of mantle sculptured with reticular matrix of cartilaginous skin ridges and tubercles at intercepting points; ventral and ventrolateral mantle surfaces in smaller females sculptured with small non-cartilaginous pit-like depressions. Mantle globose, without dorsoventral or lateral compression; pallial aperture very wide, with

points of mantle attachment dorsolateral to eyes, free of brachial crown. Head large, dorsal head musculature absent; head partially retracted into mantle, neither head nor mantle constrictions distinct. Orbits small to large (EDI about 20–40), bulbous, laterally oriented; orbits free of arm bases 2 and 3; eye aperture large. Funnel length moderate to long, tubular (FuLI about 34–72), free distal portion short to moderately long (FFLI about 12–25), projecting beyond level of arm bases and beaks. Two cephalic water pores at base of ventral arm pair, adjacent to point where funnel fuses with ventral surface of head.

Female arms stout, with flattened adoral surface; longest arms short to moderately long, length ontogenetically variable: immature females 10–55 mm ML, AL about 75% TL; to 80 mm ML, AL about 70% TL; about 50–60% TL in larger females; arms tapering to fine non-filiform, non-laminar tips; arm formula 4.1.2.3 to 1.4.2.3, arm pairs 1 and 4, and 2 and 3, of subequal length, with arms 1 and 4 appreciably longer than 2 and 3. Web absent.

Female whole-arm sucker count ontogentically variable: 6–13 in juveniles of 5 mm ML, through to 91–97 in largest female examined, with ASC less on lateral arm pairs than dorsal and ventral arm pairs; terminal portion of arms transversely ridged and devoid of suckers. Sucker size ontogenetically variable: ML < 32 mm with suckers on arms 1 and 4 about 8–11.5% ML, on arm pairs 2 and 3 about 6–9% ML; ML 38–64 mm with suckers on arm pairs 1 and 4 about 6–8% ML, and suckers on arms 2 and 3 about 4.5–5.5% ML; ML 82 mm with suckers on arms 1 and 4 about 6% ML, and on arms 2 and 3 about 5–5.5% ML; ML 230–345 mm, with suckers on arm pair 1 about 5% ML, and on arm pairs 2, 3, and 4 about 3% ML. Suckers biserial, positioned along lateral margins of arms; well spaced along arms, not deeply embedded within arm tissues; distance between suckers about 1 sucker diameter, suckers decreasing in diameter very gradually from adoral circlet to arm tip.

Male (Figs 67D, F) to 20.8 mm ML; mantle without cartilaginous matrix sculpture; ventral and ventrolateral mantle surfaces in mature males with pitlike depressions similar to indentations observed in females of ML less than 55 mm. Mantle globose, without dorsoventral or lateral compression; pallial aperture very wide, points of mantle attachment dorsolateral to eyes, free of brachial crown. Head large, dorsal head musculature absent; head partially retracted into mantle, neither head nor mantle constrictions distinct. Orbits small to large (EDI about 25–42), bulbous, laterally oriented; orbits free of arm bases 2 and 3; eye aperture large. Funnel long, tubular (FuLI about 51–63), free distal portion short to moderately long (FFLI about 16–26), projecting beyond level of arm bases and beaks. Two cephalic water pores at base of ventral arm pair, adjacent to point where funnel fuses with ventral surface of head.

Male arms stout, with flattened adoral surface; longest arms short to moderately long, length ontogenetically variable: ML >15 mm, arm length about 70% TL; ML 10–15 mm, arm length to 75% TL; arms tapering to fine, non-filiform non-laminar tips; arm pairs 1 and 4 about twice the length of arm pairs 2 and 3, with arm formula 1.4.2.3 or 4.1.2.3; arm pairs 1 and 4, and 2 and 3, of subequal length. Web absent.

Male whole-arm sucker count 15–50, ontogentically variable and with disparity between dorsal, ventral, and lateral arm pairs. ASC less on lateral arm pairs than dorsal and ventral arm pairs; terminal portion of arms transversely ridged and devoid of suckers. Suckers of small to moderate size (ASIn 2.8–10.3), biserial, positioned along lateral margins of arms; size ontogenetically variable, increasing in diameter relative to mantle length, larger on arm pairs 1 and 4, than 2 and 3. Suckers well spaced along arms, not deeply embedded within arm tissues; distance between suckers about 1 sucker diameter, suckers decreasing very gradually in diameter from midpoint of each arm (adoral circlet smaller than midarm suckers). Hectocotylus contained in large pouch set on peduncle from base of third right arm; with 2 suckers on peduncle.

Gill lamellae counts per outer demibranch are ontogenetically variable in males and females: smallest females with 15, intermediate-sized females with 16–18, and females 82–345 mm ML with 19–20 outer lamellae; males with range 9–12.

Male reproductive system (Fig. 68A) with disproportionately large, gold coloured, triangular testis sac; funnel-like structure joins testis sac with short, thick, weakly convoluted proximal vas deferens; spermatophoral gland very long, without pronounced central swelling; spermatophoral gland enters base of disproportionately large granular accessory gland; accessory gland with distal laminar volution; spermatophoric sac elongate, distally attenuated; penis and spermatophoric sac separated by constriction; penis about 25% length of spermatophoric sac, barrel-shaped, genital aperture not apparent. Female (Fig. 68B) with comparatively small ovary sac; ovarian eggs minute (< 1 mm max. length); proximal oviducts very short, thick; oviducal ball large, cylindrical, with two apparent chambers, proximal chamber with strong longitudinal striations; distal oviduct of enormous length, highly convoluted, dilating distally, particularly proximal to genital aperture.

Alimentary canal of female (Fig. 68C) with large

Table 42. Indices, formulas, and counts for male *Ocythoe tuberculata* (* denotes damage).

	NMNZ M.120109	NMNZ M.120122	NMNZ M.95282	NMNZ M.90412	NMNZ M.90459	NMNZ M.67328	NZOI Stn Z8215
MWI	84.7	81.7	65.7	65.8	72.3	72.1	52.9
HWI	73.6	73.1	52.9	65.8	66.0	63.6	49.6
HdLI	43.1	34.4	39.3	39.5	42.1	73.3	38.5
EDI	41.7	24.7	35.7	33.6	39.0	42.4	38.5
EOI	13.9	10.8	7.9	10.5	7.5	7.9	9.6
ALI1–4	12.6–63.0	20.7–75.8	17.3–72.9	22.9–75.3	22.2–77.6	26.6–82.8	27.0–72.6
AFR	4=1.2.3	1.4.2.3	4.1.2.3	1.4.2.3	4.1.2.3	4.1.2.3	*
AFL	4.1.2.3	4.1.2.3	4=1.2=3	4.1.2.3	4.1.3.2	4.1.2.3	1.4.2.3
ASC1–4	15–31	19–33	18–36	23–56	26–29*	25–50	21–49
ASIn1–4	2.8–6.9	4.3–6.5	3.6–7.1	6.6–9.2	6.3–6.9	6.1–10.3	4.8–9.6
HcLI	50	33.3	36.1	53.6	60.0	52.9	*
GiLC	*	9	10	11	12	12	12
FuLI	62.5	55.9	50.7	56.6	60.4	54.5	58.2
FFLI	26.4	21.5	22.8	21.1	16.4	17.6	20.2

Table 43. Indices, formulas, and counts for female *Ocythoe tuberculata* (* denotes damage).

	NMNZ M.74190	NMNZ M.67325	NMNZ M.95283	NMNZ M.67240	NMNZ M.118432	NMNZ M.109380	NMNZ M.91692	NMNZ M.90297	NMNZ M.67233	BM 1889. 2.11.10	NMNZ M.118416
MWI	80.0	70.4	87.3	72.3	75.7	69.3	51.1	84.7	90.2	83.6	*
HWI	80.0	72.0	73.3	65.7	69.4	56.0	43.2	62.2	52.4	44.9	*
HdLI	42.0	56.0	44.8	37.2	37.9	37.3	33.0	31.5	43.9	24.1	*
EDI	40.0	40.0	43.6	39.3	37.9	36.3	35.2	34.2	33.7	24.1	20.2
EOI	10.0	14.4	12.1	8.3	8.2	8.3	8.0	8.1	9.8	9.1	*c.*4.5
ALI1–4	13.8–57.7	26.9–74.0	39.1–76.3	41.6–75.6	44.2–75.9	*	41.9–74.3	46.0–75.4	*	46.4–68.1	49.0–61.6
AFR	4.1.2.3	4.1.2.3	4.1.2.3	4.1.2.3	4.1.2.3	*	1.4.2.3	4=1.2.3	*	1.4.2.3	*
AFL	4.1.2.3	*	4.1.2.3	4.1.2.3	4.1.2.3	*	*	4=1.2.3	*	*	*
ASC1–4	6–16	30–56	48–66	59–90	66–92	*	69–90	*	*	86–92	91–97
ASIn1–4	1.0–4.0	7.2–11.2	7.3–11.5	5.4–9.5	6.3–7.9	5.3–8.0	4.5–6.8	4.5–6.3	5.1–6.1	4.3–5.2	2.6–5.0
GiLC	15	15	17	17	17	18	19	19	19	19	20
FuLI	70.0	72.0	63.6	55.4	55.2	57.3	45.5	55.9	61.0	51.7	33.6
FFLI	-	24.8	18.2	12.4	18.6	22.7	17.0	20.2	15.9	19.8	15.9

buccal bulb; anterior salivary glands well developed (length 50% buccal bulb length), loosely applied to posterior margin of buccal bulb. Anterior oesophagus short (about 25% total oesophagus and crop length), thick walled; posterior salivary glands paired, small (length about 50% buccal bulb length), tear-drop shaped; crop massive, thin walled, with well-developed anterior diverticulum. Stomach large (length about 1.2 times buccal bulb), with thick-walled muscular basal section and thin-walled distal section, its lumen continuous; spiral caecum thin-walled (about 66% size of buccal bulb), considerably smaller than stomach (about 50% size of stomach), with single complete volution; intestine twice length of anterior alimentary canal, dilated for greatest length. Hepatic ducts paired; digestive gland large, triangular, of metallic-green colour; pancreas moderately well developed (about 25% digestive gland length), light green; ink sac large, cylindrical (length about 66% digestive gland), deeply embedded in digestive gland, surface visible throughout length; ink duct short, opening at anus. Alimentary canal of male (Fig. 67D, E) differs in having larger posterior salivary glands (about 70% buccal bulb length), a larger, massive thin-walled crop, longer oesophagus (about 50% oesophagus and crop length), and an intestine dilated for entire length, and being of equivalent length to the anterior alimentary canal.

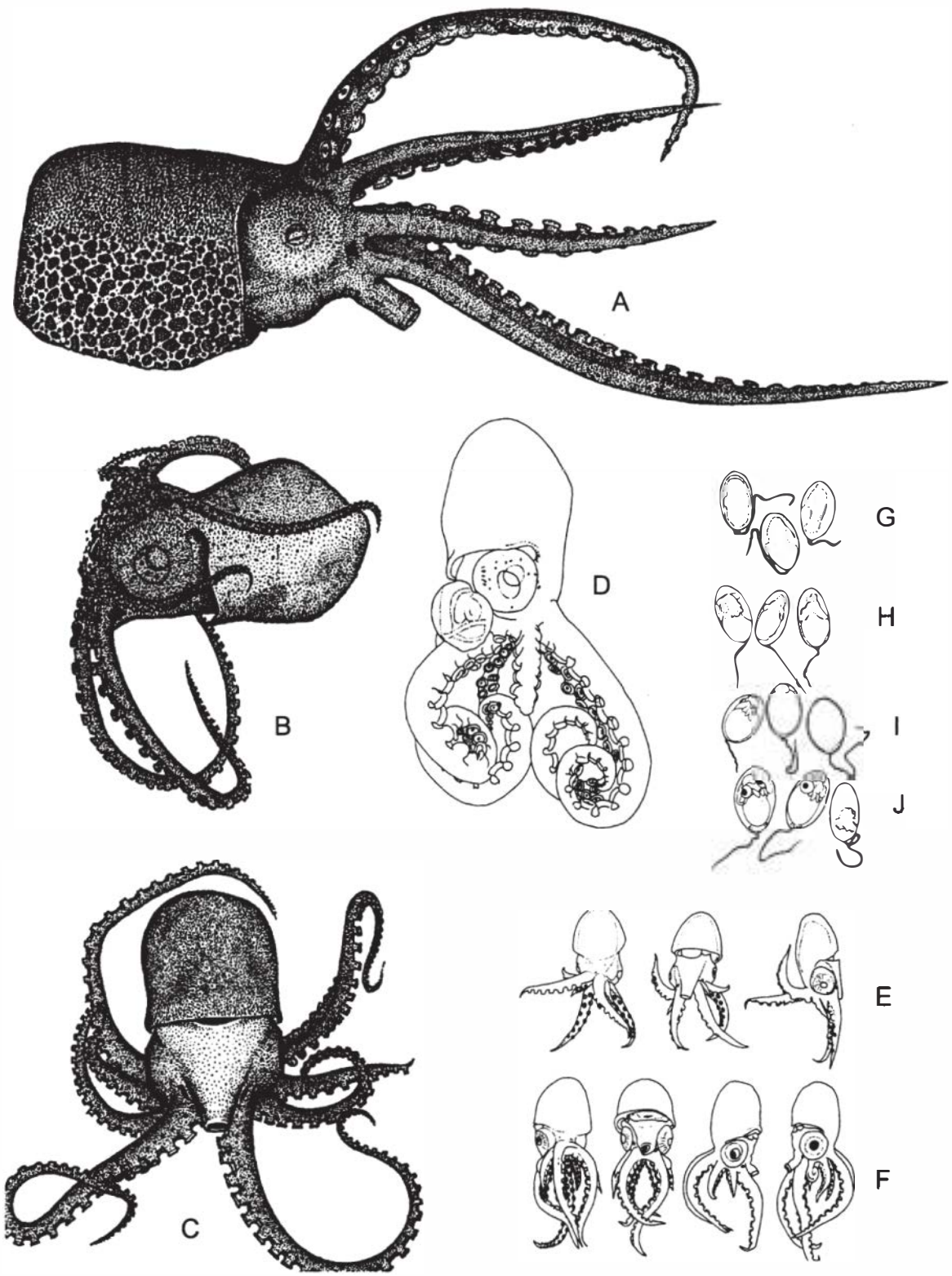


Figure 67. *Ocythoe tuberculata* Rafinesque, 1814: **A**, NMNZ M.90297, female, ML 55.5 mm. **B, C**, NMNZ M.90315, female, ML 22.5 mm. **D**, NMNZ M.67244, male, ML 14.0 mm. **E**, NMNZ M.74190, female, ML 4.4 mm. **F**, NMNZ M.120109, male, ML 7.2 mm. **G–J**, eggs recovered from distal oviducts of females. **G**, NMNZ M.118415, ML 231 mm. **H**, NMNZ M.118418, ML 231mm. **I**, NMNZ M.118417, ML 240 mm. **J**, NMNZ M.118416, ML 345 mm.

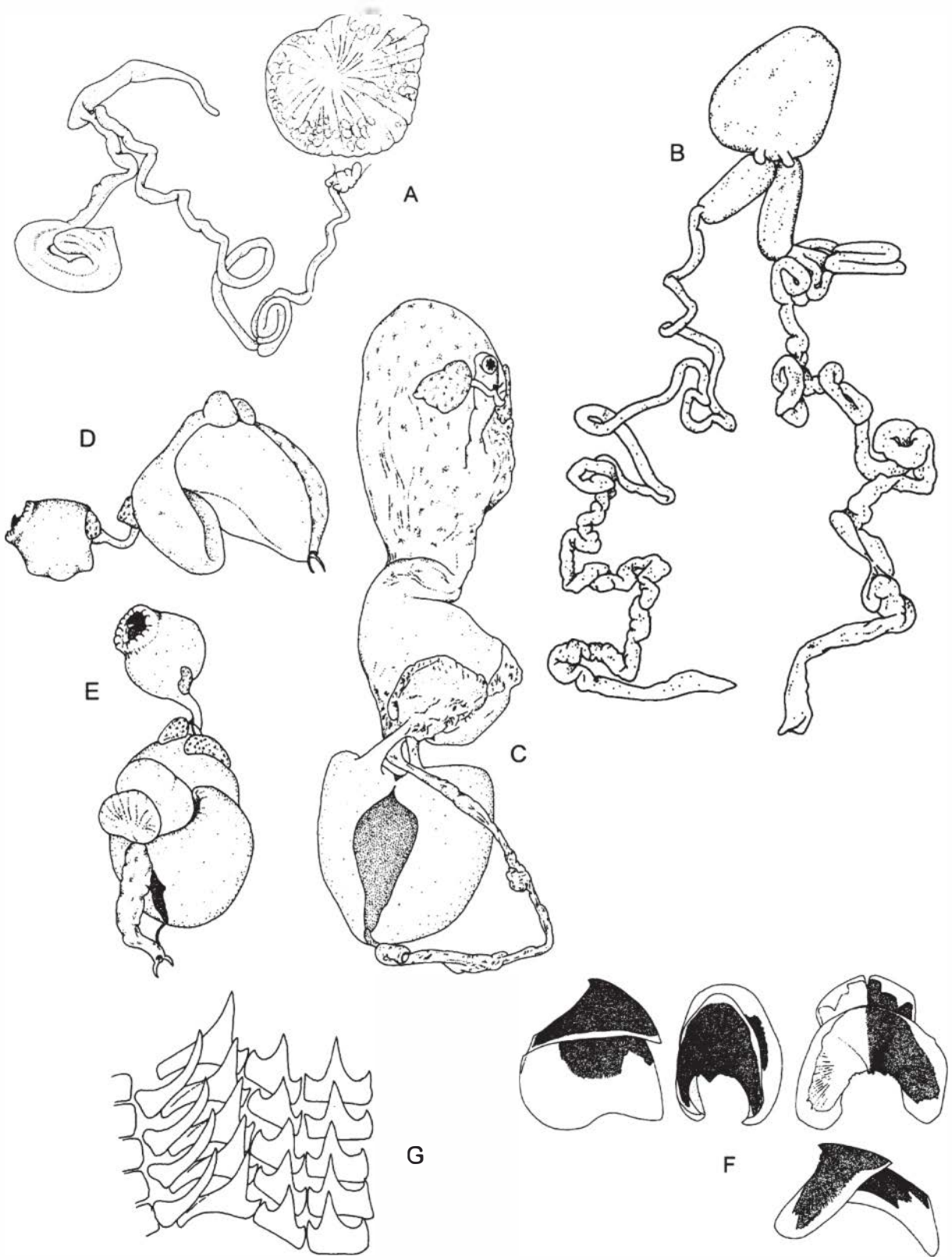


Figure 68. *Ocythoe tuberculata* Rafinesque, 1814. Anatomy: **A, D, E**, NMNZ M.90323, male, ML 18.1 mm. **B, E–G**, NMNZ M.67233, female, ML 82 mm. **A**, male reproductive system. **B**, female reproductive system. **C**, female alimentary canal. **D, E**, male alimentary canal, lateral and dorsal perspectives. **F**, female beaks. **G**, female radula.

Table 44. Raw measures for male *Ocythoe tuberculata* (* denotes damage; ASC 3R counts basal suckers on hectocotylus peduncle).

	NMNZ M.120109	NMNZ M.120122	NMNZ M.95282	NMNZ M.90412	NMNZ M.90459	NMNZ M.67328	NZOI Stn Z8215
ML	7.2	9.3	14.0	15.2	15.9	16.5	20.8
TL	23.8	29.0	48.0	49.0	67.0	64.0	100.0
MW	6.1	7.6	9.2	10.0	11.5	11.9	11.0
HW	5.3	6.8	7.4	10.0	10.5	10.5	10.3
HdL	3.1	3.2	5.5	6.0	6.7	12.1	8.0
ED	3.0	2.3	5.0	5.1	6.2	7.0	8.0
EO	1.0	1.0	1.1	1.6	1.2	1.3	2.0
AL1R/L	15.0/14.5	22.0/19.0	31.4/32.1	36.9/33.0	47.1/49.4	52.0/45.0	71.6/72.6
AL2R/L	6.8/6.3	11.0/10.8	15.0/12.5	17.0/17.5	22.6/20.5	25.1/24.1	33.1/34.5
AL3R/L	3.0/5.5	6.0/8.6	8.3/12.5	11.2/15.5	14.9/21.1	17.0/21.9	*/27.0
AL4R/L	15.0/15.5	20.0/22.0	35.0/32.1	35.6/34.0	52.0/51.0	53.0/52.0	69.1/60.9
ASC1R	31	33	36	56	*	47	45
ASC2R	18	22	20	25	29	30	29
ASC3R	2	2	2	2	2	2	2
ASC3L	15	19	18	23	26	25	21
ASC4R	29	31	36	46	*	50	49
ASn1R	0.5	0.4	1.0	1.1	1.1	1.2	2.0
ASn2R	0.5	0.4	0.5	1.0	1.0	1.0	1.4
ASn3L	0.2	0.5	0.5	1.0	1.0	1.0	1.0
ASn4R	0.4	0.6	1.0	1.4	1.1	1.7	1.7
GiLC	*	9	10	11	12	12	12
FuL	4.5	5.2	7.1	8.6	9.6	9.0	12.1
FFL	1.9	2.0	3.2	3.2	2.6	2.9	4.2

Table 45. Raw measures for female *Ocythoe tuberculata* (* denotes damage).

	NMNZ M.74190	NMNZ M.67325	NMNZ M.95283	NMNZ M.67240	NMNZ M.118432	NMNZ M.109380	NMNZ M.91692	NMNZ M.90297	NMNZ M.67233	BM 1889. 2.11.10	NMNZ M.118416
	ML	5.0	12.5	16.5	24.2	31.7	37.5	44.0	55.5	82.0	116.0
345.0	**TL**	13.0	54.0	65.5	96.0	122.0	145.0	148.0	187.0	247*	405.0
830.0	**MW**	4.0	8.8	14.4	17.5	24.0	26.0	22.5	47.0	74.0	97.0 *
HW	4.0	9.0	12.1	15.9	22.0	21.0	19.0	34.5	43.0	52.1	*
HdL	2.1	7.0	7.4	9.0	12.0	14.0	14.5	17.5	36.0	28.0	*
AL1R/L	7.4/6.1	39.0/38.0	47.0/46.5	68.5/66.1	87.5/86.9	*/*	108/110	141/141	128*/164*	276/*	*/*
AL2R/L	3.0/2.5	18.0/16.0	27.1/29.0	43.1/40.9	56.4/58.0	55.1/58.9	70/72	100/100	133*/161*	215/217	*/486
AL3R/L	1.8/2.1	16.6/14.5	25.6/28.1	39.9/39.9	53.9/55.2	53.6/*	65/62	86/92	115*/115*	188/198	*/407
AL4R/L	7.5/6.9	40.0/*	50.0/50.0	70.9/72.6	89.0/92.6	*/*	101/*	141/141	175/154*	261/264	511/493
ASC1R	16	55	63	73	82	*	90	*	*	92	*
ASC2R	8	36	58	69	74	*	75	*	*	92	L 95
ASC3R	6	30	48	59	66	*	69	*	*	86	L 91
ASC4R	13	56	66	90	92	*	81	*	*	98	L 97
ASn1R	0.2	1.3	1.9	2.0	2.5	2.5	3.0	3.5	4.8	5.8	L 17.3
ASn2R	0.05	1.0	1.5	1.5	2.0	2.1	2.0	3.0	4.5	5.0	L 10.0
ASn3R	0.05	0.9	1.2	1.3	2.0	2.0	2.2	2.5	4.2	5.0	L 9.0
ASn4R	0.2	1.4	1.7	2.3	2.5	3.0	3.0	3.3	5.0	6.0	L 10.0
GiLC	15	15	17	17	17	18	19	19	19	19	20
FuL	3.5	9.0	10.5	13.4	17.5	21.5	20.0	31.0	50.0	60.0	115.9
FFL	*	3.1	3.0	3.0	5.9	8.5	7.5	11.2	13.0	23.0	54.9
ED	2.0	5.0	7.2	8.8	12.0	13.6	15.5	19.0	27.6	28.0	69.7
EO	0.5	1.8	2.0	2.0	2.6	3.1	3.5	4.5	8.0	10.6	c.15.5

Upper beak (Fig. 68F) tall, conical (height 108% beak length), with dark-brown hood and lateral walls, pronounced W-shaped dark-brown lateral wall crest, translucent hood and lateral wall margins. Hood moderately long (depth 59% beak length), with pronounced downward-deflected rostrum, with 2 teeth in jaw; rostrum weakly pronounced, pointed. Lateral walls of rounded profile, with broadly rounded crest, deep lateral wall crease, and deep concavity in lateral wall margin. Lower beak (Fig. 68F) of low profile (height 71% width) with dark pigmented hood and proximal two-thirds of lateral wings; distal third of lateral wings and wall margin translucent. Lateral wall with deeply excavated basal notch, sharply keeled crest, 2 lateral wall thickenings, and with free corners of lateral wall little spread apart. Hood short (depth 46% beak length), broad; rostrum little projecting, pinched in laterally, slightly deflected down, and with margin comprising 5–7 sharp-pointed low-profile teeth; lateral wings long (length 88% beak length), without apparent folds.

Radula (Fig. 68G) with wide, tall-profile rachidian with 3 symmetric cusps, the central tall, delicate, the laterals shorter, more robust; 1st lateral almost as wide as rachidian, with 3 well-developed cusps, the central cusp most prominent; 2nd lateral wider than rachidian, with wide base and 2 well-developed cusps, the 2nd most prominent; marginal teeth wide, slender, cusp more delicate than that of 2nd cusp on 2nd lateral; marginal blocks short, stocky.

REMARKS: There are previous records of *Ocythoe tuberculata* recovered from gut regurgitations of the seabirds *Diomedia bulleri* and *Procellaria parkinsoni* breeding in New Zealand waters, but the food items were not necessarily taken from our waters (O'Shea 1997b). Four previous southern ocean records of *O. tuberculata* are known — one from Australia (Roper & Sweeney 1976), and three from South Africa (Voss 1967b; Nesis 1991; Smale *et al.* 1993). Records of *O. tuberculata* from the New Zealand EEZ conclusively extend the distribution of this species into the South Pacific Ocean.

Female characters subject to ontogenetic change are mantle sculpture, arm length, sucker diameter, arm sucker count, eye diameter and gill lamellae counts. The ventral cartilaginous matrix of skin ridges and tubercles is well developed in females of mantle lengths of 55 mm and greater; they appear to develop on maturity. Male ontogenetic changes are seen in sucker size, gill lamellae counts and arm length. Indentations present on the ventral mantle surface of New Zealand males have been described for Japanese specimens (Sasaki 1929), but otherwise they have been described or inferred as smooth (Robson 1932; Naef 1923).

Roper and Sweeney (1976) suggest the bathymetric distribution of *O. tuberculata* is limited to surface waters of 100–200 m depth. Several New Zealand specimens are reported from depths about 2000 m, but were taken with non-closing nets. Anecdotal evidence suggests they could have been taken deeper, however. Thomas (1977) described *Tremoctopus gelatus* from stomach contents of the mesopelagic fish *Alepisaurus ferox*, by inference considering *T. gelatus* also possibly mesopelagic; Voss (1967b) and Rancurel (1970) also described *T. violaceus* from stomach contents of *A. ferox*. The distribution of *A. ferox* is widespread throughout the North Atlantic, Gulf of Mexico, the entire Pacific, and off South and Southwest Africa, the Indian Ocean and the Coral Sea (Francis 1981). As *Ocythoe tuberculata* is known also from stomach contents of New Zealand *Alepisaurus ferox*, *Ocythoe* may have a more extensive bathymetric distribution than currently realised.

A commensal relationship between male *Ocythoe* and a pelagic salp is known for one New Zealand specimen only. This relationship, illustrated *in situ* (Jatta 1896), may have been broken during capture or earlier curation of other male specimens.

Family **TREMOCTOPODIDAE** Tryon, 1879

Dorsal and ventral cephalic water pores present; suckers biserial, small, numerous; arms 1 and 2 greatly elongate; web very deep dorsally, almost absent ventrally; sexual dimorphism pronounced, male dwarfed; entire 3rd right arm of male hectocotylised and developed in a pouch below eye, (autotomises at maturity) radula heterodont; mantle-locking apparatus well developed; funnel organ a series of ridges; shell vestige present. Family monogeneric for *Tremoctopus* delle Chiaje, 1830.

Tremoctopus delle Chiaje, 1830

DIAGNOSIS: With characters of the family.

TYPE SPECIES: *Tremoctopus violaceus* delle Chiaje, 1830

Tremoctopus robsonianus Kirk, 1883 (Figs 70, 71) (Tables 46, 47)

Tremoctopus robsonianus Kirk, 1883: 549–550; Dell 1952: 71, fig. 4.
Tremoctopus robsoni Kirk, 1883: 549.

Tremoctopus violaceus (not delle Chiaje, 1830): Suter 1913: 1065; Massy 1916a: 145–146, figs 3–4; Powell 1937: 95; Benham 1944: 294–296, pl. 40, figs 1–3; Powell 1946: 100; Dell 1951: 97; 1952: 71–73; Powell 1957: 125; 1962: 126; 1976: 133; 1979: 445.

Tremoctopus violaceus gracilis (not Eydoux & Souleyet, 1852): Spencer & Willan 1995 (*partim*): 53 (exclude specimens of Thomas 1977).

MATERIAL EXAMINED (30 specimens, 11 male [M], 17 female [F], 2 sex indet.). Neotype: NMNZ M.118407, M, ML 17.0 mm, Mayor Island, *c*. 37°1' S, 176°16' E, -/11/1981, coll. M. Potter.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.74489, 3F, ML 3.6, 3.0, 3.0 mm, sex indet, ML 1.4 mm, 28°50' S, 177°48.3' W, surface, 17/06/1976, f.r.v. *James Cook* Stn J9/31/76; NMNZ M.74488, F, ML 3.7 mm, sex indet., ML 3.0 mm, 29°15.7' S, 177°51.8' W, surface?, 16/06/1976, f.r.v. *James Cook* Stn J9/19/76; NMNZ M.91495, F, ML 7.0 mm, 32°22.8–21.3' S, 167°34.6–37.3' E, FMMWT, 115–125 m over 1002–1352 m, 23/10/1985, f.r.v. *James Cook* Stn J16/19/85; NMNZ M.74161, M, ML 5.0 mm, F, ML 6.0 mm, AUZ 082/01, noon position, 33°09' S, 176°06' E ± 16 miles from noon position, 1903–1945 hours (NZST), 1 m cone with # 18 grit gauze, 30 min tow, 100 fthm wire, 23/07/1962; BMNH 1919.12.30.64–65, 2F, ML 5.0, 4.5 mm, off Three Kings Islands, *c*. 34°10' S, 172°05' E, 26/08/1911, *Terra Nova* Exped. Stn 129; NMNZ M.90455, F, ML 13.1 mm, 37°14' S, 176°24.5' E, 305 m over 633–660 m, 13/12/1975, f.r.v. *James Cook* Stn J17/42/75; NMNZ M. 118440, M, ML 15.3 mm, washed ashore at Mayor Island, *c*. 37°18' S, 176°16' E, -/11/1965, coll. R. Grace; NMNZ M.5622, F, ML 61.0 mm, floating on sea, Crater Bay, White Island, *c*. 37°31' S, 177°11' E, coll. Oliver 06/12/1912; NMNZ M.67874, 2F, ML 34.6, 22.0 mm, 37°35.50' S, 177°49.20' E, 30 m, 20/11/1979, f.r.v. *James Cook* Stn J16/21/79; NMNZ M.131727, 4M, ML 12.6, 11.5, 9.2, 8.5 mm, 37°39' S, 177°14.6' E, 142 m, 13/12/1975, f.r.v. *James Cook* Stn J17/51/75; NMNZ M.118433, M, ML 7.0 mm, 39°01.7' S, 178°28.2' E, surface, 10/01/1980, f.r.v. *James Cook* Stn J01/004/80; NMNZ M.95284, M, ML 14.2 mm, 39°16.8–18.2' S, 178°34.6–34.7' E, FMMWT, 30 m, 06/12/1987, f.r.v. *James Cook* Stn J15/06/87; NMNZ M.120126, M, ML 11.4 mm, 40°45.0' S, 170°16.2' E, 232 over 800 m, 20/01/1976, f.r.v. *James Cook* Stn J2/31/76; NMNZ M.13337, F, ML 1370 mm, washed ashore Tory Channel, *c*. 41°14' S, 174°14' E, -/02/1959, coll. G. Perano.

UNLOCALISED NEW ZEALAND MATERIAL: NMNZ M.90365, F, ML 82.0 mm (+ 3 hectocotyls removed from mantle cavity), f.v. *Voyager*, set # 16, 17/11/1981; NMNZ M.95269, 2F, ML 61.0, 23.0 mm, f.v. *Voyager*, set # 26, 12/12/1981; NMNZ M.90432, M, ML 7.0 mm, 15 miles north of Cape Brett, 505 m, 21/11/1962; NMNZ M.93065, F, ML 78.7 mm, f.v. *Souza*, set # 63.

REFERENCE MATERIAL: *T. violaceus violaceus*, BMNH 1889.2.11.6, F, ML 70.0 mm, Nice, France; *T. violaceus violaceus*, BMNH 1995157, F, ML 62.5 mm, Messina, Sicily; SAM D17601, *T. violaceus gracilis* (det. W. Zeidler), F, ML 201 mm, midway between Section Bank and St. Kilda, north of outer harbour (prawn trawl), South Australia, col. P.D. Vickers, 29/06/1984; SAM D17602, *T. violaceus gracilis* (det. W. Zeidler), F, ML 198 mm, D'Estrees Bay beach, Kangaroo Island (washed up recently dead), South Australia, coll. K.F.H. Bell, 08/03/1986.

DISTRIBUTION (Fig. 69, p. 100): New Zealand, 28°50–40°45.0' S, 167°34.6–37.3' E to 177°48.3' W, bathymetric distribution from surface to 305 m over 1002–1352 m.

DIAGNOSIS: Sexually dimorphic; male third right arm hectocotylised, with 27 or 28 distal transverse sucker pairs.

DESCRIPTION (Female, Figs 70A, B): ML to 137 mm; skin entirely smooth; mantle ovoid, not laterally compressed; pallial aperture very wide, points of mantle attachment dorsolateral to eyes, free of arm pair 1 and 2. Head indistinct, dorsal head musculature absent; head not retracted into mantle, neither head nor mantle constrictions distinct; dorsal water pores large, crescentic, situated between arm bases 1 and 2. Orbits large to very large (EDI about 27–55), laterally flattened and oriented, situated over base of arm pairs 2 and 3; thick skin covers eyes of largest female; eye aperture small. Funnel of moderate length (FuLI about 39–44), free portion short (FFLI about 7–17); ventral water pores large, ovoid, situated at base of arm pair 3, adjacent to point where funnel fuses to ventral surface of head.

Female brachial crown and arms robust, arms stout, broadly triangular, short to moderately long (about 30–82% TL), with arm pairs 3 and 4 rapidly tapering to arm tip; arm formula 2.1.4.3, with arm pairs 1 and 2 considerably longer than pairs 3 and 4. Web shallow to very deep (WDI 9–52% longest arm length), extensive webbing in sectors A and B, and shallow webbing in sectors C–E; web formula variable, sectors A and B invariably deepest, sectors C–E shallowest.

Female whole-arm sucker count 60–181 (ASC arm pairs: 1, about 74–86; 2, about 132–181; 3, about 47–64, 4, about 60); suckers biserial, extend almost to tip of each arm, positioned along lateral margins of arms 1 and 2, but more adorally oriented along arm pairs 3 and 4; suckers at tips of dorsal arm pair 1 uniserial, papillalike; suckers very small to small (ASIn about 2–7). Suckers closely spaced within web sectors, not deeply embedded within arm tissues; distance between suckers within web about 1–3 sucker diameters; dorsal arms 1 with first 5–9 suckers largest and similar sized, thereafter about 10 suckers gradually decrease in diameter, thereafter similarly sized to arm tip; arm pair 2 with first 18 suckers largest, suckers 5–10 especially so, thereafter suckers assume pitiful proportions and extend to laminar arm tips; all suckers on arm pairs 3 and 4 to distal third of arm of similar size, sucker diameter thereafter rapidly decreases to arm tips.

Male (Figs 70C) to 17 mm ML; mantle ovoid, not laterally compressed; pallial aperture very wide, points of mantle attachment dorsolateral to eyes, free of arm pairs 1 and 2. Head indistinct, dorsal head musculature absent; head not retracted into mantle, neither head nor mantle constrictions distinct; dorsal water pores situated at base of arm pair 1. Orbits large to very large (EDI about 37–43), laterally flattened; orbits situated on base of arm pairs 2 and 3; eye aperture small. Funnel of moderate length (FuLI about 33–39), free portion short (FFLI about 5–21); ventral water pores large, within either web sector D, opening adjacent to funnel aperture.

Male brachial crown and arms robust, arms stout, broadly triangular, short to moderately long (about 27–67% TL), with arm pairs 3 and 4 rapidly tapering to arm tips; arm formula variable, with arms pairs 1 and 2 consistently longer than pairs 3 and 4. Web shallow to very deep (WDI 13–50% longest arm length), with extensive webbing in sectors A and B, and shallow webbing in sectors C–E; web formula variable, with sectors A and B invariably deepest, sectors C–E shallowest.

Male whole-arm sucker count about 30–83 (ASC arm pairs: 1, about 77–83; 2, about 79; 3, about 24–30; 4, about 29–38); suckers biserial, extending almost to tip of each arm along lateral margins of arms 1 and 2, but more adorally oriented along arm pairs 3 and 4; suckers small (ASIn about 4.2–6.5), indistinct at arm tip. Suckers closely spaced within web sectors, not deeply embedded within arm tissues; distance between suckers within web about 1 sucker diameter; with first 5 or 6 suckers on arms 1 and 2 largest, of similar size, thereafter sucker size gradually decreases to arm tip; first 5 or 6 suckers on arms 3 and 4 large, of similar size, with sucker diameter increasing to mid-arm length, thereafter rapidly decreasing to arm tips; male without abrupt sucker enlargement; hectocotylised arm (Fig. 70D–F) with 27 or 28 distal transverse sucker pairs.

Male reproductive system (Fig. 71A) with disproportionately large, gold coloured triangular testis sac; proximal vas deferens short, thick, weakly convoluted; spermatophoral gland long, with pronounced central swelling; spermatophoral gland enters base of disproportionately large, granular accessory gland; accessory gland laminar, with complete terminal volution; common spermatophoral and accessory gland duct to spermatophore sac with well-developed basal appendix; spermatophore sac cylindrical, short, distally rounded; penis and spermatophore sac separated by constriction; penis about 50% length spermatophore sac, barrel-shaped, genital aperture not discerned. Female (Fig. 71B) with large ovary sac; ovarian and distal oviduct eggs small (< 1 mm length), ovoid; proximal oviducts exceedingly short, narrow; oviducal ball cylindrical, large, without apparent chambers; distal oviduct very long, convoluted, packed with eggs, dilated proximal to genital aperture.

Alimentary canal of female (Fig. 71C) with large buccal bulb; anterior salivary glands very large (length 65% buccal bulb length), loosely applied to posterior margin of buccal bulb. Anterior oesophagus narrow, long (about 50% oesophagus and crop length); posterior salivary glands paired, small (about 33% buccal bulb length), teardrop-shaped; crop with well-developed, thin-walled anterior diverticulum. Stomach massive (about 1.7 times buccal bulb length), with thick-walled, muscular basal section and thin-walled distal section, its lumen continuous; spiral caecum thin walled, large (of equivalent size to buccal bulb), smaller than stomach (about 60% size of stomach), with single complete volution; intestine of equivalent length to anterior alimentary canal, dilated for greatest length. Hepatic ducts paired; digestive gland large, ovoid, of metallic green colour; pancreas well developed (about 33% digestive gland length), light green; ink sac large, cylindrical (length about 66% digestive gland length), deeply embedded in digestive gland with surface visible throughout length; ink duct short, opening at anus. Alimentary canal of male (Fig. 71D) differs in having large slender triangular-shaped posterior salivary glands of equivalent length to buccal bulb, massive thin-walled crop, stomach of equivalent size to buccal bulb, spiral caecum of equivalent size to buccal bulb, and an intestine constricted for its entire length.

Female upper beak (Fig. 71E) tall, conical (height 86% beak length), with dark-brown hood; rostrum indented; hood and lateral wall margins translucent; with pronounced W-shaped dark brown lateral wall crest. Hood moderately deep (depth 58% beak length), well raised from lateral walls; hood crest flattened, with faint lateral keels. Lateral walls rounded in profile, with broadly rounded crest and deep lateral wall crease, with deep concavity in lateral wall margin. Lower beak (Fig. 71E) very depressed (height 45% width), with darkly pigmented hood and proximal two-thirds of lateral wings; wings wide, flaring outwards, distal third of lateral wings and wall margins translucent. Lateral wall with deeply excavate basal notch, weak-keeled crest, 2 lateral wall creases, and with the free corners of lateral wall widely spread out. Hood short (depth 50% beak length), broad, low; forward projecting rostrum absent (rostrum with square-shaped indentation); lateral wings long (length 120% beak length), without apparent folds.

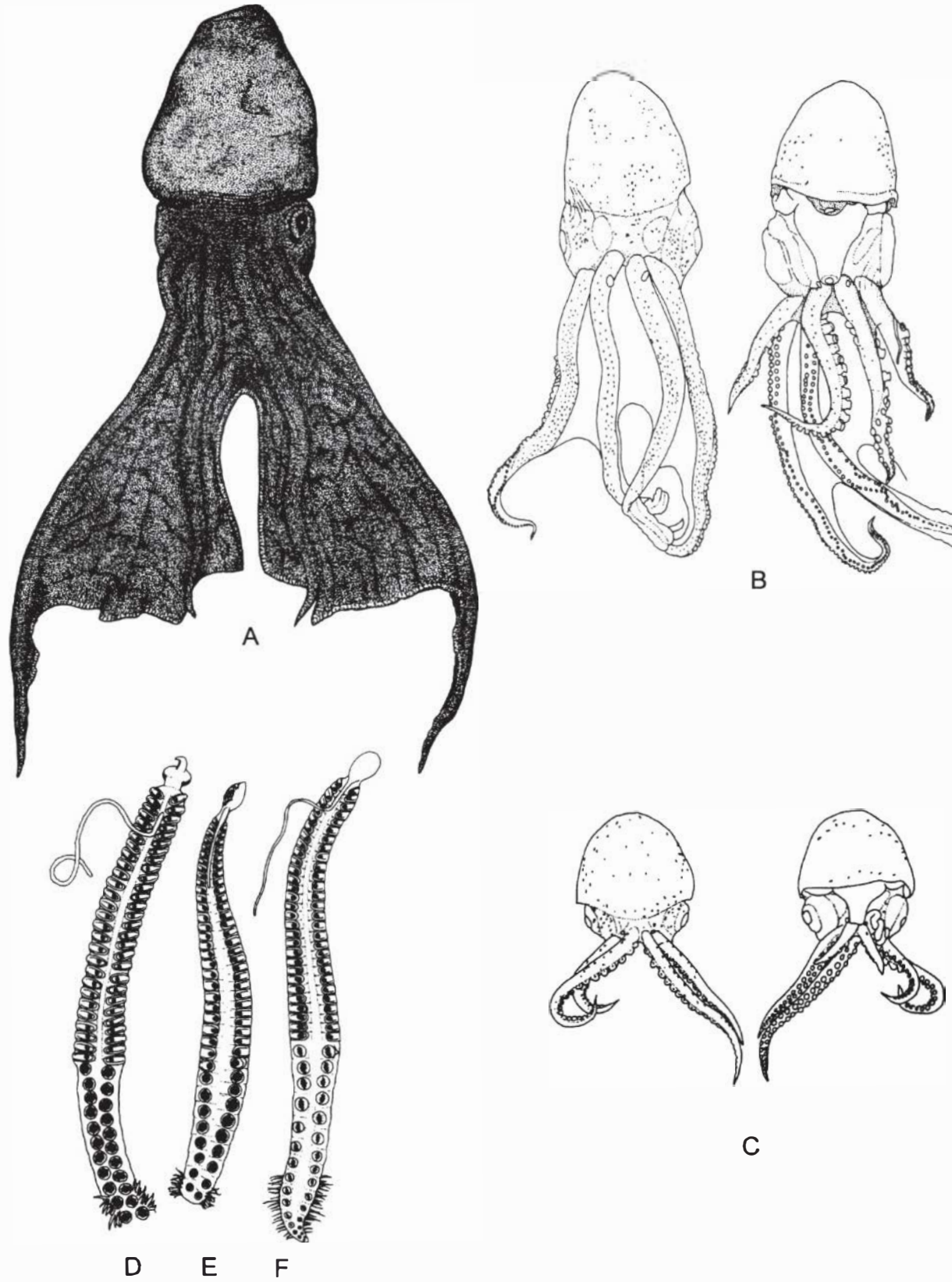


Figure 70. *Tremoctopus robsonianus* Kirk, 1883: **A**, NMNZ M.5622, female, ML 61 mm. **B**, NMNZ M.90455, female, ML 13.1 mm. **C**, NMNZ M.74161, male, ML 5 mm. **D–F**, male hectocotylii recovered from female mantle cavities. **D**, from NMNZ M.118262. **E, F**, from NMNZ M.90365.

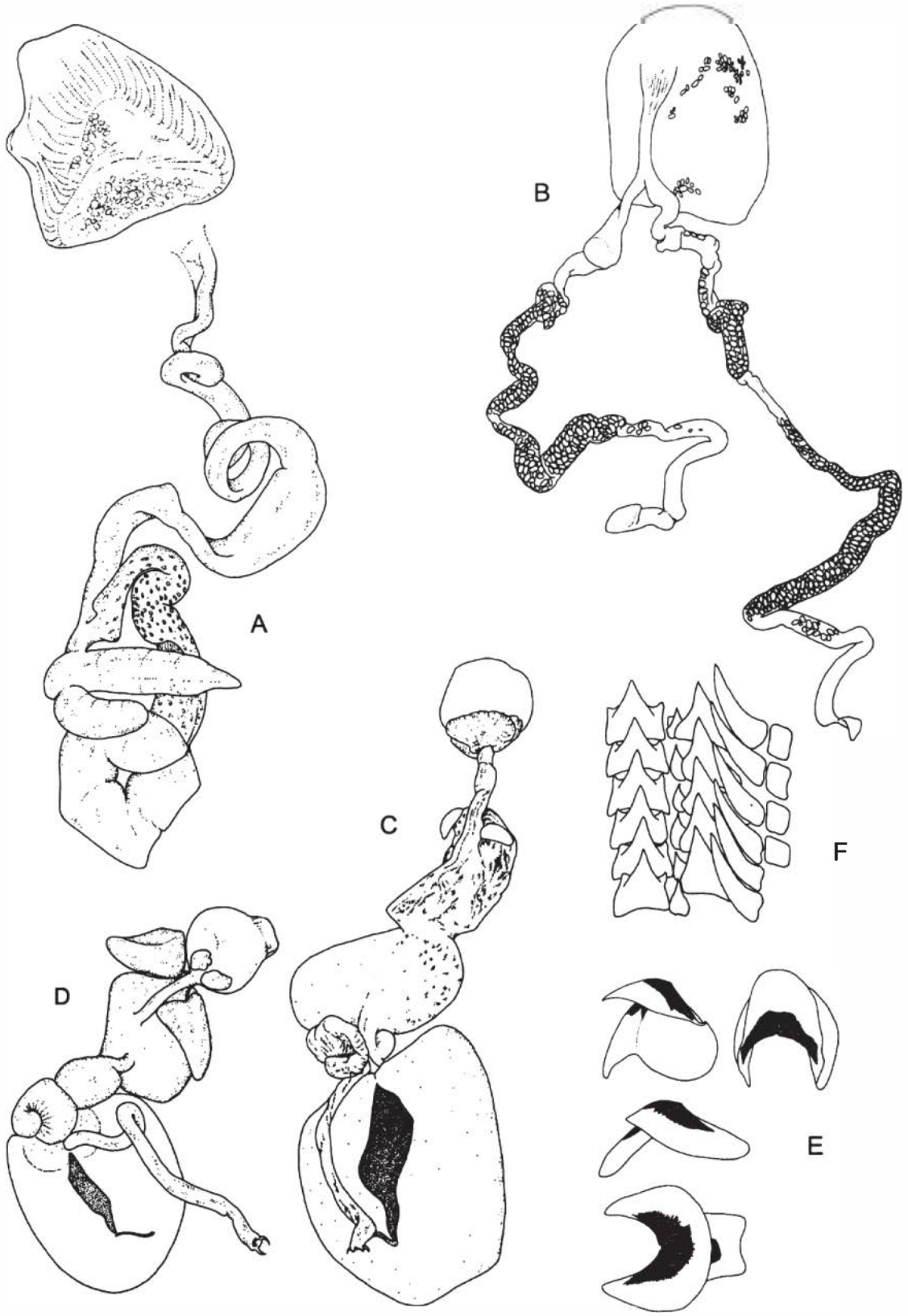


Figure 71. ***Tremoctopus robsonianus*** Kirk, 1883. Anatomy: **A, D**, NMNZ M.118440, male, ML 15.3 mm. **B, C, E, F**, NMNZ M.90365, female, ML 82 mm. **A**, male reproductive system. **B**, female reproductive system. **C**, female alimentary canal. **D**, male alimentary canal. **E**, female beaks. **F**, female radula.

Table 46. Indices, formulas, and counts for *Tremoctopus robsonianus* (* denotes damage).

	NMNZ M.131727	NMNZ M.95284	NMNZ M.118440	NMNZ M.90455	NMNZ M.67874	NMNZ M.67874	NMNZ M.95269	NMNZ M.93065
sex	M	M	M	F	F	F	F	F
MWI	66.7	69.7	62.1	76.3	68.2	81.5	73.8	77.5
HdWI	75.4	85.9	68.6	81.7	71.4	78.0	63.8	53.4*
HdLI	38.9	35.9	43.1	46.6	36.4	37.9	32.8	22.9*
EDI	38.9	36.6	43.1	55.0	37.7	37.6	27.0	*
EOI	10.3	12.7	11.8	11.5	13.2	18.2	10.5	*
ALI1–4	31.4–57.1	30.4–67.4	26.7–66.7	31.4–68.6	30.6–76.5	39.2–81.0	33.5–81.9	*
AFR	*	1.2.3.4	2.1.3.4	2.1.4.3	2.1.4.3	2.1.4.3	*	*
AFL	2.1.4.3	1.2.4.3	1.2.4.3	2.1.4.3	2.1.4.3	2.1.4.3	*	*
WDIA–E	25.0–50.0	12.9–45.2	13.3–50.0	8.6–48.6	10.8–52.3	8.6–40.6	10.2–40.3	14.4*–26.4*
WFR	B.A.D.C=E	B.A.D=E.C	*	B.A.C.D.E	B.A.D=E.C	?B.A.D.C.E	B.A.E.C.D	B.D.E.C.A
WFL	B.A.C=D.E	B.A.D=C.E	A=B.D.C.E	B.A.C.D.E	B.A.D.E.C	B.A.C.D.E	B.A.E.D.C	*
ASC1–4	*	24*–79	30–*c*.83	*c*.60–*c*.144	51*–*c*.132	*c*.60–*c*.181	*	*
ASIn1–4	4.8–5.6	4.2–5.6	5.2–6.5	6.1–6.9	1.8–5.0	2.0–6.1	2.3–5.6	1.7–5.2
FuLI	38.9	35.9	33.3	43.5	42.7	42.8	39.3	42.2
FFuI	8.7	21.1	5.2	11.5	12.3	11.6	7.4	16.5

Table 47. Raw measures for *Tremoctopus robsonianus* (* denotes damage; ‡ denotes arm enclosed in pouch; the figures in parentheses for ASn are largest of basal 4 suckers, followed by mid-arm length diameters).

	NMNZ M.131727	NMNZ M.95284	NMNZ M.118440	NMNZ M.90455	NMNZ M.67874	NMNZ M.67874	NMNZ M.95269	NMNZ M.93065
sex	M	M	M	F	F	F	F	F
ML	12.6	14.2	15.3	13.1	22.0	34.6	61.0	78.7
TL	35.0	46.0	45.0	51.0	85.0	158.0	215.0	271.0
MW	8.4	9.9	9.5	10.0	15.0	28.2	45.0	61.0
HW	9.5	12.2*	10.5	10.7	15.7	27.0	38.9	42*
HdL	4.9	5.1	6.6	6.1	8.0	13.1	20.0	18*
AL1R/L	17/19	31/31	27/30	30/33	45/45	99/95	115/100	135/125
AL2R/L	20/20	29/30	28/26	34/35	63/65	128/127	176/145	174*/155
AL3R/L	‡/11	detach/14	‡/13	16/17	28/26	62/63	25*/72	51*/68*
AL4R/L	11*/17	21/21	12/18	19/21	39/40	72/72	35*/40*	52*/71*
WDA	8.5	10.0*	14.0	13.0	17.0	46.0	29.0	25
WDBR/L	9.0/10.0	14.0*/11.0	15.0/14.0	15.0/17.0	34.0/28.0	*/52.0	71.0/62.0	43/*
WDCR/L	5.0/6.0	4.0/5.0	*/5.5	5.0/5.0	8.0/7.0	11.5/15.0	21.0/18.0	26/46
WDDR/L	6.0/5.0	5.0/6.0	*/6.0	4.5/4.5	9.0/11.0	16.0/13.5	20.0/22.0	38/45
WDE	5.0	5.0	4.0	3.0	9.0	11.0	23.0	34
ASC1R	*	77*	*c*. 83	*c*. 86	*c*. 76	*c*. 74	*	*
ASC2R	*	79	79	*c*. 144	*c*. 132	*c*. 181	*	*
ASC3R	-	*	-	*c*. 60	*c*. 63	*	*	*
ASC3L	*	24*	30		*	*c*. 64	*c*. 47	*
ASC4R	*	29*	38	*c*. 60	51*	L *c*. 60	*	*
ASn1R	(0.6)0.4	(0.6)0.4	(0.9)0.3	(0.8)0.5	(1.0)0.5	(2.1)0.7	(3.2)1.4	(3.8)1.3
ASn2R	(0.6)0.4	(0.6)0.4	(0.9)0.3	(0.9)0.5	(1.1)0.4	(2.0)0.7	(3.4)*	(4.0)*
ASn3L	(0.7)0.4	(0.6)0.6	(0.8)0.8	(0.9)0.7	(1.1)1.0	(1.9)1.9	(3.1)3.1	(4.0)4.0
ASn4R	(0.7)0.4	(0.8)0.8	(0.8)1.0	(0.9)0.9	(1.0)1.1	(1.9)2.0	(3.2)3.0	(4.1)4.1
HcL	*	*	*	F	F	F	F	F
GiLC	11	10	13	15	15	15	15	15
FuL	4.9	5.1	5.1	5.7	9.4	14.8	24	33.2
FFL	1.1	3.0	0.8	1.5	2.7	4.0	4.5	13.0
ED	4.9	5.2	6.6	7.2	8.3	13.0	16.5	*
EO	1.3	1.8	1.8	1.5	2.9	6.3	6.4	*

Radula (Fig. 71F) with wide, tall-profile rachidian with 3 symmetric cusps, the central tall, the lateral shorter; 1st lateral short, narrow, with single tall, well-developed cusp; 2nd lateral slightly shorter than rachidian, with long base and single tall, broad-based cusp; marginal teeth large, robust, cusp similar to 2nd lateral; marginal blocks stocky.

Indices, formulas, and counts for *T. robsonianus* in Table 46; raw measures in Table 47.

REMARKS: Thomas (1977) reviewed species of the genus *Tremoctopus* and recognised two valid subspecies of *T. violaceus*, *T. v. violaceus* and *T. v. gracilis*, and a second species, *T. gelatus*. Males of *T. v. violaceus* and *T. v. gracilis* can be distinguished by the number of distal transverse sucker pairs on the hectocotylised arm: the former with 15–19, the latter, 19–23; the male of *T. gelatus* is presently unknown. Each of 5 detached hectocotyli recovered from the mantle cavity of New Zealand female *T. robsonianus* have 27 or 28 distal transverse sucker pairs. Of the options available to describe New Zealand *Tremoctopus*, the one adopted here is to recognise New Zealand specimens as a separate species from either subspecies of *T. violaceus* or the poorly known *T. gelatus*; the earliest available name for the New Zealand species being *T. robsonianus* Kirk, 1883.

Female *Tremoctopus* species historically have proved difficult to distinguish (Thomas 1977). The distal oviducts of *T. robsonianus* are exceedingly long and convoluted, differing markedly from those of *T. v. violaceus*, *T. v. gracilis*, and *T. gelatus* as depicted by Thomas (1977: figs 5g and 11b), and *T. violaceus* as depicted by Sasaki (1929: fig. 10A). In each of these the distal oviducts are short, each having a pronounced distal dilation.

Tremoctopus robsonianus evidently breeds in New Zealand waters, three hectocotyli having been recovered from the mantle cavity of one female and two from another. Since the New Zealand distribution of *T. robsonianus* parallels that of *Ocythoe tuberculata*, it could be that the former also has a more extensive distribution than current records might suggest.

Family **VITRELEDONELLIDAE** Robson, 1930

Deep-sea gelatinous octopods with translucent, almost colourless body. Adults with arms about 2 or 3 times mantle length; suckers uniserial, widely distributed within web, closely set and greatly enlarged outside web; enlarged suckers to 10–17% ML; web depth 40–60% longest arm length; eyes small, narrow, almost rectangular, diameter approximately 20% mantle length; eyes directed laterally. Optic nerve very long, optic ganglia at distance from brain. Mantle aperture very wide. Radula with multicuspid rachidian and unicuspid first and second lateral teeth; liver very long, narrow, accuminate posteriorly; stomach in front of liver, ovary above it; posterior salivary gland unpaired; ink sac well developed. Third left arm hectocotylised, shorter than right, ligula short (after Nesis 1987: 323). Family monogeneric for Vitreledonella Joubin, 1918.

Vitreledonella Joubin, 1918

TYPE SPECIES: *Vitreledonella richardi* Joubin, 1918 by monotypy.

DIAGNOSIS: With characters of the family.

Vitreledonella richardi Joubin, 1918

Vitreledonella richardi Joubin, 1918: 1; Robson 1932: 321–325, fig. 79; Thore 1949: 57; Dell 1951: 96; 1952: 75; Powell 1957: 125; 1962: 126; 1976: 133; 1979: 444; Nesis 1987: 323, figs A–C; Spencer & Willan 1995: 52.

MATERIAL EXAMINED (6 specimens, 1 male [M], 5 sex indet.): NMNZ M.74170, M, ML 20.0 mm, 30°18' S, 173°03' E, 3200–3600 m, datNR, AUZ 014/04, depth questionable; NMNZ M.120117, sex indet., ML 5.2 mm, 31°24' S, 179°00' E, 1500–1700 m, 25/07/1962, AUZ 95 17, *Tui* Cruise; NMNZ M.74187, sex indet., ML 7.9 mm, 31°57' S, 177°38' E, surface over 3400–4000 m, 24/07/1962; NMNZ M.120110, 2 sex indet. ML 28.5 mm, 13.5 mm, AUZ 018 06; NMNZ M.74428, sex indet., ML 4.1 mm, 37°34.4' S, 178°21.7' E, 17 m over 46 m, 03/08/1976, f.r.v. *James Cook* Stn J11/93/1976.

DISTRIBUTION (New Zealand, Fig. 71, p. 100): 30°18–31°24' S, 173°03–179°00' E, bathymetric range from surface to 3200–3600 m over bottom depths to 4000 m. Otherwise tropical–subtropical and cosmopolitan, adults bathypelagic, juveniles epipelagic to mesopelagic (Nesis 1987: 323).

DIAGNOSIS: With characters of the family. New Zealand specimens all juvenile; mantle length attains 110 mm, total length to 450 mm (*fide* Nesis 1987: 323). The following description is based on that of Robson (1932: 321).

DESCRIPTION: With 30 uniserial suckers remaining on longest arms; adoral suckers small, widely spaced, increasing in size towards midarm, the largest numbers 12–14, thereafter suckers become smaller and more closely arranged; suckers implanted in circular transparent boss, at the apex of which lies the sucker aperture; suctorial apparatus absent. Gills comprise outer demibranch only, with 7 filaments.

Anterior salivary glands absent; posterior salivary gland single, median. Crop represented by thin vermiform caecum situated near stomach; stomach divided externally into two parts; spiral caecum separated from stomach by short section of intestine, of which it is a diverticulum; digestive gland much reduced in size; ink sac almost as large as digestive gland, largely covering the latter; intestine very slender.

Beaks small, weak and flattened; rostral lamella of lower beak deeper than gular lamella. Radula with central rachidian with two cusps aside, a bicuspid 1st lateral, the inner cusp being much broader than the outer, a unicuspid second lateral of more or less octopodan form, a more or less straight third lateral and a lozenge-shaped marginal.

Optic nerve long; peduncular and optic ganglia close together; brachial ganglion indistinct; white body present.

Proximal oviduct long, slender; the oviducal gland well developed, comprising a number of small pyriform subdivisions around a central canal; distal oviduct slender.

REMARKS: *Vitreledonella richardsoni* is represented by six juveniles of mantle length 4.1–28.5 mm.

The genus is currently considered monotypic on the basis of the most recent revision (Thore 1949), in which neither comprehensive anatomical nor morphometric information for any specimen was provided. Robson (1932) recognised four species.

Family **OCTOPODIDAE** d'Orbigny, 1845

Body muscular to gelatinous; suckers uniserial or biserial; radula heterodont, occasionally homodont; digestive gland anterior to stomach and caecum; hectocotylised arm not autotomised at maturity; mantle-locking apparatus absent; shell vestige present in some species as stylets in mantle; ink sac present or absent; light organs absent (after Hochberg *et al.* 1992: 237).

Subfamily **OCTOPODINAE** Grimpe, 1921

Littoral to bathyal octopods with biserial suckers; ink sac present, reduced or absent (*Ameloctopus* Norman, 1992a); crop large, with diverticulum extensive, reduced or absent; radula with rachidian tooth with 1–3 small lateral cusps aside tall central cusp; funnel organ W or VV (new diagnosis).

Octopus (s.s.) Lamarck, 1798 Type 1

Arms not conspicuously different in length; suckers in two rows; penis diverticula short; suckers unmodified in female; gill filaments rarely exceed 11. Small mantle and head and robust brachial crown; enlarged suckers on both lateral arm pairs 2 and 3; hectocotylised portion of male third right arm minute; female genital apertures extend over face of interpallial musculature, opening proximal to anus (corrected from Robson 1932: 57).

REMARKS: As the type species of *Octopus*, *O. vulgaris* Cuvier, is inadequately described, and for which neither type locality is known nor type material exists (*fide* Mangold & Hochberg 1991), the definition of *Octopus* (*Octopus*) employed here follows that of Robson (1929b: 57). In the absence of type material of the type species, the characteristics of *O. oliveri* are taken to be those of *Octopus* (*s.s.*). *Octopus oliveri* Berry was recognised as *Octopus* (*s.s.*) by Robson (1929: 100), though (*ibid.*: 101) he considered it to be "rather unlike the majority of the *vulgaris*-like group". The character states in which this species purportedly differed from *O. vulgaris* (narrow pallial aperture, shallow web, short arms, and web sector A deeper than E) were simple artefacts of the limited material and descriptions of this species available to Robson. In taking *O. oliveri* as the standard of reference, several additional, distinct morphologies are apparent that herein are referred to as *Octopus* (*sensu lato*) Types 2, 3, and 4. These morphotypes may represent new genera, although much additional research is required before their systematic status can be evaluated further.

Octopus oliveri (Berry, 1914) (Figs 74, 75) (Tables 48–52)

Polypus oliveri Berry, 1914: 136–137; Oliver 1915: 560, 564; Berry 1916: 49, pl. 6, fig. 2; Sasaki 1929: 42–43, text fig. 15–16, pl. 4, fig. 2, pl. 9, figs 14–18.
Octopus oliveri: Robson 1929b: 100–101; Okutani *et al.* 1987: 166–167, figs 65A, B.

TYPE MATERIAL (23 specimens, 11 male [M], 11 female [F], 1 sex indet.): Holotype, USNM 816455, F, ML 45.0 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, intertidal, coll. Oliver, 1908.

ADDITIONAL MATERIAL EXAMINED: OM A.'54.82, M, ML 44.0 mm, Kermadec Islands, pres. Oliver (labelled cotype), datNR; NMNZ M.256367, 2M, ML 48.0, 42.2 mm, AUZ 107, Meyer Island, Kermadec Islands, *c.* 29°14' S, 177°50' W, shore collecting, 28/07/1962; AK 77956, F, ML 29.2 mm, Raoul Island, Kermadec Islands, Fishing Rock, 29°15' S,

177°52' W, rock pool, 08/06/1944; AK 77955, F, ML 30.0 mm, *c.* 29°15' S, 177°52' E, 07/05/1944, Raoul Island, Boat Harbour tidal rocks; AK 77956, F, ML 38.1 mm, *c.* 29°15' S, 177°52' E, Raoul Island, Fishing Rock rock pool, 08/06/1944; NZOI Stn Z2049, 2M, ML 48.0, 47.5 mm, F, ML 69.0 mm, 29°15'S, 177°52'W, Fishing Rock, Raoul Island, pools, 18/11/1964; NZOI Stn Z2058, F, ML 41.0 mm, 29°15' S, 177°52' W, Fishing Rock, Raoul Island, pools, 13/05/1965; NZOI Stn Z2061, M, ML 48.2 mm, 29°15' S, 177°52' W, Fishing Rock, Raoul Island, pools, 20/10/1965; NMNZ M.256368, F, ML 40.0 mm, Fishing Rock, Raoul Island, Kermadec Islands, 29°15' S, 177°52' W, low tide, coll. D. Browning & N. Brown, 18/01/1968; NMNZ M.256375, M, ML 42.5 mm, 3F, ML 36.0, 35.0, 34.0 mm, tidepools, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. J. Soberg, 1954; NMNZ M.256373, M, ML 52.5 mm, rock pool, Denham Bay, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, -/02/1956; NMNZ M.56363, M, ML 15.7 mm, sex indet., ML 12.0 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, rock pool, 1975–76; NMNZ M.56372, M, ML 49.5 mm, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. R.G. Lovegrove, 1963–64; NMNZ M.256377, M, ML 47.2 mm, F, ML 38.0 mm, tide pools, Raoul Island, Kermadec Islands, *c.* 29°16' S, 177°54' W, coll. J. Soberg, 1954.

DISTRIBUTION (New Zealand, Fig. 73, p. 121): Kermadec Islands, 29°14–16' S; otherwise recorded from Japan (*fide* Sasaki 1929).

DIAGNOSIS: Small, robust-bodied, densely papillose, muscular animals with grossly but not abruptly enlarged suckers on lateral arm pairs; male with minute terminal calamus and ligula, spermatophoral groove well developed; outer gill lamellae few (7); New Zealand distribution restricted to Kermadec Islands, all known records intertidal to several metres depth.

DESCRIPTION: Adult size small (ML to 69.0 mm, TL to 262.0 mm); body small and stocky (Figs 74A–D); female attaining greater size (to 69.0 mm ML; male to 52.5 mm ML). Mantle ovoid, broader in male (male MW 74–91.5% ML; female 65.3–69.6), dorsoventral compression absent; lateral keel or fold of skin absent; ventral longitudinal groove or depression frequent. Head well developed but small, wider than long, narrower than mantle (HdL about 22–34% ML; HW about 46–72% ML), separated from mantle by moderately well-developed preocular constriction. Orbits small, dorsally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsally oriented. Funnel long (FuL about 29–41% ML), well developed, base entirely free of brachial crown. Nuchal constriction poorly developed.

Brachial crown very robust, wider than head and mantle. Arms thick, square in section, very short to very long (female about 73–87% TL; male about 51–91% TL), gradually tapering to blunt-rounded tips; web shallow to deep, about 11–34% longest arm length, with thick, well-developed web extension along dorso- and ventrolateral surfaces of each arm almost to tip; web formula variable, sectors A and E usually shallowest, sectors C, D and B deeper, with no consistent disparity in sector depths. Suckers biserial, with 11–13 suckers between beaks and web margin on dorsal arm pair 1; distal arm-tip suckers not markedly reduced in diameter. Arm sucker counts low to moderate, similar in male and female of comparable ML, ASC 95–180; suckers extend to arm tips. Sucker size sexually dimorphic, male large to very large (ASIe about 14–22), with suckers 11–13 on lateral arms 2 and 3 largest; suckers in female moderate to very large (ASIe 10–18); no suckers abruptly enlarged in either sex. Suckers with: large suction chamber; well-constricted sucker aperture; extensive, well-developed grasping ring with 27–30 faint radial grooves; crenulate sucker aperture with 11–14 well-developed teethlike processes; and slight development of muscular suction pad (Fig. 155F).

Male with third right arm hectocotylised, length shorter or equivalent in length to opposite member (OAI about 65–99); with moderate number of suckers (ASC 76–110); terminal hectocotylised portion (Fig. 75A) minute (LLI 1.6–2.2), ligula with thick cheeks enclosing narrow groove with 7 or 8 fleshy transverse rugae; calamus proportionately large (CaLI about 29–40), with groove extending entire structure length. Spermatophoral groove deeply recessed within well-developed, thickened web margin.

Dorsal and ventral surfaces of mantle, head, arms, web, and oral surface of arms and web densely papillose. Dorsal surface of mantle, head, dorsal surfaces of arms 1–3, and web sectors A–C beset with large, wartlike conical mounds, each with 11–16 small, low-profile, pimplelike prominences. Conical mounds most crowded over dorsolateral surface of mantle and dorsal surface of head, none particularly enlarged to form superocular cirri. Ventral surface of mantle, head, arms 4, and web sectors D and E with more sparsely set with small wartlike conical mounds. Dorso- and ventrolateral surfaces of arms, and oral surface of arms and web densely beset with small conical papillae. Colour (preserved specimens) over dorsal surfaces of mantle, head, arms 1–3, and web sectors A–C dark red to purple. Ventral surface of mantle, head, surfaces of arms 3 and 4 and web sectors D and E slightly paler. Oral surface of arms, web and sucker apertures light purple to tan.

Funnel organ W-shaped; outer limbs short, broad, inner V-component longer, narrow. Gills large, with 7 inner and outer lamellae per demibranch. Penis in mature male oriented towards interpallial septum, extending over renal tissue; genital aperture opening

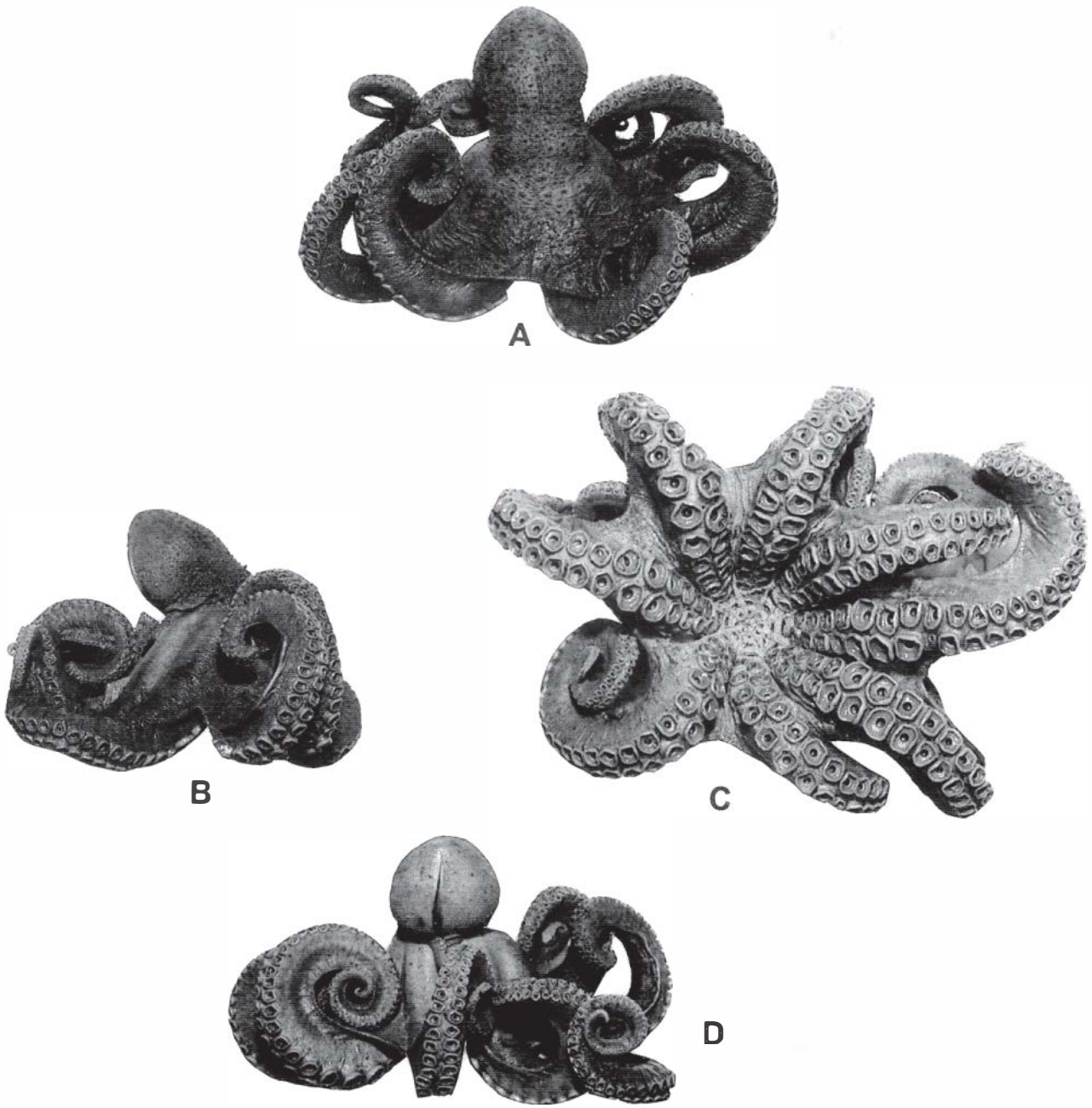


Figure 74. *Octopus oliveri* (Berry, 1914): **A-D,** NZOI Stn Z2058, female, ML 41.0 mm.

proximal to anus. Interpallial septum short, thick, muscular; membranes between renal tissue and ventral inner surface of mantle well developed, mantle cavity restricted. Anus at base of interpallial septum; saccular, thin walled, containing up to 24 spermatophores; spermatophores short, to 34 mm length. Distal vas deferens short, thick; penis diverticulum single, large, about 50% penis length; penis large, genital aperture subterminal. Mature female (Fig. 75C) with large ovary sac (about 78% ML in greatest dimension); proximal oviducts depart ovary sac through common antrum, wide (but flattened [preservation artefact] in single female dissected), thin walled, length about 65% distal duct length;

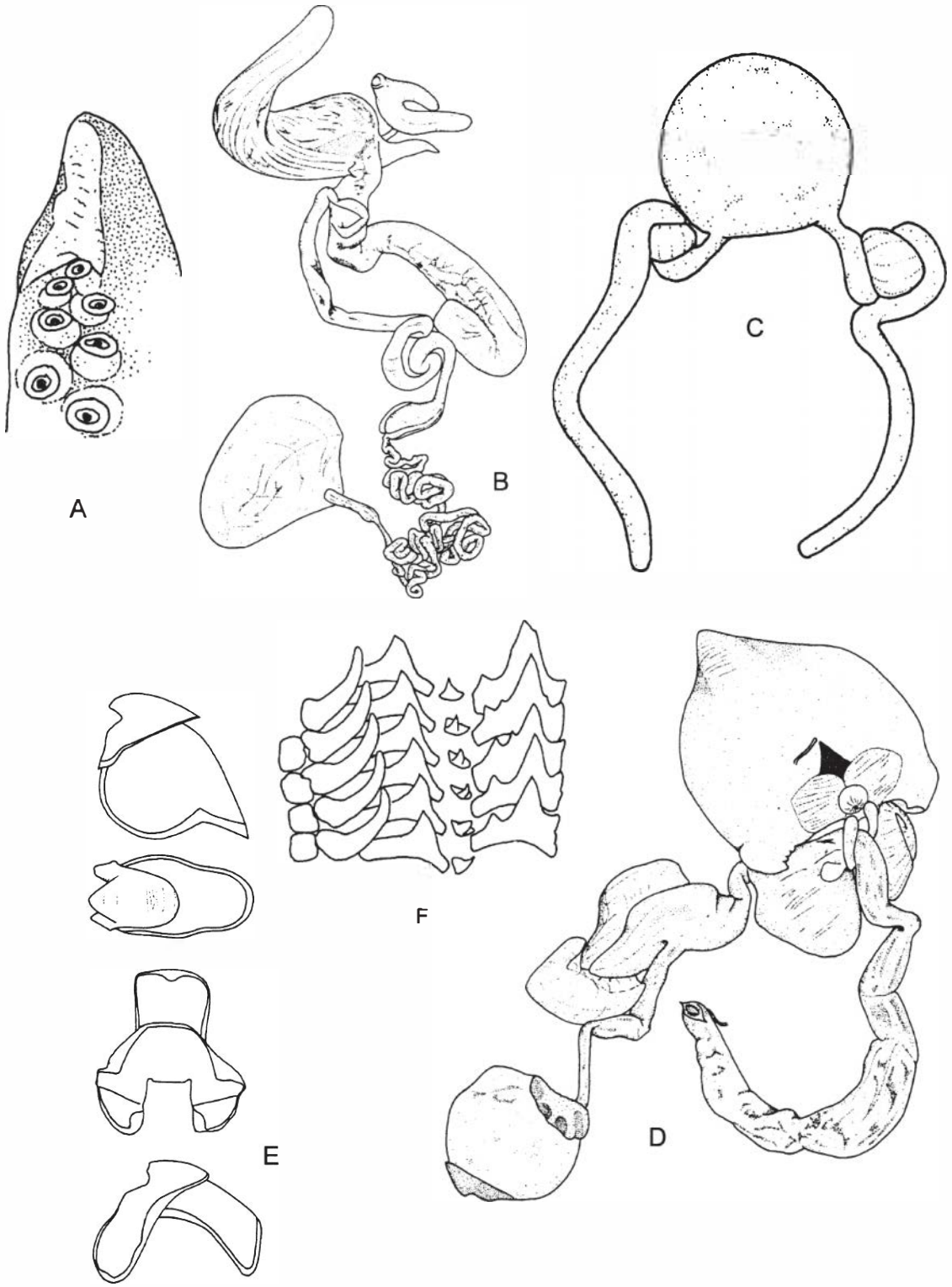


Figure 75. *Octopus oliveri* (Berry, 1914). Anatomy: **A**, **B**, **D–F**, NMNZ M.256367, male, ML 48 mm. **C**, NZOI Stn Z2049, female, ML 69 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 48. Indices, formulas, and counts for male *O. oliveri* (Berry) (* denotes damage).

	NMNZ M.256372	NMNZ M.256367	NZOI Stn Z2049	OM A.'54.82	NMNZ M.256367	NMNZ M.256363
MWI	77.0	83.3	74.0	89.5	91.5	86.6
HdLI	23.4	28.3	31.5	25.7	32.0	29.9
HdWI	56.6	54.6	56.3	60.2	52.8	71.3
EOI	3.4	4.2	4.2	2.7	7.8	3.2
ALI1–4	72.2–91.2	67.0–80.3	54.9–84.1	69.5–85.3	62. 7–78.2	50.8–78.7
AFR	2.4.1.3	*	*	2.4.1.3	2.1.4.3	2.4.1.3
AFL	2.3.1.4	4.2.1.3	*	2.3.1.4	3.1=2.4	3.2.1=4
WDIA–E	23.7–33.9	12.3–21.4	18.9–21.6	20.5–29.8	16.0–21.5	29.2–33.3
WFR	*	B.A=C.D.E	D.C.E.B.A	C.D.B.A.E	B.E.D=A.C	D.B.E.A.C
WFL	D.C.B.E.A	C.B.A.D.E	D.E.B.C.A	C.D.B=A.E	B=D.C.E.A	C.B=D.E.A
ASC1–4[1]	159–171	160–177	174–180	151–163	163–167	95–107
ASIn1–4	16.8–20.8	15.6–18.8	17.1–21.7	15.7–19.3	13.7–16.6	14.0–19.1
FuLI	32.3	31.3	35.4	28.4	37.9	34.4
FFuI	30.3	21.9	20.4	22.7	20.1	25.5
PAI	52.5	53.1	53.1	50.9	56.4	49.7

[1] Excludes ASC arm 3R

Table 49. Indices, formulas, and counts for female *O. oliveri* (Berry) (* denotes damage).

	NZOI Stn Z2058	NZOI Stn Z2049	NMNZ M.256377	NMNZ M.256368
MWI	68.3	69.6	65.3	67.8
HdLI	34.1	21.7	26.8	23.0
HdWI	57.1	45.8	50.0	51.5
EOI	3.2	3.6	5.5	5.3
ALI1–4	73.3–82.6	74.8–83.2	72.7–81.3	74.4–86.7
AFR	*	*	2.3.4.1	2.4.3.1
AFL	3.2.4.1	*	*	4.2.3.1
WDIA–E	21.1–30.6	18.3–22.9	11.2–19.9	14.1–23.7
WFR	C.D.B.E.A	B=C.D.A.E	C.D.B.E.A	D.C.B.E.A
WFL	C.B.D.E=A	D.B.C.A.E	D.C.B.A.E	C.D.B=E.A
ASC1–4	170–178	172–195	156–163	150–155
ASIn1–4	13.7–18.0	12.2–15.2	10.8–14.5	10.3–13.0
FuLI	34.1	32.6	40.5	30.0
FFuI	24.1	19.6	26.8	22.5
PAI	46.6	39.1	44.7	46.3

Table 50. Indices and counts of hectocotylised arm for male *O. oliveri* (Berry) (* denotes immature).

	NMNZ M.256372	NMNZ M.256367	NZOI Stn Z2049	OM A.'54.82	NMNZ M.256367	NMNZ M.256363
OAI	82.8	99.4	*c.* 84	83.7	80.2	64.6
ASC3R	95	105	107	103	110	76
CaLI	35.7	28.6	40.0	40.0	36.4	*
LLI	2.0	2.2	2.0	1.6	1.6	*

oviducal gland large, with 2 hemispheres, distal largest, black, with faint radial striations, proximal small, cream coloured, lumen single. Distal oviducts thick walled, slightly swollen, basal half thrown into fold, constricting towards genital apertures; genital aperture terminal, porelike, not secondarily modified. Mature ovarian eggs number thousands; individual eggs small, tear drop shaped, to 7.5 x 1.0 mm, each with short stalk; longitudinal striations not apparent in preserved ovarian eggs.

Alimentary canal (Fig. 75D) with large buccal bulb about 31% ML; anterior salivary glands large, ovoid; anterior oesophagus long, narrow, enters crop dorsally; crop well developed, with extensive anterior diverticulum about 33% total crop length. Posterior salivary glands very large, heart-shaped to ovoid (PSGL about 110% greatest buccal bulb dimension, about 35% ML). Posterior oesophagus muscular, thick walled. Stomach large, with small, thin-walled basal, thick-walled central, and thin-walled distal sections; stomach with undivided lumen. Spiral caecum smaller than stomach, with 2 complete volutions, faint radial striations apparent. Intestine long, about twice oesophagus length, thin walled, dilated for entire length, particularly central half; anal flaps small. Digestive gland large, broadly triangular, with prominent anterior peaks; pancreas well developed; ink sac narrow, short (about 17% digestive gland length), superficially embedded in surface of digestive gland; ink duct short, opening into base of anus.

Upper beak (Fig. 75E) moderately tall (height 98.0% length); hood and lateral walls black, margins translucent; hood very deep (depth 45.7% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, slightly deflected down; jaw with single broad, pronounced tooth. Lateral walls straight sided; crest squared, lateral wall fold weak. Lower beak (Fig. 75E) moderately depressed (height 72.3% width); hood, lateral wall, and wings black, lateral wing and wall margins translucent. Lateral wall with deep, acute angled, V-shaped basal notch and keeled crest. Hood very deep (depth 41.7% beak length), with flattened chisel-like to weakly bifid rostrum; hood with shallow posterior notch; lateral wings long, length equivalent to beak length; lateral wings with single strong fold.

Radular dentition (Fig. 75F) simple; rachidian well developed, broad based, with 1 or 2 asymmetric lateral cusps aside central; 1st lateral tooth small, with short inner heel with inner cusplike prominence, outer cusp larger, broad based, triangular; 2nd lateral of equivalent width to rachidian, broad based, with short inner heel with cusplike prominence, the outer cusp larger, robust; marginal tooth long, with marked curvature, cusp more delicate than that of 2nd lateral; marginal block small, rectangular, well developed. Radula ribbon with repeat seriation every 4 or 5 transverse rows.

REMARKS: In the original and subsequent descriptions of *Octopus oliveri* two specimens were recorded (Berry 1914, 1916). In the collections of the Otago Museum (NZ) is a specimen collected by Oliver labelled 'Cotype'. Given that the holotype is deposited at the National Museum of Natural History, Smithsonian Institution, and the single designated paratype (= 'Cotype' of Berry) is at the California Academy of Sciences, CASIZ-021805 [464] (*fide* Sweeney *et al.* 1988), and no additional material was recorded by Berry (1916), the Otago Museum specimen is not a type specimen (ICNZ Art. 72(a) (vii)).

Table 51. Raw measures for female *Octopus oliveri* (* denotes damage).

	NZOI Stn Z2058	NZOI Stn Z2049	NMNZ M.256377	NMNZ M.256368
TL	172	262	198	180
ML	41.0	69.0	38.0	40.0
MW	28.0	48.0	24.8	27.1
HdL	14.0	15.0	10.2	9.2
HdW	23.4	31.6	19.0	20.6
EO	1.3	2.5	2.1	2.1
AL1R/L	104*/126	179*/202	148/144	134/144
AL2R/L	115*/138	196/151*	161/159	156/151
AL3R/L	141/142	208/218	157/152*	142/147
AL4R/L	130/133	185*/166*	150/155	144/152
WDA	30	45	22	22
WDBR/L	38/30	50/48	27/18	32/30
WDCR/L	43.5/42	50/47	31/26	35/36
WDDR/L	40/39	49/50	28/32	37/35
WDE	37	40	25	30
ASC1R	L170	L193	157	152
ASC2R	L176	172	163	151
ASC3R	177	195	156	155
ASC4R	178	*	158	150
ASe1R	5.6	9.0	4.1	4.8
ASe2R	7.0	10.0	5.5	5.1
ASe3R	7.4	10.5	5.5	5.2
ASe4R	6.0	8.4	4.6	4.1
GiLC	7	7	7	7
FuL	14.0	22.5	15.4	12.0
FFL	9.9	13.5	10.2	9.0
PA	19.1	27.0	17.0	18.5

Table 52. Raw measures for male *Octopus oliveri* (* denotes damage; † denotes regrowth).

	NMNZ M.256372	NMNZ M.256367	NZOI Stn Z2049	OM A.'54.82	NMNZ M.256367	NMNZ M.256363
TL	194	233	226	177	220	61.0
ML	49.5	48.0	48.0	44.0	42.2	15.7
MW	38.1	40.0	35.5	39.4	38.6	13.6
HdL	11.6	13.6	15.1	11.3	13.5	4.7
HdW	28.0	26.2	27.0	26.5	22.3	11.2
EO	1.7	2.0	2.0	1.2	3.3	0.5
AL1R/L	160/163	106*/165	124/178	139/136	168/170	41/44
AL2R/L	173/177	187/176	190/178	151/149	178/170	48/47
AL3R/L	140/169	156/157	151/180*	123/147	138/172	31/48
AL4R/L	170/154	65*/178*	113*/184	142/131	163/164	43/44
WDA	46	33	25	35	28	14.1
WDBR/L	42/51	37/35	38/37	42/40	37/34	15.2/15.0
WDCR/L	55/56	33/40	40/36	45/41	27.5/32	14.0/16.0
WDDR/L	*/60	27/31	41/40	39/35	28/34	15.5/15.0
WDE	55	23	39	31	30	14.8
ASC1R	168	L160	L178	151	163	95
ASC2R	159	177	174	163	167	107
ASC3R	95	105	107	103	110	76
ASC4R	171	*	L180	161	166	102
ASe1R	9.0	7.5	8.2	6.9	5.8	2.7
ASe2R	9.8	9.0	10.4	8.5	7.0	3.0
ASe3R	10.3	8.0	10.4	8.4	7.0	2.2
ASe4R	8.1	7.5	8.4	7.0	6.2	2.6
LL	2.8	3.5	3.0	2.0	2.2	-
CaL	1.0	1.0	1.2	0.8	0.8	-
GiLC	7	7	7	7	7	7
FuL	16.0	15.0	17.0	12.5	16.0	5.4
FFL	15.0	10.5	9.8	10.0	8.5	4.0
PA	26.0	25.5	25.5	22.4	23.8	7.8

Octopus gibbsi sp. nov. (Figs 76–78) (Tables 53–57)

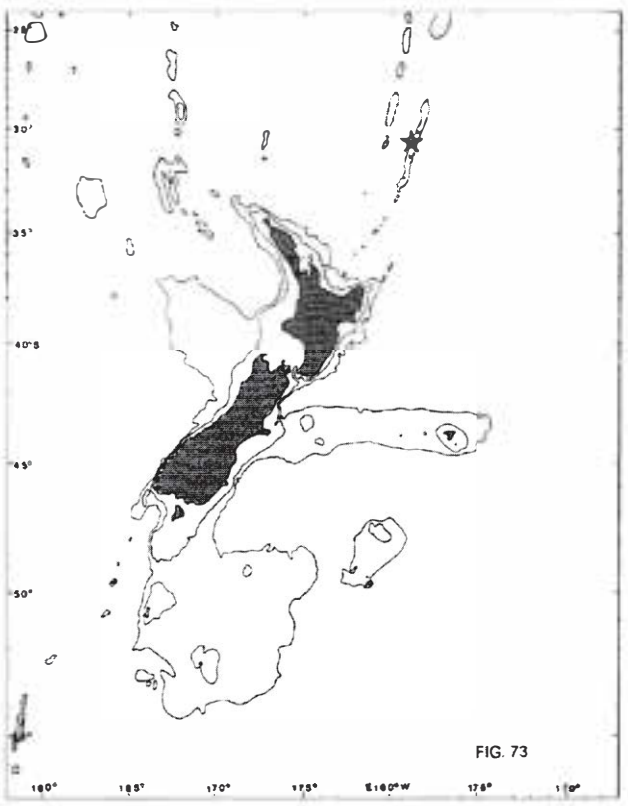
Robsonella australis (not Hoyle, 1885): Dell 1952 (*partim* = *O.* (*s.l.*) *huttoni*, Dell register specimens 23 & 26): 39, 151.

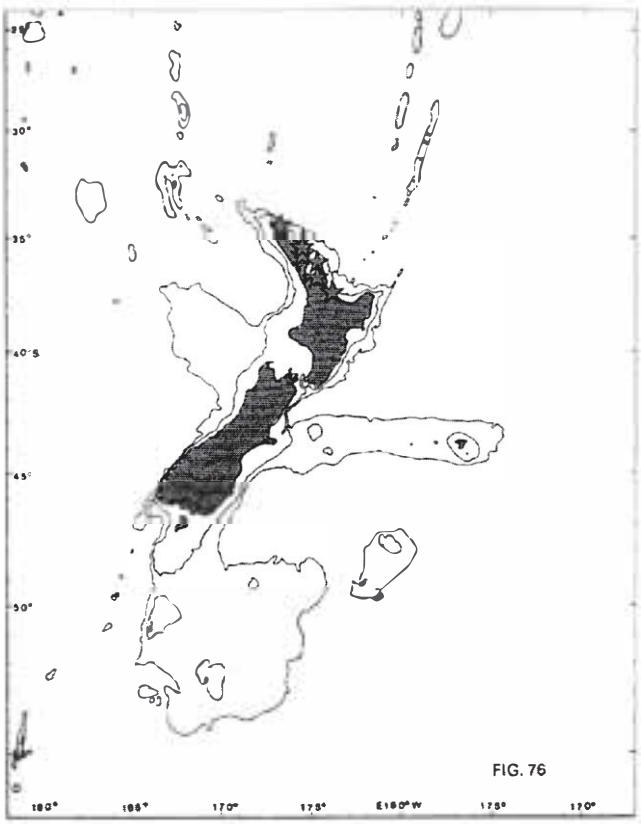
TYPE MATERIAL (20 specimens, 9 male [M], 8 female [F], 3 sex indet.): Holotype: NMNZ M.118305, M, ML 121.5 mm, Smugglers Bay, Whangarei Heads, *c.* 35°49' S, 174°30' E, rock pools, 27/05/1994. Paratypes: NMNZ M.118421, M, ML 135.5 mm, 36°48.79–48.24' S, 175°16.33–16.86' E, 34–40 m, BT 13.1°C, 27/10/1994, f.r.v. *Kaharoa* Stn KAH 9411/11; NMNZ M.118426, F, ML 137.0 mm, Ocean Beach, Whangarei Heads, *c.* 35°49' S, 174°30' E, 1 m, -/05/1993; NMNZ M.90368, F, ML 31.1 mm, BS 409, main channel entrance to Whangaroa Harbour, *c.* 35°02' S, 173°45' E, 22 m, r.v. *Acheron*, 22/02/1974.

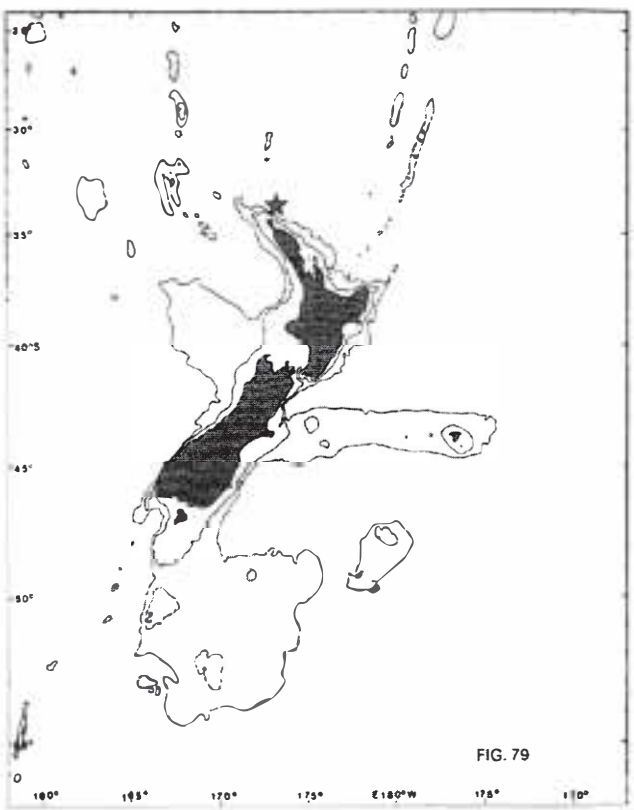
ADDITIONAL MATERIAL EXAMINED: NMNZ M.118303, F, ML 24.5 mm, *c.* 34°31' S, 172°57' E, Dog Island, Parengarenga Harbour, low water, 05/07/1993, coll. O.J. Marston; NMNZ M.117695, F, ML 112.0 mm, Cavalli Islands, Whangaroa, *c.* 34°59' S, 173°58' E, coll. J. MacDonald, -/07/1953; NMNZ M.90321, M, ML 75.4 mm, Parekura Bay, Bay of Islands, *c.* 35°15' S, 174°15' E, 2 m, R.K. Dell, -/11/1971; NMNZ M.90320, F, ML 48.0 mm, *c.* 35°16' S, 174°07' E, 1971; NMNZ M.5636, M, ML 52.0 mm, Russell, Bay of Islands, *c.* 35°16' S, 174°07' E, -/01/1939 (Dell Reg# 26); NMNZ M. 90298, 4M, ML 47.0, 39.5, 19.2, 19.0 mm, F, ML 31.8 mm, Bay of Islands, *c.* 35°16' S, 174°07' E, 6–7 m, coll. J.M. Moreland, 1961; NMNZ M.5613, F, ML 28.0 mm, Paihia, Bay of Islands, *c.* 35°17' S, 174°05' E, intertidal Pools, coll. R.K. Dell, -/01/1939 (Dell register # 23); NMNZ M.118425, M, ML 89.5 mm, Smugglers Bay, Whangarei Heads, *c.* 35°49' S, 174°30' E, rock pools, -/05/1993; NZOI Stn Z8917, F, ML 118.0 mm, 36°49.9' S, 175°45.5' E, 0 m, 08/09/1996; NMNZ M.97076, F, ML 44.1 mm, off Mount Maunganui, Tauranga, *c.* 37°37' S, 176°11' E, 1946.

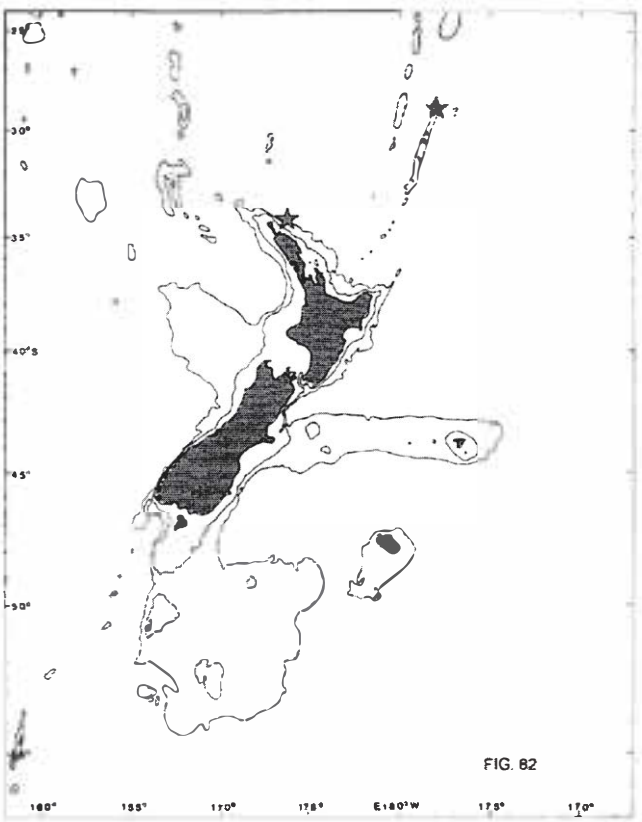
LARVAE ATTRIBUTED TO THIS SPECIES: NMNZ M.118409, 2 sex indet., ML 7.2, 7.0 mm, *c.* 36°05' S, 175°25' E, mid tide, Rangiwhakaea Bay, Great Barrier Island; NMNZ M.137778, sex indet., ML 7.0 mm, Otarawairere Bay, Ohope, under low tidal rocks, 1965, ex. B.A. Marshall colln.

RECOGNISED DISTRIBUTION (Fig. 76, p. 121): North Island east coast, 0–40 m.









Recognised distribution. **Fig. 73**, *Octopus oliveri* (Berry, 1914): type and new material. **Fig. 76**, *Octopus gibbsi* sp. nov. **Fig. 79**, *Octopus* cf. *rugosus* (Bosc, 1792). **Fig. 82**, *Octopus* sp. 2.

DIAGNOSIS: Moderate-sized, papillose-bodied animals with enlarged suckers on lateral arm pairs; web poorly developed in sector A; hectocotylised portion of male third right arm minute, penile complex small; females with genital apertures opening on lateral face of interpallial musculature, not extending to anus; with 9 outer lamellae per demibranch of the gill. Live animals with two preocular iridescent patches on dorsal surface of mantle.

DESCRIPTION: Adult attaining moderate size (ML to 137.0, TL to 676 mm), body slender to stocky (Figs 77A,B). Mantle ovoid, broad (MW about 45–75% ML), no dorsoventral compression, lateral keel fold of skin, ventral longitudinal mantle groove or depression. Head well developed, small to large, wider than long, narrower than mantle (HdL about 20–38% ML; HW about 40–63% ML), separated from mantle by weak preocular constriction. Orbits large, dorsolaterally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsally oriented. Funnel moderately long to very long (FuL about 25–49% ML), well developed, base entirely free of brachial crown. Nuchal constriction poorly developed.

Brachial crown robust, slightly wider than head. Arms thick, square in section, very short to very long (AL about 38–97% TL), gradually tapering to delicate tips; arm pairs 2 and 3 frequently longest, 4 and 1 shortest, with no consistent disparity in relative arm lengths. Web shallow to deep, about 11–32% longest arm length, with well-developed web extension along dorso- and ventrolateral surfaces of each arm almost to arm tip, wider dorsolaterally than ventrolaterally; web formula variable, sectors A and E usually shallowest, sectors C, D, and B deeper, with no consistent disparity in sector depths. Suckers biserial, with 11–13 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers minute. Arm sucker counts variable, moderately high to high, ASC 138–263; suckers extend to arm tips. Sucker size sexually dimorphic, in male moderate to very large (ASIe about 8–19), with suckers 15–17 on lateral arms 2 and 3 largest; suckers in female moderate (ASIe about 8–13); no suckers abruptly enlarged in either sex. Suckers with: small suction chamber; development of sucker aperture constriction poor; moderately well-developed grasping ring with 26–29 faint radial grooves; crenulate sucker aperture with 19–21 well-developed tooth-like processes; and well-developed muscular suction pad (Fig. 155D).

Male with third right arm hectocotylised, length shorter to slightly longer than opposite member (OAI about 77–106); with high number of suckers (ASC 142–164); terminal hectocotylised portion (Fig. 78A) minute (LLI 1.0–1.6), ligula with thin cheeks bordering extremely small triangular groove; transverse rugae indistinct; calamus proportionally large (CaLI about 40–54), with groove extending entire structure length. Spermatophoral groove narrow, bordered by slightly thickened web margin, with short series of small papilla-like structures where groove fuses with web sector D.

Dorsal surface of mantle, head, arms 1–3, and web sectors A–C beset with numerous small, wart-like conical mounds, each with 1–9 minute, low-profile, pimple-like prominences; 5 or 6 enlarged wart-like mounds present on dorsal and dorsolateral surface of mantle, with single papilla above and below each eye as super- and subocular cirri, and several thrown into longitudinal folds along dorsal surfaces of arms 1 and 2. Ventral surface of mantle, head, dorso- and ventrolateral surface of arms 4, aboral surface of web sectors D, E, and adoral surface of web sectors A–E with fine, evenly granular sculpture. Colour (preserved specimens) over dorsal surfaces of mantle, head, arms 1–3 and web sectors A–C dark red to purple. Ventral surface of mantle, head, surfaces of arms 3 and 4 and web sectors D and E slightly lighter. Oral surface of arms, web and sucker apertures light purple to tan.

Funnel organ of W-type, with thick outer limbs. Gills with 9 inner and outer lamellae per demibranch. Penis proper in mature male oriented towards interpallial septum, not extending over renal tissues or anterior visceral mass; genital aperture opening midway along interpallial musculature. Interpallial septum short, thick, muscular; membranes between renal tissue and ventral inner surface of mantle well developed, mantle cavity restricted; interpallial septum running to posterior end of mantle as thin muscular riblet. Anus at base of interpallial septum; anal flaps 3, single large ventral and 2 smaller lateral flaps. Visceral envelope and lateral muscles restraining digestive gland without chromatophores. Renal papilla short, situated at base of gill. Oviducts long, oriented parallel to anteroposterior axis of mantle, opening midway along interpallial musculature, not extending to anus.

Male with proportionally large testis sac (Fig. 78B); proximal vas deferens very long, thick, strongly convoluted; spermatophoral gland long, with pronounced swelling at junction with proximal vas deferens, with thickenings, glandular regions and constrictions for entire length, without apparent appendix proximal to junction with accessory gland; accessory gland proximally narrow, thin walled, abruptly expanding into thick, glandular, granular structure, with terminal volution incomplete. Spermatophore sac distally truncated, short, saccular, thin walled, containing up to 50 short spermatophores to 24 mm length. Distal vas deferens short, narrow; penis diverticulum single,

small, about 30% penis length, coiled in incomplete spiral; penis long, narrow, genital aperture subterminal. Mature female unknown. Sub-mature female (Fig. 78C) with small ovary sac; proximal oviducts depart ovary sac through common antrum, narrow, length about 40% distal duct length; oviducal gland small, each with small, light brown proximal and darker-brown distal hemisphere, with faint radial striations. Distal oviducts narrow, long, with moderate central dilatation, proximally and distally contracted, with moderate curvature from oviducal ball towards genital aperture; genital aperture terminal, pore-like, not secondarily modified. Immature eggs numerous, thousands, small, slender, to 0.7 mm; mature egg size unknown.

Alimentary canal (Fig. 78D) with moderate-sized buccal bulb, length about 20% ML; anterior salivary glands large, ovoid, length about 53% buccal bulb greatest dimension; anterior oesophagus long, narrow, enters crop dorsally; crop well developed, with extensive anterior diverticulum about 45% total crop length. Posterior salivary glands moderate sized, broadly triangular, length about 120% buccal bulb length, about 23% ML. Posterior oesophagus muscular, thin-walled. Stomach large, with small, thin-walled basal, thick-walled central, and large thin-walled distal sections; stomach with undivided lumen. Spiral caecum smaller than stomach, 2 complete volutions, with faint radial striations. Intestine short, about 1.1 times oesophagus length, thin-walled, dilated for proximal half, constricted for distal half; anal flaps small. Digestive gland large, broadly triangular, with prominent anterior peaks; pancreas little developed; ink sac large, broad (about 50% digestive gland length), superficially embedded in surface of digestive gland; ink duct short, opening into base of anus.

Upper beak (Fig. 78E) tall (height 107.1% length); hood and lateral walls dark brown, margins translucent; hood shallow (depth 35.0% beak length), with broadly rounded to triangular crest, without posterior notch; rostrum triangular, rostral tip blunt, not deflected down; jaw with single broad low-profile tooth. Lateral walls straight-sided; crest squared, lateral wall fold weak. Lower beak (Fig. 78E) moderately depressed (height 75.6% width); hood, lateral wall and wings dark brown, lateral wing and wall margins translucent. Lateral wall with deep, acute-angled V-shaped basal notch and broadly keeled crest. Hood deep (depth 39.9% beak length), with shallow posterior notch and flattened chisel-like rostrum; lateral wings long (length 100% beak length), with single strong fold.

Raw measures for male in Table 56; female in Table 57.

Table 53. Indices, formulas, and counts for male *Octopus gibbsi* sp. nov. (* denotes damage; † denotes regrowth).

	NMNZ M.5636	NMNZ M.118421	NMNZ M.118305	NMNZ M.118425
MWI	73.5	71.6	45.7	66.5
HdLI	32.9	19.9	29.8	28.6
HdWI	58.5	46.1	42.8	41.6
EOI	5.8	7.0	4.9	10.1
ALI1–4	69.1–81.8	65.1–81.6	66.1–77.8	49.5–72.2
AFR	2.3.4.1	*	2.3.4.1	2.4.3.1
AFL	2.3.4.1	2.3.1.4	2.3.1.4	*
WDIA–E	17. 1–29.0	11.3–26.0	13.3–25.5	10.6–26.3
WFR	C.E.D.B.A	C.D.B.E.A	C.D.B.A.E	C.D.B.A.E
WFL	C.E.D.B.A	C.D.B.E.A	C=B.A.E.D	C=D.B.A.E
ASC1–4[1]	180–191	228–239	237–263	145–186
ASIn1–4	10.6–14.4	10.4–15.7	10.0–18.8	8.4–13.0
FuLI	49.0	33.2	37.5	27.9
FFuI	27.9	21.4	18.8	18.4
PAI	53.8	46.9	41.8	33.5

[1] Exxcludes ASC arm 3R

Table 54. Indices, formulas, and counts for female *Octopus gibbsi* sp. nov. (* denotes damage).

	NMNZ M.118303	NMNZ M.90320	NMNZ M.131569	NMNZ M.118426
MWI	55.9	74.4	57.3	66.1
HdLI	34.3	37.9	26.6	27.0
HdWI	63.3	62.5	55.2	40.1
EOI	4.5	2.5	7.0	8.8
ALI1–4	37.5–82.8	66.2–97.2	62.4–75.1	54.0–72.5
AFR	2.4.1.3	*	2.3=4.1	3.4.2.1
AFL	2=3.4.1	*	*	2.3.4.1
WDIA–E	22.6–32.1	19.1–31.9	13.6–26.0	11.4–22.9
WFR	D.C.B.E.A	D.C.E.B.A	C.D.B=E.A	C.D.B.E=A
WFL	C.D.B.E.A	D=C.E.B.A	C.D.E.B.A	C.B.D.E=A
ASC1–4	138–140	203–206	145–158	205–243
ASIn1–4	8.2–11.4	10.4–12.5	8.8–12.1	8.4–12.3
FuLI	25.3	29.2	40.5	35.8
FFuI	20.0	16.7	23.5	19.7
PAI	48.6	55.2	36.8	38.0

Table 55. Indices and counts for hectocotylised arm of male *Octopus gibbsi* sp. nov. (* denotes damage).

	NMNZ M.5636	NMNZ M.118421	NMNZ M.118305	NMNZ M.118425
OAI	106.4	78.6	101.2	*
ASC3R	164	150	162	142
CaLI	*	53.7	40.0	50.0
LLI	*	1.0	1.0	1.6

Figure 77. *Octopus gibbsi* sp. nov.: Whole animal, holotype, NMNZ M.118305, male, ML 121.5 mm.

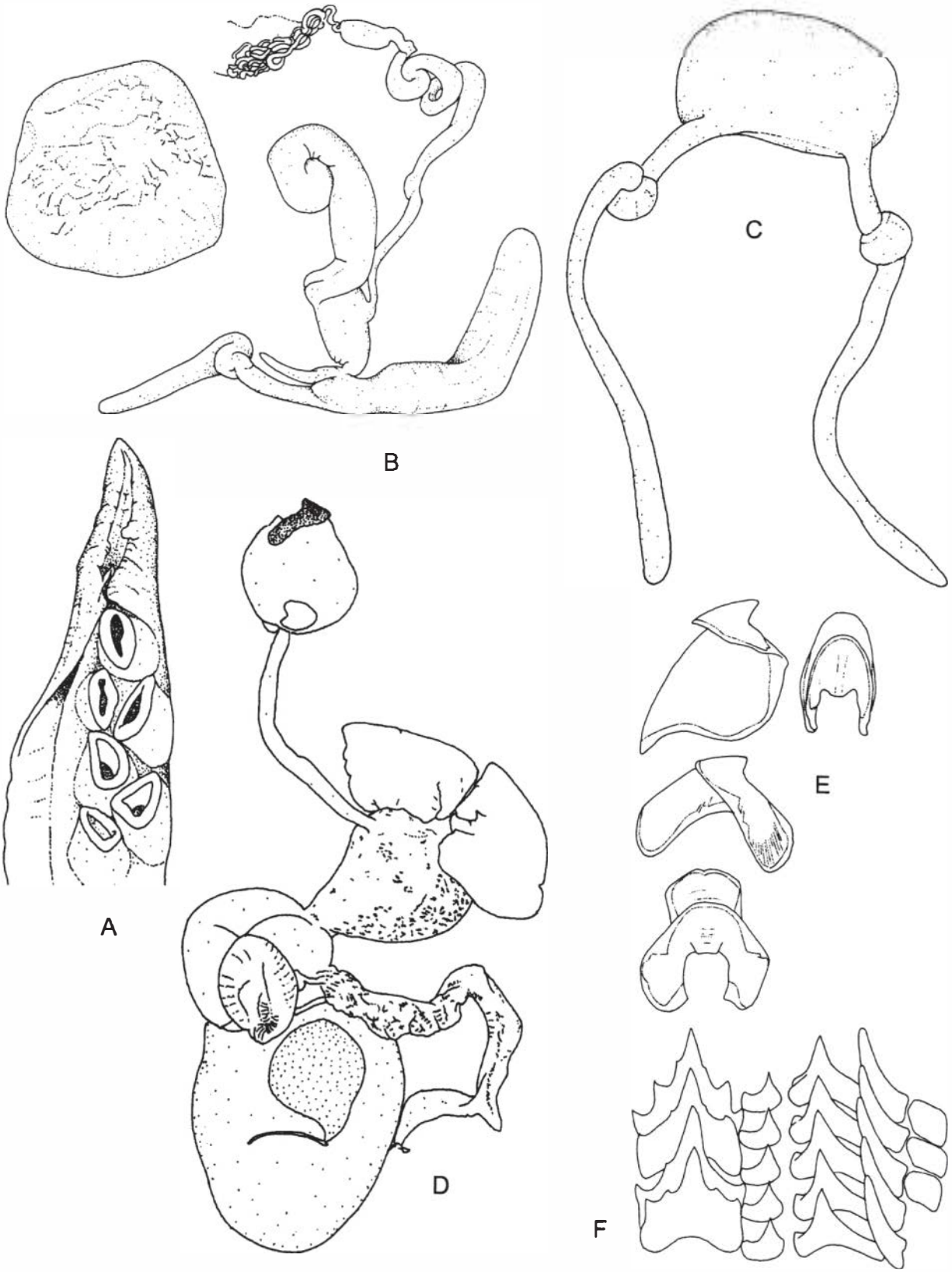


Figure 78. *Octopusgibbsi* sp. nov. Anatomy: **A**, NMNZ M.118305. **B, D**, NMNZ M.90321, male, ML 75.4 mm. **C, E–F**, NZOI Stn Z8917, **F**, ML 118 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 56. Raw measures for male *Octopus gibbsi* sp. nov. (* denotes damage).

	NMNZ M.5636	NMNZ M.118421	NMNZ M.118305	NMNZ M.118425
TL	236	670	540	327
ML	52.0	135.5	121.5	89.5
MW	38.2	97.0	55.5	59.5
HdL	17.1	27.0	36.2	25.6
HdW	30.4	62.5	52.0	37.2
EO	3.0	9.5	6.0	9.0
AL1R/L	163/168	450/438	357/377	162/38*
AL2R/L	193/183	510/547	420/415	228/218
AL3R/L	183/172	418/532	360/393	192/73*
AL4R/L	172/171	393*/436	358/367	193/236
WDA	33	62	75	31
WDBR/L	46/38	100/106	97/91	45/42
WDCR/L	56/56	116/142	107/91	62/58
WDDR/L	48/50	97/132	80/56	52/58
WDE	51	70	71	25
CaL	*	2.2	1.2	1.5
LL	*	4.1	3.0	3.0
ASC1R	180	228	237	145
ASC2R	191	229	238	186
ASC3R	164	150	162	142
ASC4R	187	239	263	171
ASe1R	5.5	14.1	12.2	7.5
ASe2R	7.5	21.3	22.9	11.5
ASe3R	7.5	21.3	17.0	11.6
ASe4R	5.7	15.2	12.2	7.6
GiLC	9	9	9	9
FuL	25.5	45.0	45.6	25.0
FFL	14.5	29.0	22.8	16.5
PA	28.0	63.5	50.8	30.0

Table 57. Raw measures for female *Octopus gibbsi* sp. nov. (* denotes damage).

	NMNZ M.118303	NMNZ M.90320	NMNZ M.131569	NMNZ M.118426
TL	64	145	205	676
ML	24.5	48.0	48.9	137.0
MW	13.7	35.7	28	90.5
HdL	8.4	18.2	13	37.0
HdW	15.5	30.0	27	55.0
EO	1.1	1.2	3.4	12.0
AL1R/L	45/45	120/96	129/128	365/383
AL2R/L	53/52	133/63*	151/154	474/490
AL3R/L	24/52	130*/141	141/89*	485/424
AL4R/L	47/46	61*/137	141/141	384/396
WDA	12	27	21	56
WDBR/L	14/14	36/37	29/28	70/98
WDCR/L	15/16	41/45	40/35	98/112
WDDR/L	17/15	45/45	32/32	80/97
WDE	12.5	39	29	56
ASC1R	138	203	156	205
ASC2R	138	210	158	224
ASC3R	140	L206	145	243
ASC4R	140	L215	153	240
ASe1R	2.0	5.0	4.5	13.0
ASe2R	2.7	6.0	5.9	16.8
ASe3R	2.8	6.0	5.4	15.1
ASe4R	2.3	5.0	4.3	11.5
GiLC	9	9	9	9
FuL	6.2	14.0	19.8	49.0
FFL	4.9	8.0	11.5	27.0
PA	11.9	26.5	18.0	52.0

ETYMOLOGY: Named for my dearest, late friend, David William "W for wonderful" Gibbs.

REMARKS: Penis and diverticulum structure in this species is similar to that of *O. vulgaris* as depicted by Robson (1929: 61, fig. 7). The three juveniles attributed to this species (NMNZ M.118409, ML 7.2, 7.0 mm; NMNZ M.137778, sex indet., ML 7.0 mm) possess two rows of chromatophores along each arm. This species is most regularly encountered in shallow water along the northeastern coast of North Island. It is seldom found on soft sediments, occurring more typically in recesses and grottos, or beneath ledges on rocky ground.

Octopus Group 1

DIAGNOSIS: Penis enormously elongate; penis diverticula paired, basal, short; male with spermatophoric gland entering spermatophoric sac separate to accessory gland; spermatophores few in number, disproportionately long relative to mantle length; spermatophoric sac correspondingly disproportionately long.

DISTRIBUTION: With certainty New Zealand, East Australia, and Japan. If all citations in synonymy of *Octopus rugosus* (Bosc) [*fide* Robson 1932: 63] are correct, the species, or species complex, has an extensive tropical to subtropical cosmopolitan distribution.

REMARKS: Anatomical character states peculiar to *Octopus* Group 1 morphology differ markedly from those of *Octopus oliveri* and *O. gibbsi* sp. nov., despite Robson's inclusion of *O. rugosus* in *Octopus* (*s. s.*). The diagnosis for this Group 1 is based almost exclusively upon a single dissected male; it is not certain if these characters are consistent in all species and /or specimens referred to *O. rugosus* by Robson.

Octopus cf. *rugosus* (Bosc, 1792) (Figs 80, 81)
(Tables 58–60)

MATERIAL EXAMINED (4 specimens, 2M, 2F): NZOI Stn Z8646, M, ML 33.5 mm, FFN, 34°23.5' S, 172°47.4' E, 36.0 m, 28/02/1997, f.v. *Ben Gunn* Stn BG9701/54; NZOI Stn Z8654, M, ML 42.5 mm, 34°23.5' S, 172°47.9' E, 37.5 m, 28/02/1997, f.v. *Ben Gunn* Stn BG9701/55; NZOI Stn Z8468, F, ML 59.2 mm, *c.* 34°25' S, 172°47' E, 40–50 m, 01/06/1996, Spirits Bay, coll. M. Cryer, D. Parkinson; NZOI Stn Z8653, F, ML 47.2 mm, FFN, 34°49.3' S, 173°14.2' E, 23 m, 03/03/1997, f.v. *Ben Gunn* Stn BG9701/G.

?FOREIGN MATERIAL EXAMINED: NZOI Stn Z8565, M, ML 87.6 mm, 22°39.72–36.75' S, 153°06.94' E, 180–200 m, -/03–08/1996.

REFERENCE MATERIAL: OM B350, *Octopus granulatus* (?ident. Berry, S.S.), F, ML 52.0 mm, Port Jackson, Australia, datNR, depNR. SAM D14028, *Octopus berrima* Stranks & Norman, 2M, ML 49.5, 34.8 mm, det. K. Gowlett-Holmes, Gulf St. Vincent, W of Aldinga, prawn trawl, 38-41 m, 4–5/05/1987, f.v. *Rivoli Queen*; SAM D14026, *O. berrima* Stranks & Norman, det. K. Gowlett-Holmes, 2M, ML 61.0, 57.0 mm, F, ML 67.0 mm, Eyre Peninsula, Coffin Bay, Black Springs, on sand at night, 1.5–3 m, 20/04/1984; SAM D14027, *O. berrima* Stranks & Norman, det. K. Gowlett-Holmes, M, ML 28.6 mm, Nuyts Archipelago, St Francis Island, cove NW of Petrel Cove, sand bottom, 40 m, 28/01/1982.

DISTRIBUTION (New Zealand, Fig. 79, p. 121): Spirits Bay, Northland, New Zealand, 23–50 m.

DIAGNOSIS: Small-bodied, densely papillose species with minimal web development in sector A; 5 to 6 suckers between beaks to web margin along arms 1; small bladelike ligula; 2 transverse white bars pass through iridescent blue-coloured orbits; enlarged suckers on lateral arm pairs.

DESCRIPTION (based on New Zealand specimens only): Adult specimens of small size (ML to 59.2, TL to 183 mm); body stocky (Figs 80A–F). Male and female with similar gross morphology; mantle globose, broad (MW about 49–72% ML), dorsoventral compression and lateral keel or fold of skin absent; ventral longitudinal groove or depression faint. Head well developed, small to large, wider than long, narrower than mantle (HdL about 21–35% ML; HW about 29–57% ML), separated from mantle by moderate preocular constriction. Orbits large, dorsally oriented, situated above base of arm pairs 1 and 2; eye aperture dorsolaterally oriented. Funnel long to moderately long (FuL about 30–41% ML), well developed, base entirely free of brachial crown. Nuchal constriction moderately well developed.

Brachial crown robust, narrower than head. Arms thick, square in section, very short to moderately long (AL about 56–78% TL), gradually tapering to delicate tips; arm pairs 3 and 4 usually longest, arms 1 and 2 shortest, with no consistent disparity between right and left sides or specimens apparent. Web shallow to deep, about 10–35% longest arm length, well-developed delicate web extension present along ventrolateral surfaces of each arm almost to arm tip, along dorsolateral surface of arm pair 4 almost to arm tip, but absent along dorsolateral surface of arm pairs 1–3; web formula variable, sectors A and B usually shallowest, sector D usually deepest, with no consistent disparity in sector depths. Suckers biserial, with 5 or 6 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers minute. Arm sucker counts variable, moderately high, ASC 129–208; suckers extend to arm tips. Sucker size sexually dimorphic, in male small to moderate (ASIe about 6–14), with suckers 9–12 from arm base on lateral arms 2 and 3 largest; suckers in female small (ASIe about 5–9); no suckers abruptly enlarged in either sex. Suckers with: large suction chamber; markedly constricted sucker aperture; well-developed grasping ring with 13 or 14 incised radial grooves; sucker aperture without toothlike processes; and muscular suction pad moderately well developed (Fig. 155E).

Male with third right arm hectocotylised, length equivalent to opposite member (OAI about 101); with moderate number of suckers (ASC 79–85); terminal hectocotylised portion (Figs 81A) short (LLI 7.5–8.2), ligula bladelike, with shallow groove with 16 or 17 faint transverse rugae; calamus of short to moderate length (CaLI about 17–27), with shallow groove extending entire structure length. Spermatophore groove deeply recessed in well-developed, thickened web margin; groove with 3 large, bifid papillae and 4 simple papillae at junction with web sector D.

Dorsal and ventral surfaces of mantle, head, dorsolateral surfaces of arm pairs 1–3, and web sectors A–E densely papillose. Dorsal and dorsolateral surfaces of mantle, head, dorsolateral surfaces of arms 1–3 and web sectors A–C beset with numerous small, blister- to wartlike mounds; warts predominant over head and dorsolateral surfaces of arms 1 and 2, blisters predominant on other dorsal surfaces; warts with 5–8 minute, low-profile, pimplelike prominences; 1 or 2 enlarged wartlike mounds present above and below either eye in form of super- and subocular cirri. Ventrolateral and ventral surfaces of mantle beset with numerous, much smaller blister-like papillae.

Colour (preserved specimens) over dorsal surfaces of mantle, head, dorsolateral surfaces of arms 1–3 and web sectors A–C mottled light green to light reddish-brown, with individual and adjacent papillae of variable colour. Dorsolateral through to ventral surfaces

Table 58. Indices, formulas, and counts for *Octopus* cf. *rugosus* (* denotes damage).

	NZOI Stn Z8565	NZOI Stn Z8468	NZOI Stn Z8653	NZOI Stn Z8654	NZOI Stn Z8646
MWI	49.1	60.0	65.9	62.8	71.6
HdLI	24.0	20.6	31.8	35.3	32.8
HdWI	36.9	29.1	49.8	56.7	55.8
EOI	6.8	6.6	4.4	8.9	6.0
ALI1–4	51.8–85.8	61.2–73.8	66.0–77.8	62.4–70.1	55.9–72.0
AFR	*	4.3.2.1	4.3.2.1	*	4.2.3.1
AFL	*	3.4.2.1	3.4.2.1	*	4.2.1.3
WDIA–E	11.3–27.2	10.4–26.7	15.2–34.8	18.3–35.4	14.9–32.8
WFR	D.C.E.B.A	D.C.B.E.A	D.E.C.B.A	D.E.C.B.A	C.D.E.B.A
WFL	D.C.B.E.A	D.C.B.E.A	D.E.C.B.A	D.C.E.B.A	D.C=E.B.A
ASC1–4	*–218	161–177	189–208	129–173	139–166
ASIn1–4	6.8–9.1	5.4–6.8	6.6–8.5	7.3–14.1	6.3–8.4
FuLI	32.0	30.4	40.9	35.3	34.3
FFuI	17.1	16.9	23.3	24.0	23.9
PAI	36.5	28.7	43.2	43.3	45.1

of mantle ,white to pink; dorsolateral surface of orbit with 2 white lines dissecting eye aperture, delimiting white to pink ventrolateral and ventral surfaces of head from dorsal, contrastingly pigmented surfaces; orbits deep blue; ventrolateral surfaces of arms 1-4, oral surfaces of arms 3 and 4, suckers and web slightly lighter, light tan to orange coloured.

Funnel organ large, W-shaped, with inner and outer limbs thick, outer appreciably shorter than inner. Gills large, with 8 or 9 inner and outer lamellae per demibranch. Penis exceedingly long, dilated for entire length, bent in semicircle oriented towards interpallial septum, extending onto right side of viscera; genital aperture proximal to anus on left side. Interpallial septum short, thick, muscular; membranes between renal tissue and ventral inner surface of mantle absent; extensive connective tissue between reproductive tissue and ventral inner surface of mantle restricts mantle cavity. Anus at base of interpallial septum; anal flaps small, paired. Visceral envelope and lateral muscles restraining digestive gland without chromatophores. Renal papilla large, situated at base of gill. Oviducts long, oriented parallel to anteroposterior axis of mantle, opening midway along interpallial musculature, not extending to anus.

Male reproductive system (Fig. 81B, C) with very long, thin, strongly convoluted proximal vas deferens; spermatophoral gland very long, slender, with thickenings, glandular regions and constrictions, opening directly into spermatophore sac, with no direct communication with accessory gland. Accessory gland long, of comparable thickness to spermatophoral gland, with distal portion slightly expanded, with incomplete terminal volution. Spermatophore sac exceedingly long, narrow, thin walled, containing 5 very long spermatophores to 113 mm length. Distal vas deferens short, narrow; penis diverticulum complex, distal vas deferens opening into base of 2 basal, thick-walled appendicular diverticula folded over upon themselves; primary diverticulum large, distally truncated, secondary smaller, distally attenuate. Penis exceedingly long, dilated for entire length, bent in semicircle; genital aperture terminal. Although neither female has fully been dissected, the distal oviducts are narrow, the genital apertures are not secondarily modified and open midway along the lateral face of interpallial musculature.

Alimentary canal (Fig. 81D) with small buccal bulb, greatest diameter about 20% ML; anterior salivary glands ovoid, large, about 45% buccal bulb diameter; anterior oesophagus long, about 70% crop length, enters crop dorsally; crop well developed, with poor anterior projection, diverticulum minute. Posterior salivary glands broadly triangular, small, about 115% buccal bulb greatest dimension, about 18% ML. Posterior oesophagus short, thick walled. Stomach small, elongate, with small, thin-walled basal, large thick-walled central, and larger thin-walled distal sections; stomach with undivided lumen. Spiral caecum larger than stomach, with single loosely coiled volution, with strong radial striations. Intestine short, about 80% oesophagus and crop length, dilated proximal half, constricted and more muscular distal half; anal flaps well developed. Digestive gland small, with prominent

Table 59. Indices and counts of hectocotylised arm for male *Octopus* cf. *rugosus* (* denotes damage).

	NZOI Stn Z8565	NZOI Stn Z8654	NZOI Stn Z8646
OAI	*	*	101.9
ASC3R	95	79	85
CaLI	13.7	16.7	26.8
LLI	4.6	8.2	7.5

anterior peaks and marked depressions to accommodate stomach, crop and posterior salivary glands; digestive gland iridescent, predominantly blue to green; pancreas well developed in recess between anterior peaks; ink sac narrow, long (about 40% digestive gland length), superficially buried beneath surface of digestive gland, most of sac deeply embedded in gland; ink duct long, opening into base of anus.

Upper beak (Fig. 81E) depressed (height about 90% length); almost entirely black to dark brown, translucent margins very narrow; hood very shallow (depth 30% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip acute, apically blunt, not deflected downwards; jaw with single broad, pronounced tooth. Lateral walls almost parallel sided; crest rounded, lateral wall with weak fold and deep sinus in basal margin. Lower beak (Fig. 81E) moderately depressed (height 74% width); hood, lateral wall, and wings black to brown pigmented, lateral wing and wall margins translucent. Lateral wall with shallow, broad-angled V-shaped basal notch and keeled crest. Hood moderately deep (depth 32.8% beak length), with blunt, chisel-like rostrum; hood with shallow posterior notch; lateral wings short (length 87.5% beak length), with single strong fold.

Radula (Fig. 81F) with well-developed rachidian, wider than tall, with 1 or 2 asymmetric, small lateral cusps aside central cusp; 1st lateral tooth with 2 well-developed cusps, inner small, at base of long inner heel, outer largest; 2nd lateral shorter than rachidian, with single large cusp; marginal tooth with moderate curvature, robust; marginal block well developed, rectangular, wider than deep (along axis of radula ribbon). Radula with repeat seriation every 6 or 7 transverse rows.

Indices, formulas, and counts in Table 58.

REMARKS: The four New Zealand specimens were fully mature at comparatively small mantle lengths. When caught, one female (NZOI Stn Z8653) was observed brooding a large clutch of eggs, which when placed in a bucket of seawater hatched. Unfortunately, through circumstances beyond control (extreme sea conditions) these larvae were lost.

The principal difference between the four New Zealand specimens and the mature male dredged from 180–200 m off Swain Reefs, Queensland (NZOI Stn Z8565) is size, although the latter also has a slightly higher hectocotylised arm sucker count than the New Zealand specimens. The New Zealand specimens differ from the specimen from Port Jackson, New South Wales in sundry characters that could equally be attributed to preservation history. Japanese specimens described and depicted as *Octopus granulatus* by Sasaki (1929) are not significantly different from the New Zealand specimens. The systematic status of both nominal species, *O. rugosus* and *O. granulatus*, requires review. Type material of neither exists (*fide* Norman 1992b: 320–321), although Robson (1929), from examination of 87 specimens from the Atlantic and Indian Oceans, Malayan, and Australasian waters variously attributed to either *O. rugosus* or *O. granulatus*, concluded a single species was represented. Pending a redescription of *O. rugosus* (Bosc) based on a neotype, I have referred the New Zealand specimens to *Octopus* cf. *rugosus* (Bosc), rather than accept uncritically the determination offered by Robson (1929b: 63–74).

Octopus sp. 2

MATERIAL EXAMINED (?8 specimens, 2 female [F], 6 sex indet.): NMNZ M.90311 (dubious), 2M, ML 14.6, 14.5 mm, F, ML 11.7 mm, 3 sex indet., ML 11.5, 10.3, 9.3 mm, 29°15' S, 177°50.9' W, between Dayrell and Chanter Islands, Herald Islets, Kermadec Islands, 31–45 m, 11/09/1976, r.v. *Acheron*; NZOI Stn Z8666, F, ML 30.5 mm, FL, 34°22.3' S, 172°43.9' E, 31–34 m, 27/02/97, f.v. *Ben Gunn* Stn BG9701/44; NZOI Stn Z8675, F, ML 34.0 mm, FL, 34°58.3' S, 173°45.9' E, 27.4 m, 26/02/97, f.v. *Ben Gunn* Stn BG9701/A.

RECOGNISED DISTRIBUTION (Fig. 82, p. 121): With certainty from the entrance of Whangaroa Harbour, Northland, New Zealand, 34°22.3–58.3' S, 27–34 m. Juvenile specimens from the Kermadec Islands are hesitantly attributed to this species.

DIAGNOSIS: Small-bodied, highly papillose species; with 5 to 6 suckers between beaks and web margin along dorsal arm pair 1; with suckers 3–20 largest, of similar size on all four arm pairs; male not known.

DESCRIPTION (based on female only): Adult size small (ML to 34.0, TL to 117 mm); body stocky (Figs 83A–F). Mantle globose to flask-shaped, broad (MW about 64–82% ML), dorsoventral compression and lateral keel or fold of skin absent; ventral longitudinal groove or

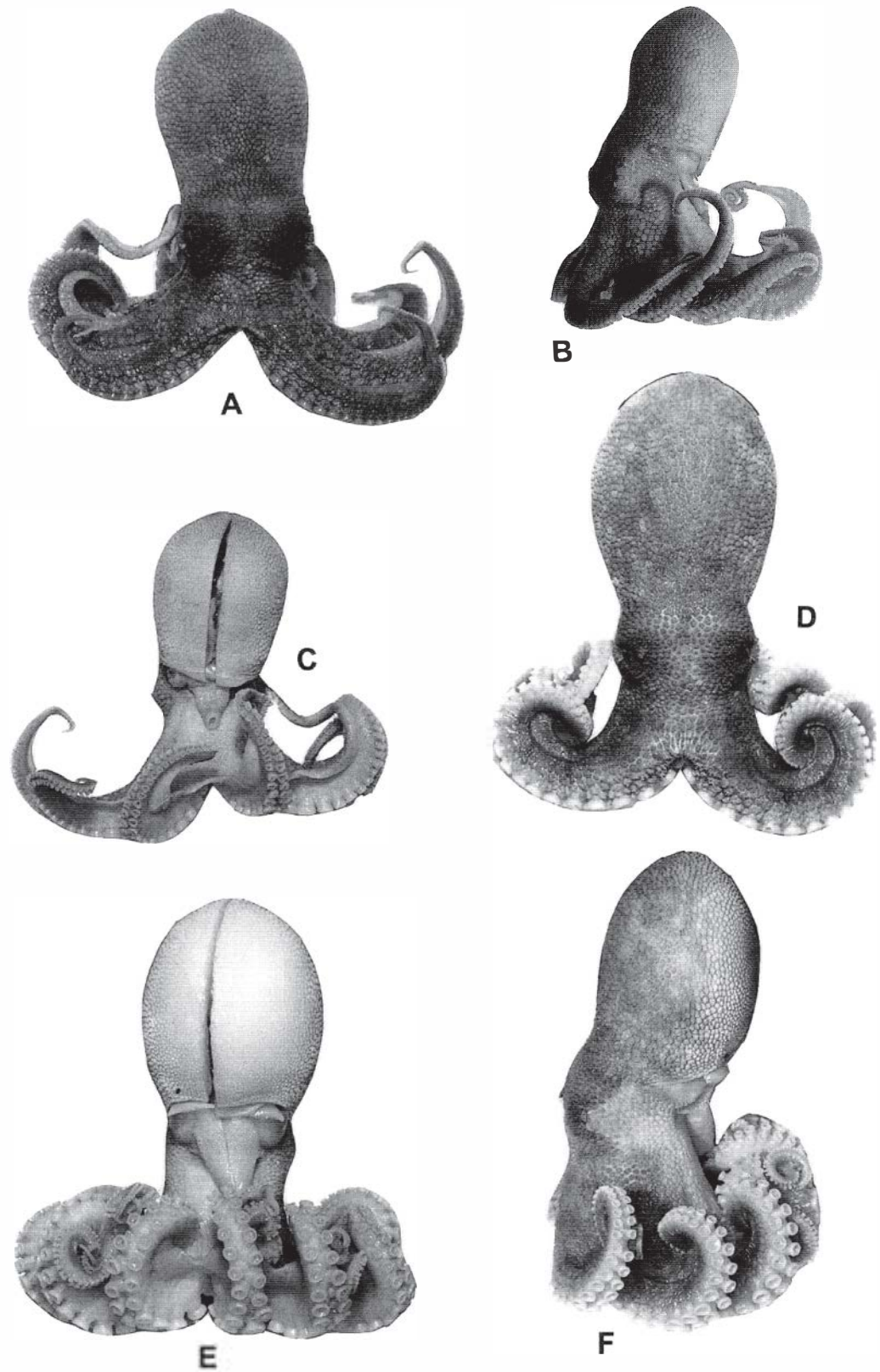


Figure 80. *Octopus* cf. *rugosus*: **A–C**, NZOI Stn Z8654, male, ML 42.5 mm. **D–F**, NZOI Stn Z8653, female, ML 47.2 mm.

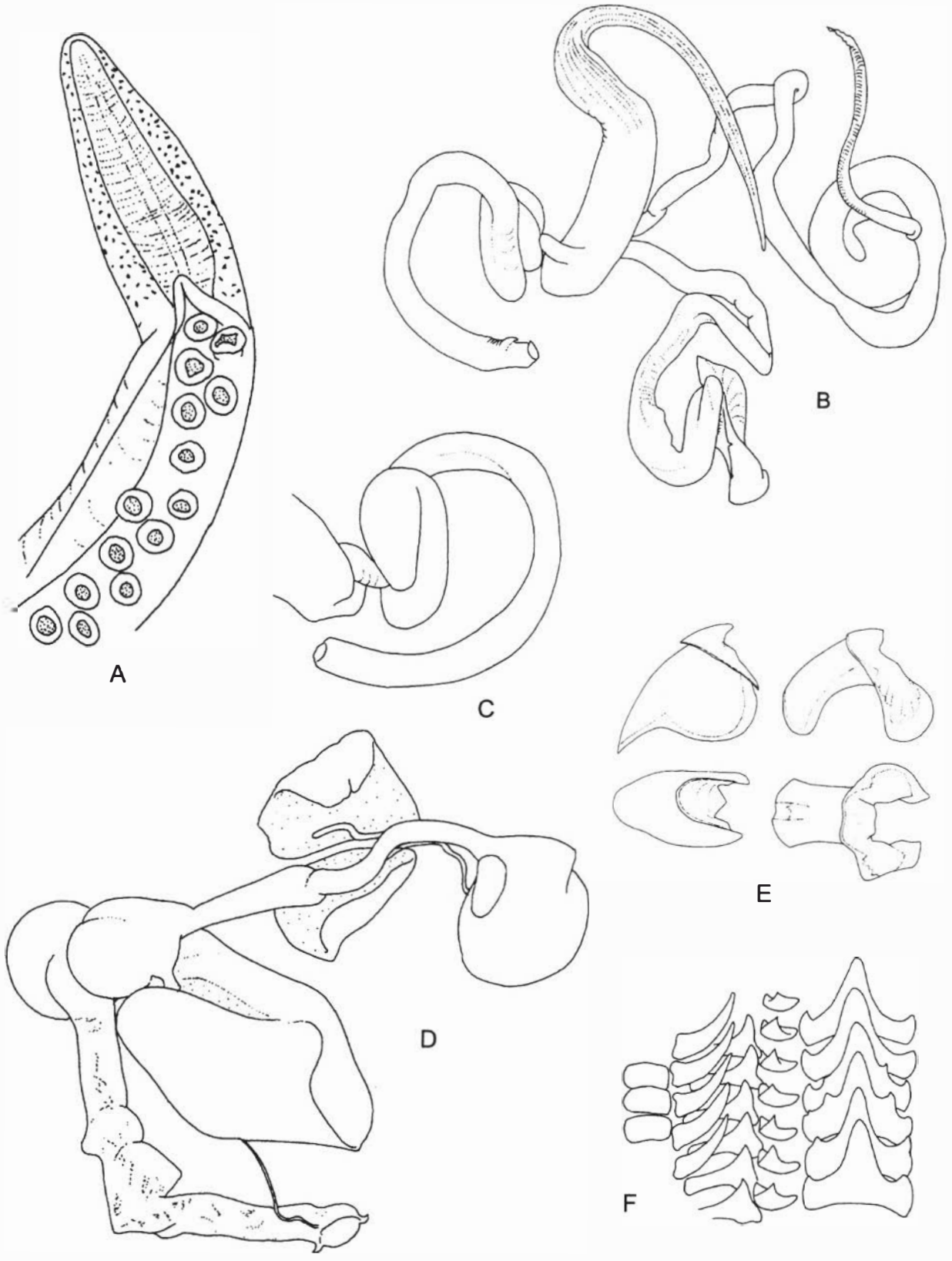


Figure 81. *Octopus* cf. *rugosus*. Anatomy: NZOI Stn Z8654, male, ML 42.5 mm. **A**, hectocotylus. **B–C**, reproductive system. **C**, penis and diverticular structure. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 60. Raw measures *Octopus* cf. *rugosus* (* denotes damage, † denotes regrowth).

	NZOI Stn Z8565	NZOI Stn Z8468	NZOI Stn Z8653	NZOI Stn Z8654	NZOI Stn Z8646
Sex	M	F	F	M	M
TL	309	183	144	117	93
ML	87.6	59.2	47.2	42.5	33.5
MW	43.0	35.5	31.1	26.7	24.0
HdL	21.0	12.2	15.0	15.0	11.0
HdW	32.3	17.2	23.5	24.1	18.7
EO	6.0	3.9	2.1	3.8	2.0
AL1R/L	64*/186†	119/112	95/99	60†/82	52/56
AL2R/L	142*/129*	126/118	105/101	70*/80	62/62
AL3R/L	160/158*	128/135	106/104	73/75†	55/54
AL4R/L	265/210	130/120	112/103	95/87†	67/64
WDA	30	14	17	15	10
WDBR/L	47/52	27/28	25/24	21/21	17/18
WDCR/L	56/54	31/33	34/34	23/27	21/20
WDDR/L	61/72	33/36	39/37	26/29	20.5/22
WDE	49	21	36	25	20
CaL	1.0	*	*	1.0	1.1
LL	7.3	*	*	6.0	4.1
ASC1R	*	161	189	L129	139
ASC2R	*	174	206	L135	161
ASC3R	95	170	208	79	85
ASC4R	218	177	194	173	166
ASn1R	L6.0	3.2	3.1	3.1	2.1
ASn2R	8.0	4.0	3.6	4.5	2.5
ASn3R	8.0	4.0	4.0	6.0	2.8
ASn4R	6.5	4.0	3.9	4.1	2.3
GiLC	9	9	9	8	9
FuL	28.0	18.0	19.3	15.0	11.5
FFL	15.0	10.0	11.0	10.2	8.0
PA	32.0	17.0	20.4	18.4	15.1

depression faint. Head well developed, small to large, wider than long, narrower than mantle (HdL about 33–40% ML; HW about 59–68% ML), separated from mantle by moderate preocular constriction. Orbits large, dorsally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsally oriented. Funnel long (FuL about 47–56% ML), well developed, base entirely free of brachial crown. Nuchal constriction well developed.

Brachial crown robust, narrower than head. Arms thick, moderately long to very long (AL about 71–91% TL), gradually tapering to not unduly delicate tips; with ventral arms longest, arm formula 4.3.2.1 or 4.2.3.1. Web very shallow to deep, about 6–30% longest arm length, with well-developed delicate web extension along ventrolateral surfaces of each arm almost to arm tip, along dorsolateral surface of arm pair 4 almost to arm tip, absent along dorsolateral surface of arm pairs 1–3; web formula variable, sector A shallowest in both specimens, otherwise no consistent disparity in sector depths. Suckers biserial, with 5 or 6 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers not markedly reduced in size. Arm sucker counts moderately high, ASC 161–202; suckers extend to arm tips. Females with suckers of moderate size (ASIn about 10–13), with suckers 3–20 largest, of similar size on all arm pairs; no suckers abruptly enlarged. Suckers with: volumetrically large suction chamber; markedly constricted sucker aperture; well-developed grasping ring with about 12 or 13 incised radial grooves; sucker aperture without toothlike processes; and moderate development of muscular suction pad.

Dorsal and dorsolateral surfaces of mantle, head, dorsolateral surfaces of arms 1–3 and web sectors A–C beset with numerous small, wartlike conical mounds; warts largest over head and dorsolateral surfaces of arms 1–3, smaller on other dorsal surfaces; warts over mantle and head frequently with tall central prominence and 4–8 lateral prominences; warts on

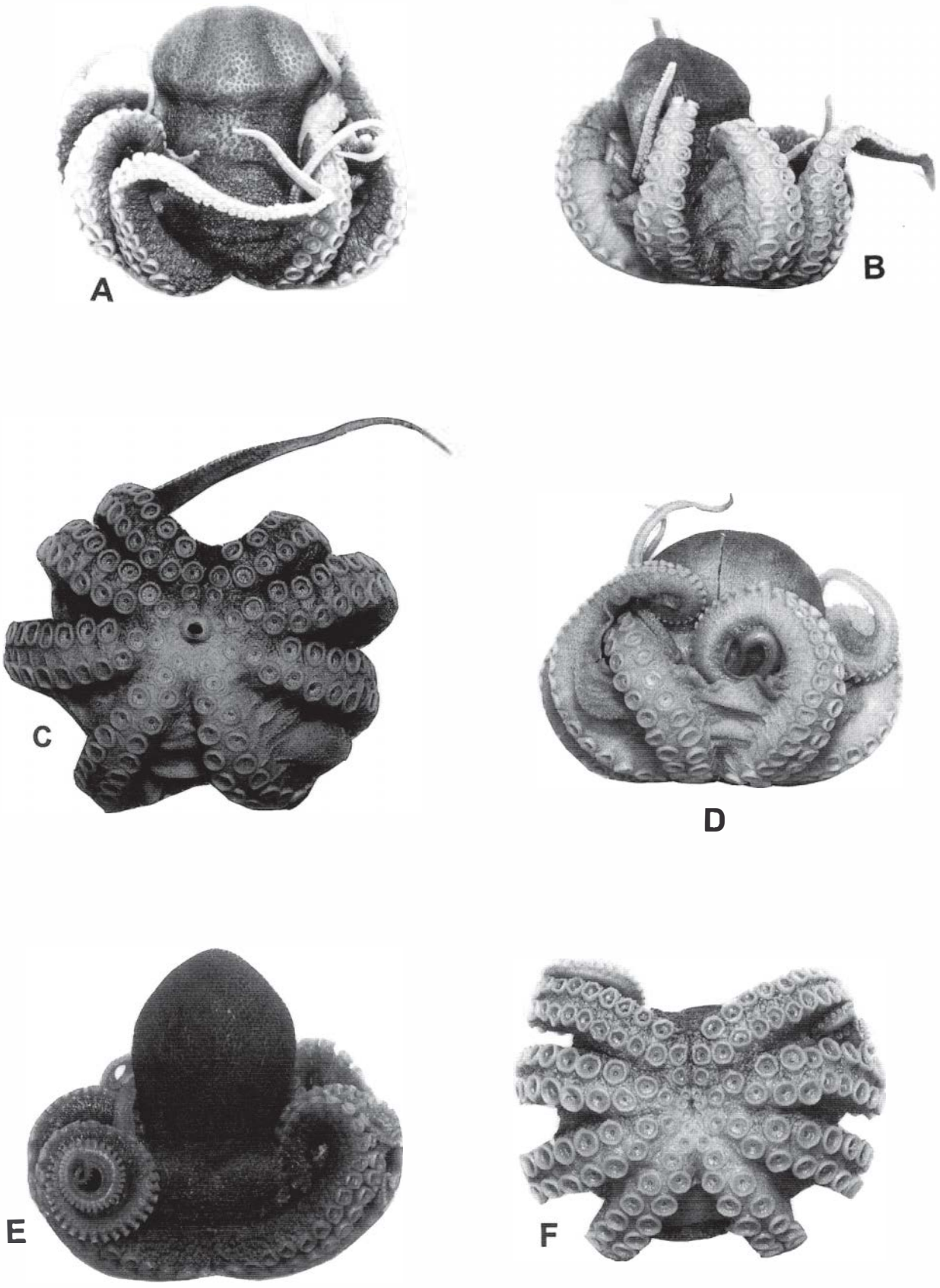


Figure 83. *Octopus* sp.: **A–C**, NZOI Stn Z8675, female, ML 34 mm. **D–F**, NZOI Stn Z8666, female, ML 30.5 mm.

Table 61. Indices, formulas, and counts for *Octopus* sp. (* denotes damage).

	NZOI Stn Z8675	NZOI Stn Z8666
MWI	82.4	64.3
HdLI	39.7	32.8
HdWI	67.6	59.0
EOI	5.3	4.9
ALI1–4	74.4–88.9	70.7–90.5
AFR	4=3.2.1	4.2.3.1
AFL	3.4.2.1	4.3.2.1
WDIA–E	11.5–29.8	6.2–25.7
WFR	C.E.D.B.A	D.C.B.E.A
WFL	*	D.C.E.B.A
ASC1–4	184–202	161–202
ASIn1–4	11.5–11.8	9.8–13.1
FuLI	47.1	56.1
FFuI	23.5	31.5
PAI	51.5	45.9

Table 62. Raw measures for female *Octopus* sp. (* denotes damage).

	NZOI Stn Z8675	NZOI Stn Z8666
TL	117	116
ML	34.0	30.5
MW	28.0	19.6
HdL	13.5	10.0
HdW	23.0	18.0
EO	1.8	1.5
AL1R/L	94/87	84/82
AL2R/L	97/97	95/96
AL3R/L	104/102	94/98
AL4R/L	104/101	105/104
WDA	12	6.5
WDBR/L	24/	23/19
WDCR/L	29/31	23.5/25
WDDR/L	25/31	26.5/27
WDE	26	21.5
ASC1R	184	185
ASC2R	201	198
ASC3R	202	161
ASC4R	200	202
ASe1R	3.9	3.0
ASe2R	3.9	3.9
ASe3R	4.0	4.0
ASe4R	4.0	3.2
GiLC	9	8
FuL	16.0	17.1
FFL	8.0	9.6
PA	17.5	14.0

dorsolateral surfaces of arms 1–3 with 9–15 somewhat irregularly disposed prominences; single enlarged wartlike mound above and below either eye in form of super- and subocular cirri. Ventrolateral and ventral surfaces of mantle, head, ventrolateral surfaces of arms 1–3, both dorso- and ventrolateral surfaces of arms 4, and oral surface of arms and web beset with numerous smaller wartlike papillae, each with a single prominence or with 1–3 small prominences either side of the taller central structure. Colour (preserved specimens) over dorsal surfaces of mantle, head, dorsolateral surfaces of arms 1–3, oral surface of arms 1 and 2, and aboral surface of web sectors A–C light red to brown, with warts on dorsolateral surfaces of arms 1–3 slightly lighter than background colour, imparting on oral and dorsolateral surface of arms a reticulate pattern. Ventral surfaces of mantle, head, ventrolateral surfaces of arms 1–3, and both dorso- and ventrolateral surfaces of arms 4, oral surfaces of arms 3–4, suckers and web sectors C–E, light tan to orange.

REMARKS: This species, represented by two mature female and possibly six immature specimens, differs from *Octopus* cf. *rugosus* in larger egg size, body sculpture, sucker diameter and enlargement along the arms, and colouration, particularly in the absence of the two white bars dissecting the orbits. The systematic status of this species, like the former, cannot be resolved until the confused systematic status of *O. rugosus* is resolved.

Pinnoctopus d'Orbigny, 1845

TYPE SPECIES: *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832)

DIAGNOSIS: Large-bodied octopods; arm formula about 1.2.3.4; sucker diameter reducing from dorsal to ventral arm pairs; gill lamellae typically exceed 11 per outer demibranch; rachidian tooth of radula multicusped, with 3 or 4 lateral cusps aside central cusp; with extensive connective tissues between renal tissue and ventral, inner surface of mantle; ligula elongate, cylindrical.

REMARKS: *Pinnoctopus* is the oldest available name for a complex of species characterised by the possession of long dorsal arms. It has frequently been referred to as the *Octopus macropus* or *Callistoctopus* complex. Although Voss (1981) concluded no valid basis existed for recognising any distinction between *Callistoctopus* and *Octopus*, reference was made to a complex of Indo-West Pacific octopuses characterised by the possession

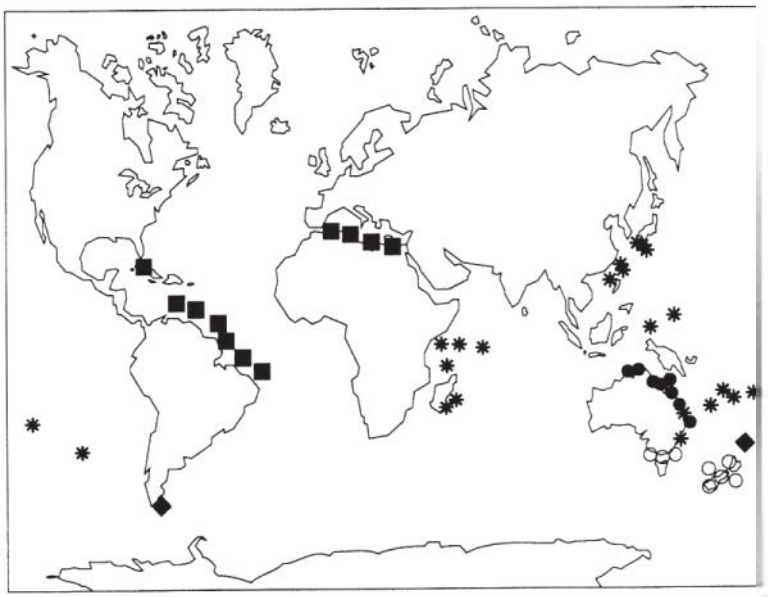


Figure 84. Recognised distribution of *Pinnoctopus*. ○ *P. cordiformis* (Quoy & Gaimard; inclusive junior synonym *O. flindersi* Cotton); ◆ *P. kermadecensis* (Berry); ✳ *O. ornatus* Gould; ■ *O. macropus* Risso; ● *Octopus* spp. (combined distribution: *O. alpheus*, *O. aspilosomatis*, *O. dierythraeus*, *O. graptus*, all Norman, 1992). Sourced: *P. cordiformis* and *P. kermadecensis* (pers. obs.); *O. ornatus*, *O. alpheus*, *O. aspilosomatis*, *O. dierythraeus*, *O. graptus* (Norman 1992); *O. macropus* (Roper & Sweeney 1984, with corrections *fide* Norman 1992).

of "long arms I". Toll (1991b), concluded otherwise, accepting *Macroctopus* Robson (based on the New Zealand *Octopus maorum* Hutton), and *Callistoctopus* Taki, as valid genera, albeit in abstract form; Toll (*loc. cit.*), however, considered *Pinnoctopus* to be synonymous with *Octopus*. Since *O. maorum* is a junior synonym of *O. cordiformis*, and *O. cordiformis* is the type species of *Pinnoctopus* and typical of the *O. macropus* group, *Macroctopus* and *Callistoctopus* are both junior synonyms of *Pinnoctopus*. Given that the holotype of *P. cordiformis* is not extant (Lu *et al.* 1995) a neotype is designated for it to stabilise the concept of *Pinnoctopus*.

Pinnoctopus cordiformis (Quoy & Gaimard, 1832)

Octopus cordiformis Quoy and Gaimard, 1832: 87, pl. 6, fig. 3; Gray 1843; Spencer & Willan 1995: 53.

Robsonella australis Benham (not Hoyle): Dell 1952: (*partim*, Dell register # 17 only): 39, 151.

Pinnoctopus cordiformis: d'Orbigny 1845: 193; Adams 1858: pl. 1, fig. 3; Chenu 1859: 14, fig. 5; Tryon 1879: 128, pl. 40, fig. 64; Hutton 1880: 2; Hoyle 1886: 14; 1888: 222; 1909 (*partim*, exclude Campbell Island record): 261; 1910: 411 (*pars.*); Suter 1913: 1065; 1915: pl. 70, fig. 3; Robson 1929 (*partim*, exclude Campbell Island record of Filhol 1885): 185; 1929a: 607; Powell 1937: 95; 1946: 100; Dell 1951: 97; 1952 (*partim*, exclude citation Filhol 1885): 31; Powell 1957: 125; 1962: 125; 1976: 133; 1979 (*partim*, *fide* Dell 1952): 44.

Octopus maorum Hutton, 1880: 1 (*partim*, exclude paralectotype by designation Suter 1913): Parker 1885: 586; Hoyle 1886: 13, 220; 1888: 221; Dell 1951: 97, fig. 1, 3, 4, 20; Batham 1957 (*partim*, exclude type *Paroctopus zealandicus* Benham): 629–638, figs 1–9; Powell 1957: 125; 1962: 125; 1976: 133; 1979: 444; Kubodera 1990: 349, fig. 277; Hochberg *et al.* 1992: 255–256, fig. 265a–c; Spencer & Willan 1995: 53.

Octopus (*Octopus*) *maorum*: Dell 1952 (*partim*, exclude type *Paroctopus zealandicus* Benham):15–28, pl. 1, figs 1–6, pl. 2, figs 1–3, pl. 3, figs 1–4.

Polypus maorum: Hoyle 1909: 260; Suter 1913 (*partim*, exclude Campbell Island citation of Filhol 1885): 1064; Powell 1937: 95.

Macroctopus maorum: Robson 1928: 257–264, figs 1–4, 6; 1929a: 607; Benham 1943: 139–153, pl. 22, figs 1–2, pls 23, 24, figs 1–15.

Octopus (*Macroctopus*) *maorum*: Robson 1929b: 174–175; Adam 1941: 18, 19; Powell 1946: 100.

Octopus communis Park, 1885: 198–199; Hoyle 1886: 13, 220; 1888: 221; Suter 1913: 1063–1064.

Polypus communis: Powell 1937: 95.

Octopus (*Macroctopus*) *communis*: Robson 1929b: 175; Adam 1941: 18, 19.

Octopus flindersi Cotton, 1932 (*fide* Norman 1992).

Removed from Synonymy:

Octopus maorum (not Hutton, 1885): Filhol 1885.

Paroctopus zealandicus Benham, 1944a.

TYPE MATERIAL (71 specimens, 37 male, 32 female, 2 sex indet.; 1 pair beaks): Neotype (here selected): NZOI H-668, M, ML 120.0 mm, 41°09.14–07.78' S, 173°15.07–11.76' E, 23–24 m, 21/03/1997, f.r.v. *Kaharoa* Stn KAH9701/01, NZOI Stn Z829; *Octopus maorum* Hutton, 1880, lectotype (selected by Suter, 1913), animal putrefied, beaks only.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.118434, M, ML 15.2 mm, Bay of Islands, *c.* 35°20' S, 174°00' E, -/02/1961, 6–7 m, coll. J. Moreland; NMNZ M.118304, M, ML 141.0 mm,

Smugglers Bay, Whangarei Heads, *c.* 35°49' S, 174°30' E, intertidal, 27/05/1994; NMNZ M.118420, F, ML 166.0 mm, 35°53.32–53.9' S, 174°36.10–36.13' E, 49 m, BT 13.8°C, 30/10/1994, f.r.v. *Kaharoa* Stn KAH 9411/034; NMNZ M.118424, M, ML 212.0 mm, 4F, ML 200.0, 160.0, 107.0, 72.0 mm, Mokohinau Islands, *c.* 35°55' S, 175°07' E, *c.* 200 m, datNR; NMNZ M.118270, 3F, ML 155.0, 150.0, 160.0 mm, 35°58.8' S, 174°31.3' E, 20 m, 07/11/1993, f.r.v. *Kaharoa* Stn 93/026; NMNZ M.118267, M, ML 228.0 mm, F, ML 165.0 mm, 36°02.7' S, 175°11.3' E, 90 m, 04/11/1993, f.r.v. *Kaharoa* Stn 93/04; NMNZ M.118172, F, ML 190.0 mm, off Little Barrier Island, *c.* 36°12' S, 175°05' E, 40 m, 18/10/1991; NMNZ M.118269, F, ML 158.0 mm, 36°26.6' S, 175°0.8' E, 50 m, datNR, f.r.v. *Kaharoa* Stn 9301/025; NMNZ M.118419, M, ML 151.0 mm, 36°28.07–27.50' S, 175°10.05–10.54' E, 50 m, 28/10/1994, BT 13.5°C, f.r.v. *Kaharoa* Stn KAH 9411/017; NMNZ M.118422, F, ML 218.0 mm, 36°28.44–36°27.94' S, 175°29.29–29.87' E, 52–57 m, BT 3.7°C, 29/10/1994, f.r.v. *Kaharoa* Stn KAH 9411/018; NMNZ M.118268, M, ML 154.0 mm, F, ML 139.0 mm, 36°35.0' S, 175°08.0' E, 46 m, 06/11/1993, f.r.v. *Kaharoa* Stn KAH 93/024; NMNZ M.118243, M, ML 165.0 mm, 36°35' S, 176°08' E, 260 m, 08/01/1994; NMNZ M.118255, F, ML 145.0 mm, 36°36.8' S, 175°38.56' E, 49 m, 05/11/1993; NMNZ M.118279, F, ML 180.0 mm, off Ponui Island, Hauraki Gulf, *c.* 36°52' S, 175°11' E, 20 m, -/08/1993; NMNZ M.90445, sex indet., ML 14.8 mm, 37°21.3' S, 176°08.3' E, 16 m ov. 52 m, (MWT), 14/08/1975, f.r.v. *James Cook* Stn J12/31/75; NMNZ M.94803, M, ML 37.7 mm, F, ML 31.5 mm, West of Waiaka Bay, *c.* 37°32' S, 178°13' E, 3 m, tide pool, 02/03/1988, coll. G.S. Hardy, C. Ward; NMNZ M.118437, M, ML 26.2 mm, 2F, ML 41.0 mm, W. of Waiaka Bay, *c.* 37°32' S, 178°13'' E, 3 m, tide pool, 02/03/1988, coll. G.S. Hardy, C. Ward; NMNZ M.90299, F, ML 65.5 mm, BS 728, 37°51.8–51.7' S, 176°56.8–55.0' E, 39–34 m, 21/01/1979, f.r.v. *Tangaroa* (NZOI Stn R86); NMNZ M.119115, F, ML 227.0 mm, 38°24.8' S, 173°54.9' E, 105 m, 07/01/1995, f.v. *Ikuku Maru*; NZOI Stn Z8587, M, ML 128.0 mm, 38°42.04–40.67' S, 174°30.16–30.94' E, 41–40 m, 30/10/1996, f.r.v. *Kaharoa* Stn KAH9615/102; OM A.'89.07. Portland Island (Benham Ref 'F'', F, ML 18.0 mm, sex indet. ML 12.5, *c.* 39°17' S, 177°52' E, datNR, depNR; NMNZ M.110972, M, ML 136.0 mm, N. side Bare Island, Napier, *c.* 39°50' S, 177°02' E, 10 m, 11/12/1990, coll. C. Duffy; NZOI Stn Z8288, M, ML 150.0 mm, off Arapawaita, west coast of Kapiti Island, *c.* 40°50' S, 174°55' E, 70–72 m, coll. D. Watson, 19/04/1995; NMNZ M.118167, F, ML 179.0 mm, 40°56' S, 170°29' E, 160–165 m, 28/09/1976, f.r.v. *James Cook* Stn J15/026/76; NZOI Stn Z8828, M, ML 125.0 mm, 40°58.38–59.77' S, 173°11.65–15.18' E, 36–38 m, 21/03/1997, f.r.v. *Kaharoa* Stn KAH9701/03; NMNZ M.118001, M, ML 173.0 mm, 41°04.5' S, 173°33.5' E, Whangamoa, Nelson, 3–6 m, 17/11/1993, coll. C. Paulin, C. Roberts, A. Stewart; NZOI Stn Z8829, 2M, ML 168.0, 120.0 mm, 41°09.14–07.78' S, 173°15.07–11.76' E, 23–24 m, 21/03/1997, f.r.v. *Kaharoa* Stn KAH9701/01; NMNZ M.95409, M, ML 30.5 mm, Flat Point, Wairarapa, *c.* 41°15' S, 175°58' E, coll. B.A. Marshall, 16–19/01/1989; NMNZ M.5635, M, ML 13.8 mm, Lyall Bay, Wellington, *c.* 41°20' S, 174°48' E, among stones, R.K. Dell, 27/12/1947; NMNZ M.5634, ?M, ML 21.4 mm, Lyall Bay, Wellington, *c.* 41°20' S, 174°48' E, among stones, R.K. Dell, 27/12/1947 (Dell register # 17); NMNZ M.117882, F, ML 108.0 mm, Island Bay, Wellington, *c.* 41°21' S, 174°47' E, 1.5 m, rockpool, 11/01/1994, coll. C. Roberts; NMNZ M.5693, F, ML 113.5 mm, Island Bay, Wellington, *c.* 41°21' S, 174°47' E, datNR, depNR; NMNZ M.5646, F, ML 115.0 mm, Island Bay, Wellington, *c.* 41°21' S, 174°47' E, craypot, 1950; NMNZ M.118000, M, ML 161.0 mm, 41°44.5' S, 174°15.0' E, 3 m, 16/11/1993, coll. C. Paulin, A. Stewart, C. Roberts; NZOI Stn Z8374, 9M, ML 215.0 (2), 207.0, 188.0, 186.4, 180.3, 170.0, 165.5, 148.0 mm, *c.* 42°20' S, 173°30' E, 25 m, SCUBA, 15/08/1995, coll. B. Noye; NZOI Stn E779 TAM, F, ML 91.0 mm, 42°44.0' S, 170°07.0' E, 229–219 m, 16/10/1967; NZOI Stn Z8830, M, ML 162.0 mm, 43°41.68–41.45'' S, 169°04.00–08.10' E, 125–130 m, 25/03/1997, f.r.v. *Kaharoa* Stn KAH9701/21; NMNZ M.111818, F, ML 135.0 mm, 43°48.4' S, 176°52.4' W, Tangoio Bay, Chatham Islands, 0–2 m, 11/02/1991, coll. T. Robb; NMNZ M.111819, M, ML 158.0 mm, 44°07.3' S, 176°37.8' W, off The Horns, Cape Leveque Bay, Chatham Islands, 16–21 m, 12/02/1991, craypot, f.v. *Journeyman*; FSFRL EA439 (14–2–3), F, ML 149.0 mm, 44°45.5' S, 172°12' E, 138 m, 21/09/1974, f.v. *Kaiburu Maru*; NMNZ M.90367, M, ML 40.0 mm, BS 550, 45°44' S, 170°48' E, off Taiaroa Heads, 27 m, f.r.v. *Munida*, 25/09/1976; NMNZ M.118246, M, ML 160.0 mm, F, ML 215 mm, 45°59.71' S, 170°55.12' E, 139 m, 16/03/1993, f.v. *Lady Dorothy*; NMNZ M.90372, M, ML 31.3 mm, 46°34.9' S, 167°51.9' E, Foveaux Strait, 52 m, datNR, coll. B.M. Barry, f.v. *Lachlan* Stn 51/81; NMNZ M.118168, M, ML 208.0 mm, off Port Pegasus, Stewart Island, *c.* 47°12' S, 167°41' E, -/02/1972; NZOI Stn Z8373, 2F, ML 208.0, 158.0 mm, FPT, *c.* 47°12' S, 167°41' E, 15 m, -/04/1996; NMNZ M.118166, M, ML 218.0 mm, 47°54.6' S, 168°42.4' E, 140 m, f.v. *Sokolinoe*, coll. S. Tong; NMNZ M.118175, F, ML 248.0 mm, 48°15.7' S, 168°17.6' E, 300 m, 24/03/1994, f.v. *Sokolinoe*, coll. S. Tong.

RECOGNISED DISTRIBUTION (New Zealand, Fig. 85, p. 148): North Island (south of Leigh), South, Stewart, and Chatham Islands (*c.* 35°20–48°15.7' S), 0–300 m. Not known from Auckland, Campbell, or Bounty Islands. Also known from South Australia (*fide* Norman 1992).

DIAGNOSIS: Massive, papillose octopus with long, slender arms; arm formula about 1.2.3.4, suckers enlarged on dorsal arm pair, diameter twice that of ventral arm suckers, sucker formula 1.2.3.4, sucker diameter about 5–16% ML; hectoctylised arm sucker counts 82–103, non-hectocotylised arm sucker counts to 326; outer gill lamella number 12–14; hectocotylus with cylindrical calamus with thick lateral walls, length to about 11% hectocotylised arm.

DESCRIPTION: Adult animal attains massive size (ML to 248.0 mm, TL to about 1.5 m); body slender to stocky (Figs 86–88). Mantle elongate to ovoid (MW about 36–95% ML), dorsoventral compression absent; lateral keel or fold of skin absent in live- or narcotised-fixed specimens but often present in postmortem-fixed material. Head small to moderately long, narrow to broad (HdL about 19–33% ML; HW about 26–56% ML)

narrower than mantle, separated from mantle by well-developed preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head; eye apertures dorsolaterally oriented. Funnel long (FuLI 34–53), well developed, base entirely free of brachial crown. Nuchal constriction well developed.

Brachial crown robust, slightly narrower to wider than head. Arms slender, very short to long (female about 58–83% TL; male about 32–84% TL), gradually tapering to delicate tips; arms 1 and 2 usually longest, 3 and 4 shortest, without consistent disparity in relative arm lengths. Web shallow to deep, about 7–35% longest arm length, usually about 8–20% longest arm length, with wide, well-developed membranous extension down both dorso- and ventrolateral faces of each arm to distal third arm length, thereafter both dorso- and ventrolateral web extensions seemingly fusing into common riblet to arm tip; web formula variable, sector E usually shallowest, sectors A and B deepest, without consistent disparity in relative sector depths. Suckers biserial, distal 10–20 suckers at arm tips minute; non-hectocotylised arm tips of males not secondarily modified in any discernible way. Arm sucker counts very high, greater in mature females than males, female ASC to 326, male to 278, range (both sexes) 164–326; suckers extend to arm tips. Suckers small to moderate sized, ASIn 5.1–16.4, largest on dorsal arms, gradually decreasing to ventral arms, suckers on ventral arm pair about 50% diameter of those on dorsal arm pair. Suckers with: well-developed, small suction chamber; pronounced constriction of sucker aperture; extensive, well-developed grasping ring with about 18 complete radial grooves and an equal number of incomplete finer inter-radial grooves; and massive muscular suction pad (Fig. 155A).

Male with third right arm hectocotylised, length shorter than (mature specimens) to equivalent (juveniles) opposite member (OAI about 52–96); with moderate number of suckers (ASC 82–103); terminal hectocotylised portion (Fig. 89A) short to long, increasing with maturity (LLI 2.7–10.7); ligula with thick cheeks enclosing deep, narrow, V-shaped groove, with inner surface with about 10 thick, incomplete, opposing fleshy corrugations, alternating with those on opposite side; calamus moderate to large (CaLI about 16–35), with groove extending entire length. Spermatophore groove narrow, with thickened web margin weakly differentiated from web sector D.

Dorsal and ventral surfaces of mantle, head, arms and web densely beset with small, soft-topped, conical papillae; dorsal surfaces of mantle, head and base of arms 1 and 2 with scattered larger conical mounds, each with 5–9 small, lateral, low-profile pimplelike prominences; two are particularly enlarged to form superocular cirri (one dorsolateral to each eye), two enlarged to lesser extent around dorsal margin of eye aperture. Live-preserved specimens with small dome-shaped red pigment spots in web sectors A–E and along dorso- and ventrolateral surfaces of arms 1–4. Colour (live-preserved specimens) over dorsal and ventral surfaces of mantle, head, arms 1–4 and web sectors A–E, variable — light, dark brown or red; oral surface of arms, web and sucker apertures slightly lighter brown to red. Colour (postmortem, particularly post-thaw-fixed specimens) over dorsal surfaces of mantle, head, arms 1–3 and web sectors A–D light pinks, oranges, reds, and browns; ventral surface of mantle, head, dorso- and ventrolateral surfaces of arms 4, oral surface of arms 1–4 and web sectors A–E, aboral surface of web sector E, and sucker apertures lighter pink to orange, with darker orange to red blotches.

Gills with 12–14 lamellae per outer demibranch; funnel organ W-shaped, with thick inner and outer limbs; outer limbs slightly shorter than to equivalent length of inner limbs. Male with long penis, penis diverticula oriented towards interpallial septum. Female with narrow distal oviducts extending over face of viscera parallel to interpallial musculature, genital apertures open proximal to anus. Extensive connective tissue developed between renal tissues and ventral inner mantle musculature. Visceral envelope with sparse, small black chromatophores; skin over lateral muscles restraining digestive gland without apparent chromatophores.

Male reproductive system (Fig. 89B) with very long, thick, strongly convoluted proximal vas deferens; spermatophoral gland long, with thickenings, glandular regions and constrictions, without apparent appendix proximal to junction with accessory gland. Accessory gland long, thick, with distal portion rapidly expanded, terminal volution incomplete; common spermatophoral and accessory gland duct to spermatophore sac with well-developed appendicular diverticulum. Spermatophore sac long, narrow, thin walled, distally rounded, containing up to 5 spermatophores; spermatophores very long, to 164 mm. Distal vas deferens short, narrow; penis diverticula complex, double, with large primary diverticulum doubled over on itself, and small appendicular secondary diverticulum sandwiched between folds of primary diverticulum; penis large, long, distally expanding, genital aperture subterminal. Mature female (Fig. 89C) with large ovary sac; proximal oviducts depart ovary sac through common antrum; proximal ducts narrow, length about 20% that of distal ducts; oviducal gland large, with 2 clearly defined hemispheres, distal largest, blackened, with about 30 radial striations, proximal light coloured, with faint radial striations. Distal oviducts proximally narrow,

Figure 86. ***Pinnoctopus cordiformis*** (Quoy & Gaimard): **A**, NZOI Stn Z8374, male, ML 207 mm. **B**, NZOI Stn Z8374, male, ML 188 mm.

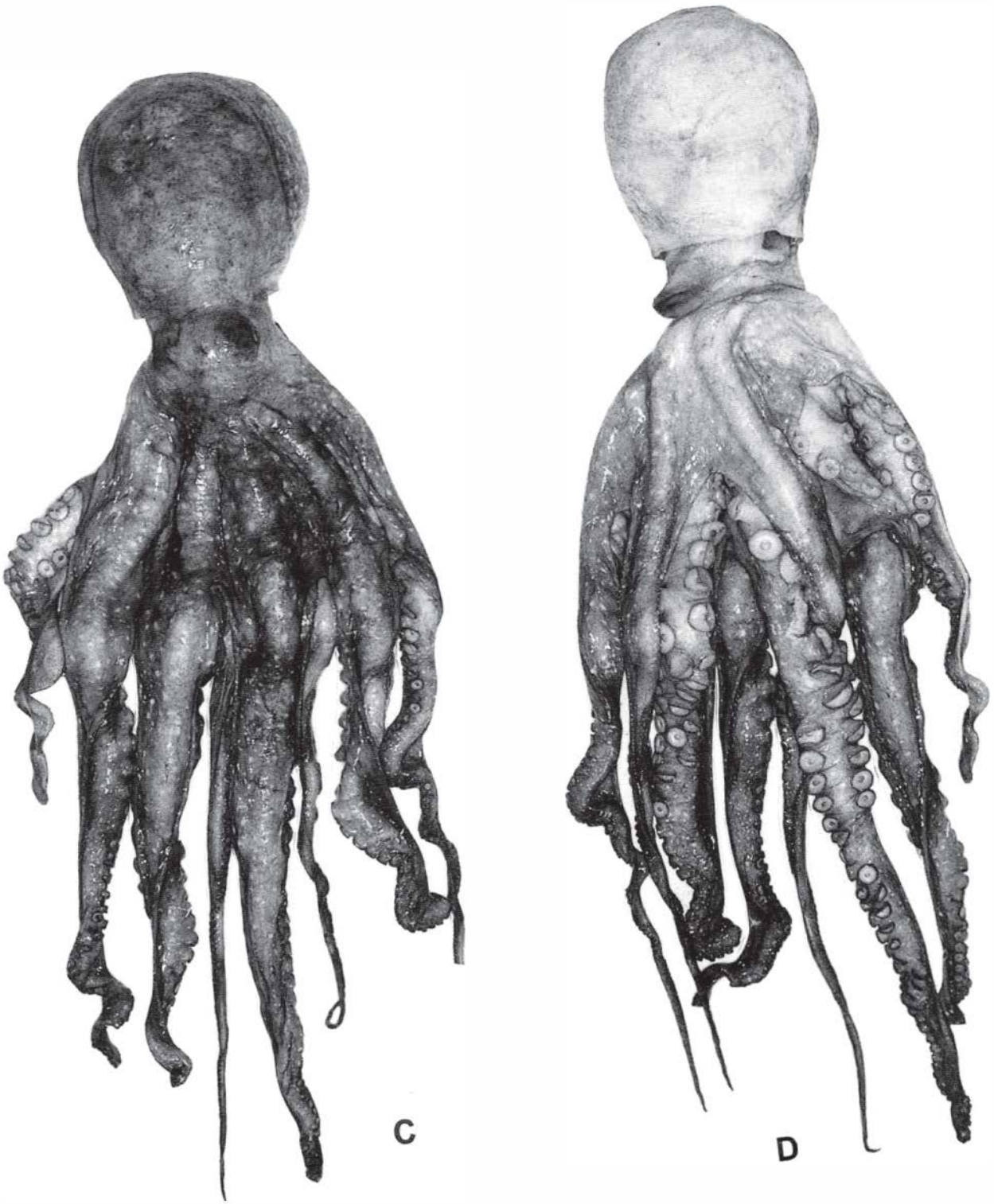


Figure 87. *Pinnoctopus cordiformis* (Quoy & Gaimard): C–D, NZOI Stn Z8374, male, ML 215 mm.

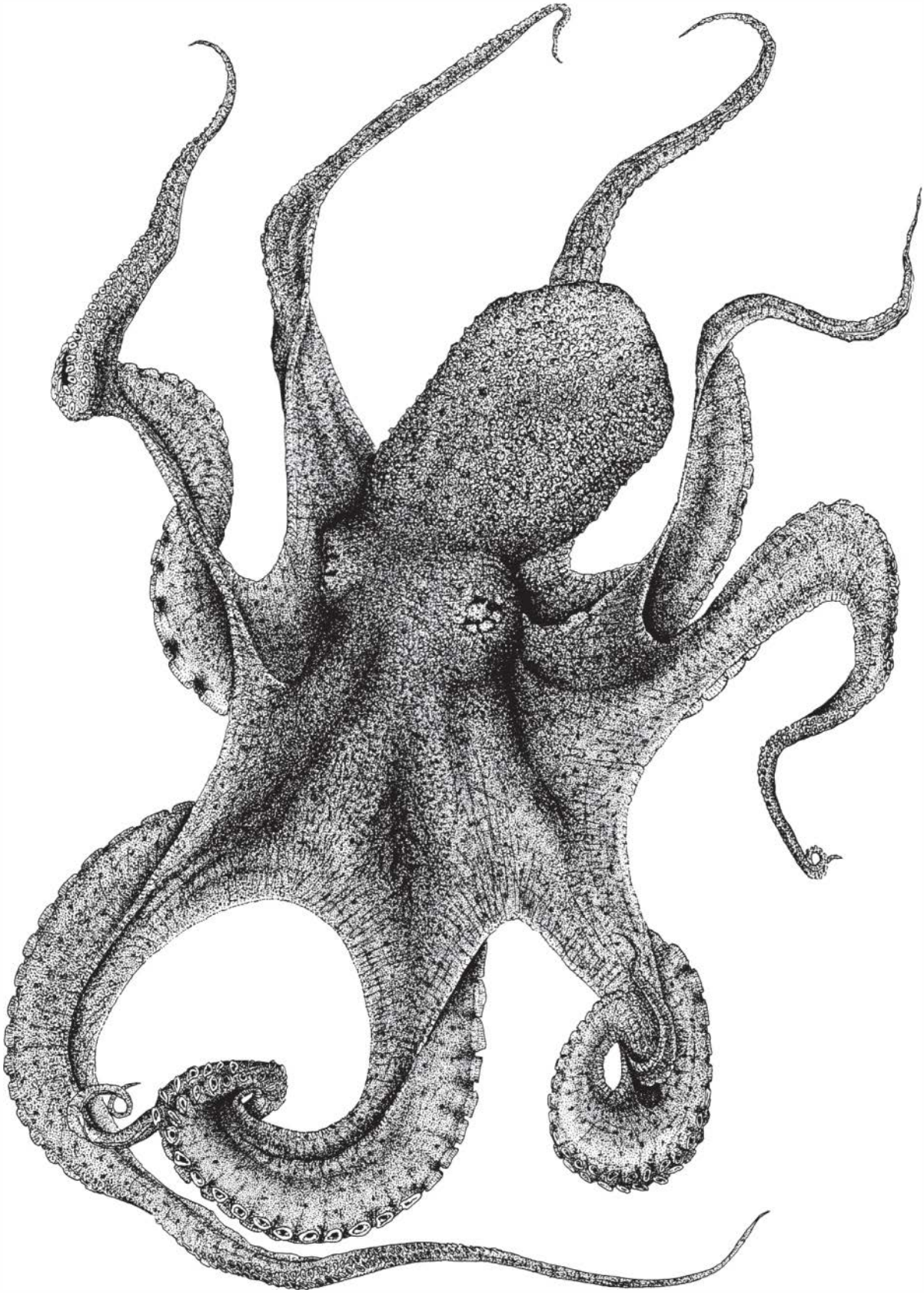


Figure 88. ***Pinnoctopus cordiformis*** (Quoy & Gaimard, 1832): NMNZ M.90299, female, ML 65.5 mm, live-fixed individual.

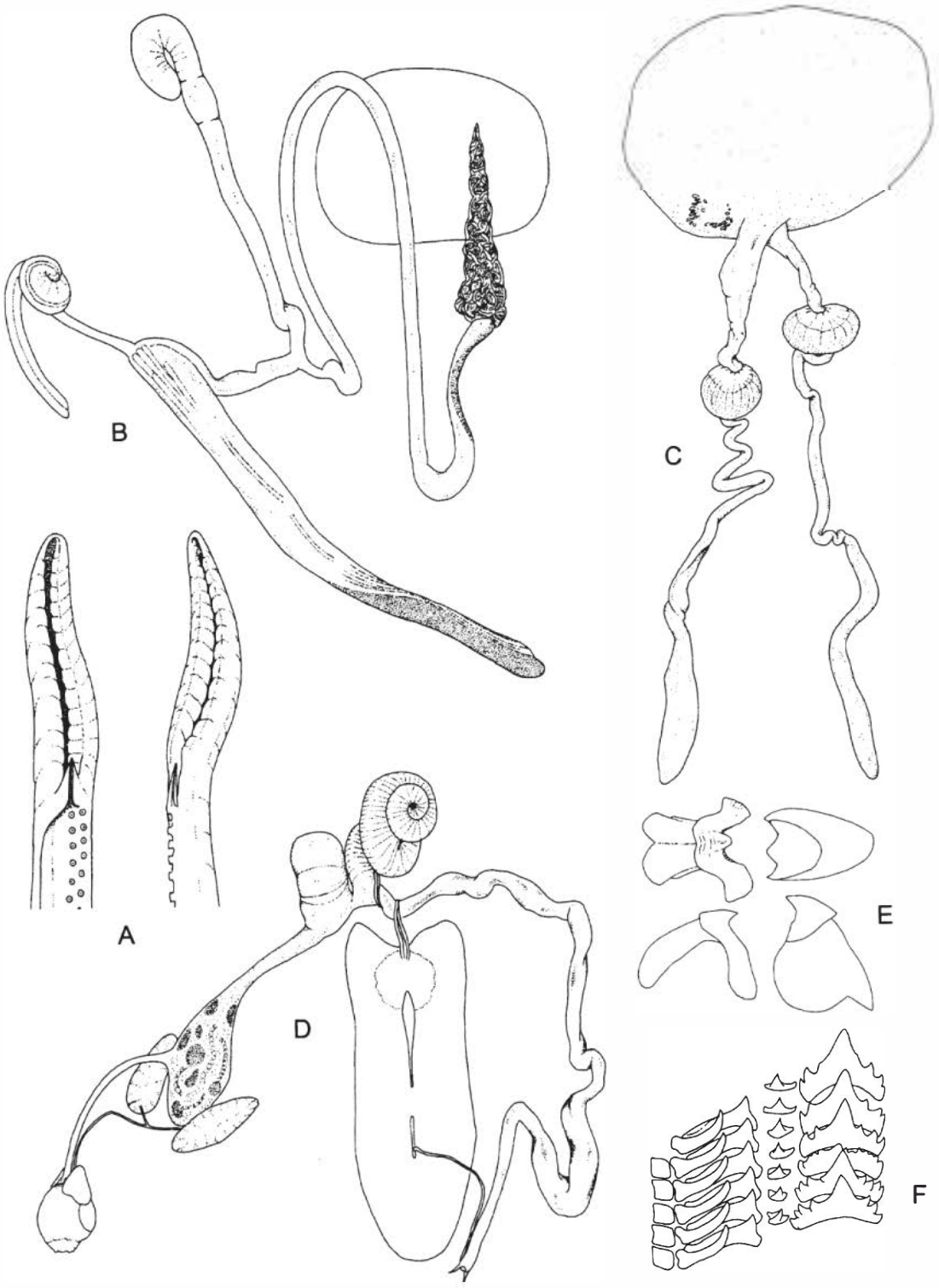


Figure 89. ***Pinnoctopus cordiformis*** (Quoy & Gaimard, 1832): **A–B**, NMNZ M.118268, male, ML 154 mm. **C**, **F**, NMNZ M.118268, female, ML 139 mm. **E**, holotype ***Octopus maorum*** Hutton. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 63. Indices, formulas, and counts for male *P. cordiformis* (Quoy & Gaimard) (* denotes damage).

	NZOI Z8374	NZOI Z8829	NZOI Z8830	NZOI Z8587	NZOI Z8828	NMNZ M.95409	NZOI Z8829
MWI	45.6	33.8	55.2	55.9	65.6	95.1	45.8
HdLI	19.1	19.6	21.6	21.9	23.6	29.5	25.8
HdWI	30.0	31.3	29.9	37.5	45.6	66.2	45.8
EOI	7.9	5.1	4.6	5.9	6.5	3.3	8.3
ALI1–4	*	33.6–79.6	35.4–73.7	35.5–77.3	39.6–78.3	31.6–84.2	52.9–77.2
AFR	*	1.2.4.3	*	1.2.4.3	*	1=2.4.3	2.1.4.3
AFL	*	2.1.?3.4	1.3.2.4	1.2.4.3	*	1.3.4.2	1.2.3.4
WDIA–E	*	7.0–20.2	10.1–35.0	11.6–18.7	7.9–15.2	9.7–17.6	7.1–18.1
WFR	A.B.D.C.E	B.A.C.D.E	C.E.B.A.D	A.B.C.D.E	B.A.C.D.E	B.A.C.D.E	C.D.B.E.A
WFL	A.B.C.D.E	B=C.A.D.E	D.C.E.A.B	B.A.C.D.E	B.D.A.C.E	A=B.C.D.E	B.C.E.A.D
ASC1–4	*–278	187–270	252–262	258–274	234–255	174–186	236–266
ASIn1–4	7.4–14.4	5.1–12.0	5.9–12.3	6.3–11.0	8.8–16.4	7.2–16.1	6.5–13.3
FuLI	33.5	35.1	38.3	37.5	40.8	52.5	41.7
FFuI	16.7	15.2	26.9	17.2	26.0	31.8	24.2
PAI	26.5	26.2	28.8	28.1	38.7	54.1	27.5

Table 64. Indices, formulas, and counts for female *P. cordiformis* (Quoy & Gaimard) (* denotes damage).

	NZOI Z8373	NZOI Z8373	NMNZ M.90299	NMNZ M.14992	NMNZ M.118437
MWI	51.4	60.1	62.6	65.4	46.3
HdLI	28.8	23.4	32.8	27.8	23.7
HdWI	25.5	35.2	55.7	49.8	42.7
EOI	4.6	4.9	3.1	5.2	7.6
ALI1–4	60.9–75.8	57.7–80.1	56.6–78.4	*	66.5–82.8
AFR	2.1.4.3	*	1.2.3.4	?1.2.4.3	2.1.3.4
AFL	1.2.3.4	*	1.2.4.3	?1.2.3.4	1.2.3.4
WDIA–E	10.8–18.2	8.5–18.4	14.5–23.7	*	6.9–15.4
WFR	A.B.D.C.E	B.A.C.E.D	A.C.D.B.E	B.C.A.D.E	B.D.E.A.C
WFL	A.D.C.B.E	A.B.D.C.E	B.A.C.D.E	B.C.A=D.E	B.D.C.E.A
ASC1–4	276–310	306–326	261–272	186–211	164–171
ASIn1–4	5.5–8.4	5.2–11.5	7.6–13.7	8.2–13.4	4.9–9.8
FuLI	40.6	36.4	38.2	40.8	33.9
FFuI	14.9	20.3	20.0	31.9	19.5
PAI	17.1	31.9	36.8	40.0	27.8

Table 65. Indices and counts of hectocotylised arm for male *P. cordiformis* (Quoy & Gaimard) (* denotes damage).

	NZOI Stn Z8374	NZOI Stn Z8829	NZOI Stn Z8830	NZOI Stn Z8587	NZOI Stn Z8828	NZOI Stn Z8829	NMNZ M.90367	NMNZ M.95409	NMNZ M.118434
OAI	*	62.9	52.3	83.1	*	63.1	73.5	48.8	96.2
ASC3R	94	97	94	98	103	95	102	82	96
CaLI	15.7	22.9	21.7	26.4	24.8	19.4	29.4	34.5	*
LLI	10.7	6.3	8.2	5.7	9.7	6.5	2.8	4.7	*

distally swelling to genital aperture; genital aperture terminal, pore-like, not secondarily modified. Mature ovarian eggs number thousands, each small, elongate, to 5.5 x 1.0 mm in size, with long stalk and about 8–10 longitudinal striations running the entire egg length.

Alimentary canal (Fig. 89D) with large buccal bulb, length about 27% ML; anterior salivary glands very large, ovoid, length about 64% greatest buccal-bulb dimension; anterior oesophagus exceptionally long (length equivalent to crop), enters crop dorsally; crop well developed, with extensive anterior diverticulum about 33% crop length. Posterior salivary glands elliptical to narrowly triangular, very large, length about 163% buccal bulb greatest dimension, to about 44% ML (in live-fixed specimens). Posterior oesophagus narrow, thick walled. Stomach large, with large, thin-walled basal, thick-walled central, and larger thin-walled distal sections; stomach with undivided lumen. Spiral caecum smaller than stomach, with 3 complete radially striate volutions. Intestine long (about twice oesophagus and crop length), thinwalled, proximally constricted, dilated centrally, secondarily constricted, dilated distally and again constricted proximal to anus; anal flaps paired, conspicuous. Digestive gland massive, elongate, with prominent anterior peaks; pancreas well developed; ink sac narrow, long (about 40% digestive gland length), exposed anteriorly, superficially buried beneath surface of digestive gland for greatest length; ink duct long, opening into base of anus.

Upper beak (Fig. 89E) moderately tall (height equivalent to length); hood and lateral walls black, margins translucent; hood shallow (depth 33.3% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, not deflected down; jaw with single broad pronounced tooth. Lateral walls slightly rounded; crest squared, lateral wall without apparent fold, with shallow sinus in basal margin. Lower beak (Fig. 89E) tall (height 75.6% width); hood, lateral wall and wings black, lateral wing and wall margins translucent. Lateral wall with deep, acutely angled, V-shaped basal notch and keeled crest. Hood shallow (depth 28.0% beak length); rostrum broadly triangular, apex blunt; hood with shallow posterior notch; lateral wings moderately long (length 93.1% beak length), with single strong fold.

Radula (Fig. 89F) with massive, broad-based rachidian with 3 or 4 small asymmetric, lateral cusps beside large prominent central cusp; 1st lateral tooth with 2 cusps, inner small, at base of long inner heel, outer largest; 2nd lateral robust, broad based, with single large cusp; marginal tooth long, comparatively delicate relative to 2nd lateral tooth cusp; marginal block well developed, rectangular, wider than deep (along axis of radula ribbon). Radula with repeat seriation every 6 or 7 transverse rows.

Indices, formulas, and counts for male and female *P. cordiformis* in Tables 63 and 64; for hectocotylised arm of male in Table 65; raw measures for male and female in Tables 66 and 67 (p. 144 and 145).

REMARKS: A recent and extensive trawling survey on scallop beds along the east coast of Northland between Leigh and Spirits Bay failed to capture a single specimen of this otherwise common species. The distribution of *P. cordiformis* appears discontinuous along the North Island east coast.

Pinnoctopus kermadecensis (Berry, 1914) (Fig. 91) (Tables 68, 69)

Polypus (*Pinnoctopus* ?) *kermadecensis* Berry, 1914:138–139, pls 7, 8.
Polypus kermadecensis: Berry 1916: 49.

TYPE MATERIAL (2 specimens, 1 male [M], 1 female [F]): Holotype USNM 00816461, M, ML 50.0 mm, 29°50' S, 178°15' W, 03 April 1913.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.256374, F, ML 78.0 mm, Raoul Island, Kermadec Islands, R.S. Bell, 1910, ex. W.R.B. Oliver colln.

RECOGNISED DISTRIBUTION (Fig. 90, p. 148): Raoul Island, Kermadec Islands, intertidal.

DESCRIPTION: Adult probably attains moderate size (known specimens to ML to 78.0 mm, TL to 424 mm); body slender (Figs 91A–E). Mantle slender to ovoid (MW about 38–67% ML), no dorsoventral compression; lateral keel and fold of skin absent in live-fixed specimen (lateral keel an artefact of post-mortem-fixed material apparent in holotype). Head large, narrow (HdL about 22–34% ML; HW about 35–46% ML), narrower than mantle, separated from mantle by well-developed preocular constriction. Orbits large, neither unduly raised from surface of head nor meeting across dorsal midline; eye apertures dorsolaterally oriented. Funnel long (FuLI 34–36), well developed, with basal portion fused to base of ventral arm pair 4. Nuchal constriction well developed.

Brachial crown robust, slightly wider than head. Arms slender, hectocotylised arm very short, non-hectocotylised arms short to moderately long (combined about 48–79% TL), gradually tapering to delicate tips; arms 1 and 2 longest, 3 and 4 shortest, arm formula 1.2.3.4 to 1.2.4.3. Web shallow to moderate, about 7–19% longest arm length, with extensive membranous extension down both dorso- and

Table 66. Raw measures for male *Pinnoctopus cordiformis* (Quoy & Gaimard) (* denotes damage, † denotes regrowth).

	NZOI Stn Z8374	NZOI Stn Z8829	NZOI Stn Z8830	NZOI Stn Z8587	NZOI Stn Z8828	NZOI H-668	NMNZ M.90367	NMNZ M.95409	NMNZ M.118434
TL	1002	807	790	691	756	674	236	196	91
ML	215.0	168.0	162.0	128.0	125.0	120.0	40.0	30.5	15.2
MW	98.0	56.7	89.5	71.5	82.0	55.0	35.0	29.0	12.5
HdL	41.0	33.0	35.0	28.0	29.5	31.0	17.0	9.0	6.0
HdW	64.5	52.5	48.5	48.0	57.0	55.0	29.5	20.2	10.2
EO	17.0	8.5	7.4	7.5	8.1	10.0	1.5	1.0	0.8
AL1R/L	770*/401*	642/555	465/582	534/525	592/153*	436/520	220/219	142/165	74/72
AL2R/L	204*/540*	561/620	525/487	485/465	447*/485	500/445	251/194	142/93	63/63
AL3R/L	476/608*	271/431	280/535	245/295	299/175*	275/436	122/166	62/127	51/53
AL4R/L	672/677	326†/216*	78*/458	442*/452	166†/435	410/400	168/138	118/107	52/50
WDA	170	100	68	92	72	50	43	22	15
WDBR/L	150/154	130/104	72/60	87/100	85/90	70/94	41/38	29/22	15/15
WDCR/L	122/116	88/104	78/92	73/85	64/68	91/65	39/26	21/20	15/17
WDDR/L	132/115	72/80	59/98	66/80	62/81	71/37	30/32	19/18	14/14
WDE	68	45	76	62	47	56	29	16	15
CaL	8.0	3.9	5.0	3.7	7.2	3.5	1.0	1.0	*
LL	51.0	17.0	23.0	14.0	29.0	18.0	3.4	2.9	*
ASC1R	*	270	L252	258	236	266	235	174	134
ASC2R	*	220	252	274	L234	236	211	186	124
ASC3R	94	97	94	98	103	95	102	82	96
ASC4R	278	187	262	L262	L255	248	224	177	116
ASe1R	31.0	20.1	20.0	14.1	20.5	15.9	L7.1	4.9	2.2
ASe2R	L23.0	14.5	15.0	10.5	14.1	12.3	L5.0	3.9	1.5
ASe3R	18.5	11.5	11.0	8.2	12.1	7.8	3.9	L2.9	1.3
ASe4R	16.0	8.5	9.5	8.0	L11.0	7.8	3.4	2.2	1.1
GiLC	12	14	13	14	12	14	13	14	13
FuL	72.0	59.0	62.0	48.0	51.0	50.0	24.3	16.0	9.7
FFL	36.0	25.5	43.5	22.0	32.5	29.0	7.5	9.7	5.0
PA	57.0	44.0	46.7	36.0	48.4	33.0	22.2	16.5	8.4

ventrolateral faces of each arm almost to arm tips, both dorso- and ventrolateral web extensions appear separate along entire arm length; web formula with no consistent disparity in sector depths in two available specimens. Suckers biserial, distal 10–20 suckers at arm tips minute. Arm sucker counts moderate to high, female ASC to 21 0; suckers extend to arm tips. Suckers small to moderate-sized, ASIn 4.0–11.7, largest on dorsal arms, gradually decreasing to ventral arms, suckers on ventral arm pair 50–75% diameter of those on dorsal arm pair. Suckers with: large suction chamber; moderately constricted sucker aperture; moderately well-developed grasping ring with 18 faint radial grooves; and moderately to weakly developed muscular suction pad (Fig. 155B).

Gills with 11 or 12 lamellae per outer demibranch; funnel organ W-shaped, limbs slender, outer limbs shorter than central V-component. Distal oviducts narrow, extending parallel to and over lateral musculature of interpallial septum; genital apertures open proximal to anus. Extensive connective tissue present between renal tissues and ventral inner mantle musculature; visceral envelope and lateral muscles ensheathing and restraining digestive gland respectively, without apparent chromatophores.

Dorsal and ventral surfaces of mantle, head, arms and web densely beset with small, soft-topped, blisterlike, low-profile papillae; none particularly enlarge to form superocular cirri. Colour over dorsal and ventral surfaces of mantle, head, arms 1–4 and web sectors A–E dark rustic brown; oral surface of arms, web and sucker apertures slightly lighter brown.

REMARKS: The type specimen, initially described by Berry as an immature female, is actually an immature male. The "adventitious" fold of skin around the mantle described for this specimen is very obvious, but is, however, absent on the only other known specimen identified as this species. This lateral fold

Table 67. Raw measures for female *Pinnoctopus cordiformis* (Quoy & Gaimard) (* denotes damage).

	NZOI Stn Z8373	NZOI Stn Z8373	NMNZ M.90299	NMNZ M.14992	NMNZ M.118437
TL	1116	836	334	310	227
ML	208.0	158.0	65.5	61.2	41.0
MW	107.0	95.0	41.0	40.0	19.0
HdL	60.0	37.0	21.5	17.0	9.7
HdW	53.0	55.6	36.5	30.5	17.5
EO	9.5	7.7	2.0	3.2	3.1
AL1R/L	730/846	526/670	254/262	235*/215*	176/179
AL2R/L	760/801	434*/592	237/243	245*/222	188/173
AL3R/L	680/765	120*/522*	195/202	211/214	155/161
AL4R/L	740/723	482/446*	189/206	221/202	151/135
WDA	154	122	60	40	13
WDBR/L	127/103	123/94	46/62	49/49	23/33
WDCR/L	118/116	71/80	59/58	47/47	11/28
WDDR/L	125/121	57/86	53/54	38/40	18/29
WDE	91	58	38	25	17
ASC1R	276	L313	261	*	171
ASC2R	297	L306	269	L186	167
ASC3R	292	*	272	202	164
ASC4R	310	L326	269	211	171
ASe1R	17.4	L18.2	9.0	8.2	4.0
ASe2R	14.0	L13.2	7.2	7.0	3.0
ASe3R	12.0	L9.5	5.7	5.5	2.4
ASe4R	11.5	L8.2	5.0	5.0	2.0
GiLC	13	13	13	12	13
FuL	84.5	57.5	25.0	25.0	13.9
FFL	31.0	32.0	13.1	19.5	8.0
PA	35.5	50.4	24.1	24.5	11.4

Table 68. Indices, formulas, and counts for *Pinnoctopus kermadecensis* (Berry).

	Holotype	NMNZ M. 256374
MWI	38.0	66.7
HdLI	22.0	33.5
HdWI	35.0	46.4
EOI	7.0	1.9
ALI1–4	47.5–75.3	61.3–78.8
AFR	?1.2.4.3	?1.2.3.4
AFL	1.2.3.4	1.2.3.4
WDIA–E	6.5–19.0	13.5–16.8
WFR	A.B.C.E.D	A.D.C.E.B
WFL	A.B.E.C.D	B=C.D.A.E
ASC1–4	144–155	196–210
ASIn1–4	4.0–10.0	7.9–11.7
FuLI	34.0	35.9
FFuI	19.0	13.1
PAI	20.0	37.8

of skin has already been attributed to an artefact of preservation in *P. cordiformis*. The single female described herein has not been dissected.

Octopus (sensu lato) Group 2

DIAGNOSIS: Hectocotylised arm with 6–11 enlarged distal-most sucker pairs, elevated from arm surface, disposed on laterally compressed section of arm; ligula deeply excavate, scooplike, with thickened lateral walls; calamus short; calamus groove extending to calamus tip; ligula floor with longitudinal rows of papillae. Penis with two diverticula; second diverticulum small; primary diverticulum large, long, cylindical, oriented towards interpallial septum; female genital apertures swollen, opening beneath base of gills.

REMARKS: The Group 2 morphotype is proposed as distinct from that of *Octopus* (*s.s.*) on both morphological and anatomical character combinations. The

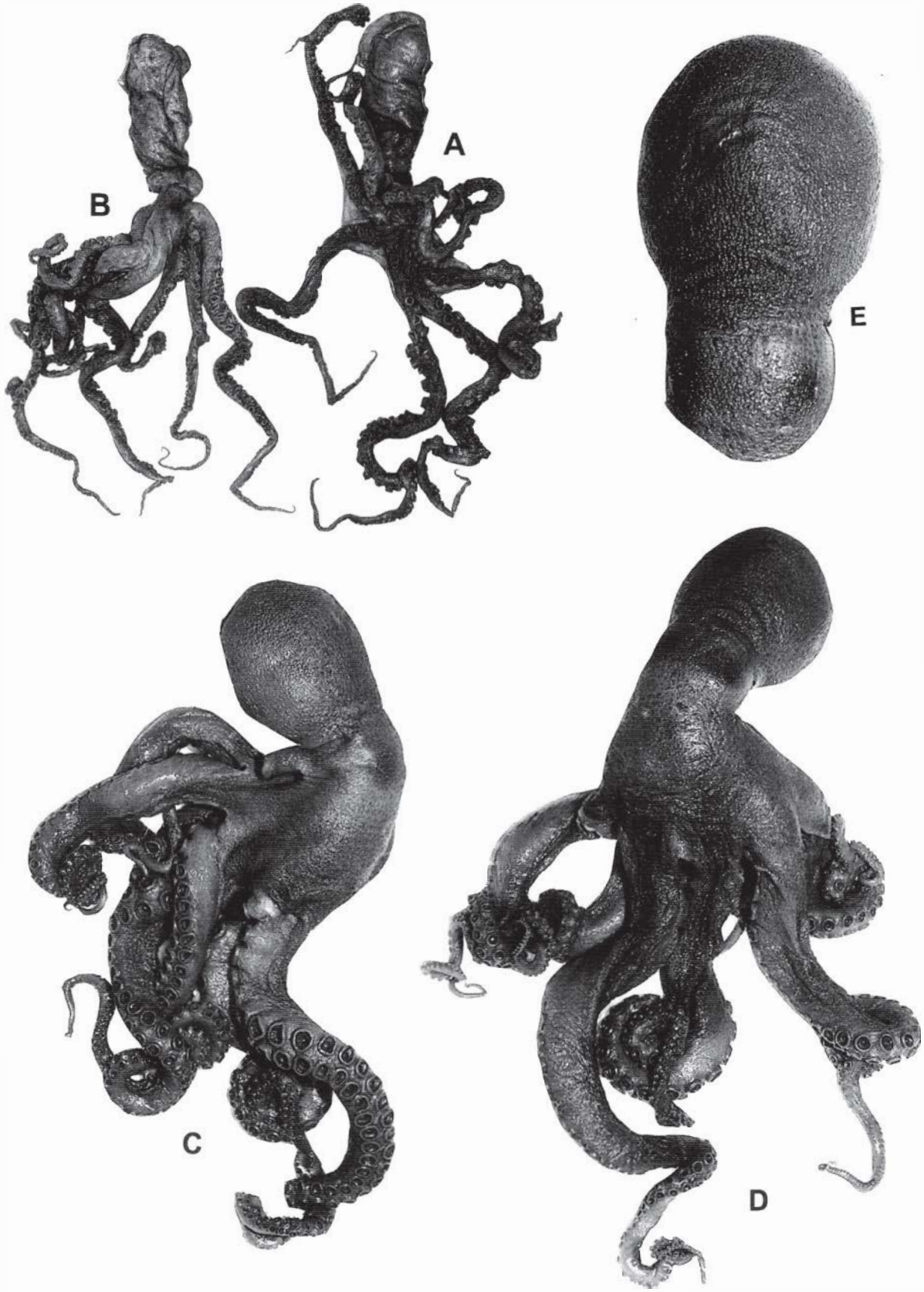
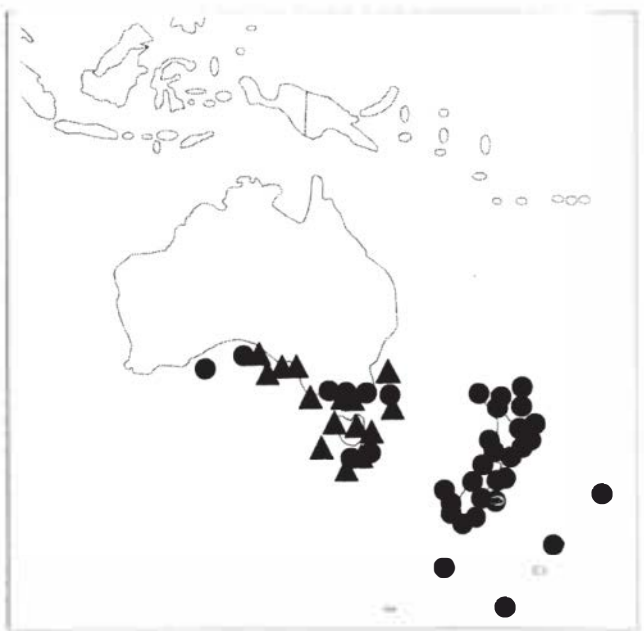


Figure 91. ***Pinnoctopus kermadacensis*** (Berry, 1914): **A, B**, holotype, USNM 00816461, male, ML 50 mm. **C–E**, NMNZ M.256374, female, ML 78 mm.

Table 69. Raw measures for *Pinnoctopus kermadecensis* (Berry) (* denotes damage).

	Holotype	NMNZ MF 56374
TL	223	424
ML	50.0	78.0
MW	19.0	52.0
HdL	11.0	26.1
HW	17.5	36.2
EO	3.5	1.5
AL1R/L	158/168	334/331
AL2R/L	143/147	49*/318
AL3R/L	106/125	291/283*
AL4R/L	86*/118	272/260
WDA	32	53
WDBR/L	28/22	45/56
WDCR/L	22/19	48/56
WDDR/L	11/15	50/54
WDE	20	46
ASn1R	5.0	9.1
ASn2R	3.7	L8.1
ASn3R	2.5	6.2
ASn4R	2.0	6.2
ASC1R	155	196
ASC2R	144	L204
ASC3R	91	204
ASC4R	*	210
GiLC	12/9?	11/10
LL	1.5	F
CaL	0.2	F
PA	10.0	29.5
FuL	17.0.	28.0
FFuL	9.5	10.2



hectocotylised male arm is unique in its secondary modification, the distal section expanded, laterally compressed with sucker pairs both slightly enlarged and markedly elevated from the arms surface. The penis is massive, with two diverticula, the primary diverticulum oriented towards the interpallial septum, away from the base of the right gill. The recognised distribution of this genus includes New Zealand and South Australian waters, with the inclusion of South Australian *O. huttoni* (inclusive junior synonym *O. warringa* Stranks) and *O. berrima* Stranks & Norman.

Octopus huttoni (Benham, 1943) (Figs 93–95) (Tables 70–74)

Polypus maorum (Hutton, 1880: 1) (*partim*, paralectotype, Suter 1913: 1064).

Polypus australis (not Hoyle, 1885): Massy 1916a (*partim*, "Terra Nova" Stn 134 specimens only): 149–151, figs 9–10; Robson 1929 (*partim*, "Terra Nova" Stn 134 specimens only, exclude type *O. campbelli* Smith, footnote synonymy: 144–145; Powell 1937: 95.

Robsonella australis (not Hoyle, 1885): Benham 1942 (*partim*, exclude holoype *O. campbelli* Smith): 227–235, figs 3–14; Powell 1946: 100; Dell 1951: 97, fig. 2; 1952 (*partim*, *fide* Benham and exclude Dell reg. # 17): 32–39, pl. 4, figs 2–6, pl. 5, figs 1, 3, 4, pl. 7, figs 1–8; 1959: 95; Pickford 1955 (*partim*, *fide* Benham, Dell): 165–166; Powell 1957: 125; 1962 (*partim*, *fide* Benham, Dell): 125; Brough 1965: 7–19, figs 1–9; Powell 1967: 125; 1976: 133; 1979 (*partim*, *fide* Benham, Dell): 444; Tait 1981: 15, 1 9–20; Voight 1993: 222.

Polypus duplex (not *Octopus duplex* Hoyle, 1885): Berry 1917: 11, fig. 5.

Robsonella huttoni Benham, 1943: 53–57, figs 1–7; Powell 1946: 100; Dell 1951: 98; 1952 (*partim*, exclude Dell Reg. # 71, pl. 9): 39–41; Pickford 1955 (*partim*, *fide* Dell): 165–166; Powell 1957: 125; 1962: 125; 1967: 125; 1976: 133; 1979 (*partim*, *fide* Dell): 444; Voight 1993 (*partim*, *fide* Dell): 222.

Octopus huttoni (Benham): Spencer & Willan 1996 (*partim*, *fide* Dell): 53.

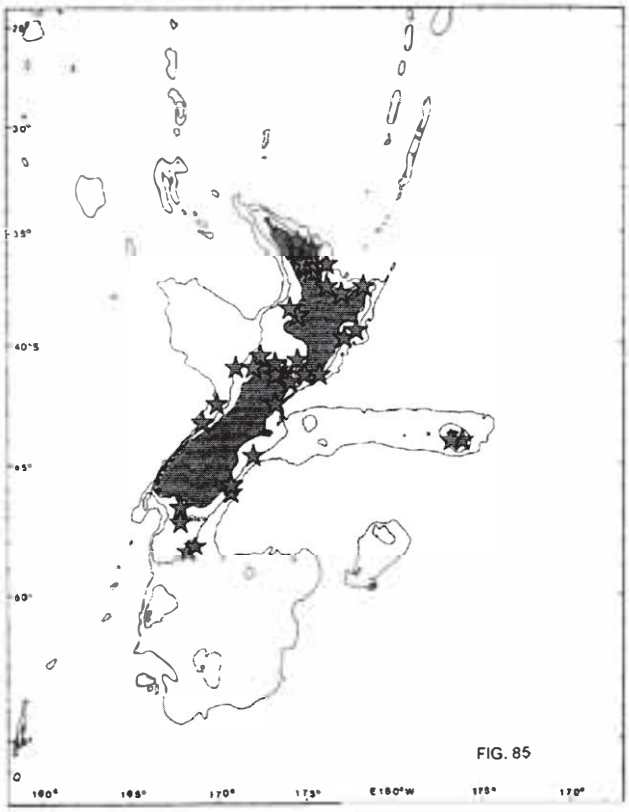
Octopus otagoensis Benham, 1943: 57.

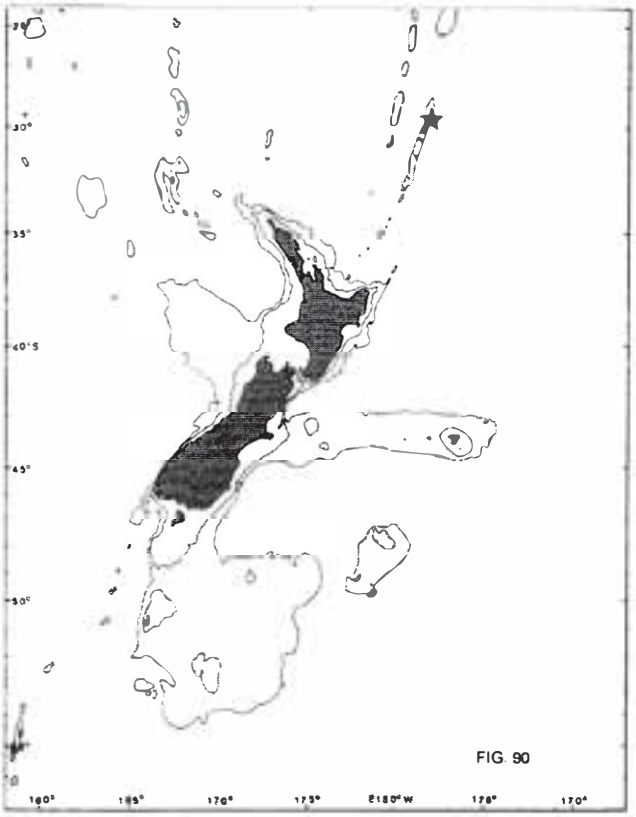
Octopus adamsi Benham, 1944: 259–261, fig. 5; Powell 1946: 100; Dell 1951: 97, fig. 21; 1952: 29, pl. 6, fig. 1; Powell 1957: 125; 1962: 125; 1967: 125; 1976: 133; 1979: 444; Spencer & Willan 1996: 53.

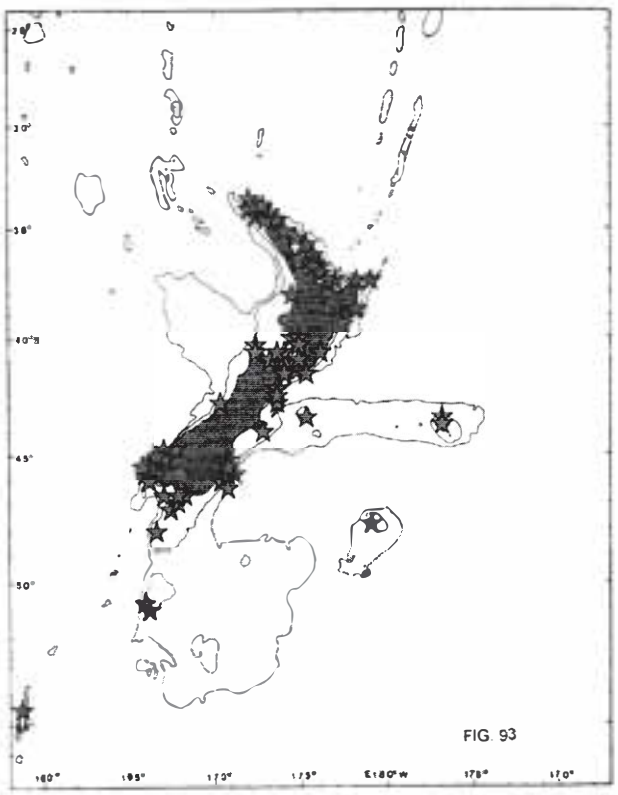
Octopus warringa Stranks, 1989 (*partim*, exclude AMS C40887): 457; Spencer & Willan 1996 (*partim*, *fide* Stranks): 53.

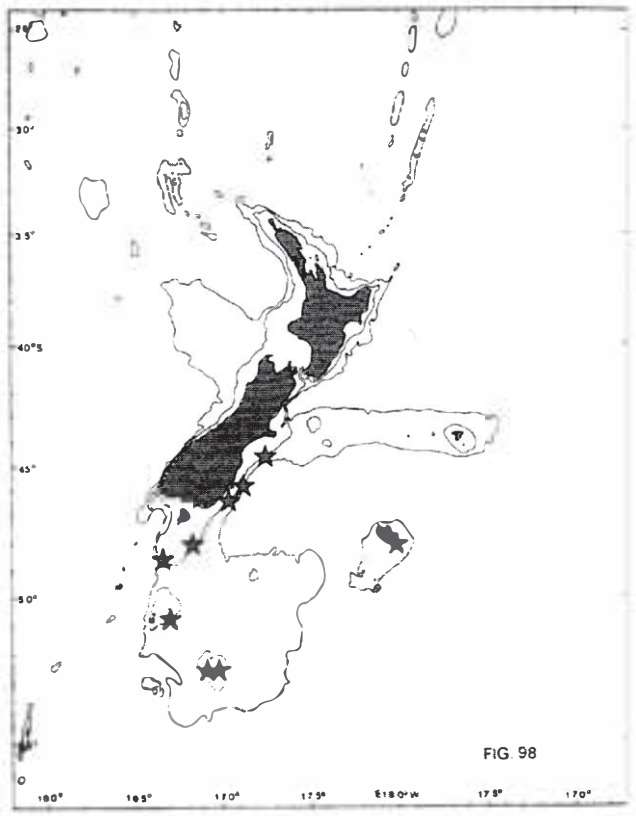
Octopus campbelli (not Smith, 1902): Toll 1991a: 116–117.

Figure 92 (opposite). Recognised distribution of *Octopus* (*s.l.*) Type 2: ▲ *O. berrima* Stranks & Norman, 1992 (*fide* Stranks & Norman 1992); ● *O. huttoni* (Benham, 1943; inclusive synonym *O. warringa* Stranks, 1990).









Recognised distribution. **Fig. 85**, *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832). **Fig. 90**, *Pinnoctopus kermadecensis* (Berry, 1914): type and new material. **Fig. 93**, *Octopus huttoni* (Benham, 1943). **Fig. 98**, *Octopus campbelli* (Smith, 1902).

TYPE MATERIAL: *Octopus maorum* Hutton (paralectotype) Canterbury Museum, M, ML 44.0 mm, Dunedin. *Robsonella huttoni* Benham, 1943: holotype, OM A.44.16, M, ML 38.7 mm, Otago. *Octopus adamsi* Benham, 1943: holotype (here designated) OM 44.18, F, ML 42.3 mm; paralectotype A.44.17, F, ML 42.0 mm, Otago. *Octopus warringa* Stranks, 1990: holotype NMV F57444, male, ML 16.5 mm.

ADDITIONAL MATERIAL EXAMINED (New Zealand: 183 specimens, 77 male [M], 87 female [F], 19 sex indet.): NMNZ M.90450, M, ML 7.9 mm, BS904, 33°57.0' S, 172°19.0' E, King Bank, N.E. of Three Kings Islands, 128 m, 01/02/1981, r.v. *Tangaroa* (NZOI Stn O650); NMNZ M.118342, F, ML 15.9 mm, W. end Great Island, Three Kings Islands, 3–7 m, *c.* 34°09' S, 172°09' E, 28/11/83, SCUBA, coll. G.S. Hardy & A.L. Stewart; NMNZ M.90415, M, ML 18.0 mm, BS397, *c.* 34°10' S, 172°09' E, sublittoral, Tasman Bay, Great Island, coll. A.N. Baker *et al*, 19/02/1974; NMNZ M.90413, F, ML 10.4 mm, BS396, off Three Kings Islands, 260 m, 34°13' S, 172°11.5' E, r.v. *Acheron*, 19/02/1974; NZOI Stn Z8662, M, ML 27.0 mm, F, ML 15.5 mm, FFN, 34°21.4' S, 172°46.2' E, 54.5 m, 27/02/1997, f.v. *Ben Gunn* Stn BG9701/41; NZOI Stn Z8645, M, ML 15.5 mm, 2F, ML 18.1, 16.3 mm, FFN, 34°22.2' S, 172°48.0' E, 51.3 m, 27/02/1997, f.v. *Ben Gunn* Stn BG9701/37; NZOI Stn Z8657, M, ML 10.0 mm, FFN, 34°22.7' S, 172°45.6' E, 43 m, 28/02/1997, f.v. *Ben Gunn* Stn BG9701/68; NMNZ M.90437, sex indet., ML 7.9 mm, BS 912, 34°22.8' S, 172°24.6' E, NW of Cape Reinga, 121 m, 02/02/1981, r.v. *Tangaroa* (NZOI Stn O658); NZOI Stn Z8676, 2F, ML 22.0, 19.0 mm, FFN, 34°22.9'S, 172°54.0'E, 52 m, 27/02/1997, f.v. *Ben Gunn* Stn BG9701/34; NZOI Stn Z8660, F, ML 12.9 mm, FFN, 34°23.6' S, 172°53.6' E, 38 m, 27/02/1997, f.v. *Ben Gunn* Stn BG9701/32; NZOI Stn Z8663, M, ML 19.0 mm, F, ML 15.5 mm, FFN, 34°23.8' S, 172°53.3' E, 37.5 m, 27/02/1997, f.v. *Ben Gunn* Stn BG9701/31; NMNZ M.90394, M, ML 18.0 mm, *c.* 34°25' S, 172°47' E, Spirits Bay, 4 m, coll. R.K. Dell, -/11/1963; NZOI Stn F920, F, ML 10.0 mm, 34°26' S, 172°49.5' E, 14–16 m, 13/10/1968; NZOI Stn Z8656, sex indet., ML 6.0 mm, FFN, 34°47.7' S, 173°19.0' E, 30 m, 02/03/1997, f.v. *Ben Gunn* Stn BG9701/82; NZOI Stn Z8665, M, ML 19.5 mm, FFN, 34°48.0' S, 173°12.3' E, 24 m, 02/03/1997, f.v. *Ben Gunn* Stn BG9701/76; NZOI Stn Z8655, sex indet., ML 7.6 mm, FFN, 34°50.0' S, 173°14.0' E, 20 m, 03/03/1997, f.v. *Ben Gunn* Stn BG9701/F; NZOI Stn Z8664, 2M, ML 13.8, 11.5 mm, F, ML 17.1 mm, FFN, 34°58.1' S, 173°45.5' E, 28.4 m, 26/02/1997, f.v. *Ben Gunn* Stn BG9701/D; NZOI Stn Z8675, 3F, ML 18.0, 14.2, 13.9 mm, FFN, 34°58.3' S, 173°45.9' E, 27.4 m, 26/02/97, f.v. *Ben Gunn* Stn BG9701/A; NZOI Stn Z8658, sex indet., ML 6.1 mm, FFN, 34°59.1' S, 173°49.7' E, 31 m, 26/02/1997, f.v. *Ben Gunn* Stn BG9701/30; NZOI Stn Z8661, M, ML 15.5 mm, FFN, 34°59.4' S, 173°50.5' E, 33 m, 26/02/1997, f.v. *Ben Gunn* Stn BG9701/28; NZOI Stn Z8639, sex indet., ML 7.2 mm, FFN, 34°59.46' S, 173°58.20' E, 41 m, 03/03/1997, f.v. *Ben Gunn*; NZOI Stn Z8659, F, ML 8.5 mm, FFN, 34°59.7' S, 173°45.5' E, 17.5 m, 26/02/1997, f.v. *Ben Gunn* Stn BG9701/B; NMNZ M.90284, M, ML 24.6 mm, 2F, ML ML 23.0, 21.9 mm, Tauranga Bay, Whangaroa, 2 m, *c.* 35°03' S, 173°45' E, coll. R.K. Dell, 11/11/1963; NMNZ M.90428, sex indet., ML 8.1 mm, Tauranga Bay, *c.* 35°03' S, 173°45' E, 4 m, coll. R.K. Dell, 11/11/1963; NMNZ M.90422, F, ML 11.0 mm, BS337, *c.* 35°12' S, 174°18' E, datNR, outer Deepwater Cove; NZOI Stn I4 TB, F, ML 10.0 mm, 35°47.8–48.8' S, 175°13–16.2' E, 151–153.4 m, 02/05/1975; NMNZ M.90352, 3M, ML 13.1, 12.0, 11.9 mm, 2F, ML 21.0, 15.5 mm, Mar. Dept. Stn 65/64, *c.* 36°20' S, 175°05' E, Cradock Channel, Hauraki Gulf, 62–68 m, 17/11/1964; NMNZ M.90362, F, ML 37.2 mm, *c.* 36°2' S, 175°05' E, datNR, Hauraki Gulf, N.Z., ex. Mar. Dept; NMNZ M.90414, F, ML 17.2 mm, BS358, 36°25' S, 175°28' E, Colville Channel, 44 m, r.v. *Acheron*, 10/02/1974; NMNZ M.5616, M, ML 17.0 mm, *c.* 36°50' S, 175°35' E, off Coromandel Peninsula, 50 m, 20/02/1916, coll. Oliver; NZOI Stn Z8523, F, ML 33.2 mm, 36°52.13–55.32' S, 176°16.77–16.90' E, 380–386 m, 17/04/1996, f.r.v. *Kaharoa* Stn KAH9604/33; AK 77684, F, ML 29.6 mm, 37°05' S, 176°14' E, 380 m, 03/02/1992, f.r.v. *Kaharoa* Stn 9202/06; NMNZ M.90336, M, ML 18.0 mm, BS701, 37°30.4' S, 177°09.7' E, White Island, 83–92 m, 19/01/1979, r.v. *Tangaroa* (NZOI Stn R59); NMNZ M.117698, M, 21.2 mm, 2F, ML 18.5, 13.0 mm, Waiaka Bay, *c.* 37°32' S, 178°13' E, 15–20 m, 01/05/1992; NMNZ M.90440, M, ML 13.2 mm, BS837, 37°35.0' S, 178°52.8' E, 31–48 m, 22/01/1981, r.v. *Tangaroa* (NZOI Stn O582); NMNZ M.90304, F, ML 37.5, BS680, 37°35.0–34.5' S, 178°51.6–53.5' E, 39–50 m, 17/01/1979, r.v. *Tangaroa* (NZOI Stn R38); NMNZ M.90423, M, ML 18.1 mm, BS678, 37°36.3' S, 178°53.1' E, Ranfurly Bank, 74 m, 17/01/1979, r.v. *Tangaroa* (NZOI Stn R36); NMNZ M.90426, F, ML 10.4 mm, BS737, 37°40.4–40.7' S, 176°24.3–24.5' E, 44 m, 21/01/1979, r.v. *Tangaroa* (NZOI Stn R95); NMNZ M.90388, M, ML 16.0 mm, BS732, 37°46.5–47.0' S, 176°38.5–38.2' E, SE Plate Island, 39 m, 21/01/1979, r.v. *Tangaroa* (NZOI Stn R90); NMNZ M.90425, sex indet., ML 6.4 mm, BS729, 37°49.4' S, 176°39.0' E, 29 m, 21/01/1979, r.v. *Tangaroa* (NZOI Stn R87); NMNZ M.90410, M, ML 17.0 mm, *c.* 38°02' S, 174°47' E, off Kahu Rocks, East Coast, 73 m, coll. F. Abernethy, -/10/1956; NMNZ M.5614, F, ML 24.2 mm, *c.* 38°40' S, 178°01' E, datNR, Tatepouri, Gisborne; NMNZ M.90400, sex indet., ML 6.0 mm, *c.* 39°07' S, 177°12' E, 1 mile off Mohaka River, Hawke Bay, -/02/1955; NMNZ M.5619, 2F, ML 24.5, 15.0 mm, Hawke Bay, *c.* 39°20' S, 177°30' E, dredged, -/03/1917, coll. W.J. Phillips; NMNZ M.90371, F + eggs, ML 20.0 mm, BS490, 39°57' S, 174°34' E, *c.* 10 miles SW of Waitotara River mouth, 33–35 m, r.v. *Acheron*, 02/03/1976; NMNZ M.90355, F, ML 28.0 mm, BS485, 40°09' S, 174°54' E, *c.* 11 miles SW of Whangaehu River mouth, 55–57 m, r.v. *Acheron*, 01/03/1976; NZOI Stn B686 TAL, 2F, ML 26.2, 15.0 mm, 40°16.0' S, 172°32.3' E, 126 m, 28/10/1962; NMNZ M.90309, M, ML 19.0 mm, BS492, 40°18' S, 174°59' E, *c.* 13 miles W of Rangitikei River mouth, 75–82 m, r.v. *Acheron*, 02/03/1976; NMNZ M.90277, F (+ eggs), ML 19.8 mm, BS535, 40°28' S, 172°48' E, 51 m, 10/03/1976, r.v. *Acheron*; NMNZ M.90447, F, ML 15.4 mm, 5.5–11 m, off Puponga, *c.* 40°32' S, 172°44' E, N. Nelson, coll. L. Climo, 10–20/03/1971; NMNZ M.90281, F, ML 20.0 mm, BS510, 40°38.5' S, 174°01' E, N. of Stephens Island, 183–187 m, 04/03/1976, r.v. *Acheron*; NMNZ M.17947, M, ML 22.3 mm, VUZ 9, 40°44' S, 174°E, off Rangitoto Island, Cook Strait, 90 m, 09/12/1954; NMNZ M.17945, M, ML 14.8 mm, VUZ Stn 4, 40°44' S, 174°E, off Rangitoto Island, Cook Strait, 73–91 m, 18/12/1954; NMNZ M.90314, 3M, ML 23.2, 21.6, 21.5 mm, F, ML 10.5 mm, BS512, 40°44' S, 173°48' E, off W. coast D'Urville Island, between Nile Head and Greville

Harbour, 62 m, r.v. *Acheron*, 05/03/1976; NMNZ M.118435, F, ML 16.0 mm, intertidal, Mataikona Coast, *c.* 40°47' S, 176°16' E, 14/11/1965; NMNZ M.90429, M, ML 9.5 mm, BS505, 40°47' S, 174°10.5' E, Marlborough Sounds, 73 m, 04/03/1976, r.v. *Acheron*; NMNZ M.90305, 2F, ML 22.1, 19.9 mm, N of Kapiti Island, 55 m, *c.* 40°52' S, 174°54' E, coll. F. Abernethy, 05/09/1956; NMNZ M.5623, M, ML 25.0 mm, *c.* 40°57' S, 173°03' E, Torrent Bay, Nelson, coll. P.A. Lush, 30/12/1950; NMNZ M.90403, 2F, ML 18.3, 15.8 mm, Admiralty Bay, *c.* 40°57' S, 173°52' E, coll. W.F. Ponder, -/08/1959; NMNZ M.90427, 3 sex indet., ML 10.0, 8.4, 7.0 mm, BS500, 40°57.5' S, 174°18' E, 139–144 m, 03/03/1976, r.v. *Acheron*; NMNZ M.90308, F, ML 13.5 mm, BS 14, 40°57.5' S, 174°01.5' E, 29 m, r.v. *Acheron*, 05/03/1976; NMNZ M.90411, M, ML 11.0 mm, BS514, 40°57.7' S, 174°01.5' E, 29 m, 05/03/1976, r.v. *Acheron*; O.M. 'A.O.97, Benham ref. 'G', *c.* 41°00' S, 173°20' E, Tasman Bay, between Nelson and Stephens Island, 20–60 m, datNR; NMNZ M.90300, M, ML 31.6 mm, Pukerua Bay, Wellington, *c.* 41°02' S, 174°54' E, 13/04/1957; NMNZ M.13322, F, ML 32.9 mm, Kaiwharawhara, Wellington Harbour, *c.* 41°16' S, 174°47' E, 5 m, 16/01/1959; NMNZ M.90326, M, ML 26.0 mm, 2F, ML 19.1, 15.1 mm, Lyall Bay, Cook Strait, *c.* 41°20' S, 174°48' E, 3–4 m, 11/11/1962; NMNZ M.90418, M, ML 11.5 mm, BS776, 41°26.1' S, 174°15.9' E, Cloudy Bay, 59–64 m, 28/01/1979, r.v. *Tangaroa* (NZOI Stn R134); NMNZ M.118408, sex indet., ML 8.5 mm, BS775, 41°27.0–25.7' S, 174°08.6–10.8' E, Cloudy Bay, 27–28 m, 28/01/1979, r.v. *Tangaroa* (NZOI Stn R133); NMNZ M.17944, F, ML 12.5 mm, VUZ Stn 99, 41°34.30' S, 174°43.30' E, 274 m, 29/08/1957; NMNZ M.118431, M, ML 24.5 mm, F, ML 25.0 mm, VUZ Stn 55, 41°39.30' S, 175°13' E, off Cape Palliser, 146–182 m, 23/02/1956; NMNZ M.118430, F, ML 21.4 mm, off Cape Campbell, *c.* 42°15' S, 173°40' E, 91–220 m, -/7/1925; NMNZ M.90279, 2M, ML 19.0, 13.5 mm, *c.* 42°25' S, 173°41' E, off Kaikoura, 73 m, coll. F. Abernethy, -/05/1953; NZOI Stn G156, M, ML 26.0 mm, 42°58' S, 173°30' E, 110 m, 13/11/1967; NMNZ M.90330, F, ML 25.0 mm, off Wanganui, 73 m, *c.* 43°01' S, 170°30' E, f.v. *Admiral*, -/04/1957; NMNZ M.90406, 2M, ML 7.8, 7.0 mm, F, ML 11.0 mm, BS 657, 43°13.3' S, 175°23.6' E, Mernoo Bank, 94–99 m, 12/01/1979, r.v. *Tangaroa* (NZOI Stn R15); NMNZ M.90453, M, ML 7.5 mm, Chatham Islands Expedition Stn 23, 43°32.5' S, 176°47.5' W, 60 m, 29/01/1954; NMNZ M.111847, M, ML 25.1 mm, 43°48.5' S, 176°42.3' W, Pine Tree Point, Port Hutt, Chatham Islands, 5 m, 03/02/1991, coll. A.L. Stewart; NMNZ M.111931, M, ML 35.8 mm, 43°48.6' S, 176°53.0' W, Te Raki Bay, Chatham Islands, 8–10 m, 11/02/1991; NMNZ M.90278, 2M, 45.6, 44.2 mm, *c.* 43°51' S, 176°42' W, Port Hutt, Chatham Islands, -/09/1950; NMNZ M.90348, F, ML 18.2 mm, BS556, 43°52' S, 173°06' E, E of Pompeys Pillar, 44 m, 27/09/1976, r.v. *Acheron*; NMNZ M.119904, F, ML 24.3 mm, 44°58.55' S, 167°25.60' E, George Sound, 6–16 m, 22/03/1995, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.119905, F, ML 13.2 mm, 45°02.61' S, 167°15.26' E, Caswell Sound, 8–20 m, 24/03/1995; NMNZ M.119907, M, ML 25.3 mm, 45°05.63' S, 167°08.45' E, Charles Sound, 7–20 m, 25/03/1995; NMNZ M.90283, M, ML 25.7 mm, F, ML 28.0 mm, 15–20 miles off Oamaru, *c.* 45°06' S, 170°58' E, 119 m, coll. J.M. Moreland, 13/11/1952; NMNZ M.119908, F, ML 54.0 mm, 45°10.37' S, 167°05.92' E, Nancy Sound, 5–18 m, 26/03/1995; NMNZ M.117691, M, ML 31.4 mm, F, ML 40.0 mm, 45°24.95' S, 166°51.30' E, Dagg Sound, 0–25 m, 29/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.119909, M, ML 57.0 mm, FFN, 45°26.62' S, 167°08.22' E, Doubtful Sound, 6–15 m, 30/03/1995, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M. 117687, M, ML 37.6 mm, 45°33.75' S, 166°52.05' E, Breaksea Sound, 6–15 m, 20/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.117688, M, ML 38.4 mm, F, ML 42.0 mm, FFN, 45°34.55' S, 166°57.96' E, Breaksea Sound, 2–18 m, 21/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.8958, M, ML 18.0 mm, BS189, 45°35.8' S, 171°02' E, off east Otago coast, 219 m, M.V. *Alert*, 14/08/1955; NMNZ M.117690, M, ML 42.0 mm, 45°37.00' S, 166°58.25' E, Wet Jacket Arm, 2–20 m, 28/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.117689, M, ML 40.0 mm, F, ML 16.1 mm, 45°39.00' S, 166°51.90' E, Wet Jacket Arm, 0–33 m, 28/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.117692, M, ML 42.3 mm, 45°43.55' S, 166°46.50' E, Dusky Sound, 0–17 m, 22/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.117693, F, ML 18.6 mm, 45°43.78' S, 166°56.56' E, Dusky Sound, 2–20 m, 22/03/1993, coll. C.D. Paulin, C.D. Roberts, A.L. Stewart; NMNZ M.90390, F, ML 9.0 mm, *c.* 45°44' S, 166°53' E, in Nine Fathom Passage, Dusky Sound, 18 m, m.v. *Alert*, 10/01/1952, coll. W.H. Dawbin; NMNZ M.118441, M, ML 23.2 mm, BS202, N 66° E of Taiaroa Head, Otago, 45°44' S, 171°02' E, 137 m, m.v. *Alert*, 23/01/1957; NMNZ M.16729, M, ML 32.3 mm, *c.* 45°44' S, 171°02' E, off Taiaroa Head, 113 m, 29/11/1962; NMNZ M.90354, M, ML 25.4 mm, *c.* 45°52' S, 170°40' S, 50 m, North Otago, ex. J. Graham colln; NZOI Stn B485, F, ML 10.8 mm, 46°04.1' S, 166°24.5' E, 58 m, 06/06/1961; NZOI Stn G689, M, ML 37.0 mm, 46°09' S, 170°48' E, 133 m, 20/01/1970; NZOI Stn B230 GLO, F, ML 28.0 mm, 46°40.0' S, 168°02.50' E, 26 m, 22/03/1960; NZOI B220, 2M, ML 9.5, 7.2 mm, 46°40' S, 168°09.8' E, 37 m, 21/05/1960; NMNZ M.90404, sex indet., ML 8.0 mm, 46°44' S, 168°07.5' E, Foveaux Strait, 12/01/1951, HMNZS *Lachlan*; NZOI Stn B225, M, ML 8.2 mm, 46°50' S, 168°18' E, 31 m, 21/05/1960; NMNZ M.90398, 4 sex indet., ML 11.0, 9.1, 8.5, 8.1 mm, Paterson Inlet, Stewart Island, *c.* 46°55' S, 168°03' E, coll. B.M. Bary, 04/02/1951; NMNZ M.90294, 2F, ML 21.0, 10.6 mm, Paterson Inlet, Stewart Island, *c.* 46°55' S, 168°03' E, r.v. *Acheron*, 07–14/02/1977, coll. J.R. Richardson; NMNZ M.90392, M, ML 7.5 mm, F, ML 7.0 mm, BS142, in channel between Ulva Island and Bradshaw Peninsula, Paterson Inlet, Stewart Island, *c.* 46°56' S, 168°04' E, 33 m, m.v. *Alert*, 12/01/1952; NMNZ M90442, 4M, ML 10.8, 10.0, 9.8, 9.8 mm, 3F, ML 9.7, 9.6, 9.0 mm, *c.* 47°00' S, 167°57' E, off anchor cable, HMNZS *Lachlan*, Cape Edwardson, Stewart Island, coll. B.M. Bary, 05/02/1951; NMNZ M.90290, F, ML 19.4 mm, sex indet., ML 8.2 mm, BS283, N. arm, *c.* 47°00' S, 167°57' E, Port Pegasus, Stewart Island, 40–45 m, r.v. *Acheron*, 25/02/1972; NMNZ M.90389, 2M(?), ML 7.2, 6.7 mm, *c.* 47°10' S, 167°33' E, Easy Harbour, SW coast Stewart Island, 7–20 m, 24/02/1972, r.v. *Acheron*; NMNZ M.90288, 2F, ML 24.4, 17.0 mm, *c.* 47°42' S, 179°04' E, Proclamation Island, Bounty Islands, New Zealand, 18 m, 09/11/1978, coll. D.S. Horning; NMNZ M.90280, M, ML 25.5 mm, *c.* 47°42' S, 179°04' E, Proclamation Island, Bounty Islands, New Zealand, 17 m, 16/11/1978, coll. D.S. Horning; NMNZ M.95263, M, ML

29.1, 8F, ML 23.0, 22.9, 21.2, 20.3, 19.3, 18.0, 14.1, 12.1 mm, *c.* 48°01' S, 166°35' E, Cod Cavern, Snares Islands, 6–9 m, 05/12/1984, coll. A.L. Stewart; NMNZ M.90306, M, ML 27.9 mm, *c.* 48°01' S, 166°35' E, Snares Expedition, 1984, -/11–12/1984; NMNZ M.90310, F, ML 18.5 mm, *c.* 48°01' S, 166°35' E, 18 m, 06/12/1984, Ho Ho Bay, Snares Islands, coll. G.S. Hardy; NMNZ M.90337, F, ML 20.1 mm, SA-3469, *c.* 48°01' S, 166°35' E, NW corner Ho Ho Bay, Snares Islands, 10 m, 19/12/1976, coll. G.D. Fenwick; NMNZ M.90391, M, ML 12.1 mm, *c.* 50°40' S, 166°30' E, Ranui Cove, Auckland Islands, on *Durvillea*, 08/01/1963; NMNZ M.90417, M, ML 19.0 mm, intertidal, Ranui Cove, Auckland Islands, *c.* 50°40' S, 166°30' E, coll. J.C. Yaldwyn, -/01/1963; NMNZ M.90430, M, ML 13.2 mm, outer Ranui Cove, *c.* 50°40' S, 166°30' E, 3.5 m, Auckland Islands, coll. J.C. Yaldwyn, 02/01/1963; NMNZ M.90344, M, ML 21.2 mm, F, ML 18.0 mm, *c.* 50°40' S, 166°30' E, tide pool, Enderby Island, Port Ross, Auckland Islands, 17/03/1954, coll. R.K. Dell; NMNZ M.90356, M, ML 37.0 mm, *c.* 50°40' S, 166°30' E, N of Dundas Island, Auckland Islands, crab pot, 10 m, 04/02/1970, coll. L.D. Ritchie; NZOI D184, F, ML 31.6 mm, 50°50' S, 166°05' E, 62 m, 22/01/1964; NZOI Stn D15, sex indet., ML 7.8 mm, 54°29.5' S, 158°58.0' E, DepNR, 22/04/1963.

NON-TYPE, NON-NEW ZEALAND (CONSPECIFIC) MATERIAL EXAMINED: AM C134083, M, ML 23.5 mm, Bells Beach, South of Geelong, Victoria, -/02/1972; AM C134084, M, ML 14.2 mm, N side of Eaglehawk Neck, Pirates Bay, SE Tasmania, 30/03/1970.

REFERENCE MATERIAL (Australia). SAM D14028, *Octopus berrima* Stranks & Norman, 2M, ML 49.5, 34.8 mm, det. K. Gowlett-Holmes, Gulf St. Vincent, W of Aldinga, prawn trawl, 38–41 m, 4–5/05/1987, f.v. *Rivoli Queen*; SAM D14026, *O. berrima*, det. K. Gowlett-Holmes, 2M, ML 60.1, 57.0 mm, F, ML 67.0 mm, Eyre Peninsula, Coffin Bay, Black Springs, on sand at night, 1.5–3 m, 20/04/1984; SAM D14027, *O. berrima*, det. K. Gowlett-Holmes, M, ML 28.6 mm, Nuyts Archipeligo, St Francis Island, cove NW of Petrel Cove, sand bottom, 40 m, 28/01/1982; SAM D14033, *O. kaurna* Stranks, det. Stranks, 2F, ML 30.0, 35.8 mm, sex indet., ML 9.5 mm, Eyre Peninsula, Second Creek, S of Tumby Bay, stranded in intertidal pool, sand and seagrass, 19/01/1985; SAM D17988, *O. kaurna*, det. Stranks, M, ML 37 mm, Spencer Gulf, Tiparra Reef, depNR, -/-/1975; SAM D14024, *O. pallidus* Stranks, det. K. Gowlett-Holmes, 2M, ML 89.5, 87.2 mm, 2F, ML 100.0, 58.5 mm, Gulf St Vincent, W of Aldinga, 38–41 m, 4–5/05/1987, prawn trawl, f.v. *Rivoli Queen*.

RECOGNISED DISTRIBUTION (New Zealand, Fig. 93, p. 148): Spanning about 18° latitude, 17° longitude, between 33°57.0– 50°50' S, 166°05' E–176°53.0' W, off Three Kings, North, South, Chatham, Stewart, Snares, Auckland, and Bounty Islands; 0–386 m; larval specimen taken off Macquarie Island. Also southern Australia.

DIAGNOSIS: Small-bodied, moderately long-armed species; dorsal arms typically shortest. Head well developed, with 1 or 2 large, multiple-branched ocular cirri. Mantle, head, arms and web densely papillose, individual papilla generally low in profile, rounded. Suckers enlarged on all arms at level of 10–13th sucker from arm base (at web margin) in mature specimens, diameter 14.0–16.6% ML; enlarged suckers not excessively elevated from arm surface. Distal 6–11 sucker pairs on hectocotylised arm enlarged, elevated from arm surface; hectocotylised arm sucker count 69–74. Gill lamellae number 6–8 per outer demibranch.

DESCRIPTION: Adult animal attaining small size (ML to 57.0 mm, TL to 236 mm), robust, muscular (Figs 94A–L). Mantle globose to ovoid (stages J–L[1]), broad (MW about 67–89% ML), dorsoventral compression and lateral keel or fold of skin absent; ventral longitudinal groove or depression well developed. Head large, wider than long, narrower than mantle (HdL about 25–38% ML; HW about 44–72% ML), separated from mantle by well-developed preocular constriction. Orbits large, bulbous, dorsolaterally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsolaterally to laterally oriented. Funnel moderately long to very long (FuL about 23–56% ML), well developed, base entirely free of brachial crown. Nuchal constriction well developed.

Brachial crown robust, equivalent in width to slightly wider than head. Arms thick, rectangular in section, short to very long (male AL about 52–87% TL), gradually tapering to somewhat delicate tips; dorsal arm pair 1 regularly shortest, otherwise with no consistent disparity between arm lengths. Web shallow to deep (WDI about 10–33% longest arm length), with little development along dorsolateral face of arms 1-4, moderate development to mid-arm length along ventrolateral faces of arms 1-4; web extension narrow, wider ventrolaterally than dorsolaterally; web formula variable, sectors A and E usually shallowest, sectors C and D deepest, with no consistent disparity in relative sector depths. Suckers biserial, with 9–12 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers not minute. Arm sucker counts onto genetically variable, counts similar for comparable-sized male and female (ML 37–57 mm, ASC 112–175; ML 20–37, ASC 69–141); suckers extend to arm tips. Sucker size sexually dimorphic, in male moderate to large (ASIn about 8–16), females moderate (ASIn about 8–12), with suckers on lateral arms slightly larger than those on dorsal or ventral arm pairs; no suckers abruptly enlarged in either sex. Suckers with: well-developed, small suction chamber; pronounced constriction of sucker aperture; extensive, well-developed grasping ring with about 16–18 complete radial grooves and few incomplete interradials; and massive muscular suction pad (Fig. 155G).

[1] Stages as depicted by Hochberg *et. al* 1992: fig. 235, p. 215.

Specimens live-, narcotised- or postmortem-fixed without lateral keel or fold of skin around mantle; dorsal and ventral surfaces of mantle, dorsal and dorsolateral surfaces of head, arms 1–4 and web sectors A–D densely and uniformly beset with simple, low-profile blister-like papillae without hardened apical structures; 6 secondarily enlarged papillae present on mantle, one preocular papilla anterior to eye on either dorsolateral surface of mantle, and 4 enlarged papilla in diamond formation on dorsal surface of mantle (the anterior papilla forming a mantle peak); enlarged multiple-branching papilla present above either eye as superocular cirrus; ventral surfaces of head, ventrolateral surface of arms 1–3, both dorso- and ventrolateral surfaces of arms 4, and aboral surface of web sector E with fine, simple papillae; adoral web surfaces A–E smooth. Dorsal and dorsolateral surfaces of mantle and head, dorsal and dorsolateral surfaces of arms 1–3 and to a lesser extent arms 4, oral surface of arms 1–3 outside web margin, and web sectors A–C, dark brown to red with irregular darker blotches; ventrolateral to ventral surfaces of mantle, funnel, head, ventrolateral surfaces of arms 1–4, web sectors D and E, light red to cream; oral surface of arms 1-4 within web light pink to red; sucker apertures cream to white. Live animals with two preocular mid-dorsal iridescent mantle patches. Juveniles (ML < 10 mm) with single row of black chromatophores running down each arm.

Gills with 7 inner and outer lamellae per demibranch; funnel organ W-shaped, limb thickness moderate, outer limbs slightly shorter than central V-component. Male with massive primary penis diverticulum oriented towards interpallial septum; penis large. Female with short distal oviducts not extending over lateral interpallial musculature, with genital apertures opening beneath gill. Extensive connective tissue is developed between renal tissues and ventral inner mantle musculature; visceral envelope and lateral muscles, ensheathing and restraining digestive gland respectively, without apparent chromatophores.

Terminal 7–10 sucker pairs on hectocotylised arm closely spaced, slightly enlarged, elevated from arm surface, disposed on laterally compressed section of arm (Fig. 95A). Spermatophoral groove deep, thick, with 5 or 6 enlarged papillae in recess at junction of spermatophoral groove with web sector D. Hectocotylised portion from distal sucker to tip of ligula of moderate length, about 6–10% arm length; hectocotylised arm about 66–89% length opposite arm. Ligula of moderate length (LLI about 6–10), with well-developed lateral walls enclosing deep ligula groove, 4–6 faint transverse rugae and several indistinct longitudinal rows of papillae; calamus large (CaLI about 43–60), apex acutely pointed; ligula groove shallow, running entire structure length.

Male reproductive system (Fig. 95B) with long, thin, strongly convoluted proximal vas deferens; spermatophoral gland long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Terminal portion of accessory gland expanded, with incomplete volution differentiated from accessory gland by weak constriction. Spermatophore sac long, saccular, thin walled, containing up to 4 short spermatophores to 39 mm length; spermatophore sac with small anterior appendix. Distal vas deferens short, thick; 2 penis diverticula: primary large, about 50% penis length, secondary small, appendicular, positioned between primary diverticulum and penis; penis large, genital aperture subterminal. Mature female (Fig. 95C) with large ovary sac, about 67% ML in greatest dimension; proximal oviducts depart ovary sac through common antrum, ducts narrow, length about 50% distal duct length; oviducal gland large, with two obvious hemispheres, basal cream coloured, distal khaki coloured; both hemispheres with faint radial striations. Distal oviducts appreciably swollen, bent into pronounced U-shape; genital aperture terminal, porelike, not secondarily modified. Mature eggs numerous, tear-drop shaped, small, to 3.1 x 1 mm, each with short stalk; longitudinal striations not apparent in preserved material.

Alimentary canal (Figs 95D, E) with large buccal bulb, about 29% ML; anterior salivary glands large, ovoid; anterior oesophagus long, narrow, enters crop dorsally; crop well developed, with extensive anterior diverticulum about 40% crop length. Posterior salivary glands broadly triangular, large, length about 87% buccal bulb greatest dimension, about 26% ML. Posterior oesophagus muscular, thick walled. Stomach large, with small, thin-walled basal, thick-walled central, and large thin-walled distal sections; stomach with undivided lumen. Spiral caecum larger than stomach, with single volution and faint radial striations. Intestine long, about twice oesophagus and crop length, thin walled, dilated for central half, constricted either side in proximal and distal quarters; anal flaps paired, small. Digestive gland large, broadly triangular; anterior peaks prominent; pancreas poorly developed; ink sac large, broad (about 57% digestive gland in length), superficially embedded in surface of digestive gland; ink duct short, opening into base of anus.

Upper beak (Fig. 95F) tall (height 107.6% length); hood and lateral walls dark brown, margins translucent; hood moderately deep (depth 35.5% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip pointed, slightly

deflected down; jaw with single broad, low profile tooth. Lateral walls straight sided; crest squared, lateral wall fold weak. Lower beak (Fig. 95F) moderately tall (height 73.2% width); hood, lateral wall and wings dark brown, lateral wing and wall margins translucent. Lateral wall with deep V-shaped basal notch and keeled crest. Hood deep (depth 38.6% beak length), with bifid rostrum; hood without posterior notch; lateral wings long (length 100% beak length); lateral wings with single strong fold.

Radula (Fig. 95G) with rachidian tooth taller than broad, 2 large asymmetric lateral cusps beside central cusp; 1st lateral well developed, with 2 cusps, inner heel with short basal cusp, outer cusp largest, comparatively slender; 2nd lateral wider than rachidian, with long, slender base, pronounced uncusped inner heel and large, robust secondary cusp; marginal teeth tall, well developed, with cusp of comparable size to that on 2nd lateral; marginal plates poorly developed rectangular blocks. Radula with repeat seriation every 3 or 4 transverse rows.

Indices, formulas, and counts for live-fixed male in Table 70, live/narcotised-fixed female in Table 71, and male hectocotylised arm in Table 72. Raw measures for male and female in Tables 73 (p. 157) and Table 74 (p. 158).

REMARKS: Much morphological variation apparent in this species can be attributed to the animal's small size, which lends itself to dropping live, narcotised, or dead animals into whatever convenient, various-sized containers and preservatives are available in the field. Nevertheless, the species varies appreciably in absolute size, with relatively gigantic specimens occurring in Fiordland, sporadically off the southern North Island and throughout the South Island, whilst fully mature 'midget' specimens are common elsewhere; currently only 'midget' specimens are known from South Australia. Absolute size no doubt is influenced by environmental factors, and large-bodied specimens are assumed to be ecotypic variants.

The specimen illustrated by Dell (1952: pl. 9) from Ewing Island, Auckland Islands, is unique, its identity not known. Although this specimen is not further described it is not referable to *Octopus huttoni* (Benham), and is removed from that synonymy.

Octopus huttoni is similar in gross morphology to *O. gibbsi* sp. nov., both species having partly overlapping distributions off the northeast coast of North Island. Males of both species can be distinguished, however, on the basis of hectocotylus detail and penis shape (Fig. 95B), while females differ markedly in the relative positions of both genital apertures and oviducts to the interpallial septum (Fig. 95C).

Octopus huttoni differs from the South Australian *O. berrima* most obviously in relative ligula size, considerably longer in *O. berrima* than *O. huttoni*. The relationship between *Octopus huttoni* and other recently described species from Australian waters, *O. kaurna*, *O. bunorong* and *O. pallidus* is, however, less clear. *Octopus bunurong* has enlarged suckers on the dorsal arm pair, gradually decreasing to the ventral arm pair; *O. kaurna* has a peculiar hectocotyl that lacks the terminal secondary enlargement and elevation of arm suckers characteristic of *Octopus* Group 2, with suckers small on all arm pairs; *O. pallidus* has a most distinctive hectocotyl, similarly lacking secondary enlargement of distal arm suckers, and with the ligula hooked orally. All three species have a penis diverticulum oriented towards the interpallial septum. This latter character state does not alone separate *Octopus* Group 2 from *Octopus* (*s.str.*), and *Octopus* Group 1, with the penis diverticulum in the latter two groups oriented towards the interpallial septum; it is the combination of sucker enlargement on the lateral arm pairs, secondary hectocotylisation of the males third right arm, and penis diverticulum orientation relative to the interpallial septum that distinguish *Octopus* Group 2 from other octopus groups. *Octopus bunurong* could most easily be accommodated in *Pinnoctopus*, but the systematic status of *O. kaurna* and *O. pallidus* in this schema is less obvious.

Despite considerable variation in penis and penis diverticulum shape and orientation described for *Octopus hummelincki* Adam (Burgess 1966: fig. 22, p. 806), similar variation is not apparent in *O. huttoni*, although there is ontogenetic variation in penis and diverticulum size.

Octopus (*sensu lato*) Group 3

DIAGNOSIS: Hectocotylised arm with 4–10 compact terminal sucker pairs on thickened distal section of arm; suckers not appreciably elevated from arm surface. Hectocotylus proper with shovel and thumb arrangement; ligula with thick but not markedly inrolled sides; primary diverticulum long, oriented away from interpallial septum, extending over base of left gill; second penis diverticulum small, appendicular.

REMARKS: The characters unique to these small-bodied octopods were first discerned by Robson (1929), who recognised three species — *Octopus campbelli* Smith, 1902, an assortment of specimens attributed to *Octopus australis* Hoyle, 1885, and misidentified specimens attributed to *Octopus fontanianus* d'Orbigny, 1835; *O. fontanianus* Robson (not d'Orbigny) was then designated the type species of a new genus, *Joubinia* Robson,

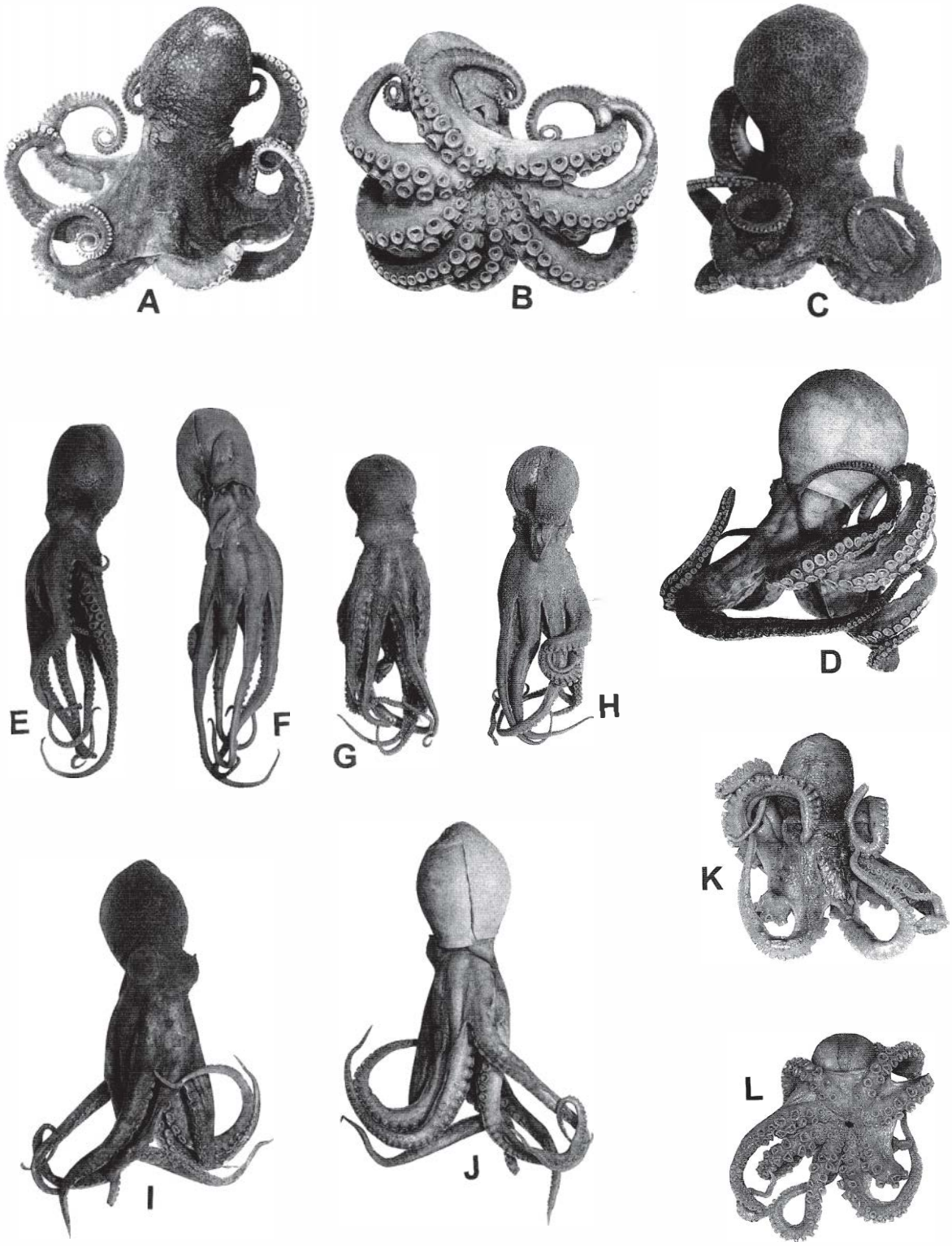


Figure 94. *Octopus huttoni* (Benham, 1943): **A, B**, NMNZ M.117689, male, ML 40 mm. **C, D**, NMNZ M.119908, female, ML 54 mm. **E–H**, NMNZ M.90283. **E, F**, female, ML 28 mm. **G, H**, male, ML 25.7 mm. **I, J**, NMNZ M.117688, female, ML 42 mm. **K, L**, AM C134083, male, ML 23.5 mm.

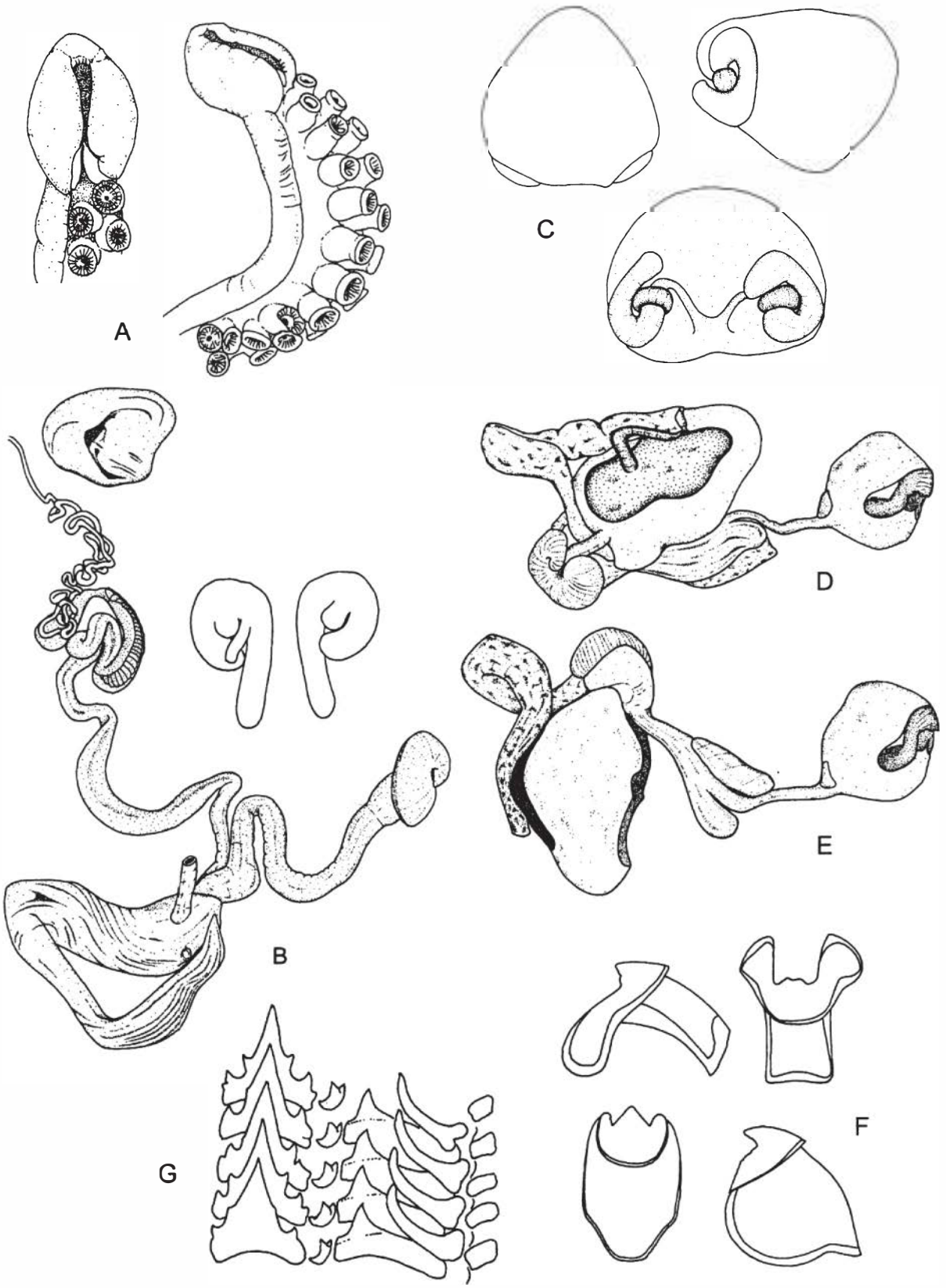


Figure 95. *Octopus huttoni* (Benham, 1943). Anatomy: **A**, NMNZ M.119909, male, ML 57 mm. **B, D–G**, NMNZ M.117688, male, ML 38.4 mm. **C**, NMNZ M.117688, female, ML 42 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D, E**, different views alimentary canal. **F**, beaks. **G**, radula.

Table 70. Indices, formulas, and counts for live-fixed male *Octopus huttoni* (Benham) (* denotes damage).

	NMNZ M.119909	NMNZ M.117692	NMNZ M.117689	NMNZ M.117687	NMNZ M.117691	NMNZ M.90314	NMNZ M.90314	NMNZ M.117698	NMNZ M.90314
MWI	79.8	77.2	76.9	82.4	84.1	71.1	78.3	66.7	85.2
HdLI	30.5	30.0	32.8	34.6	37.9	27.2	34.8	38.1	24.8
HdWI	55.8	64.4	65.9	62.5	68.5	66.5	65.7	67.6	71.4
EOI	4.7	4.7	5.1	5.3	11.1	4.6	3.9	6.7	5.2
ALI1–4	54.7–76.3	65.6	58.2–79.5	55.8–85.5	58.8–79.4	52.0–69.3	58.6–76.3	58.8–75.0	59.7–76.1
AFR	*	*	1.3.4.2	2.4.3.1	4.2.1.3	*	*	*	2.4.1.3
AFL	3.4.2.1	*	*	3.2.4.1	*	*	*	2=3=4.1	*
WDIA–E	17.8–21.1	13.6–22.7	17.2–25.8	16.1–25.4	12.0–22.2	19.2–30.8	22.4–27.6	19.6–27.5	25.5–27.5
WFR	D.C.E.B.A	C=D.A.B.E	C.D.B.A.E	C.B.A.D.E	C.D.B.A.E	D.C.B.A.E	B=C=D.A=E	C=D.B=E.A	A=B=C=D.E
WFL	B=C=D=E.A	D.B.C.A.E	C.D.B.A.E	D.C.A.B.E	C.D.B.A.E	D.C.B.A.E	C=D.B.A=E	D.C.B.E.A	A=C=D.B=E
ASC1–4	127–155	*	137–153	112–175	133–141	94–103	127	69–114	113–120
ASIn1–4	13.9–14.0	11.6–12.1	12.8–13.3	15.1–16.0	11.1–13.1	12.6–14.2	11.7–13.0	6.7–8.1	13.3–14.3
FuLI	45.6	41.6	41.0	39.9	44.9	22.6	36.1	29.5	28.6
FFuI	21.9	16.5	23.3	23.9	22.9	9.6	17.4	14.3	21.4
PAI	42.2	53.5	47.9	46.8	44.6	49.0	50.0	38.1	50.0

Table 71. Indices, formulas, and counts for live-/narcotised fixed female *Octopus huttoni* (Benham) (* denotes damage).

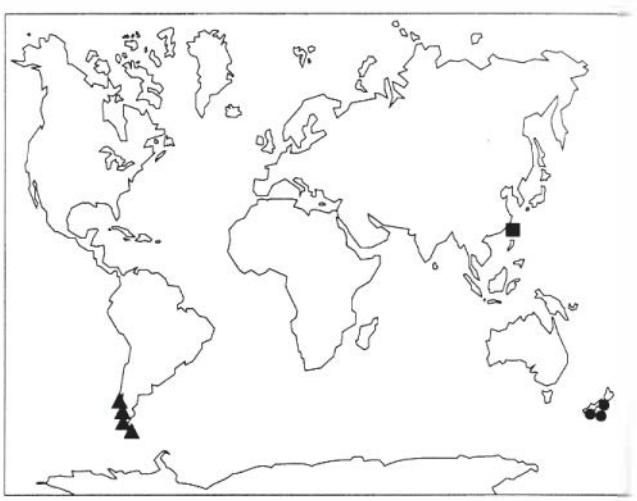
	NMNZ M.119908	NMNZ M.117688	NMNZ M.90362	NMNZ M.90355	NZOI Stn B686	NMNZ M.5614	NMNZ M.90305	NMNZ M.90344	NZOI Stn B686
MWI	88.9	69.0	67.2	75.5	87.8	86.1	82.9	89.4	80.0
HdLI	27.8	31.0	25.5	32.3	30.5	32.5	30.0	33.3	32.7
HdWI	58.3	53.1	44.4	61.0	59.2	64.9	69.3	72.2	66.7
EOI	4.1	4.8	8.3	8.9	7.6	10.8	7.5	3.9	6.7
ALI1–4	64.7–81.4	59.5–76.1	55.9–74.8	57.3–70.0	67.1–78.9	75.5–87.2	66.7–74.1	60.7–75.4	68.3–78.0
AFR	*	3.2.4.1	*	*	2.3.4.1	3.2.4.1	3.4.2.1	2.3.4.1	3.4.2.1
AFL	*	*	*	3.2=4.1	3.2.4.1	4.3.1=2	*	*	2=3=4.1
WDIA–E	18.1–23.5	17.7–23.4	15.8–27.4	20.8–32.5	23.3–28.3	9.8–23.2	18.3–25.0	19.6–28.3	20.3–28.1
WFR	C.B.D.A.E	D.E.C.A.B	A.D.B=C.E	C.D.B.E.A	D.A=B.C=E	C.A=B=D.E	D.C.B.E.A	C=D.B=E.A	C.A=B=D.E
WFL	C.A.E.B.D	D=E.B.C.A	C.B=D.A.E	C.B=D.E.A	C.D.A=B.E	A=C.D.B.E	C.D.A=E.B	D.C.B=E.A	B.A.C.D.E
ASC1–4	155–166	115–169	125–128	119–128	116–133	122–138	107–113	108–117	98–105
ASIn1–4	9.6–10.9	8.3–9.8	7.8–8.6	10.6	8.4–10.7	10.8–11.7	9.5–10.1	11.1–11.7	8.7–10.0
FuLI	42.7	40.5	25.8	45.0	38.2	48.5	52.8	55.6	30.7
FFuI	20.2	21.9	14.2	28.0	23.3	11.7	32.2	28.9	20.0
PAI	46.3	41.0	29.3	36.2	51.5	50.6	54.8	50.6	53.3

Table 72. Indices and counts of hectocotylised arm for male *Octopus huttoni* (Benham) (* denotes damage).

	NMNZ M.119909	NMNZ M.117692	NMNZ M.117689	NMNZ M.117687	NMNZ M.117691	NMNZ M.90314	NMNZ M.90314	NMNZ M.117698	NMNZ M.90314
OAI	71.7	*	73.3	66.1	*	89.1	*	78.4	80.0
ASC3R	67	71	70	74	71	55	64	69	66
CaLI	50.0	50.0	60.0	42.9	54.7	45.0	50.0	50.0	56.3
LLI	7.8	5.9	7.6	9.0	8.0	9.8	9.0	7.5	8.0

Table 73. Raw measures for male *Octopus huttoni* (Benham) (* denotes damage).

	NMNZ M.119909	NMNZ M.117692	NMNZ M.117689	NMNZ M.117687	NMNZ M.117691	NMNZ M.90314	NMNZ M.90314	NMNZ M.117698	NMNZ M.90314
TL	236	154	146	138	136	75	76	68	67
ML	57.0	43.0	39.0	37.6	31.4	23.9	23.0	21.0	21.0
MW	45.5	33.2	30.0	31.0	26.4	17.0	18.0	14.0	17.9
HdL	17.4	12.9	12.8	13.0	11.9	6.5	8.0	8.0	5.2
HdW	31.5	27.7	25.7	23.5	21.5	15.9	15.1	14.2	15.0
EO	2.7	2.0	2.0	2.0	3.5	1.1	0.9	1.4	1.1
AL1R/L	148*/172	52*/108*	47*/103	77/100	95/68*	21*/13*	18*/32*	42/47	44/47
AL2R/L	160*/173	106*/113*	108/114	110/112	100/62*	20*/52	41*/58	50/51	51/37*
AL3R/L	129/180	101/132*	85/116	78/118	80/84*	41/46	44.5/26*	40/51	40/50
AL4R/L	170/174	121*/120*	107/100*	100/108	108*/37*	39/41	53/27*	41*/51	50/38*
WDA	32	22	22	26	18	12	13	10	14
WDBR/L	33/35	21/27	23/26	27/23	21/20	13/13	14/14	11/12	14/13
WDCR/L	37/35	28/26	27/30	30/26	24/23	15/15	14/16	14/13	14/14
WDDR/L	38/32	28/30	24/27	25/27	22/21	16/16	14/16	14/14	14/14
WDE	35	18	20	19	13	10	13	11	13
ASC1R	L152	*	L137	112	141	*	*	92	113
ASC2R	L155	*	153	175	133	L103	L127	114	120
ASC3R	67	71	70	74	71	55	64	69	66
ASC4R	127	*	148	166	*	94	127	L114	119
ASe1R	7.9	5.2	5.2	5.7	3.5	3.0	2.7	1.4	2.9
ASe2R	8.0	5.2	5.2	6.0	4.1	3.2	3.0	1.7	2.9
ASe3R	8.0	5.0	5.2	5.9	4.0	3.4	3.0	1.5	3.0
ASe4R	8.0	5.2	5.0	6.0	3.5	3.4	2.9	1.6	2.8
GiLC	7	7	7	7	7	7	7	7	7
FuL	26	17.9	16.0	15.0	14.1	5.4	8.3	6.2	6.0
FFL	12.5	7.1	9.1	9.0	7.2	2.3	4.0	3.0	4.5
PA	24.1	23.0	18.7	17.6	14.0	11.7	11.5	8.0	10.5
CaL	5.0	3.0	3.9	3.0	3.5	1.8	2.0	1.5	1.8
LL	10.0	6.0	6.5	7.0	6.4	4.0	4.0	3.0	3.2



1930. Unfortunately, the largest specimen d'Orbigny found and designated as lectotype of *O. fontanianus tanianus* was an immature female of another species of *Pinnoctopus* d'Orbigny. All reference to specimens of *O. fontanianus* d'Orbigny by and subsequent to Robson (1929) actually refer to an undescribed species hereafter referred to as *Octopus (s.l.)* sp. nov. (= *Octopus fontanianus* Robson, 1929, not d'Orbigny, 1835). The small female attributed to *Octopus fontanianus* var. *africanus* (Robson, 1929), is immature and related to *Octopus (s.s.) vulgaris*, not to the Type 3 *Octopus* group. Given *Joubinia* Robson was preoccupied by *Joubinia* Berger, *Joubinia* Robson and *Robsonella* Adam, 1938 (the replacement name for the preoccupied *Joubinia* Robson) are synonyms of *Pinnoctopus* d'Orbigny. No existing genus is therefore available to characterise this novel *Octopus (s.l.)* Type 3 morphology.

Figure 96 (opposite). Recognised distribution of ***Octopus (s.l.)*** Group 3 ▲ *O.* sp. nov. (= *O. fontanianus* Robson *et al.*, not d'Orbigny); ● *O. campbelli* (Smith, 1902); ■ *O.*cf. *oshimae* Sasaki, 1929.

Table 74. Raw measures for female *Octopus huttoni* (Benham) (* denotes damage).

	NMNZ M.119908	NMNZ M.117688	NMNZ M.90362	NMNZ M.90355	NZOI Stn B686	NMNZ M.5614	NMNZ M.90305	NMNZ M.90344	NZOI Stn B686
TL	204	163	127	110	76	94	81	61	41
ML	54.0	42.0	37.2	28.2	26.2	23.1	19.9	18.0	15.0
MW	48.0	29.0	25.0	21.3	23.0	19.9	16.5	16.1	12.0
HdL	15.0	13.0	9.5	9.1	8.0	7.5	6.0	6.0	4.9
HdW	31.5	22.3	16.5	17.2	15.5	15.0	13.8	13.0	10.0
EO	2.2	2.0	3.1	2.5	2.0	2.5	1.5	0.7	1.0
AL1R/L	122*/119*	97/72*	61*/41	63/63	51/53	71/71	54/26*	39/22*	28/28
AL2R/L	125*/151	116/70*	81/71	72/72	58/57	80/71	57/48*	46/43	30/30
AL3R/L	166/163	120/124	82*/55*	51*/77	57/60	82/80	60/60	44/43	32/30
AL4R/L	154/132	108/107	95/86	76/72	55/55	78/81	59/57	40/37	31/30
WDA	34	23	23	16	15	18	11	9	8.5
WDBR/L	37/32	22/26	18/24	21/20	15/15	18/16	13/11	10/10	8.5/9
WDCR/L	39/37	27/25	15/26	25/23	14/17	19/18	14/14	13/12	9/8
WDDR/L	35/30	29/28	20/24	24/20	17/16	18/17	15/13	13/13	8.5/7
WDE	33	28	18	19	14	8	12	10	6.5
ASC1R	*	115	*	119	L116	138	107	108	98
ASC2R	L162	150	125	126	L124	132	111	117	102
ASC3R	166	168	*	L128	133	130	113	115	103
ASC4R	155	169	128	127	129	122	111	113	105
ASe1R	5.2	3.9	3.1	3.0	2.5	2.5	1.9	2.0	1.3
ASe2R	5.6	4.0	2.9	3.0	2.8	2.7	2.0	2.0	1.3
ASe3R	5.9	4.1	3.2	3.0	2.5	2.6	2.0	2.1	1.5
ASe4R	5.4	3.5	3.0	3.0	2.2	2.6	1.9	2.0	1.4
GiLC	7	7	7	7	7	7	7	7	7
FuL	23.1	17.0	9.6	12.7	10.0	11.2	10.5	10.0	4.6
FFL	10.9	9.2	5.3	7.9	6.1	2.7	6.4	5.2	3.0
PA	25.0	17.2	10.9	10.2	13.5	11.7	10.9	9.1	8.0

Octopus rapanui Voss, 1979, described with two penis diverticula, differs from New Zealand species in radula dentition, higher gill lamellae count, and lower beak rostrum detail. It is yet uncertain whether *Octopus rapanui* is referable to the *Octopus (s.l.)* Type 3 group.

Octopus campbelli (Smith, 1902)

(Figs 99, 100)
(Tables 75–79)

Polypus campbelli Smith, 1902: 201, pl. 24, figs 7–11; Hoyle 1909: 259; Suter 1913: 1063; 1915: pl. 69, fig. 3; Powell 1937: 94.

Joubinia campbelli: Robson 1929: 190–191, figs 73, 74.

Robsonella campbelli: Adam 1938: 223.

Robsonella australis (not Hoyle, 1885): Benham 1942, 228–229, pl. 18, figs 1–2; Dell 1952 (*partim, fide* Benham 1942, Type *O. campbelli* Smith): 32; Powell 1957 (*partim, fide* Benham): 125; 1962 (*partim, fide* Benham): 125; 1976 (*partim, fide* Benham): 133; 1979 (*partim, fide* Benham): 444.

Octopus campbelli: Powell 1946: 100; Stranks & Norman 1992: 361–370, figs 12–14.

MATERIAL EXAMINED (30 specimens, 13 male, 16 female, 2 sex indet.). Holotype: BMNH 1902.5.16.2, M, ML 27.0 mm, Campbell Island, *c.* 52°30' S, 169°00' E, r.v. *Southern Cross*.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.67827, M, ML 33.0 mm, F, ML 24.0 mm, 44°38' S, 172°38' E, 365 m, 17/11/1976; NMNZ M.67834, 2M, ML 30.0, 29.5 mm, F, ML 16.0 mm, 44°38' S, 172°38' E, 365 m, 17/11/1976; NMNZ M.90327, M, ML 11.7 mm, 3F, ML 18.9, 14.0, 11.0 mm, BS 202, 45°44' S, 171°02' E, 137 m, m.v. *Alert*, 23/01/1957; NMNZ M.8961, M, ML 32.0 mm, 3F, ML 32.0, 31.5, 30.0 mm, 45°47' S, 171°07' E, 500–600 m, 16/08/1955; NMNZ M.8960, 2M, ML 32.0, 21.0 mm, 3F, ML 23.0, 17.5, 16.0 mm, 2 sex indet., ML 12.0, 11.5 mm, 45°47' S, 171°07' E, 500–600 m, 16/08/1955; NZOI Stn B197, F, ML 11.5 mm, 46°14.1–13.5' S, 170°32–32.5' E, depNR, 18/10/1959; NZOI Stn F97, 2M, ML 17.2, 15.5 mm, 48°00' S, 168°32' E, 134 m, 17/01/1965; NZOI Stn I671, M, ML 19.0 mm, F, ML 13.9 mm, 48°00.0–01.5' S, 180°00.0–179°58.5' W, 280 m, 13/03/1979; NZOI Stn D139, M, ML 21.5 mm, 48°20.50' S, 167°46.50' E, 141 m, 13/01/1964; NMNZ M.118290, 3F, ML 26.5, 28.0, 18.0 mm, 50°40' S, 167°06' E, 367–410 m, -/03/1994, f.v. *Peterson*; AIM 75675, M, ML 36.0 mm, 52°33' S, 169°09' E, 43 m, 04/01/1952.

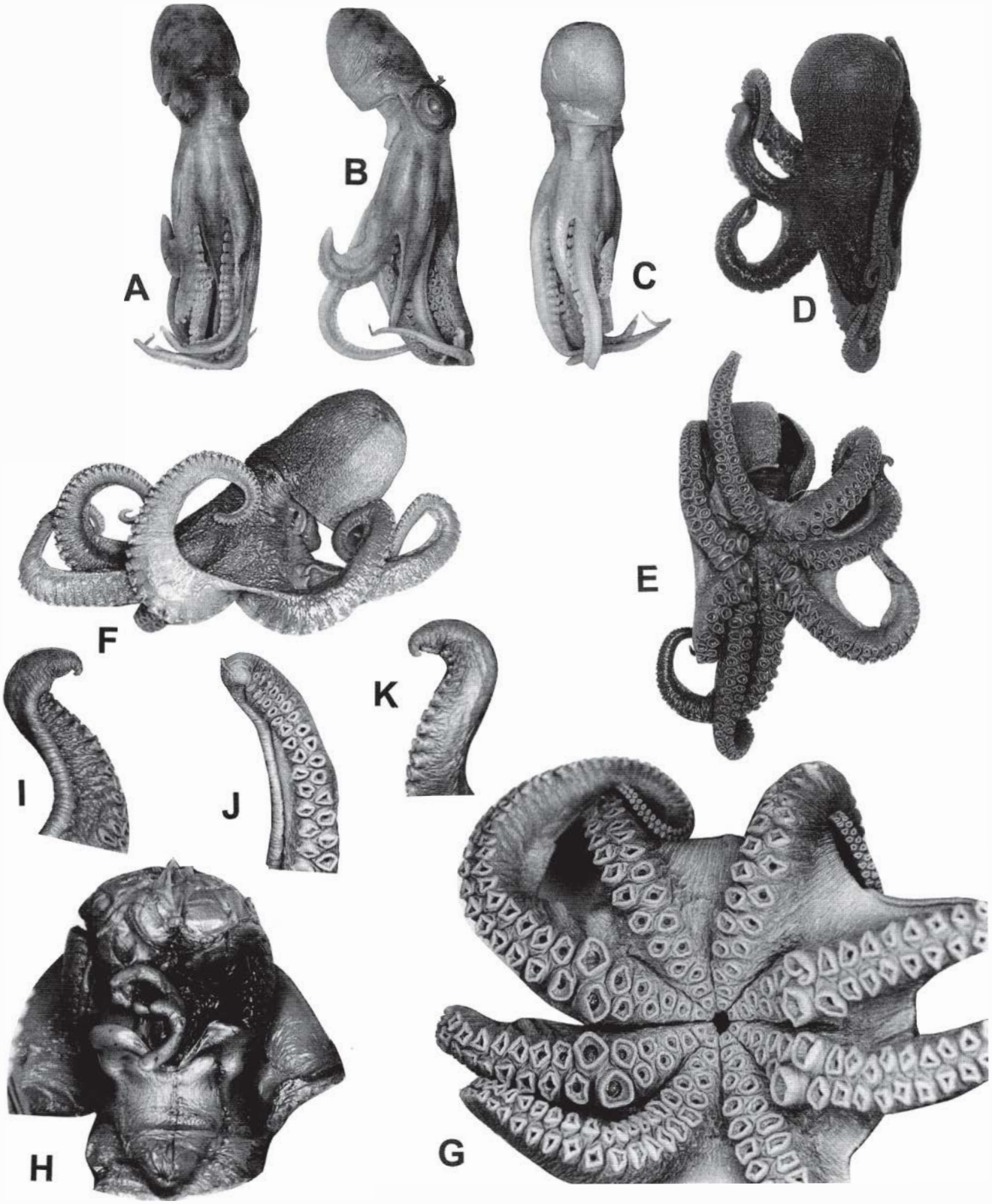


Figure 97. ***Octopus (s.l.)*** spp: **A–C**, *Octopus* cf. *oshimae* Sasaki, male, ML 29 mm. **D–K**, *Octopus* sp. nov. (= *O. fontanianus* Robson *et al*., not d'Orbigny): **D–F**, dorsal, oral and lateral perspectives, USNM 731397, male, ML 31.5 mm. **G**, oral view web and enlarged lateral arm suckers, USNM 731255, male, ML 27.5 mm. **H**, USNM 731397, male, ML 28.5 mm, mantle cavity. **I–K**, hectocotyl, USNM 731397, male, ML 31.5 mm.

REFERENCE MATERIAL: *Octopus* (*s.l.*) n. sp. A (= *Octopus fontanianus* Robson, 1929: 187–189, figs 71, 72, not d'Orbigny, 1835). BMNH 1848.6.16.2, F, ML 36.1 mm, Bay of Valparaiso, coll. Mr Bridges; BMNH 1899.8.31.84, F, ML 21.2 mm, coast of Chile, Leg. Dr Delfin; BMNH 1869.6.5.62, 65, 69, M, 14.1 mm, F, ML 21.2 mm, sex indet. 12.3 mm, Coquimbo Bay, coll. Dr Cunningham, pres. Lords of the Admiralty; BMNH 1869.6.5.63, F, ML 26.0 mm, Lota, Peru, col. Dr Cunningham, pres. Lords of the Admiralty 1868; BMNH 1851.1.24.5, M, ML 33.0 mm, Chile, Leg. Charles Darwin Esq; BMNH 1869.6.5.64, M, ML 22.1 mm, Halt-adura, coll. Dr Cunningham, pres. Lords of the Admiralty, -/03/1868; USNM 731255, M, ML 27.5, Chile, Valparaiso, 1 m, rotenone Stn (fig. 97G); USNM 731397, M, ML 31.5 mm, F, ML 24.5 mm (figs 97D–F, H–K); USNM 731251, M, ML 25.0 mm; USNM 731263, M, ML 47.0 mm, Chile, Talca-huano, 36°43'S, 73°07'W. *Octopus* (*s.l.*) cf. *oshimae* Sasaki, M, ML 29 mm, unregistered specimen, Taiwan, C.C. Lu collection (Figs 97A–C).

RECOGNISED DISTRIBUTION (Fig. 98, p. 148): New Zealand. Off east coast of South Island, Auckland, and Campbell Islands (44°38'S to 52°33'), depth range 43–600 m.

DIAGNOSIS: Small papillose-bodied octopus; super-ocular cirrus single, multiple branching; arms short; web shallow; normal suckers small in both sexes; 1 or 2 grossly, abruptly enlarged suckers present on lateral arm pairs of male; secondary modification of male arm 3R with up to 8 slightly enlarged sucker pairs; hectocotylised arm sucker count 56–71, non-hectocotylised arm sucker counts 124–164. Female with distal oviducts oriented parallel to interpallial septum, genital apertures opening on lateral inter-pallial musculature between 2 thick cheeks.

DESCRIPTION: Adult attaining small size (ML to 34 mm, TL to 135 mm), robust, muscular (Figs 99A–F). Mantle ovoid, broad (MW about 65–105% ML), dorsoventral compression, lateral keel or fold of skin, and ventral longitudinal groove or depression absent. Head well developed, large, wider than long, nar-rower than mantle (HdL about 31-40% ML; HW about 50–83% ML), separated from mantle by well-developed preocular constriction. Orbits large, bul-bous, dorsolaterally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsolaterally to laterally oriented. Funnel moderately long to very long (FuL about 16–51% ML), well developed, base entirely free of, or with slight membranous attach-ment to base of ventral arms 4. Nuchal constriction well developed.

Brachial crown robust, slightly wider than head. Arms thick, rectangular in section, short to long (AL about 48–83% TL), gradually tapering to not unduly delicate tips; arms of subequal length, without consistent disparity in relative length. Web shallow to deep (WDI about 12–28% longest arm length), developed along dorsolateral face of arms 1-4 about 50% arm length, extensively developed to arm tips down ventrolateral surfaces of arms 1–4; more extensive ventrolaterally than dorsolaterally; web formula variable, sector E usually shallowest, sectors B and C deepest, with no consistent disparity in relative sector depths. Suckers biserial, with 13–15 suckers between beaks and web margin on dorsal arm pair 1; distal arm-tip suckers not minute. Arm sucker counts moderate, ontogenetically variable, counts similar for comparable-sized male and female (ML 18–36 mm, ASC 124–164); suckers extend to arm tips. Normal suckers in both sexes small (ASIn 5.3–5.8), with 1 or 2 abruptly enlarged suckers on lateral arms of male (ASIe 9.6–21.3), most often being the 10th to 11th sucker that is enlarged (range 8–11). Normal and enlarged sucker morphology similar, suckers with well-developed, large suction chamber; moderately constricted sucker aperture; extensive, well-developed grasping ring with about 20 complete radial grooves; and moderately weak muscular suction pad (Figs 155I, J).

Specimens live, narcotised or postmortem fixed without lateral keel or fold of skin around mantle; dorsal surfaces of mantle, dorsal and dorsolateral surfaces of head, arms 1–3, and web sectors A–C densely and uniformly beset with simple, low-profile blister-like papillae without hardened apical structures; 3 secondarily enlarged papillae present on mantle, comprising a single preocular papilla on dorsolateral surface of mantle, and single enlarged papilla at anteromost dorsal surface of mantle, forming anterior mantle peak; an enlarged, almost foliose multiple-branching papilla present over either eye as super-ocular cirrus. Ventral surfaces of head, ventrolateral surface of arms 1–3, both dorso- and ventrolateral surfaces of arms 4, aboral surface of web sectors D and E and adoral web surfaces A–E smooth. Dorsal and dorsolateral surfaces of mantle and head, arms 1–3 and to a lesser extent arms 4, oral surface arms 1–3 outside web margin, and web sectors A–C, light brown to brick-orange, papillae darker orange; ventrolateral to ventral surfaces of mantle, funnel, head, ventrolateral surfaces of arms 1–4, oral surface of arms, suckers and web sectors D and E, light tan to pink.

Gills with 9 or 10 lamellae per outer demibranch; funnel organ (Fig. 100A) W-shaped, with thick inner and outer limbs of subequal length. Primary penis diverticulum long, oriented away from interpallial septum, extending over base of left gill; second diverticulum small, appendicular, positioned in U-shaped bend of primary diverticulum and penis. Female with distal oviducts oriented parallel to interpallial septum, genital apertures opening on lateral interpallial

musculature between two thick cheeks. Skin over visceral envelope and lateral muscles ensheathing and restraining digestive gland without chromatophores.

Terminal 6–8 sucker pairs on hectocotylised arm well spaced, slightly enlarged, slightly elevated from arm surface and disposed on thickened section of arm. Hectocotylised portion (Fig. 100B) of moderate length, from distal sucker to tip of calamus about 7–11% arm length, from the 8th enlarged sucker pair, 20–28% arm length; hectocotylised arm about 72–83% length opposite arm. Ligula large (LLI 10.6–15.9), with well-developed lateral walls, with shallow depression and 4–6 weak transverse rugae; calamus large (CaLI 35.3–69.0), fleshy, apex acutely pointed; calamus groove deep, running entire structure length.

Male reproductive system (Figs 100C, D) with moderately long, thin, weakly convoluted proximal vas deferens; spermatophoral gland long, with small swelling at junction with proximal vas deferens; spermatophore sac elongate, long; accessory gland long, with partial terminal volution; distal vas deferens short. Penis proper long, tubular, with subterminal genital aperture; primary penis diverticulum large, long, slender; second diverticulum small, appendicular. All available females immature; immature ovary sac small (Fig. 100E); proximal oviducts with common antrum; ducts short, narrow; oviducal glands small, with two hemispheres; distal oviducts about 3 times longer than proximal ducts, comparatively swollen; genital aperture terminal, bordered by 2 large, swollen cheeks. Eggs numerous, small, about 1.7 x 0.3 mm, each with small stalk. Alimentary canal (Fig. 100F) with large buccal bulb about 28% ML; anterior salivary glands of moderate size, length about 46% buccal bulb greatest dimension, rectangular, loosely applied to rear of buccal bulb. Anterior oesophagus long, about 50% total oesophagus and crop length, narrow; posterior salivary glands large, about 106% buccal bulb greatest dimension, about 29% ML, heart-shaped; crop with well-developed anterior diverticulum, about 33% total crop length; stomach with 3 internal sections: basal small, thin walled, central large, thick walled, distal large, thin walled; spiral caecum large, of equivalent size to stomach, with single loose coil, radially striate; intestine long, about twice oesophagus and crop length; anal flaps number 2. Digestive gland constricted laterally, with pronounced anterior peaks and depressions (imparted by stomach, crop and posterior salivary glands); with iridescent surface. Ink sac large, about 43% digestive gland length, narrow, superficially buried beneath iridescent surface of digestive gland; ink duct short. Gut contents identify a diet primarily consisting of small bivalves.

Upper beak (Fig. 100G) very tall (height 113.6% length); hood dark brown, lateral walls light brown, margins translucent; hood very deep (depth 45.9% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip pointed, slightly deflected down; jaw straight, without apparent teeth. Lateral walls straight sided; crest rounded, lateral wall fold weak; lateral wall margin with shallow sinus. Lower beak (Fig. 100G) moderately tall (height 74.0% width); hood dark brown, lateral wall and wings light brown, lateral wing and wall margins translucent. Lateral wall with deep V-shaped basal notch and keeled crest. Hood deep (depth 36.0% beak length), with bifid rostrum; hood without posterior notch; lateral wings short (length 86.0% beak length); lateral wings with single strong fold.

Radula (Fig. 100H) with well-developed rachidian with 1 or 2 asymmetric lateral cusps aside central cusp; 1st lateral with 2 cusps; 2nd lateral with single large cusp and long base; marginal teeth tall, well developed; marginal plates well developed. In one specimen both 1st and 2nd lateral teeth fused on one side of radula into a single abnormally large tooth.

REMARKS: Male sucker enlargement occurs on both left and right dorso- and ventrolateral arm pairs, affects 1 or 2 suckers per arm for a total not exceeding 5 per animal, and suckers are always successive, (numbers 8–9, 9–10 or 10–11 from the arm base). Both Smith (1902) and Robson (1929) described the holotype of *Octopus campbelli* Smith, as having enlargement of 7th sucker pair, although Smith's accompanying figure illustrates enlargement of suckers 10–11, i.e., the 5th pair. This error was evidently perpetuated by Robson (*loc. cit.*) without direct enumeration from the type specimen. The gross enlargement of these suckers in the male clearly distinguishes this species from all other small-bodied octopodids known from New Zealand waters. The otherwise small size of normal suckers in both sexes further serves to distinguish this species from other known small-bodied species.

Octopus (sensu lato) Group 4

DIAGNOSIS: Large-egged, deep-water species with mantle cavity lacking connective membranes between renal tissues and ventral inner surface of mantle. Penis and diverticulum massive, diverticulum oriented towards base of left gill, away from interpallial septum; third right arm of male hectocotylised, calamus and ligula well developed. Female with expanded distal oviducts; genital apertures opening proximal to anterior base of interpallial

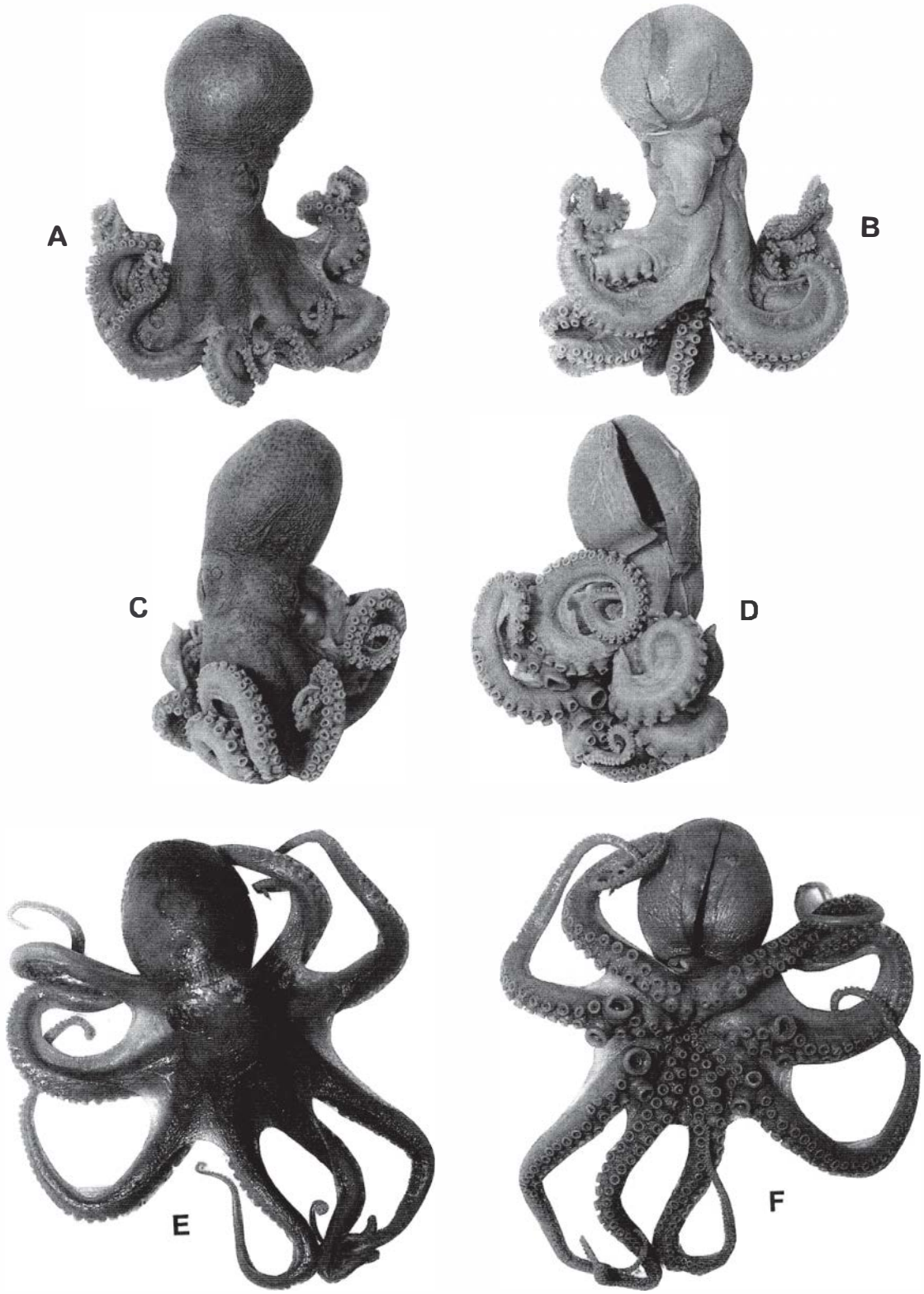


Figure 99. *Octopus campbelli* (Smith, 1902): **A–D**, NMNZ M.8961, **A, B, F**, ML 32 mm. **C–D**, male, ML 32 mm. **E–F**, AIM 75675, male, ML 36 mm.

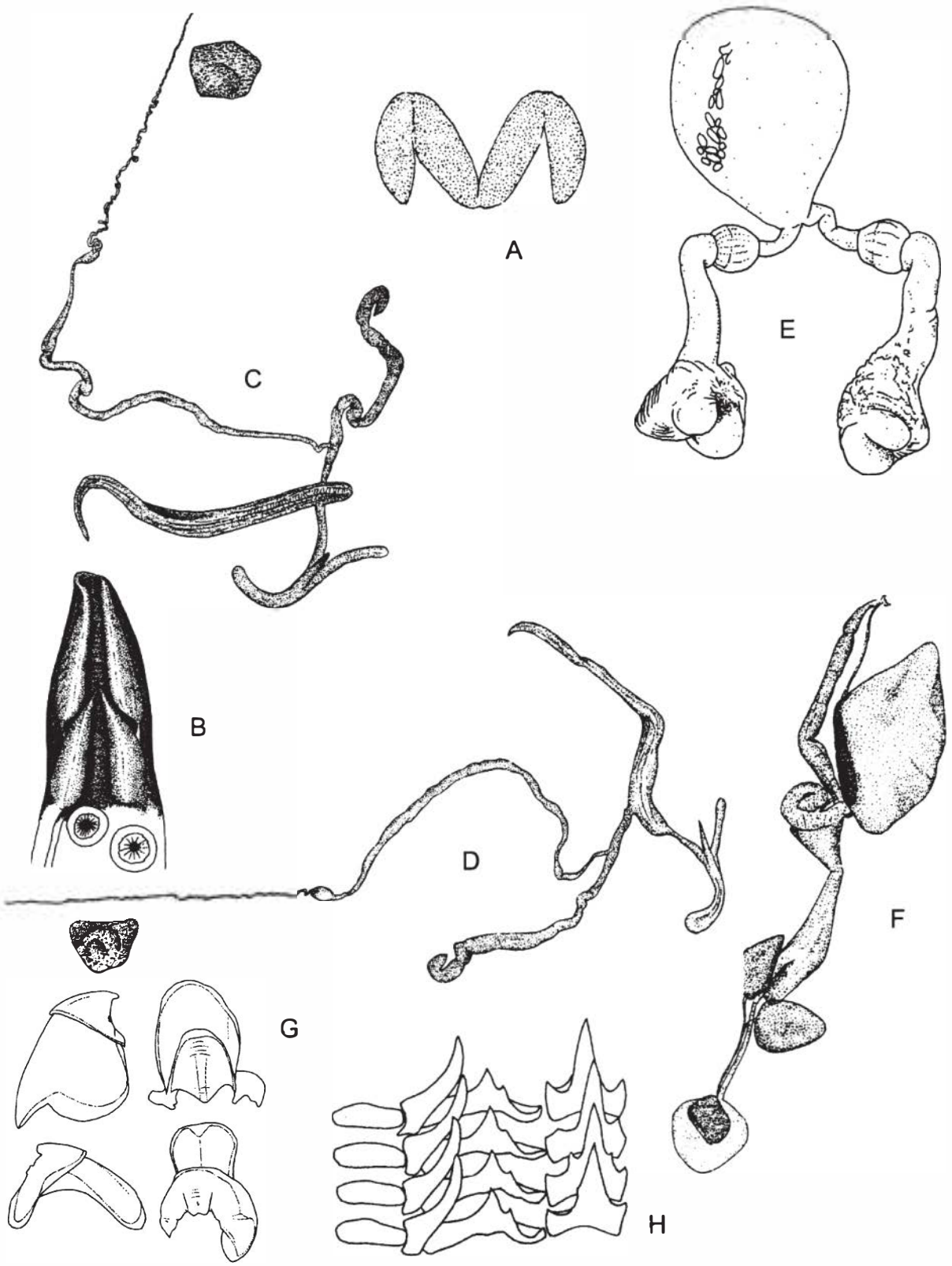


Figure 100. *Octopus campbelli* (Smith, 1902): **A–C**, NMNZ M.67834, male, ML 30 mm. **D, F–H**, NMNZ M.67827, male, ML 33 mm. **E**, NMNZ M.8961, female, ML 31 mm. **A**, funnel organ. **B**, hectocotyl. **C**, male reproductive system. **D**, male reproductive system. **E**, female reproductive system. **F**, alimentary canal. **G**, beaks. **H**, radula.

Table 75. Indices, formulas, and counts for live-fixed male *Octopus campbelli* (Smith) (* denotes damage).

	AIM 75675	NMNZ M.8960	NMNZ M.8961	NMNZ M.8960	NZOI Stn F97
MWI	69.4	65.2	67.7	81.8	104.7
HdLI	30.8	34.2	32.3	36.4	39.5
HdWI	52.8	51.0	54.8	61.4	82.6
EOI	3.9	7.2	12.9	9.1	5.8
ALI1–4	56.9–75.9	55.3–77.2	48.8–71.5	48.4–74.7	50.6–74.1
AFR	2.4.1.3	2=4.1.3	2.1.4.3	*	2.4.1.3
AFL	4.3.1.2	4.3.1=2	1=3.2.4	4.2.3.1	*
WDIA–E	13.5–22.1	18.9–25.3	18.2–28.4	20.6–25.0	18.3–23.3
WFR	C=D.B.A.E	C=D.E.B.A	A=C.D.B.E	B=C=D.A=E	A.E.B=C=D
WFL	C=D.A=B.E	C=E.D.B=A	C.D.B.A.E	C.D.B.A=E	A.E.C.B=D
ASC1–4	138–146	154–160	139–146	124–136	139–146
ASIn1–4	5.8–15.6	5.8–9.3	6.5–14.8	7.2–13.6	7.0–12.2
FuLI	36.1	43.5	48.4	39.1	59.3
FFuI	19.2	20.0	25.8	15.9	28.5
PAI	41.7	40.3	47.1	50.0	77.9

Table 76. Indices, formulas, and counts for live-fixed female *Octopus campbelli* (Smith) (* denotes damage).

	NMNZ M.8961	NMNZ M.8961	NMNZ M.8961	NMNZ M.90327	NMNZ M.8960	NMNZ M.8960
MWI	74.5	85.5	84.0	69.3	72.3	76.1
HdLI	31.7	32.3	36.3	34.4	30.7	35.0
HdWI	50.0	59.7	56.7	57.1	56.0	65.0
EOI	9.6	9.7	1.9	13.8	12.0	8.5
ALI1–4	64.6–75.4	70.2–80.7	61.9–72.0	61.3–73.8	55.0–66.7	69.4–83.3
AFR	4.3.2=1	*	1=2.4.3	3.2.4.1	2.3.4.1	*
AFL	1.2.3.4	1.2.3.4	1=3.4.2	2.1=3.4	2.1.4.3	*
WDIA–E	19.4–24.5	17.4–23.9	18.8–25.9	11.9–23.7	20.0–27.5	13.3–26.7
WFR	B.C=D.A=E	B.A=C.D.E	B=C.A=D.E	A.B=C.D.E	B=D.C.A.E	C=D=E.B.A
WFL	B=C.A=E.D	A.B.C=D.E	C.D.A.E.B	A.C=D.B.E	B.A=C=D.E	B.C=E.A.D
ASC1–4	157–160	128–159	148–164	124–133	93–109	80–92
ASIn1–4	5.9–6.5	6.16.5	6.3–6.7	7.9–9.0	6.0–6.6	7.7–8.5
FuLI	34.2	45.8	46.7	51.3	42.8	35.0
FFuI	7.8	20.3	17.0	35.4	18.7	25.6
PAI	46.6	48.4	51.7	42.3	49.4	52.1

Table 77. Indices and counts of hectocotylised arm, for male *Octopus campbelli* (Smith) (* denotes damage).

	AIM 75675	NMNZ M.8960	NMNZ M.8961	NMNZ M.8960	NZOI Stn F97
OAI	81.3	74.7	71.4	74.6	*
ASC3R	68	71	56	68	67
CaLI	50.0	61.2	46.2	69.0	35.3
LLI	8.5	7.2	10.8	6.6	8.3

Table 78. Raw measures for male *Octopus campbelli* (Smith) (* denotes damage).

	AIM 75675	NMNZ M.8960	NMNZ M.8961	NMNZ M.8960	NZOI Stn F97
TL	137	123	123	91	81
ML	36.0	34.5	31.0	22.0	17.2
MW	25.0	22.5	21.0	18.0	18.0
HdL	11.1	11.8	10.0	8.0	6.8
HdW	19.0	17.6	17.0	13.5	14.2
EO	1.4	2.5	4.0	2.0	1.0
AL1R/L	92/94	85/84	82/84	30*/58	53/51
AL2R/L	104/92	91/84	88/83	78*/60	60/57
AL3R/L	78/96	68/91	60/84	44/59	41/24*
AL4R/L	103/99	91/95	80/81	68/62	58/59
WDA	20	18	21	14	14
WDBR/L	21/20	19/18	19/22	15/15	12/11
WDCR/L	23/23	24/21	21/25	15/17	12/12
WDDR/L	23/23	24/20	20/23	15/16	12/11
WDE	14	21	16	14	13
ASC1R	143	154	139	L124	139
ASC2R	138	160	146	L132	146
ASC3R	68	71	56	68	67
ASC4R	146	155	145	136	146
ASe1R	2.1	2.0	2.0	1.6	1.4
ASe2R	L5.6	3.2	4.0	2.5	1.5
ASe3R	5.1	2.5	4.6	3.0	2.1
ASe4R	2.7	2.0	2.0	1.6	1.2
GiLC	9	9	9	9	9
FuL	13.0	15.0	15.0	8.6	10.2
FFL	6.9	6.9	8.0	3.5	4.9
PA	15.0	13.9	14.6	11.0	13.4
CaL	3.3	3.0	3.0	2.0	1.2
LL	6.6	4.9	6.5	2.9	3.4

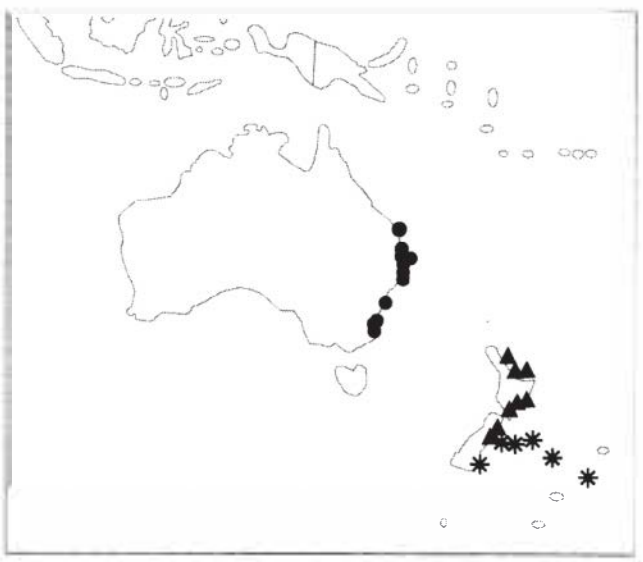


Figure 101. Recognised distribution of ***Octopus (s.l.)*** Group 4: ● *O. australis* (Hoyle) (distribution *fide* Stranks & Norman 1992); ▲ *O. kaharoa* sp. nov.; ✳ *O. mernoo* sp. nov.

septum, not extending over lateral interpallial musculature nor opening proximal to anus.

REMARKS: Group 4 octopodids may prove to be more closely related to species placed in the genera *Bathypolypus* and *Benthoctopus* than to species of *Octopus* (*s.s.*), *Octopus* (*s.l.*) Groups 1–3, or *Pinnoctopus*.

Octopus mernoo sp. nov. (Figs 103–105) (Tables 80–85)

TYPE MATERIAL (347 specimens, 74 male [M], 273 female [F]): Holotype: NZOI H-666, M, ML 33.5 mm, 43°51.19' S, 178°58.81' E, 480 m, 13/09/1989, NZOI Stn V374. Paratype: NZOI P-1120, M, ML 30.1 mm, 43°51.19' S, 178°58.81' E, 480 m, 13/09/1989, NZOI Stn V374.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.131729, M, ML 36.0 mm, 42°19.30' S, 174°00.20' E, 440 m, 04/07/1989, f.r.v. *James Cook* Stn JO5/17/89; NZOI Stn Z8529, 30M, ML 35.5–61.0 mm, 116F, ML 30.2–84.9 mm, 42°54–43°08' S, 176°26–177°05' E, 368–411m, 27/12/1994, f.v. *Peterson*; NMNZ M.118854, 34M, ML 30.0–57.0 mm, 107F, ML 25.6–

Table 79. Raw measures for female *Octopus campbelli* (Smith) (* denotes damage).

	NMNZ M.8961	NMNZ M.8961	NMNZ M.8961	NMNZ M.90327	NMNZ M.8960	NMNZ M.8960
TL	130	114	118	80	60	36
ML	32.2	31.0	30.0	18.9	16.6	11.7
MW	24.0	26.5	25.2	13.1	12.0	8.9
HdL	10.2	10.0	10.9	6.5	5.1	4.1
HdW	16.1	18.5	17.0	10.8	9.3	7.6
EO	3.1	3.0	3.0	2.6	2.0	1.0
AL1R/L	84/93	83/91	85/81	53/52	34/36	25/24
AL2R/L	84/89	74*/88	85/73	56/55	39/40	15*/12*
AL3R/L	94/86	92/86	76/81	59/52	38/33	26/27
AL4R/L	98/84	83/80	77/77	55/49	36/35	30/25
WDA	20	21	19	14	9	6
WDBR/L	24/21	22/20	20/16	13/10	11/19	6.5/8
WDCR/L	23/21	21/16	20/22	13/12	10/9	7/7
WDDR/L	23/19	20/16	19/21	12/12	11/9	7/4
WDE	20	17	18	7	8	7
ASC1R	158	128	158	124	93	90
ASC2R	155	152	164	133	106	*
ASC3R	160	159	164	129	109	92
ASC4R	157	159	*c.* 148	126	105	*c.* 80
ASe1R	2.0	1.9	2.0	1.5	1.1	0.9
ASe2R	2.0	2.0	2.0	1.7	1.1	1.0
ASe3R	2.1	2.0	2.0	1.6	1.0	1.0
ASe4R	1.9	1.9	1.9	1.5	1.0	1.0
GiLC	9	10	10	9	10	10
FuL	11.0	14.2	14.0	9.7	7.1	4.1
FFL	2.5	6.3	5.1	6.7	3.1	3.0
PA	15.0	15.0	15.5	8.0	8.2	6.1

85.0 mm, 42°54–43°08' S, 176°26–177°05' E, 368–411m, 27/12/1994, f.v. *Peterson*; NMNZ M.118991, 3M, ML 46.4–59.5 mm, 27F, ML 32.5–73.0 mm, 42°54–43°08' S, 176°26–177°05' E, 368–411m, 27/12/94, f.v. *Peterson*; NMNZ M.118333, M, ML 50.6 mm, 12F, ML 32.5–69.5 mm, 43°00' S, 176°47' E, Chatham Rise, 378–380 m, -/03/1994, f.v. *Peterson*; NMNZ M.118334, M, ML 54.0 mm, 9F, ML 33.0–79.0 mm, 43°00.0' S, 176°47' E, 378–380 m, -/03/1994, f.v. *Peterson*; NMNZ M.90170, M, ML 38.0 mm, 43°14.7' S, 174°41.6' E, 468–439 m, 27/08/1987, f.v. *Banchu Maru 8*; NMNZ M.90346, F, ML 18.0 mm, 44°35.5' S, 176°04' W, *c.* 550 m, 03/01/1954; NMNZ M.8946, M, ML 20.0 mm, F, ML 39.5 mm, BS 190, 45°45.4' S, 171°05' E, off east Otago coast, Canyon B, 550 m, m.v. *Alert*, 16/08/1955.

RECOGNISED DISTRIBUTION (Fig. 102, p.172): New Zealand, between latitudes 42°19.30–45°45.4' S, off the southern east coast of North Island to the east coast of South Island, Chatham Rise; 368–550 m.

DIAGNOSIS: Small-bodied, weakly papillose, subgelatinous species; gill lamellae number 8 per outer demibranch; hectocotylised arm sucker count very low, ASC 41–48, non-hectocotylised arm sucker counts very low for species with 2 sucker rows, ASC 78–125; sucker type characterised by extremely weak musculature, particularly poorly developed suction pad; female attains larger size than male; sex ratio skewed towards female.

DESCRIPTION: Adult animal of small size (ML to 84.9 mm, TL to 260.0 mm); body slender to stocky (Figs 103A–E, 104); live-fixed specimens with extensive subgelatinous deposits; subgelatinous deposits not apparent in post-thaw-fixed specimens. Male and female of dissimilar gross morphology; female attaining greater size (to 84.9 mm ML; male to 61.0 mm ML), with a stocky body; male body slender. Mantle ovoid (MW about 45–75% ML), dorsoventral compression absent; lateral keel or fold of skin apparent in live-fixed specimens only. Head small to large (HdL about 20–40% ML; HW about 30–55% ML), narrower than mantle; in male separated from mantle by well-developed preocular constriction, in female by poor constriction. Orbits large, bulbous, not meeting across dorsal midline of head; eye apertures dorsolaterally oriented. Funnel long (FuL about 30–48% ML), well developed, with funnel base entirely free of brachial crown. Nuchal constriction moderately well developed.

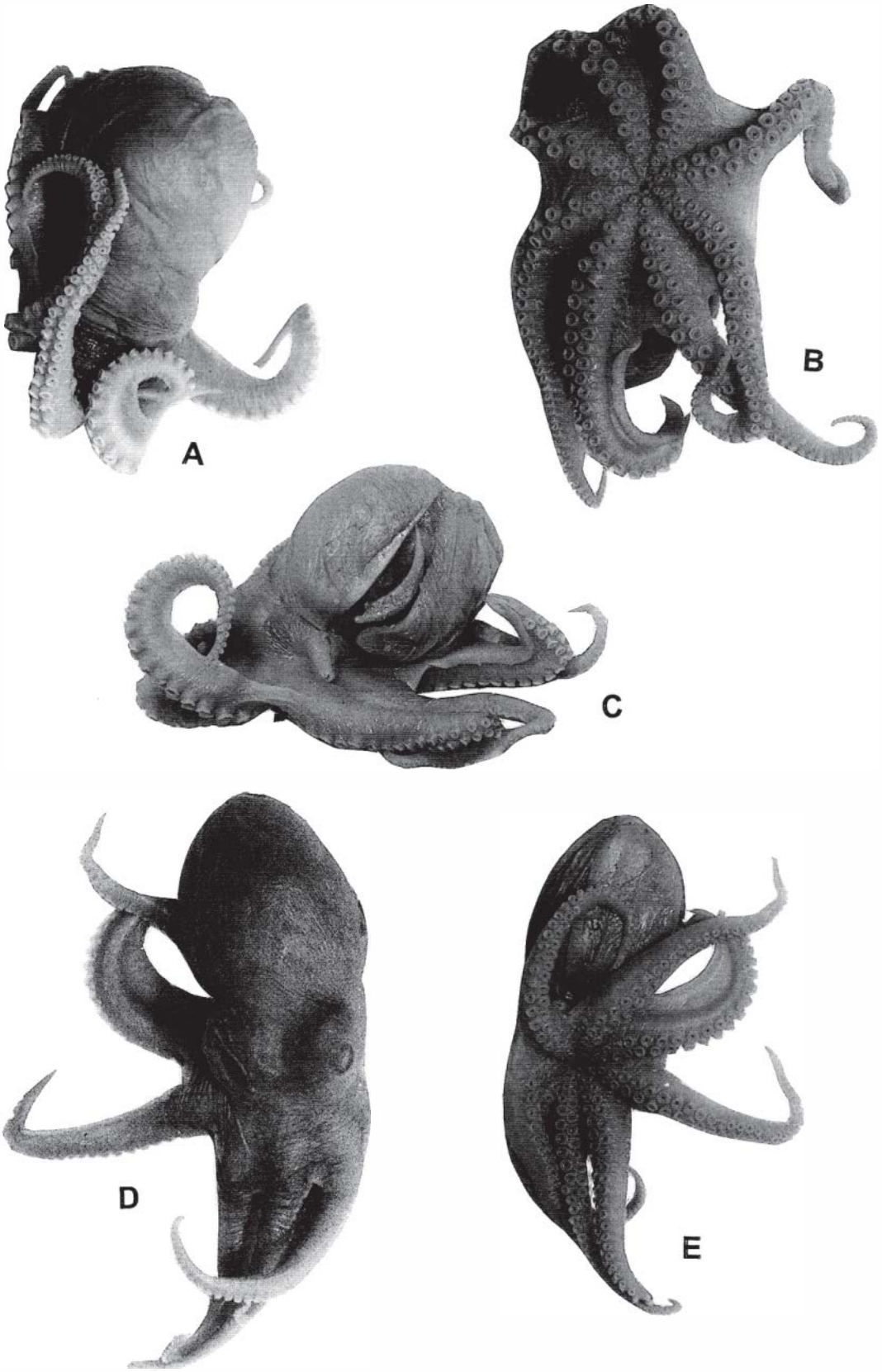


Figure 103. *Octopus mernoo* sp. nov.: **A–E**, NZOI Stn V374. **A–C**, holotype H-666, male, ML 33.5 mm. **D–E**, paratype P-1120, male, ML 30.1 mm.

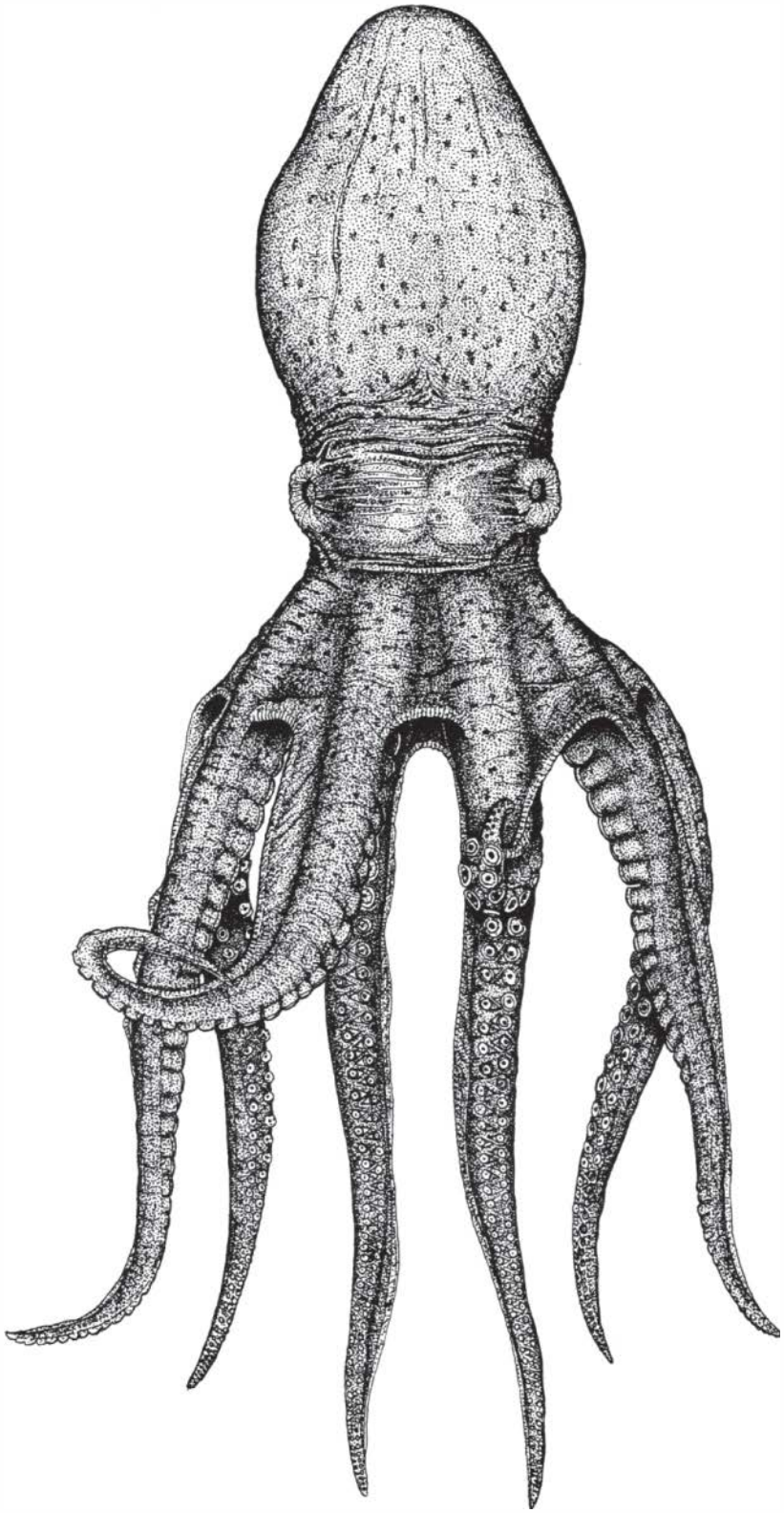


Figure 104. *Octopus mernoo* sp. nov.: NMNZ M.8946, female, ML 39.5 mm.

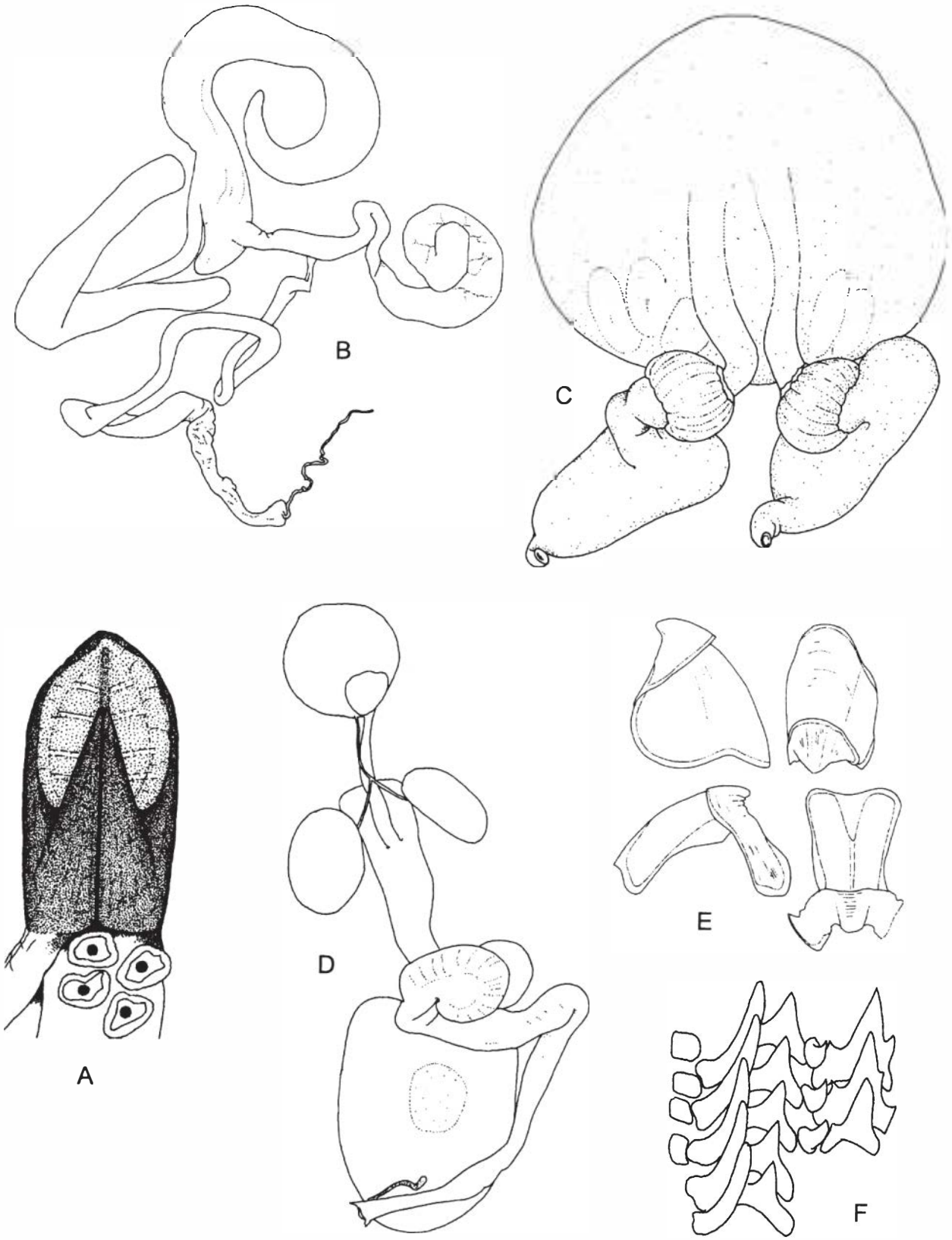


Figure 105. *Octopus mernoo* sp. nov. Anatomy: **A**, NMNZ M.8946, male, ML 21 mm. **B, D–F**, NZOI Stn Z8529, male, ML 50 mm. **C,** NZOI Stn Z8529, female, ML 80 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. E, beaks. **F**, radula.

Table 80. Indices, formulas, and counts for post-thaw-fixed male *Octopus mernoo* sp. nov.

	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529
MWI	63.1	50.7	66.0	69.4	59.6	74.8
HdLI	27.9	34.7	30.5	29.2	37.0	33.3
HdWI	41.4	30.7	55.5	50.3	42.4	51.4
EOI	7.5	8.5	13.2	8.9	11.6	7.8
ALI1–4	39.3–62.5	38.8–62.1	45.6–62.4	44.4–68.4	43.6–59.8	43.8–68.6
AFR	*	*	1.2.4.3	4.2.1.3	1.4.2.3	4.1.3.2
AFL	*	2.3.1.4	2.1.3.4	2.1.4.3	*	1.2.3.4
WDIA–E	15.2–21.0	16.7–25.0	17.9–25.6	16.2–23.8	15.7–22.9	13.9–23.6
WFR	C.B.D.A.E	B.A.C=D=E	B.C.D.A.E	D.C.B.E.A	D.A=B.C.E	C=D.B.A.E
WFL	C.B=A=D.E	A.B=C.D=E	C.D.A=B.E	D.C.E.B.A	D.A=B.C.E	A=B=C.D.E
ASC1–4	103–105	87–98	86–89	78–96	84–94	87–92
ASIn1–4	4.9–5.6	3.7–4.8	4.9–5.1	5.6	5.6	6.2
FuLI	30.1	32.0	43.1	41.7	42.4	47.7
FFuI	22.8	18.9	13.5	22.2	24.0	15.6

Brachial crown robust, wider than head. Arms slender, very short to short (female about 55–70% TL; male about 40–70% TL), gradually tapering to filiform tips; arms of subequal length, arm pairs 1 and 2 frequently longest, 3 and 4 shortest, with no consistent disparity in relative arm lengths. Web shallow to deep, about 10–30% longest arm length, with poorly developed membranous extension along basal half of each arm; web formula variable, sectors A–E usually subequal, with no consistent disparity in relative sector depths. Suckers biserial; non-hectocotylised arm tips of males not secondarily modified in any discernible way. Arm sucker counts low, greater in mature females than males, female ASC 88–125, male 78–105; suckers extend to arm tips. Suckers small, ASIn 3.7–7.7, not enlarged in male; distal 5–10 suckers minute; suckers with: large suction chamber; well-developed sucker aperture constriction; moderately well developed grasping ring with about 20 faint radial grooves; and poor development of muscular suction pad (Fig. 155O).

Male third right arm hectocotylised, shorter than opposite member (OAI 63.4–95.1). Arm sucker count 41–48; no suckers demonstrably enlarged though distal 4–6 suckers proximal to calamus slightly enlarged relative to adjacent sucker pairs. Spermatophoral groove well developed, continued over oral surface of web sector D, with conspicuously thickened, transversely ridged web margin. Hectocotylised portion large (Fig. 105A), ligula about 11–18% arm length, with shallow excavation, poorly marked lateral cheeks, and apparent absence of transverse rugae; calamus very large, about 55–80.0% ligula length, with thick cheeks and central groove running entire calamus length to acute-pointed tip.

Indices, formulas, and counts for post-thaw-fixed male and female in Tables 80 and 82, for live-fixed male in Table 81, and for male hectocotylised arm details in Table 83.

Specimens fixed live or narcotised possess a moderately well-developed lateral keel or fold of skin around mantle; low-profile papillae are distributed over dorsal surfaces of mantle, head, dorsal and dorsolateral surfaces of arms 1 and 2, dorsolateral surface of arms 3, and aboral surfaces of web sectors A–C; ventral surfaces of mantle, head, ventrolateral surface of arms 3, both dorso- and ventrolateral surfaces of arms 4, aboral surface of web sectors D and E, and adoral web surfaces A–E smooth. Papillae densest over head, pre- and postocular regions of mantle and brachial crown, outer surfaces of arms 1 and 2 and web sectors A and B; individual papillae of low profile, dome-shaped, with single flat-topped central prominence; enlarged ocular cirri not apparent. Specimens fixed post-thaw comparatively smooth bodied, papillae not raised. Live-fixed specimens with dorsal surfaces of mantle, funnel, dorsal and ventral surfaces of arms 1–3, dorsolateral surface arms 4, oral surface arms 1–3, and web sectors A–D red to orange-brown; papillae lighter orange (live fixed) to darker orange (post-thaw fixed); dorsolateral to ventral surfaces of mantle (below lateral keel) iridescent-pinkish to blue; ventrolateral surfaces of arms 4 and web sector E, light brown; dorsal and lateral surfaces of orbits with purple to bluish tinge. Specimens fixed post-thaw pinkish-red with irregular scribbling of purple over dorsal surfaces of mantle, head, brachial crown, arms 1–3, and web sectors A–D; traces of papillae orange; ventral surfaces of mantle, head, funnel, arms 4, web

Table 81. Indices, formulas, and counts for live-fixed male *Octopus mernoo* sp. nov.

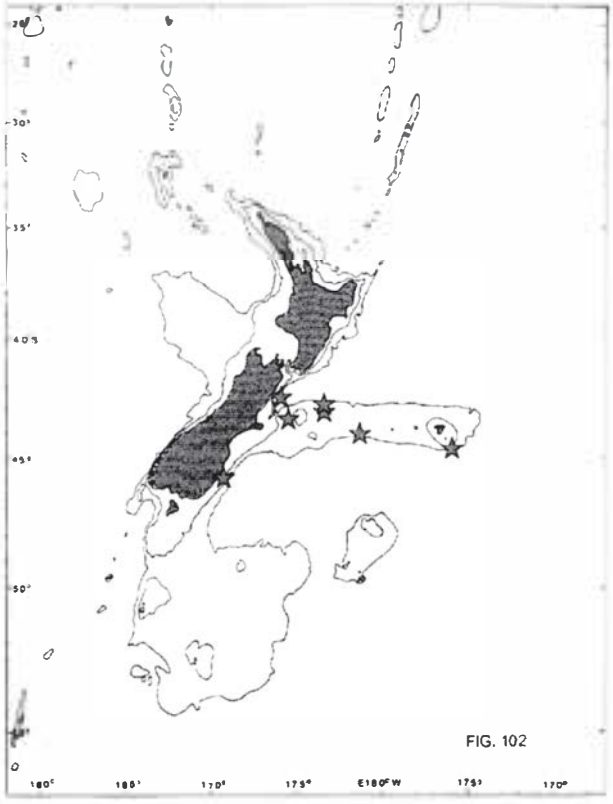
	NZOI Stn V374	NZOI Stn V374	NMNZ M.8960	NMNZ M.8946
MWI	80.6	64.1	56.5	81.0
HdLI	38.8	39.9	37.0	42.9
HdWI	59.7	56.8	39.1	67.1
EOI	4.2	5.0	10.4	7.1
ALI1–4	56.0–67.0	52.0–61.3	48.5–64.7	47.0–69.7
AFR	2=4.1.3	2.1=4.3	2.1.4.3	2.1.4.3
AFL	3.1=2.4	1=2.4.3	2.1.4.3	2.1.4.3
WDIA–E	26.2–32.8	21.7–30.4	25.0–28.4	23.9–30.4
WFR	C.D.E=B.A	D.C.A.B.E	A=B=D.C.E	C.A=B.D.E
WFL	B=C=E.A=B	A=B.C.D=E	A=B=C.D.E	C.A.B=D.E
ASC1–4	83–86	69–75	69–76	78–83
ASIn1–4	6.0	5.3–6.0	6.5–8.7	7.6–8.6
FuLI	31.3	33.2	43.9	42.9
FFuI	16.4	16.6	26.1	26.2
PAI	41.8	30.2	37.4	47.6

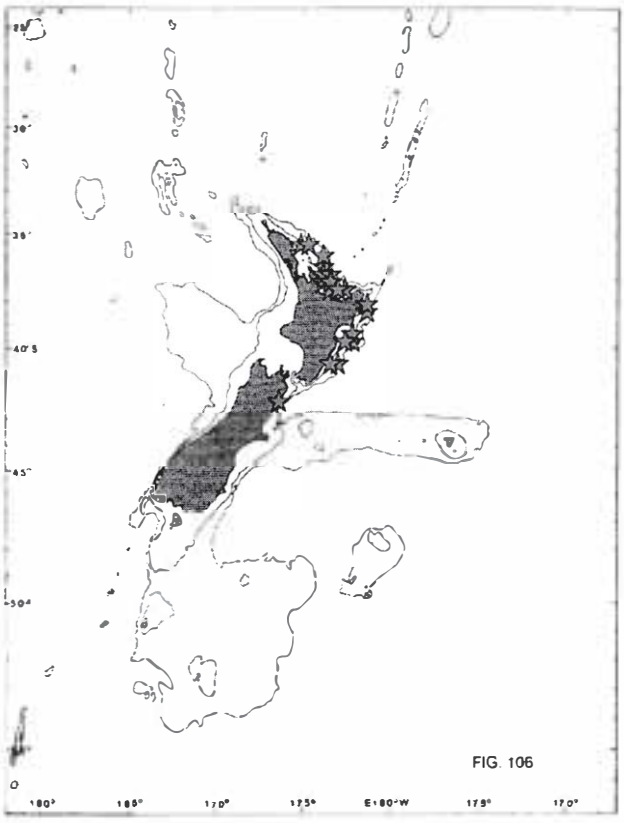
Table 82. Indices, formulas, and counts for post-thaw-fixed female *Octopus mernoo* sp. nov. (* denotes damage).

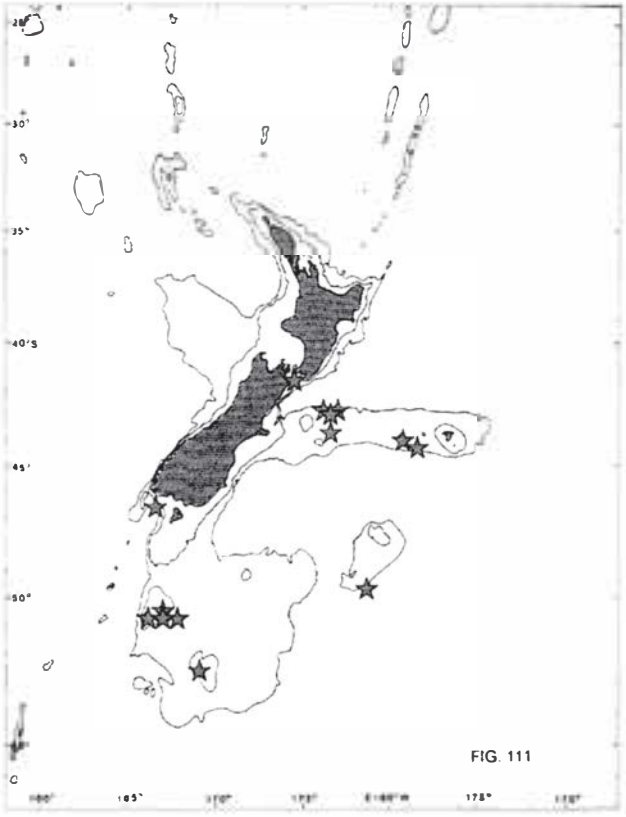
	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NMNZ M.8946	NZOI Stn Z8529
MWI	45.6	62.3	65.8	59.4	57.7	71.7
HdLI	19.5	26.6	21.9	26.5	34.6	38.2
HdWI	34.9	39.4	33.2	47.3	55.1	55.8
EOI	5.9	6.5	6.6	6.5	4.9	15.1
ALI1–4	59.3–63.6	58.5–67.4	55.8–69.2	55.7–62.9	58.4–64.0	59.4–72.3
AFR	*	*	*	2.1=3=4	*	*
AFL	*	2=3.4.1	*	2=3.4.1	*	*
WDIA–E	20.0–22.7	15.1–22.6	17.8–18.9	18.2–25.0	17.5–30.0	11.0–17.8
WFR	A=D.C.E.B	A=D.B.C.E	B=C=D=E.A	C=D.A=B=E	B=C.D=A.E	*
WFL	A.B=D.C=E	A=B.C.E.D	D.E.A=B=C	A=C=B=D.E	B=C.A.D.E	A=B=C.D.E
ASC1–4	120–121	119–125	114–125	102–104	102–105	88–94
ASIn1–4	3.8–4.7	4.4	5.2–5.6	4.3–6.0	7.4–7.7	5.2–6.8
FuLI	29.0	33.5	40.2	34.4	43.6	51.8
FFuI	19.4	18.2	15.8	12.9	21.5	27.9
PAI	35.6	48.9	39.4	42.2	41.5	43.8

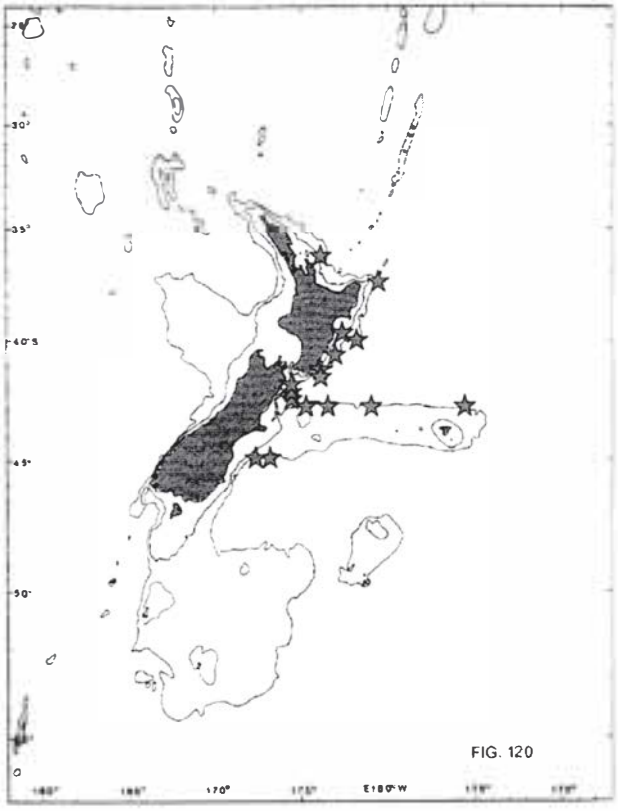
Table 83. Indices and counts for male *Octopus mernoo* sp. nov. (* denotes damage).

	NZOI Stns V374	NZOI V374	NZOI Z8529	NZOI Z8529	NZOI Z8529	NZOI Z8529	NZOI Z8529	NZOI Z8529	NMNZ M.8960	NMNZ M. 8946
OAI	91.4	95.1	*	63.4	81.4	77.6	*	63.9	86.8	88.6
ASC3R	43	41	44	48	45	44	45	44	41	42
CaLI	61.3	64.5	70.0	60.3	54.7	61.5	60.0	60.8	80.0	70.7
LLI	14.2	15.9	18.2	15.1	13.2	12.5	11.8	11.1	10.6	13.2









Recognised distribution. **Fig. 102**, *Octopus mernoo* sp. nov. **Fig. 106**, *Octopus kaharoa* sp. nov. **Fig. 111**, *Enteroctopus zealandicus* (Benham, 1944). **Fig. 120**, *Benthoctopus tegginmathae* sp. nov.

sector E, and oral surfaces of arms and web, light pink. Dorsal surfaces of mantle, head and arms darker than ventral and oral surfaces of arms and web.

Pallial aperture wide, mantle attaches anterior to ventral surface of orbit; funnel moderately long, slender; adsiphonal pouches moderately well developed. Mantle musculature thick. Funnel collar well developed; funnel retractor muscles large; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting renal tissue to ventral and inner surface of mantle absent. Male penis and diverticulum disproportionately large; penis extends along anteroposterior axis of mantle for entire mantle length, diverticulum oriented away from interpallial septum, over base of left gill, and of length equivalent to mantle length. Ovary sac large, with weak fibrous connection to ventral and inner surface of mantle musculature; genital apertures open at anterior base of interpallial septum, not extending to anus; anus with small anal flaps. Gills small, with 8 lamellae per inner and outer demibranch. Lateral muscles restraining digestive gland, visceral envelope, renal papilla and anal region without obvious chromatophores. Funnel organ difficult to interpret, indistinct even in live-fixed specimens, resembles VV-shaped structure with thick inner and outer limbs, the outer limbs slightly shorter than the inner limbs.

Male reproductive system (Fig. 105B) with short, thick, weakly convoluted proximal vas deferens; spermatophoral gland long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Accessory gland granular, distally thickened, expanded, with large complete terminal volution. Spermatophore sac large, long, thin walled, containing 3 spermatophores. Distal vas deferens long, thin, connects to penis and diverticulum in U-bend; penis diverticulum single, long, with single spermatophore; penis large, genital aperture subterminal (aperture not apparent). Mature female (Fig. 105C) with large ovary sac (about 50% ML in greatest dimension); proximal oviducts appear to depart ovary sac separately; proximal ducts long, narrow, slightly swelling into anterior face of oviducal ball; oviducal gland large, with 2 apparent hemispheres, proximal very small, cream coloured, distal large, black, radially striate; distal oviducts about 33% longer than proximal ducts, considerably dilated; spermatophores frequent in distal half of distal oviduct; genital aperture terminal, porelike without secondary modification. Mature eggs few in number (< 20), very large, teardrop-shaped, to 23.5 x 6.0 mm, each with short stalk and about 15 longitudinal striations running the entire egg length; egg-capsules unknown.

Alimentary canal (Fig. 105D) with moderate-sized buccal bulb, length about 20% ML; anterior salivary glands well developed, very large, length about 60% greatest buccal bulb dimension; anterior oesophagus long, narrow; crop with well-developed anterior diverticulum about 25% total crop length. Posterior salivary glands ovoid, moderate sized, length about 106% buccal bulb greatest dimension, about 21% ML. Posterior oesophagus muscular, thick walled. Stomach with 3 apparent sections, basal thin walled, central thick walled, distal thin walled; stomach with undivided lumen. Spiral caecum with single complete volution, and faint radial striations. Intestine moderately long, length 1.5 times that of oesophagus and crop, thick-walled, dilated for proximal two-thirds, slightly constricted distal third; anal flaps small. Digestive gland large, broadly triangular, with large anterior peaks, and depressions (to accommodate stomach and crop); pancreas small; ink sac small, length about 20% digestive gland length, superficially invested in surface tissues of gland; ink duct long, narrow, opening into base of anus. Stomach contents identify a diet consisting primarily of polychaete worms.

Upper beak (Fig. 105E) very tall (height 120.0% length); hood dark brown, lateral walls light brown, hood and lateral wall margins translucent; hood very shallow (depth 29.7% beak length), with squared crest without posterior notch; rostrum triangular, rostral-tip blunt, slightly deflected downwards, with single low-profile tooth in jaw. Lateral walls straight sided; crest broadly rounded, lateral wall fold absent. Lower beak (Fig. 105E) very depressed (height 63.2% width); hood dark brown, lateral wall and wings lighter brown, lateral wing and wall margins translucent. Lateral wall with deep, acute angled V-shaped basal notch and keeled-triangular crest. Hood moderately deep (depth 31.3% beak length), forward projecting, with flattened chisel-like to weakly bifid rostrum; hood with shallow posterior notch; lateral wings very short (length 81.3% beak length), with single weak fold.

Radula (Fig. 105F) with delicate rachidian, as wide as tall, with 1 or 2 asymmetric lateral cusps aside the larger central cusp, 1 lateral cusp consistently larger than the other; 1st lateral with 2 spikelike cusps, inner and outer cusp of similar size; 2nd lateral robust, with pronounced inner uncusped heel, long base and offset-centre large cusp; marginal teeth tall, with moderate curvature, cusp less robust than that of 2nd lateral tooth; marginal plates well developed rectangular blocks.

Raw measures for male and female in Tables 84 and 85.

Table 84. Raw measures for male *Octopus mernoo* sp. nov. (* denotes damage).

	NZOI Z8529	NZOI Z8529	NZOI Z8529	NZOI Z8529	NZOI Z2859	NZOI V374	NZOI Z8529	NZOI V374	NMNZ M.8960	NMNZ M. 8946
TL	168	116	125	117	117	91	105	75	68	66
ML	53.1	37.5	37.1	36.0	35.4	33.5	32.1	30.1	23.0	21.0
MW	33.5	19.0	24.5	25.0	21.1	27.0	24.0	19.3	13.0	17.0
HdL	14.8	13.0	11.3	10.5	13.1	13.0	10.7	12.0	8.5	9.0
HdW	22.0	11.5	20.6	18.1	15.0	20.0	16.5	17.1	9.0	14.1
EO	4.0	3.2	4.9	3.2	4.1	1.4	2.5	1.5	2.4	1.5
AL1R/L	105/104	50*/70	78/73	53/70*	70/62	56/61	65/65	45/44	38/41	43/42
AL2R/L	79*/102	65/72	77/75	71/80	62/58	51/59	68/65	46/44	42/44	46/45
AL3R/L	66/73*	45/71	57/70	52/67	51/67*	53/58	46/72	39/41	33/38	31/35
AL4R/L	90/72*	66/64	70/66	74/71	68/33*	57/57	68/59	45/42	35/40	37/40
WDA	17	15	15	13	15	16	12	12	12	13
WDBR/L	20/17	18/14	20/15	14/14	15/15	17/17	16/12	11/12	12/12.5	13/12
WDCR/L	22/18	12/14	19/17	17/17	14/14	20/17	17/12	13/11	11/12	14/14
WDDR/L	18/17	12/12	16/16	19/19	16/16	19/16	17/11	14/10	12/11	12/12
WDE	16	12	14	15	11	17	10	10	10	11
ASC1R	103	L90	88	78	94	84	88	73	69	83
ASC2R	L105	98	86	96	84	86	92	75	76	83
ASC3R	44	48	45	44	45	43	44	41	41	42
ASC4R	103	*c.* 87	89	95	94	83	*c.* 87	69	76	78
ASn1R	2.9	1.4	1.8	2.0	2.0	2.0	2.0	1.6	1.5	1.8
ASn2R	3.0	1.8	1.9	2.0	2.0	2.0	2.0	1.8	2.0	1.8
ASn3R	2.6	1.7	1.9	2.0	2.0	2.0	2.0	1.8	1.5	1.6
ASn4R	2.6	1.7	1.8	2.0	2.0	2.0	2.0	1.6	1.5	1.7
GiLC	8	8	8	8	8	8	8	8	8	8
FuL	16.0	12.0	16.0	15.0	15.0	10.5	15.3	10.0	10.1	9.0
FFL	12.1	7.1	5.0	8.0	8.5	5.5	5.0	5.0	6.0	5.5
PA	21.7	14.5	16.9	16.9	16.0	14.0	15.5	9.1	8.6	10.0
CaL	8.4	4.1	4.1	4.0	3.6	4.6	3.1	4.0	2.8	2.9
LL	12.0	6.8	7.5	6.5	6.0	7.5	5.1	6.2	3.5	4.1

ETYMOLOGY: After Mernoo Bank, Chatham Rise, New Zealand, where this species appears most abundant.

REMARKS: This species possesses a number of bathypolypodine traits, especially its large egg size, simple radula, absence of connective membranes between the renal tissue and the ventral inner surface of mantle, low gill lamellae counts, presence of subgelatinous deposits beneath the skin, and low arm sucker counts. As a rule, however, bathypolypodine species have a single hemisphere to the oviducal ball, whereas *O. mernoo* has two hemispheres. It differs further from recognised bathypolypodine genera in the peculiar penis and diverticulum configuration, a feature atypical of any recognised bathypolypodine genus or species. The systematic status of this species appears transitional between the classifications of Voss (1988a) and Robson (1932).

Octopus kaharoa sp. nov. (Figs 107–109) (Tables 86–90

TYPE MATERIAL (80 specimens, 23 male [M], 57 female [F]): Holotype: NZOI H-665, M, ML 49.0 mm, FPT, 36°50.7–53.74' S, 176°17.61–17.87' E, 439-440 m, BT 10.3°C, 09/04/1996, f.r.v. *Kaharoa* Stn KAH9604/11, NZOI Stn Z8530. Para-types: NZOI P-1115, F, ML 62.0 mm, FL, 36°59.05–52.90' S, 176°16.51–17.11' E, 395 m, 18/10/1996, f.v. *Drysdale* Stn DRY9602/01, NZOI Stn Z8567; NZOI P-1116, F, ML 66.0 mm, FL, 37°00.69–54.34' S, 176°16.50–17.64' E, 418-423 m, 19/10/1996, f.v. *Drysdale* Stn DRY9602/05, NZOI Stn Z8571; NZOI P-1110, F, ML 90.0 mm, FPT, 39°42.58-43.56' S, 177°41.63–37.94' E, 410–440 m, 30/01/1995, BT 9.7°C, f.r.v. *Kaharoa* Stn KAH9501/110, NZOI Stn Z8467.

ADDITIONAL MATERIAL EXAMINED: AK 79830, F, ML 58.0 mm, *c.* 37°25' S, 176°31' E, 384 m, 07/06/1979; AK78079, M, ML 73.5 mm, *c.* 35°14' S, 174°53' E, 355–388 m, 14/09/1971, f.r.v. *Ikatere*; NMNZ M.90379, F, ML 60.0 mm, 35°23' S, 175°06' E, *c.* 402-475 m, 16/01/1969, F.I.B. Northern Prawn Cruise Stn 32; NMNZ M.118281, F, ML 42 mm, FPT, 36°04.5' S, 176°12.5' E, 340 m, 04/01/1994, 10.0°C, f.r.v. *Kaharoa* Stn KAH9401/06; NZOI Stn Z8520, 2F, ML 67.0, 66.5 mm, FPT, 36°05.80-08.27' S, 176°14.16–13.99' E, 419–428 m, 05/01/1995, BT. 10.2°C, f.r.v. *Kaharoa* Stn KAH9501/07; NZOI Stn Z8428, M, ML 42.5 mm, 4F, ML 78.8, 61.5, 54.0, 52.5, FPT,

Table 85. Raw measures for female *Octopus mernoo* sp. nov. (* denotes damage).

	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NZOI Stn Z8529	NMNZ M.8946	NZOI Stn Z8529
TL	236	236	260	140	125	101
ML	84.5	79.0	75.2	46.5	39.5	25.1
MW	38.5	49.2	49.5	27.6	22.5	18.0
HdL	16.5	21.0	16.5	12.3	13.5	9.6
HdW	29.5	31.1	25.0	22.0	21.5	14.0
EO	5.0	5.1	5.0	3.0	1.9	3.8
AL1R/L	124*/125*	118*/138	168/145	86/78	76/46*	64/60
AL2R/L	138*/140	148/149	180/155	88/85	80/77	73/22*
AL3R/L	136*/150	159/148	160/148	86/86	80/73	23*/61
AL4R/L	133*/117*	147/145	126*/140*	86/81	65*/73	66/47
WDA	34	36	32	20	19	12
WDBR/L	30/32	32/36	34/32	21/19	24/21	10/13
WDCR/L	33/31	29/34	34/33	22/20	24/22	*/12
WDDR/L	34/32	35/24	34/38	22/18	20/17	*/10
WDE	31	26	34	16	14	8
ASC1R	*	L121	116	103	100	92
ASC2R	L121	122	114	104	105	94
ASC3R	L120	119	125	102	102	L88
ASC4R	*	125	*	103	L102	94
ASn1R	3.6	3.5	4.0	2.0	3.0	1.7
ASn2R	4.0	3.5	3.9	2.8	3.0	1.4
ASn3R	3.5	3.5	4.2	2.0	2.9	L1.3
ASn4R	3.2	3.5	3.9	2.0	2.9	1.6
GiLC	8	8	8	8	8	8
FuL	24.5	26.5	30.2	16.0	17.0	13.0
FFL	16.4	14.4	11.9	6.0	8.4	7.0
PA	30.1	38.6	29.6	19.6	16.2	11.0

36°09.66–12.69' S, 176°13.33–13.47' E, 370–380 m, BT 10.9°C, 05/01/1995, f.r.v. *Kaharoa* Stn KAH9501/08; NZOI Stn Z8433, M, ML 64.0 mm, FPT, 36°11.05–08.03' S, 176°08.80–08.68' E, 236–250 m, BT 12.3°C, 04/01/1995, f.r.v. *Kaharoa* Stn KAH9501/02; NZOI Stn Z8517, M, ML 40.8 mm, F, ML 70.0 mm, FPT, 36°12.27–09.30' S, 176°14.84–15.41' E, 450–470 m, 05/01/1995, BT. 10.8°C, f.r.v. *Kaharoa* Stn KAH9501/09; NZOI Stn Z8260, 2F, ML 58.0, 51.0 mm, FPT, 36°14.3' S, 176°12.1' E, 360 m, BT 9.5°C, f.r.v. *Kaharoa* Stn KAH 9401/12; NZOI Stn Z8424, M, ML 55.6 mm, F, ML 60.0 mm, FPT, 36°14.53–15.80' S, 176°10.45–07.77' E, 306–315 m, BT 11.0°C, 06/01/1995, f.r.v. *Kaharoa* Stn KAH9501/12; NZOI Stn Z8438, F, ML 52.5 mm, FPT, 36°16.23–17.83' S, 176°12.81–11.73' S, 430–435 m, 08/01/1995, BT. 10.5°C, f.r.v. *Kaharoa* Stn KAH9501/14; NZOI Stn Z8435, M, ML 63.2 mm, 2F, ML 80.5, 55.0 mm, FPT, 36°25.50–28.49' S, 176°07.21–06.90' E, 313–348 m, BT 11.2°C, 08/01/1995, f.r.v. *Kaharoa* Stn KAH9501/16; NMNZ M.118277, 4F, ML 77.0, 74.0, 67.0, 62.0 mm, FPT, 36°38' S, 176°13' E, 410 m, 08/01/94, BT 9.0°C, f.r.v. *Kaharoa* Stn KAH9401/017; NZOI Stn Z8530, M, ML 32.0 mm, FPT, 36°50.7–53.74' S, 176°17.61–17.87' E, 439–440 m, BT 10.3°C, 09/04/1996, f.r.v. *Kaharoa* Stn KAH9604/11; NZOI Stn Z8523, F, ML 73.0 mm, FPT, 36°52.13–55.32' S, 176°16.77–16.90' E, 380–386 m, 17/04/1996, f.r.v. *Kaharoa* Stn KAH9601/33; NZOI Stn Z8515, M, ML 61.0 mm, F, ML 71.0 mm, FPT, 36°54.43–57.44' S, 176°17.33–17.31' E, 409–427 m, 09/01/1995, BT 10.0°C, f.r.v. *Kaharoa* Stn KAH9501/24; NZOI Stn Z8522, M, ML 53.5 mm, 3F, ML 71.0, 61.8, 41.7 mm, FPT, 36°55.06–52.06' S, 176°16.43–16.39' E, 348–352 m, BT 11.1°C, 09/04/1996, f.r.v. *Kaharoa* Stn KAH9604/10; AK 78078, 2M, ML 52.5, 50.0 mm, 4F, ML 73.6, 68.6, 61.0, 56.0, mm, *c*. 36°56' S, 176°08' E, 366–475 m, 08/06/1969, f.v. *Valkyrie*; NZOI Stn Z8535, M, ML 67.0 mm, F, ML 68.0 mm, 36°56.97–57.73' S, 176°17.09–16.89' E, 406–409 m, 28/09/1995, f.r.v. *Kaharoa* Stn KAH9511/049; NMNZ M.90349, F, ML 32.0 mm, 37°01' S, 176°14' E, 210–373 m, 01/01/1969, FIB Northern Prawn Cruise, Stn 7; NMNZ M.90370, F, ML 53.0 mm, 37°11' S, 176°19' E, 329–475 m, 09/01/1969, F.I.B. Northern Prawn Cruise Stn 28; NZOI Stn Z8516, 2F, ML 78.0, 58.0 mm, FPT, 37°24.77–24.76' S, 178°11.20–07.41' E, 340–355 m, 29/01/1995, BT 10.4°C, f.r.v. *Kaharoa* Stn KAH9501/106; NZOI Stn Z8421, 2F, ML 78.0, 47.6 mm, FPT, 37°26.09–25.48' S, 177°57.23–178°00.92' E, 408–424 m, BT 9.7°C, 29/01/1995, f.r.v. *Kaharoa* Stn KAH9501/108; NZOI Stn Z8526, M, ML 52.5 mm, FPT, 37°26.18–26.40' S, 178°13.17–09.41' E, 208–255 m, BT 13.3°C, 29/01/1995, f.r.v. *Kaharoa* Stn KAH9501/105; NZOI Stn Z8427, M, ML 63.5 mm, F, ML 67.0 mm, FPT, 37°32.44–33.36' S, 177°04.33–07.91' E, 325–327 m, BT 11.0°C, 14/01/1995, f.r.v. *Kaharoa* Stn KAH9501/48; NZOI Stn Z8519, F, ML 92.7 mm, FPT, 37°35.12–34.68' S, 177°00.40–04.17' E, 201–230 m, 14/01/1995, BT. 13.0°C, f.r.v. *Kaharoa* Stn KAH9501/47; NZOI

Stn Z8431, 2F, ML 61.5, 56.5 mm, FPT, 38°07.36–10.34' S, 178°49.18–48.64' E, 318–330 m, BT 11.0°C, 28/01/1995, f.r.v. *Kaharoa* Stn KAH9501/102; NZOI Stn Z8426, 2M, ML 47.6, 47.0, F, ML 50.0 mm, FPT, 38°08.86–05.86' S, 178°45.75–45.72' E, 210–231 m, BT 12.2°C, 28/01/1995, f.r.v. *Kaharoa* Stn KAH9501/103; NZOI Stn Z8521, F, ML 60.0 mm, FPT, 38°37.57-39.93' S, 178°38.10–35.89' E, 429–440 m, 27/01/1995, BT. 10.2°C, f.r.v. *Kaharoa* Stn KAH9501/99; NZOI Stn Z8432, 3F, ML 77.0, 76.3, 61.0 mm, FPT, 38°37.63–39.81' S, 178°37.60–35.29' E, 384–397 m, BT 10.6°C, 27/01/1995, f.r.v. *Kaharoa* Stn KAH9501/97; NZOI Stn Z8434, F, ML 66.6 mm, FPT, 38°39.38–38.01' S, 178°31.62–35.03' E, 234–251 m, BT 11.7°C, 27/01/1995, f.r.v. *Kaharoa* Stn KAH9501/98; NZOI Stn Z8430, F, ML 54.5 mm, FPT, 39°37.66–39.84' S, 177°48.75–46.06' E, 315–317 m, BT 10.3°C, 17/01/1995, f.r.v. *Kaharoa* Stn KAH9501/60; NZOI Stn Z8425, 2M, ML 48.5, 46.8 mm, 2F, ML 61.0, 58.2 mm, FPT, 39°44.29–45.59' S, 177°33.38–29.74' E, 311–354 m, BT 10.5°C, 17/01/1995, f.r.v. *Kaharoa* Stn KAH9501/62; NZOI Stn Z8423, M, ML 56.0 mm, F, ML 66.9 mm, FPT, 40°29.28–32.28' S, 176°51.68–51.60' E, 224–230 m, BT 11.4°C, 22/01/1995, f.r.v. *Kaharoa* Stn KAH9501/83; NZOI Stn Z8422, 2M, ML 63.5, 30.0 mm, F, ML 64.5 mm, FPT, 40°36.50–33.91' S, 176°49.92–51.91' E, 256–268 m, BT 10.8°C, 23/01/1995, f.r.v. *Kaharoa* Stn KAH9501/85; NZOI Stn Z8518, M, ML 52.0 mm, FPT, 40°37.51–35.32' S, 176°47.19–49.89' E, 221–224 m, 23/01/1995, BT. 11.5°C, f.r.v. *Kaharoa* Stn KAH9501/84; NMNZ M.90374, F, ML 83 mm, c. 41°44' S, 174°17' E, 80 m, -/11/1952; NMNZ M.117697, 2F, ML 85.6, 66.0 mm, *c.* 42°15' S, 173°40' E, Sth of Cape Campbell, 73 m, 21/02/1952, f.v. *Phyllis*.

RECOGNISED DISTRIBUTION (Fig. 106, p. 172): New Zealand, east coast of North and South Islands, from Poor Knights Islands to Kaikoura (35°23' S, 175°06' E to about 42°15' S, 173°40' E), 7–540 m; recorded bottom temperature range 7.0–11.8°C.

DIAGNOSIS: Small to medium sized, muscular, slender-bodied papillose octopus; superocular cirrus triangular, with small flat-topped lateral prominences; lateral keel of skin prominent in live animals; gills with 8 or 9 outer lamellae per demibranch; hectocotylised arm sucker count very low, ASC 46–53, non-hectocotylised arm sucker counts low to moderate, ASC 100–182; female attains larger size than male; sex ratio skewed towards female.

DESCRIPTION: Adult animal of small to medium size (ML to 91.2 mm, TL to 394.0 mm), female attaining larger size than male; body slender (Figs 107A–E, 108); mantle globose to flask-shaped (stages J–M[1]), slender to broad (MW about 38–68% ML), dorsoventral compression weak; lateral keel or fold of skin prominent in live animals, apparent in live or narcotised-fixed animals, not apparent in specimens fixed post-mortem thaw; ventral longitudinal groove or depression absent. Head small to large, wider than long, narrower than mantle (HdL about 10–35% ML; HW about 28–47% ML), separated from mantle by variably developed preocular constriction, little apparent in live or narcotised-fixed specimens, most prominent in post-thaw-fixed specimens. Orbits large, dorsolaterally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsolaterally oriented. Funnel moderately long to very long (FuL about 30–46% ML), base entirely free of brachial crown. Nuchal constriction variably developed, little apparent in live or narcotised-fixed specimens, most prominent in post-thaw fixed specimens.

Brachial crown robust, slightly wider than head. Arms thick, square in section, very short to long (AL about 38–79% TL), gradually tapering to delicate tips; arm pairs 2 and 3 frequently longest, arms 1 and 4 shortest, with no consistent disparity in relative arm lengths. Web very shallow to moderately deep, about 8–25% longest arm length, with little development down dorsolateral surfaces of arms 1–3, moderate development (to distal quarter) along ventrolateral surfaces of arms 1–3, and both dorso- (to basal half) and ventrolateral (to distal quarter) surfaces of arms 4; web extension narrow, wider ventrolaterally than dorsolaterally; web formula variable, sectors A and E usually shallowest, sectors B, C and D deeper, with no consistent disparity in relative sector depths. Suckers biserial, with 15–17 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers minute. Arm sucker counts variable, lower in male than female (male ASC 100–141, ML 32.2–63.0 mm; female ASC 108–182, ML 39.8–91.2 mm); suckers extend to arm tips. Suckers small, size sexually dimorphic, larger in male (male ASIn about 4.5–8.0; female ASIn 4.0–6.3), suckers on lateral arms slightly larger than those on dorsal or ventral arm pairs; no suckers abruptly enlarged in either sex. Suckers with: reduced suction chamber; moderately constricted sucker aperture; well-developed grasping ring with about 26 faint radial grooves, and crenulate sucker aperture with similar number of rounded toothlike processes; well-developed muscular suction pad (Fig. 155H).

Specimens fixed live or narcotised have a well-developed lateral keel or fold of skin around the mantle; low profile and enlarged erect papillae are distributed over dorsal surfaces of mantle, head, dorsal and dorsolateral surfaces of arms 1–3, and web sectors A–D; ventral surfaces of mantle, head, ventrolateral surface of arms 3, both dorso- and ventrolateral surfaces of arms 4, aboral surface of web sector E and adoral web surfaces A–E are smooth. Papillae densest over head, pre- and postocular

[1] Stages as depicted by Hochberg *et al.* 1992: fig. 235, p. 215.

regions of mantle and brachial crown, over surfaces of arms 1 and 2 and web sectors A and B; papillae either low profile, with single small central prominence, or erect, with central element and 1–6 smaller lateral prominences; enlarged erect conical papilla present over either eye as superocular cirrus; smaller erect papilla below either eye as subocular cirrus. Specimens fixed post-thaw comparatively smooth bodied, papillae not raised. Dorsal and dorsolateral surfaces of mantle and head, dorsal and ventral surfaces of arms 1–3, dorsolateral surface of arms 4, oral surface of arms 1–3, dorsolateral surface of arms 4, and web sectors A–D orange-brown; papillae lighter orange (live fixed) to darker orange (post-thaw fixed); ventrolateral to ventral surfaces of mantle below lateral keel, funnel, head, ventrolateral surfaces of arms 4 and web sector E, off-white to light pink; orbits with bluish tinge.

Hectocotylised arm about 60–75% opposite arm length, with low ASC, 46–53 suckers in total; spermatophoral groove well developed, wide, flaring, with thickened web margin. Hectocotylised portion moderately long (Fig. 109A); ligula length moderate (LLI 8.3–13.1), cheeks prominent, depression shallow, transverse rugae not apparent; calamus large (CaLI 44.4–62.5), fleshy, apex with blunt point; calamus groove deep, running entire structure length.

Gills small, compact, with 8 or 9 outer lamellae per demibranch (excluding terminal). Funnel organ difficult to interpret, indistinct even in live-fixed specimens, resembles W-shaped structure with thick inner and outer limbs, the outer limbs slightly shorter than central V-shaped component. Penis in mature male extending anteriorly over viscera, parallel to interpallial septum; primary penis diverticulum long, with pronounced curvature away from interpallial septum, over base of left gill; secondary penis diverticulum small, appendicular, enclosed within arch of primary diverticulum and penis. Interpallial septum short, thick, muscular; membranes between renal tissue and ventral inner surface of mantle absent, interpallial septum running to posterior end of mantle as thin muscular riblet. Anus at base of interpallial septum; anal flaps small, paired. Visceral envelope and lateral muscles restraining digestive gland without chromatophores. Renal papilla elongate, erect, right papilla situated in recess between penis proper and distal vas deferens. Oviducts open at base of kidney tissue, not extending along or over face of interpallial musculature.

Male reproductive system (Fig. 109B) with short, thick, weakly convoluted proximal vas deferens. Spermatophoral gland long, with small swelling at junction with proximal vas deferens; spermatophore sac long, slender. Accessory gland long, with complete distal volution. Distal vas deferens short, thin, tubular. Penis long, cylindrical, with subterminal genital aperture; primary penis diverticulum large, elongate; secondary diverticulum appendicular, of small to large size (depending on reproductive maturity). Female with large ovary sac (Fig. 109C), when mature distended with numerous large eggs (to 18.0 x 5.0 mm), each with 11–13 longitudinal striations. Proximal oviducts of equivalent length to distal ducts, narrow, depart sac through common antrum; oviducal ball small, with small anterior hemisphere and large distal hemisphere, the distal one brown to black, with faint radial striations. Distal oviducts with pronounced U-shaped bend, distally dilatating; genital apertures simple, on dome-shaped terminal face of distal duct.

Alimentary canal (Fig. 109D) with small buccal bulb, length about 17% ML; anterior salivary glands rectangular, loosely applied to posterior margin of buccal bulb, very large, length about 60% buccal bulb greatest dimension. Anterior oesophagus extensive, opening into crop mid-dorsally. Posterior salivary glands small, length about 102% buccal bulb greatest dimension, about 17% ML; left posterior salivary gland teardrop-shaped, with acute distal point, right salivary gland rectangular, with slightly tapered ends. Crop with prominent anterior diverticulum, length about 29% total crop length. Stomach small, with 3 apparent sections, basal thin walled, central thick walled, distal thin walled; lumen continuous. Spiral caecum large, with single loose, radially striate coil. Digestive gland large, elongate, surface iridescent, with pronounced depressions imparted by stomach, caecum, crop and posterior salivary glands, and lateral constrictions imparted by lateral restraining muscles; gland equivalent in length to anterior alimentary tract, from oesophagus to stomach. Ink sac large, about 50% digestive gland length, superficially buried beneath iridescent tissues of digestive gland; ink duct short. Intestine long, about 2.3 times longer than oesophagus and crop, thick walled, dilated for greatest length, particularly proximal third; 2 anal flaps.

Upper beak (Fig. 109E) very tall (height 118.0% length); hood and lateral walls dark brown, hood and lateral wall margins translucent; hood shallow (depth 35.3% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip pointed, strongly deflected down; without tooth in jaw. Lateral walls straight sided; crest broadly rounded, lateral wall fold very weak; with shallow sinus in lateral wall margin. Lower beak (Fig. 109E) depressed (height 70.0% width); hood, lateral wall and wings dark brown, lateral wing and wall margins translucent. Lateral wall with deep, acute angled basal

Table 86. Indices, formulas, and counts for post-thaw-fixed male *Octopus kaharoa* sp. nov. (denotes damage).

	NZOI Stn Z8433	NZOI Stn Z8422	NZOI Stn Z8435	NZOI Stn Z8515	NZOI Stn Z8423	NMNZ M.11665	NZOI Stn Z8530	NZOI Stn Z8426	NZOI Stn Z8426	NZOI Stn Z8530
MWI	49.2	45.5	55.4	59.0	47.2	59.4	49.0	46.1	38.3	60.2
HdLI	25.4	23.9	26.3	24.9	28.5	29.2	29.4	27.3	26.2	26.4
HdWI	39.7	37.1	39.1	31.3	41.0	44.5	37.5	35.8	33.0	41.9
EOI	10.3	7.3	8.2	9.2	6.4	6.8	9.6	8.4	6.4	9.3
ALI1–4	39.2–69.8	39.9–64.3	42.8–67.9	45.3–64.6	42.7–71.4	47.4–79.2	41.7–72.2	40.6–64.0	46.6–70.8	38.1–73.8
AFR	*	*	*	*	2.1.4.3	4.2.1.3	2.4.1.3	2.1.4.3	*	2.4.1.3
AFL	*	*	*	*	*	*	2.3.1.4	1=3.2.4	*	2.3.1=4
WDIA–E	14.6–20.2	13.9–21.9	15.3–20.0	16.1–24.8	11.7–21.9	13.8–18.4	13.3–20.0	13.4–17.9	13.3–22.8	12.9–20.4
WFR	C=B.E.D.A	C=D.B.E.A	B.A=D.C=E	B.C.A=D=E	A=B.C.D.E	C=D.B.E.A	C=D.B=E.A	C=D.B.E.A	C.A.B.D.E	B.C.A=D.E
WFL	C=D=E.B.A	D.B.E.C.A	C.B.D.A.E	A=B=E.D.C	B.C.A=D.E	B.D.C=E.A	B.E.A=C.D	C=D.B=E.A	B.A=C.D.E	D.C.A.B.E
ASC1–4	112–135	120	132	125	124–135	125–131	115–141	100–131	113–130	100–112
ASIn1–4	6.7–7.9	5.6–6.5	6.7–8.0	5.1–6.6	7.1–7.3	5.7–7.7	5.4–6.3	5.9–6.3	6.2–6.4	4.7–5.6
FuLI	34.9	40.2	45.9	36.1	41.4	43.8	41.7	40.5	35.3	40.4
FFuI	16.8	18.2	19.8	16.1	23.4	25.1	14.6	16.6	13.8	21.7
PAI	33.2	25.8	36.1	31.0	38.5	32.3	34.8	31.9	27.7	32.6

Table 87. Indices, formulas, and counts for post-thaw-fixed female *Octopus kaharoa* sp. nov. (* denotes damage).

	NZOI Stn P1110	NMNZ M.117697	NZOI Stn Z8435	NZOI Stn Z8434	NMNZ M.117697	NMNZ M.90379	NZOI Stn Z8527	NZOI Stn Z8431	NMNZ M.5632
MWI	63.6	43.3	43.4	53.9	47.0	68.3	64.3	53.4	61.6
HdLI	18.4	18.0	23.3	19.4	27.3	30.2	23.8	25.1	35.4
HdWI	40.2	29.2	28.3	31.4	36.4	45.2	40.1	36.2	46.7
EOI	8.8	6.0	7.7	7.6	3.3	5.0	10.0	9.0	5.0
ALI1–4	49.5–72.6	51.0–69.8	48.6–66.3	53.7–71.0	57.8–70.4	43.9–78.0	57.0–75.2	61.1–75.5	61.1–77.1
AFR	*	2.3.4.1	2.3.4.1	2.4.1.3	2.3.4.1	*	*	*	2.3.1.4
AFL	*	*	*	3.1.4.2	2.1.4.3	2.3.1.4	2.3.1.4	*	2.3.1.4
WDIA–E	11.9–18.9	12.6–18.1	11.2–19.9	14.5–20.7	15.3–21.0	14.1–17.8	8.2–16.0	9.3–14.9	14.8–20.9
WFR	C.D.B.E.A	*	E.D.A=C.B	C.B=D.E.A	C=D.E.B.A	B=D.A.C.E	B.C.A=D.E	C.D.B.A.E	B.C.D.A.E
WFL	C.D.B.E.A	E.C.D.B.A	C=D.B.E.A	D.E=B.A.C	B.C.D.E.A	C.D.A.B.E	B.C.D.A.E	D.C.E.B.A	B.C.A.D.E
ASC1–4	155–161	112–137	145–175	118–153	108–141	149–182	144–159	132–148	122–143
ASIn1–4	4.7–5.5	4.0–4.6	4.8–5.2	4.5–5.5	4.5–5.0	4.7–5.2	5.0–5.2	4.5–5.4	5.3–6.3
FuLI	45.3	30.5	42.8	40.2	31.1	30.7	36.2	37.8	35.2
FFuI	24.1	16.4	22.6	26.8	15.2	23.3	19.6	22.2	26.4
PAI	38.4	29.2	22.6	32.0	33.9	43.5	33.2	26.9	41.5

Table 88. Indices and counts of hectocotylised arm for male *Octopus kaharoa* sp. nov. (* denotes damage).

	NZOI Stns Z8433	NZOI Z8422	NZOI Z8435	NZOI Z8515	NZOI Z8423	NMNZ M.11665	NZOI Z8530	NZOI Z8426	NZOI Z8426	NZOI Z8530
OAI	65.4	*	63.0	75.6	59.9	59.9	62.9	70.3	69.4	60.0
ASC3R	48	46	53	52	49	52	51	48	48	53
CaLI	45.6	56.0	49.5	51.3	48.2	44.4	54.9	54.8	61.7	62.5
LLI	10.8	10.7	9.7	8.3	10.1	10.9	9.1	13.1	10.8	10.0

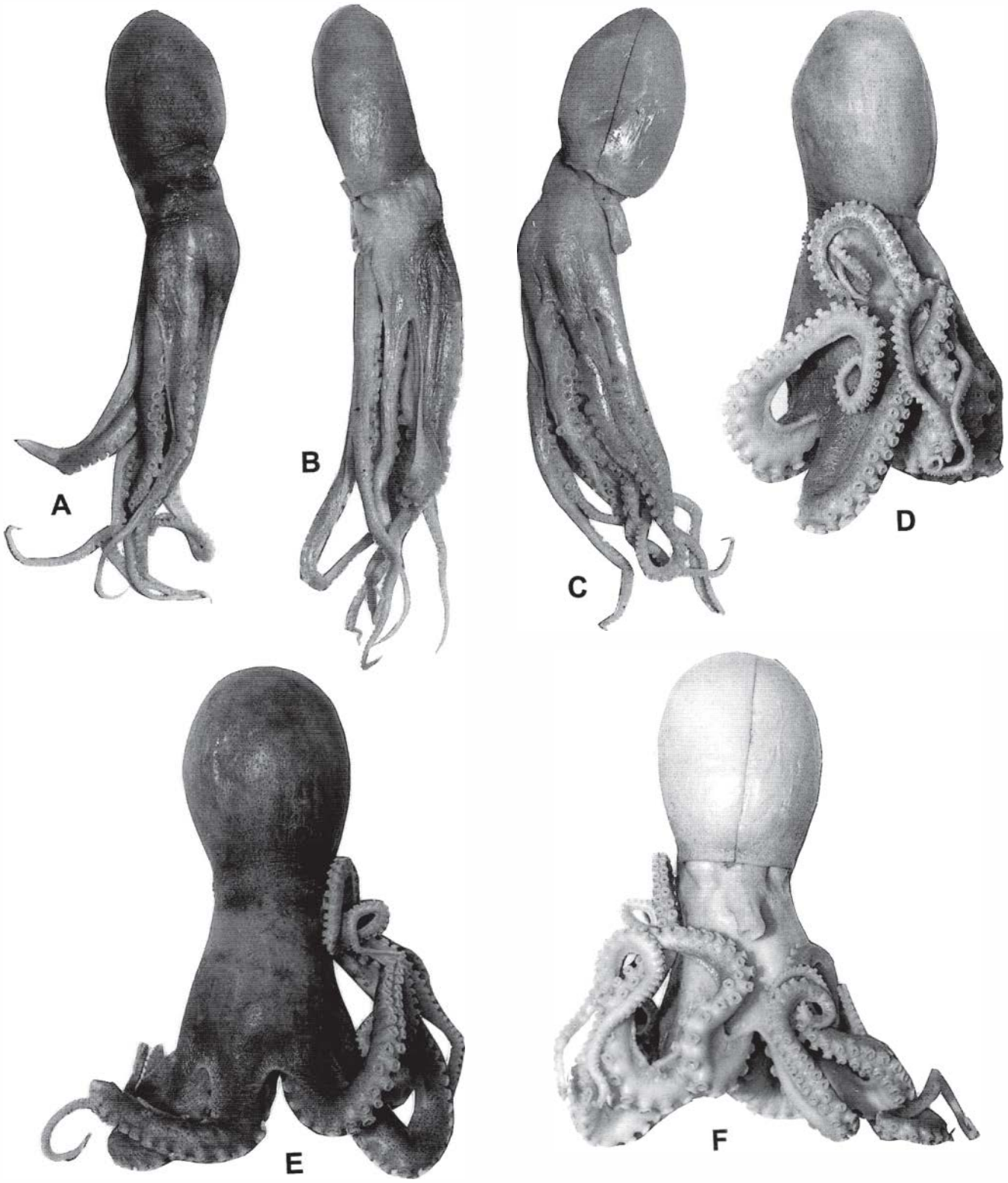


Figure 107. ***Octopus kaharoa*** sp. nov.: **A–C**, Holotype, NZOI H-655, male, ML 49 mm. **D–F**, Paratype NZOI P-115, female, ML 62 mm.

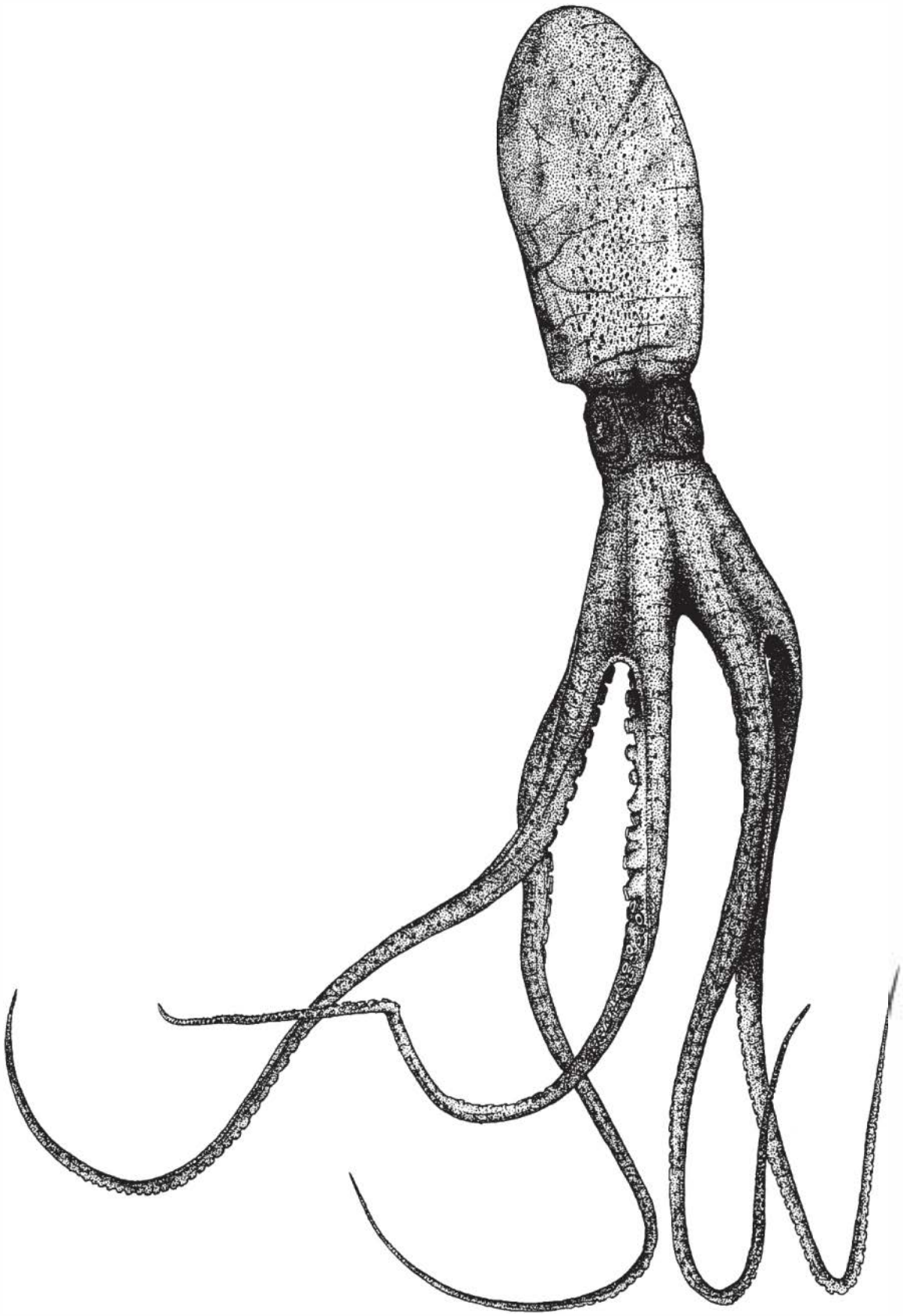


Figure 108. ***Octopus kaharoa*** sp. nov.: NMNZ M903374, female, ML 83 mm.

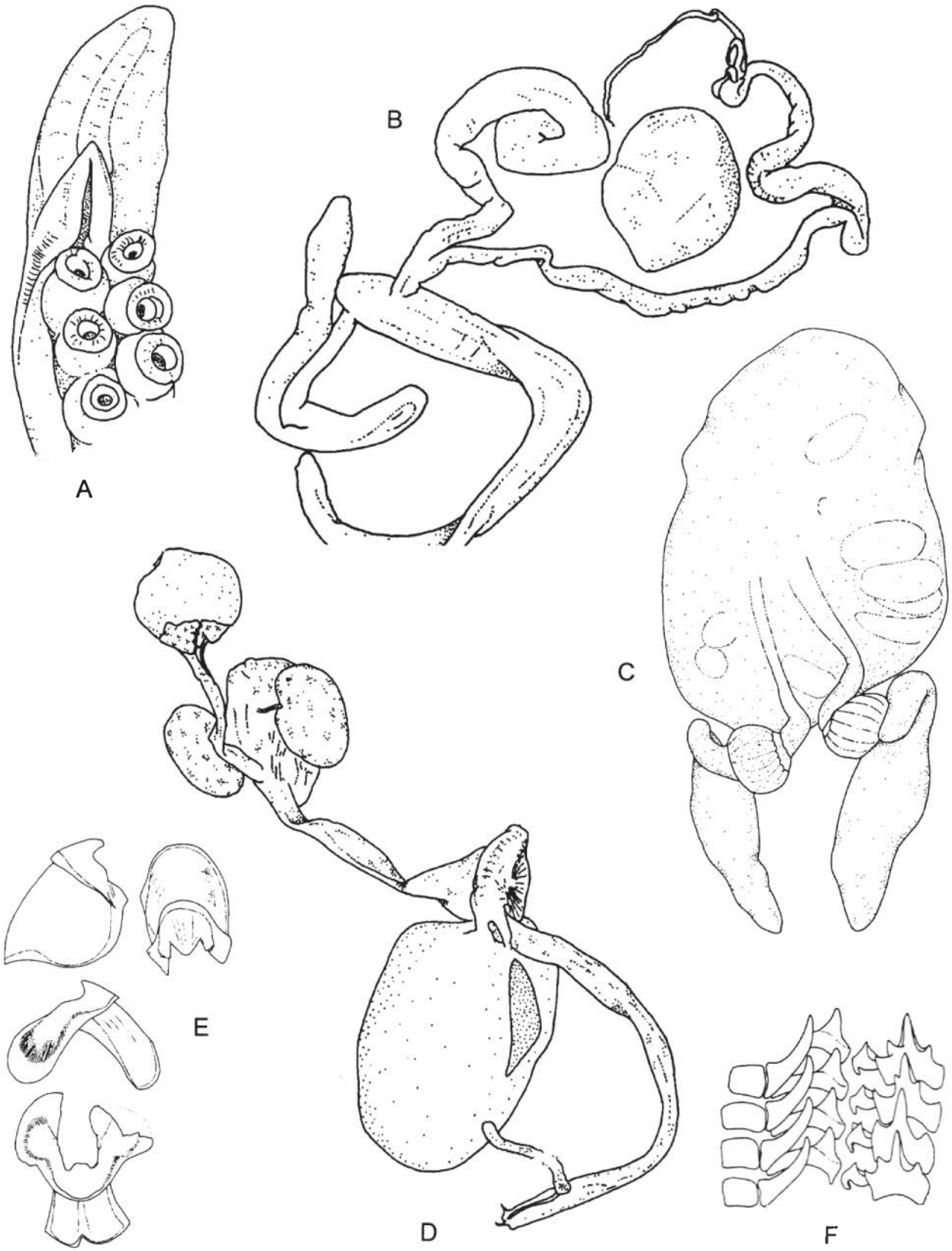


Figure 109. ***Octopus kaharoa*** sp. nov. Anatomy: **A, B**, NZOI Stn Z8515, male, ML 61 mm. **C–F**, NZOI Stn Z8535, female, ML 68 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 89. Raw measures for male *Octopus* (*s.l.*) *kaharoa* sp. nov. (* denotes damage).

	NZOI Z8433	NZOI Z8422	NZOI Z8435	NZOI Z8515	NZOI Z8423	NMNZ M.11665	NZOI Z8530	NZOI Z8426	NZOI Z8426	NZOI Z8530
TL	255	213	243	212	192	192	187	175	161	126
ML	63.0	62.0	61.2	61.0	56.1	53.0	48.0	47.7	47.0	32.2
MW	31.0	28.2	33.9	36.0	26.5	31.5	23.5	22.0	18.0	19.4
HdL	16.0	14.8	16.1	15.2	16.0	15.5	14.1	13.0	12.3	8.5
HdW	25.0	23.0	23.9	19.1	23.0	23.6	18.0	17.1	15.5	13.5
EO	6.5	4.5	5.0	5.6	3.6	3.6	4.6	4.0	3.0	3.0
AL1R/L	102*/120*	77*/116*	170/161	90*/100*	122/122	128/131	96/120	98/101	39*/66*	71/72
AL2R/L	178/163	118*/83*	90*/139*	137/133*	132/85*	135/80*	134/135	112/96	114/112	88/93
AL3R/L	100/153	85/100*	104/165	96/127	82/137	91/152	78/124	71/101	75/108	48/80
AL4R/L	131/131	137/124*	148/160	88*/121*	111/111	137/137	115/108	75/84	97/94	72/72
WDA	26	19	28	27	27	21	23	15	24	15
WDBR/L	35/27	27/26	30/30	34/27	27/30	26/28	24/26	19/16	23/26	19/13
WDCR/L	36/32	30/24	27/34	32/22	26/28	27/24	27/23	20/17	26/24	16/16
WDDR/L	29/31	30/28	28/29	27/26	24/27	27/26	27/18	20/17	20/23	15/19
WDE	31	25	26	27	16	24	24	16	15	12
ASC1R	*	*	138	*	126	125	L121	112	*	104
ASC2R	135	*	*	125	135	131	141	131	130	112
ASC3R	48	46	53	52	49	52	51	48	48	53
ASC4R	112	120	132	*	124	131	115	*c.* 100	*c.* 113	*c.* 100
ASe1R	5.0	4.0	4.5	3.1	4.1	3.5	2.6	2.8	3.0	1.8
ASe2R	5.0	4.0	4.6	4.0	4.1	4.1	3.0	3.0	3.0	1.8
ASe3R	4.5	4.0	4.9	3.3	4.1	3.9	3.0	3.0	3.0	1.5
ASe4R	4.2	3.5	4.1	3.1	4.0	3.0	2.8	2.8	2.9	1.5
GiLC	9	9	9	9	9	9	9	9	9	9
FuL	22.0	24.9	28.1	22.0	23.2	23.2	20.0	19.3	16.6	13.0
FFL	10.6	11.3	12.1	9.8	13.1	13.3	7.0	7.9	6.5	7.0
PA	20.9	16.0	22.1	18.9	21.6	17.1	16.7	15.2	13.0	10.5
CaL	4.6	5.1	5.0	4.1	4.0	4.4	3.9	5.1	5.0	3.0
LL	10.8	9.1	10.1	8.0	8.3	9.9	7.1	9.3	8.1	4.8

notch and acutely keeled, triangular crest. Hood moderately deep (depth 34.1% beak length), projecting forward, with flattened bifid rostrum; hood with shallow posterior notch; lateral wings short (length 89.0% beak length); lateral wings with single weak fold.

Radula variable (Fig. 109F); rachidian asymmetric, either with single central cusp or with 1 or 2 asymmetric lateral cusps beside central cusp; 1st lateral bicuspid, inner heel with slight basal cusp, outer cusp largest; 2nd lateral with long base and single large cusp; marginal tooth tall, well developed; in one specimen an accessory marginal tooth developed; marginal plates well developed, rectangular.

ETYMOLOGY: After the NIWA fisheries research vessel *Kaharoa* as a token of gratitude for the excellent specimens this vessel has collected.

REMARKS: One of the most obvious characters differentiating this species from *Octopus australis* Hoyle, (in numeric terms), is mature hectocotylised arm sucker counts, this number being lower in *Octopus kaharoa* than *O. australis* Hoyle, 46–53 and 62–77 respectively (HASC *O. australis*, sourced Stranks & Norman 1992). In other respects these two species are sufficiently similar to be considered congeneric in a revised classification of the Octopodidae. *Octopus kaharoa* differs from the preceding species, *O. mernoo*, in hectocotylised arm and absolute arm sucker counts.

Enteroctopus Gould, 1852

TYPE SPECIES: *Enteroctopus megalocyathus* Gould, 1852

DIAGNOSIS (new): Species attain massive proportions; arms subequal in length; all arm pairs possess enlarged suckers of similar size; posterior salivary glands large; diverticulum of crop reduced or absent; penis and penis diverticulum of exagerated length, penis diverticulum oriented along anteroposterior axis of mantle, extending over renal and reproductive

Table 90. Raw measures for female *Octopus kaharoa* sp. nov. (* denotes damage).

	NZOI P-1110	NMNZ M.117697	NZOI Stn Z8435	NZOI Stn Z8434	NMNZ M.117697	NZOI Stn Z8425	NMNZ M.90379	NZOI Stn Z8527	NZOI Sn Z8431	NMNZ M.5632
TL	394	308	329	272	223	262	237	258	257	149
ML	91.2	85.6	79.5	67.1	66.0	62.0	60.0	59.6	55.8	39.8
MW	58.0	37.1	34.5	36.2	31.0	37.0	41.0	38.3	29.8	24.5
HdL	16.8	15.4	18.5	13.0	18.0	14.0	18.1	14.2	14.0	14.1
HdW	36.7	25.0	22.5	21.1	24.0	22.5	27.1	23.9	20.2	18.6
EO	8.0	5.1	6.1	5.1	2.2	5.0	3.0	6.0	5.0	2.0
AL1R/L	195/226	160/157	160/205	165/171	129/143	162/187	110/154	163/152	157/132*	104/96
AL2R/L	190*/286	215/175*	218/241*	193/158	157/156	216/232	148/185	102*/194	194/185	115/115
AL3R/L	276*/243*	196/203	211/210*	146/180	151/132	193/184*	143*/174	168/167	131*/178	106/105
AL4R/L	231/141*	182/166	210/210	175/166	131/137	181/162	138/104	147/149	157/160	91/95
WDA	34	27	38	30	24	45	29	23	18	20
WDBR/L	45/46	39/30	27/44	37/31	25/32	42/43	30/28	31/28	25/20	24/24
WDCR/L	49/54	20*/37	38/48	40/28	33/31	45/41	28/33	27/27	28/26	22/21
WDDR/L	47/52	37/35	40/48	37/32	33/31	45/40	30/30	23/25	26/29	21/19
WDE	40	39	42	31	29	38	26	16	22	17
ASC1R	L156	112	1L 145	139	114	*	L150	144	137	126
ASC2R	L161	137	175	153	119	161	L174	L159	148	143
ASC3R	*	*c.* 126	159	*c.* 118	141	154	L182	158	L145	*c.* 134
ASC4R	155	131	148	141	108	141	149	148	132	*c.* 122
ASe1R	4.4	3.9	4.1	3.2	3.3	3.1	3.0	3.0	2.9	2.1
ASe2R	5.0	3.8	4.1	3.7	3.1	3.4	3.0	3.1	3.0	2.5
ASe3R	5.0	3.4	4.0	3.0	3.0	4.0	3.1	3.0	2.5	2.2
ASe4R	4.3	3.8	3.8	3.0	3.0	3.1	2.8	3.0	3.0	2.1
GiLC	9	9	9	9	8	9	9	9	9	8
FuL	41.3	26.1	34.0	27.0	20.5	25.8	18.1	21.6	21.1	14.0
FFL	22.0	14.0	18.0	18.0	10.0	8.3	14.0	11.7	12.4	10.5
PA	35.0	25.0	18.0	21.5	22.4	22.2	26.1	19.8	15.0	16.5

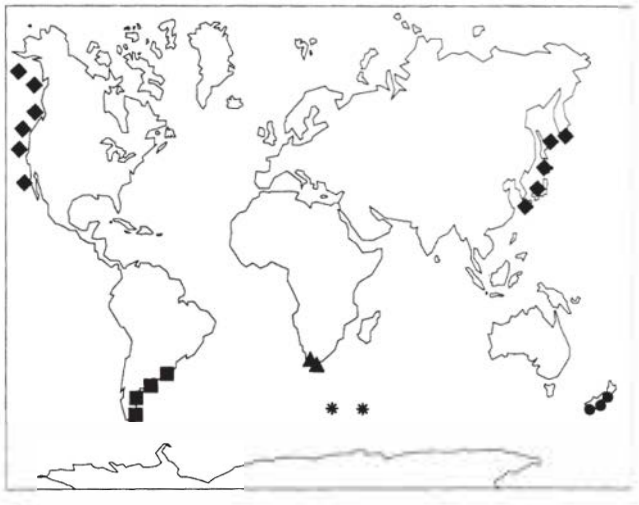


Figure 110. Recognised distribution of ***Enteroctopus***. ● *E. zealandicus* (Benham); ▲ *E. magnificus* (Villaneuva *et al.*); ✳ *E.* cf. *magnificus* (Villanueva *et al.*); ■ *E. megalocyathus* (Gould); ◆ *E. dofleini* (Wülker) species complex.

tissues to anteriormost point of visceral mass; membranes between renal tissue and ventral inner surface of mantle absent, interpallial septum extends to anteriormost point along ventral inner surface of mantle.

Enteroctopus zealandicus (Benham, 1944)

(Figs 112–114)
(Tables 91–95

Pinnoctopus cordiformis (not Quoy and Gaimard): Filhol 1885: 521.

Octopus maorum (not Hutton): Filhol 1885: 520–521; Dell 1952 (*fide* Filhol): 15; Batham 1957 (*partim*, type *Paroctopus zealandicus* Benham): 636–637.

Paroctopus zealandicus Benham, 1944a: 256–259, pl. 40, figs 1–4; Powell 1946: 100.

Octopus zealandicus: Dell 1951: 97, fig. 19; 1952: 28–29, pl. 6, figs 2–4; Powell 1957: 125; 1962: 125; 1976: 133; 1979: 444.

Octopus dofleini (not Wülker, 1910): Imber 1992: 248; Spencer & Willan 1995: 53.

TYPE MATERIAL: (37 specimens, 19 male [M], 16 female [F], 1 sex indet., 3 beaks): Neotype: NMNZ M.118251, M, ML

270.0 mm, *c.* 50°40' S, 167°10' E, 522 m, -/05/1992, f.v. *Peterson*.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.67300, M, ML 15.0 mm, 41°43.2' S, 174°27.1' E, 47 m, 15/12/1978, f.r.v. *James Cook* Stn J19/033/78; NMNZ M.118990, 3F, ML 202.0, 201.0, 141.0 mm, 42°05–43°08' S, 176°26–177°05' E, 368–411 m, 27/12/1994–18/01/1995; NMNZ M.118853, M, ML 247.0 mm, 42°53–43°08' S, 176°04–177°00' E, 370–420 m, -/12/1994, f.v. *Peterson*, coll. A. France; NZOI Stn Z8529, 2M, ML 90.1, 70.2 mm, 42°54–43°08'S, 176°26–177°05'E, 368–411m, 27/12/1994, f.v. *Peterson*; NMNZ M.118329, M, ML 250.0 mm, 43°00' S, 176°47' E, 378–380 m, -/03/1994, f.v. *Peterson*; NMNZ M.117881, F, ML 270.0 mm, 43°46.33' S, 176°32.53' E, 451–461 m, 16/01/1994, f.r.v. *Tangaroa* Stn 9401/84; NMNZ M.117883, M, ML 228.0 mm, 44°01.51' S, 179°08.66' W, 290–300 m, 11/01/1994, f.r.v. *Tangaroa* Stn 9401/55; NZOI Stn Z8677, F, ML 165.0 mm, FPT, 44°08.54–08.13' S, 178°37.83–41.97' W, 482–483 m, BT 6.9°C, 13/01/1997, f.r.v. *Tangaroa* Stn TAN9701/059; NMNZ M.90402, M, ML 10.5 mm, 46°32.5' S, 166°41' E, 389–420 m, Foveaux Strait, 20/11/1970, f.r.v. *James Cook* Stn J22/033/1970; NZOI Stn A723, M, ML 9.8 mm, 49°42' S, 178°50.3' E, 119 m, 07/11/1962; NMNZ M.90339 M, ML 16.1 mm, Ringdove Bay, Antipodes Islands, *c.* 49°43' S, 178°49' E, coll. R.K. Dell, 07/11/1950; NMNZ M.110992, F, ML 97.6 mm, 50°37' S, 167°12' E, 155 m, 10/03/1990, f.v. *Pravoved*, tow 156; NMNZ M.118322, 2M, ML 143.0, 99.0 mm, 50°40' S, 167°06' E, 367–528 m, -/02/1994, f.v. *Peterson*; NMNZ M.118336, M, ML 95.0, 78.4 mm, F, ML 62.2 mm, 50°40'S, 167°06'E, 367–528 m, -/02/1994, f.v. *Peterson*; CM AQ 115, 3 beaks, *c.* 50°40' S, 166°30' E, Auckland Islands, 18/01/1943 (ex. stomach contents sea lion); NMNZ M.118251, 3M, ML 272.0, 270.0, 155.0 mm, 3F, ML 280.0, 250.0, 108.5 mm, *c.* 50°40' S, 167°10' E, 522 m, -/05/1992, f.v. *Peterson*; NMNZ M.109065 2M, ML 140.5, 98.5 mm, 50°44.1' S, 166°57.1' E, 164 m, 14/04/1994, f.v. *Banshu Maru 8*, Stn 88/82/329; NMNZ M.118812, M, ML 31.1 mm, 51°10' S, 166°37' E, 490–510 m, 31/10/1994, f.v. *Peterson*; NMNZ M.95256, M, ML *c.* 61 mm, Campbell Island, between Camp Garden Coves, after tidal wave, *c.* 52°30' S, 169°05' E, 24/05/1960, coll. Rae Poppleton; NMNZ M.90373, M, ML 39.0 mm, Campbell Island, *c.* 52°30' S, 169°05' E, 28/10/1965, coll. C.M. Clark; NMNZ M.90439, M, ML 12.4 mm, Campbell Island, *c.* 52°30' S, 169°05' E, 01/02/1968, coll. P.E. Roberts; NMNZ M.24120, F, ML 194.0 mm, *c.* 52°33' S, 169°07' E, dead, washed up Tucker Stream, Campbell Island; NMNZ M.93099, F, ML 19.5 mm, Tucker Cove jetty, Campbell Island, *c.* 52°33' S, 169°07' E, coll. A. Wright, 03/01/1963; NMNZ M.11015, F, ML 118.5 mm, *c.* 52°34' S, 169°12' E, Perserverance Harbour, Campbell Island, 1956, coll. Poppleton; NMNZ M.90351, F, ML 24.0 mm, 0–4 m, beside wharf, Perseverance Harbour, Campbell Island, *c.* 52°34' S, 169°12' E, coll. P.E. Roberts, 01/02/1968; NMNZ M.90408, sex indet., ML 19.5 mm, Perseverance Harbour, Campbell Island, 8 m, *c.* 52°34' S, 169°12' E, coll. J.M. Moreland, 17/01/1961; NMNZ M.90301, F, ML 84.0 mm, Perseverance Harbour, Campbell Island, *c.* 52°34' S, 169°12' E, sublittoral.

REFERENCE MATERIAL (*Enteroctopus* sp.): BMNH 1868.7.10.12, F, ML 22.6 mm, Sandy Point, Straits of Magellan, coll. Dr Cunningham, pres. Lords of the Admiralty; BMNH 1851.1.24.9, sex indet., ML 7.8 mm, Tierra del Fuego, *c.* 3 m, Leg. Charles Darwin Esq.

RECOGNISED DISTRIBUTION (Fig. 111, p. 172): New Zealand, east coast of South Island, Chatham Rise, Campbell Plateau, Stewart, Auckland and Antipodes Islands. Southernmost specimens frequently littoral, extending down to *c.* 530 m, northernmost specimens usually bathyal, *c.* 300–522 m, although known from 47 m.

DIAGNOSIS: Massive, smooth-bodied octopods with short to long subequal arm length, about 48–81% TL; non-hectocotylised arm sucker counts 135–252, hectocotylised arm sucker counts 80–91; moderate to large suckers on all 4 arm pairs (ASe about 10–18% ML); 12 or 13 outer gill lamellae per demibranch; hectocotylised third right arm with ligula of exaggerated length, in mature specimens to about 20% arm length; penis and diverticulum of exaggerated length.

DESCRIPTION: Adult animal attains massive size (ML to 272 mm, TL to 1362 mm); body slender to stocky (Figs 112A, B, 113A, B). Mantle ovoid, broad (MW about 51–123% ML), dorsoventral compression, lateral keel or fold of skin, and ventral longitudinal groove or depression absent. Head well developed, small to large, wider than long, narrower than mantle (HdL about 19–37% ML; HW about 29–76% ML), separated from mantle by weak preocular constriction. Orbits large, dorsolaterally oriented, situated above base of arm pairs 1 and 2; eye apertures dorsolaterally oriented. Funnel moderately long to very long (FuL about 26–53% ML), well developed, base entirely free of brachial crown. Nuchal constriction poorly developed.

Brachial crown robust, wider than head. Arms thick, square to ovoid in section, very short to long (AL about 48–81% TL), gradually tapering to not unduly delicate tips; no consistent disparity in relative arm lengths apparent. Web shallow to deep, about 10–30% longest arm length, with well-developed web extension along ventrolateral surfaces of each arm almost to arm tip, extending little along dorsolateral face of arms 1–4; web formula variable, sectors A and E usually most shallow, sectors C, B deepest, with no consistent disparity in relative sector depths. Suckers biserial, with 10–13 suckers between beaks and web margin on dorsal arm pair 1; distal arm tip suckers not minute. Arm sucker counts variable, moderately high to high, ASC 135–252; suckers extend to arm tips. Sucker size similar in male and female, size moderate to very large (ASIe about 10–18); no suckers abruptly enlarged in either sex. Suckers with: reduced suction chamber; moderately well-constricted sucker aperture with 17–20 toothlike structures; extensively developed grasping ring with about 24–26 complete radial grooves and similar number of incomplete grooves; moderate development of muscular suction pad (Fig. 155K).

Male with third right arm hectocotylised, length shorter than opposite member (OAI about 73–81); with moderate number of suckers (ASC 80–91); terminal hectocotylised portion very long (Fig. 114A), length increasing with maturity (LLI 5.8–19.8), ligula with thick cheeks enclosing shallow groove, the inner surface of which (proximal to the calamus) bears 3 longitudinal rows of large, blocklike papillae, distally becoming indistinct and marked by 3 longitudinal central ridges; transverse rugae indistinct; calamus short (CaLI about 7.7–13.2), with groove extending entire structure length. Spermatophoral groove narrow, with thickened, crenulate web margin, with 10–12 erect papillae at junction with web margin; spermatophoral groove not markedly differentiated from web sector D.

Specimens fixed live or narcotised entirely smooth bodied; enlarged ocular cirri not apparent. Post-thaw-fixed specimens with entire dorsal and ventral body surfaces light orange coloured.

Pallial aperture wide, mantle attaches superior and anterior to dorsolateral surface of orbit; ad-siphonal pouches moderately well developed. Mantle musculature thick. Funnel collar moderately well developed; funnel retractor muscles large; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera as thin muscular riblet; membranes connecting renal tissue to ventral and inner surface of mantle absent. Penis and diverticulum disproportionately long; penis extends along antero-posterior axis of mantle; diverticulum extends anteriorly over viscera to testis sac, its length in mature males exceeding mantle length. Female with large ovary sac with slight connective tissue development with ventral and inner surface of mantle; genital apertures open at about 45° angle to interpallial septum, not extending to anus; anus with small, paired anal flaps. Gills large, with 12 or 13 lamellae per outer demibranch. Lateral muscles restraining digestive gland, visceral envelope, renal papilla and anal region without chromatophores. Funnel organ not preserved on any large post-thaw-fixed specimen; live-fixed juveniles with large W-shaped organ, with narrow inner and outer limbs, the outer slightly shorter than the inner.

Male reproductive system (Fig. 114B) with long, thick, strongly convoluted proximal vas deferens; spermatophoral gland very long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Distal half of accessory gland moderately expanded, without apparent terminal modification or volution. Spermatophore sac exceedingly long, slender, thin walled, containing up to 3 exceedingly long spermatophores to 316 mm length. Distal vas deferens short, thick; penis diverticulum single, large, long, thick walled; penis large, stout, about 50% diverticulum length, genital aperture subterminal. Mature female (Fig. 114C) with large ovary sac (about 67% ML in greatest dimension); proximal oviducts depart ovary sac through common antrum, ducts narrow, length about 50% that of distal ducts; oviducal gland large, with large radially striate blackened distal hemisphere and smaller lighter coloured proximal hemisphere. Distal oviducts appreciably swollen, with moderate U-twist; genital aperture terminal, porelike, without secondary modification. Mature eggs numerous, thousands, teardrop-shaped, small, to 12.5 x 2.3 mm, each with long stalk and about 7 or 8 longitudinal striations running the entire egg length.

Alimentary canal (Fig. 114D) with large buccal bulb, length about 29% ML; anterior salivary glands large, heart-shaped, loosely applied to posterior margin of buccal bulb, of length about 53% buccal bulb greatest dimension; anterior oesophagus long, narrow, enters crop dorsally; posterior salivary glands heart-shaped to broadly triangular, large, length about 97% buccal bulb greatest dimension, about 28% ML. Crop well developed, anterior diverticulum variably developed, present as short anterior prominence or absent. Posterior oesophagus muscular, thick-walled. Stomach massive, with 3 apparent sections, basal thin walled, central thick walled, and distal thin walled; stomach with undivided lumen. Spiral caecum smaller than stomach, of 1.5 radially striate volutions. Intestine long, about 1.5 times oesophagus length, thin walled, dilated for entire length, particularly central half; anal flaps paired, small. Digestive gland large, broadly heart-shaped, with anterior peaks; pancreas well developed; ink sac narrow, long, about 44% digestive gland length, superficially embedded in surface of digestive gland; ink duct short, opening into base of anus. Stomach contents identify a diet large comprising brachyuran crabs.

Upper beak (Fig. 114E) depressed (height 90.4% length); hood and lateral walls black, margins translucent; hood moderately deep (depth 39.2% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, slightly deflected down; jaw with single broad, low tooth. Lateral walls straight sided; crest squared, without lateral wall fold. Lower beak (Fig. 114E) moderately tall (height 70.7% width); hood, lateral wall and wings black, lateral wing and wall margins translucent. Lateral wall with deep, acute-angled V-shaped basal notch and keeled crest. Hood moderately deep (depth 34.8% beak length), with flattened chisel-like to weakly bifid

Table 91. Indices, formulas, and counts for post-thaw-fixed male *Enteroctopus zealandicus* (Benham) (* denotes damage).

	NMNZ M.118251	NMNZ M.118251	NMNZ M.118251	NMNZ M.109065	NZOI Stn Z8529	NMNZ M.90373
MWI	51.5	81.5	64.2	66.6	57.7	94.9
HdLI	19.1	23.0	25.2	24.9	31.1	37.2
HdWI	28.5	44.4	43.2	34.2	41.1	73.6
EOI	3.9	8.3	8.5	9.3	10.3	9.0
ALI1–4	61.7–76.0	55.8–72.2	*	54.3–74.7	47.7–78.6	66.7–80.0
AFR	?2.1.3.4	2.4.1.3	*	*	*	?1=2.4.3
AFL	?3.2.1.4	*	*	*	2.1.4.3	2.1.4.3
WDIA–E	17.4–30.4	14.4–20.0	*	12.9–28.0	11.6–20.2	17.4–28.0
WFR	A.B.E.C.D	D.C.E.B.A	C.D.B.E.A	B.D.C.A.E	C.B.A.D.E	B.A.C.D.E
WFL	D.C.A.E.B	D.C.B.E.A	E.D.C.B.A	C.D.B.A.E	B.C.D.A.E	B.C=A.D.E
ASC1–4	212–218	246–248	*	207–209	149–179	154–174
ASIn1–4	11.6–13.2	15.6–17.6	13.6–14.5	12.8–15.7	10.0–11.1	15.4–17.9
FuLI	26.3	26.3	52.8	32.0	30.5	41.3
FFuI	9.6	23.1	17.9	8.9	8.0	5.1
PAI	29.2	44.4	43.9	30.9	29.9	60.5

Table 92. Indices, formulas, and counts for post-thaw-fixed female *Enteroctopus zealandicus* (Benham) (* denotes damage).

	NZOI Stn Z8677	NMNZ M.11015	NMNZ M.118251	NMMZ M. 110992
MWI	123.0	62.4	75.1	46.3
HdLI	27.3	23.8	24.4	30.2
HdWI	76.4	38.8	47.9	40.8
EOI	7.6	12.3	9.2	13.3
ALI1–4	66.9–80.5	51.5–74.4	56.0–72.0	56.8–73.7
AFR	1.2.4.3	*	1.3.4.2	*
AFL	*	*	2.1.4.3	*
WDIA–E	10.7–23.9	10.4–22.1	14.9–23.7	19.0–25.7
WFR	B.C.D.A.E	D.C.B.E.A	C.B=D.A.E	D.C.B.E.A
WFL	C.B=D.A.E	C.B=E.D.A	A.B.C=D.E	D.C.B.E.A
ASC1–4	194–252	161–240	179–202	135–199
ASIn1–4	16.1–17.0	11.1–11.4	10.1–12.9	10.2–11.8
FuLI	39.4	37.6	35.9	36.4
FFuI	27.9	16.5	15.7	19.0
PAI	74.5	39.4	46.1	35.3

Table 93. Indices and counts for male *Enteroctopus zealandicus* (Benham) (* denotes damage).

	NMNZ M.118251	NMNZ M.118251	NMNZ M.118251	NMNZ M.109065	NZOI Stn Z8529
OAI	81.2	77.9	*	72.7	78.4
ASC3R	91	85	81	85	80
CaLI	10.2	7.7	13.2	10.3	8.3
LLI	19.8	17.5	15.7	11.7	5.8

Table 94. Raw measures for male *Enteroctopus zealandicus* (Benham) (* denotes damage, † denotes regrowth).

	NMNZ M.118251	NMNZ M.118251	NMNZ M.118251	NMNZ M.109065	NZOI Stn Z8529	NMNZ M.90373
TL	908	1362	702	632	440	201
ML	272.0	270.0	155.0	140.5	90.1	39.0
MW	140.0	220.0	99.5	93.6	52.0	37.0
HdL	52.0	62.0	390.	35.0	28.0	14.5
HdW	77.5	120.0	67.0	48.0	37.0	28.7
EO	10.5	22.5	13.2	13.0	9.3	3.5
AL1R/L	641/678	907/983	305*/500*	456/432	266/278	161/151
AL2R/L	678/689	910*/175*	540*/245*	442/272†	169†/346	161/159
AL3R/L	560/690	760/975	438/460*	343/472	210/268	57*/143
AL4R/L	592*/580*	912/945*	380†/506	267†/417*	299/269	134/145
WDA	155	142	83	86	58	41
WDBR/L	145/120	143/150	110/85	116/107	63/70	45/42
WDCR/L	132/190	165/180	154/93	95/132	66/65	38/41
WDDR/L	126/210	191/197	138/100	97/115	54/62	35.5/35
WDE	134	160	108	61	40	28
CaL	11.3	10.2	9.1	4.1	2.0	*
LL	111.0	133.0	68.9	40.0	12.1	*
ASC1R	212	248	*	207	149	154
ASC2R	218#	*	*	209	L168	174
ASC3R	91	85	81	85	80	*
ASC4R	*	246	L226	*	179	168
ASe1R	36.0	43.4	21.1	19.1	10.0	6.5
ASe2R	34.0	47.5	22.1	20.0	L10.0	7.0
ASe3R	35.0	47.0	22.5	22.1	10.0	6.4
ASe4R	31.5	42.0	22.4	18.0	9.0	6.0
GiLC	12	12	12	13	12	12
FuL	71.4	71.0	81.9	45.0	27.5	16.1
FFL	26.0	62.3	27.8	12.5	7.2	2.0
PA	79.4	120.0	68.0	43.4	26.9	23.6

rostrum; hood with shallow posterior notch; lateral wings very long (length 104.2% beak length); lateral wings with single weak fold.

Radular dentition simple (Fig. 114F); rachidian well developed, narrow based, with 2 asymmetrically disposed lateral cusps; 1st lateral tooth with long inner heel and single outer cusp; 2nd lateral broad based, wider than rachidian, with short inner heel and large cusp; marginal tooth slender, long, cusp less robust that that of 2nd lateral; marginal block rectangular, well developed. Repeat seriation every 3 or 4 transverse rows.

REMARKS: At the time Benham described *E. zealandicus* his eyesight was failing (Dell pers. com.), which probably accounts for the inconsistency in the number of outer gill lamellae cited for the holotype by Benham (9), and Batham (1957), 12 or 13. Batham considered insufficient differences existed between *E. zealandicus* and *Octopus maorum* Hutton to warrant their separation, affecting the cursory synonymy of these two species in the concluding paragraphs of her paper. Although the type of *Paroctopus zealandicus* (Benham) has been destroyed, several characters described for this species are clearly inconsistent with those of *Pinnoctopus cordiformis* (= *Octopus maorum*). A neotype for *Enteroctopus zealandicus* (Benham) is designated here.

Enteroctopus zealandicus, like *E. megalocyathus* (*fide* Re 1980), probably migrates from shallow to deeper waters to breed; juvenile *E. zealandicus* is common in littoral subantarctic waters, whereas mature specimens are only encountered in considerably deeper waters. Whereas *E. megalocyathus* has large ovarian eggs 9–17 mm in length, indicative of benthic young (Re 1994), *E. zealandicus* has smaller ovarian eggs to 12.5 mm, and like *E. dofleini*, planktonic young. In other respects *E. zealandicus* and *E. megalocyathus* are extremely similar.

Although the holotype of *O. dofleini* is lost, Pickford considered the type to be an immature male of the giant Japanese species. Okutani *et al.* (1987) cited for the latter species: large size, TL up to 3 m; ovoid mantle, with ML in excess of MW; ornamentation of

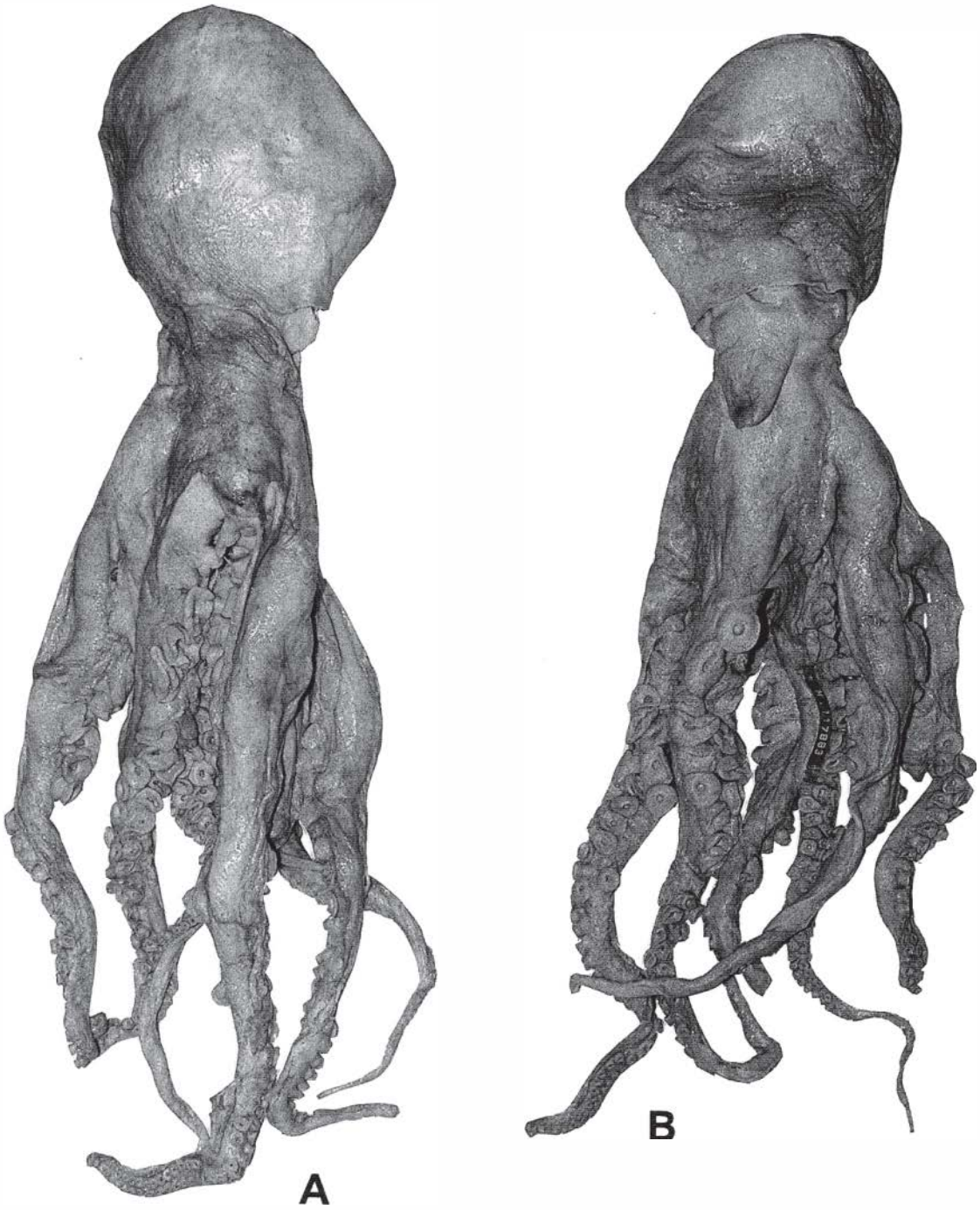


Figure 112. ***Enteroctopus zealandicus*** (Benham, 1944): **A, B**, NMNZ M.117883, male, ML 228 mm.

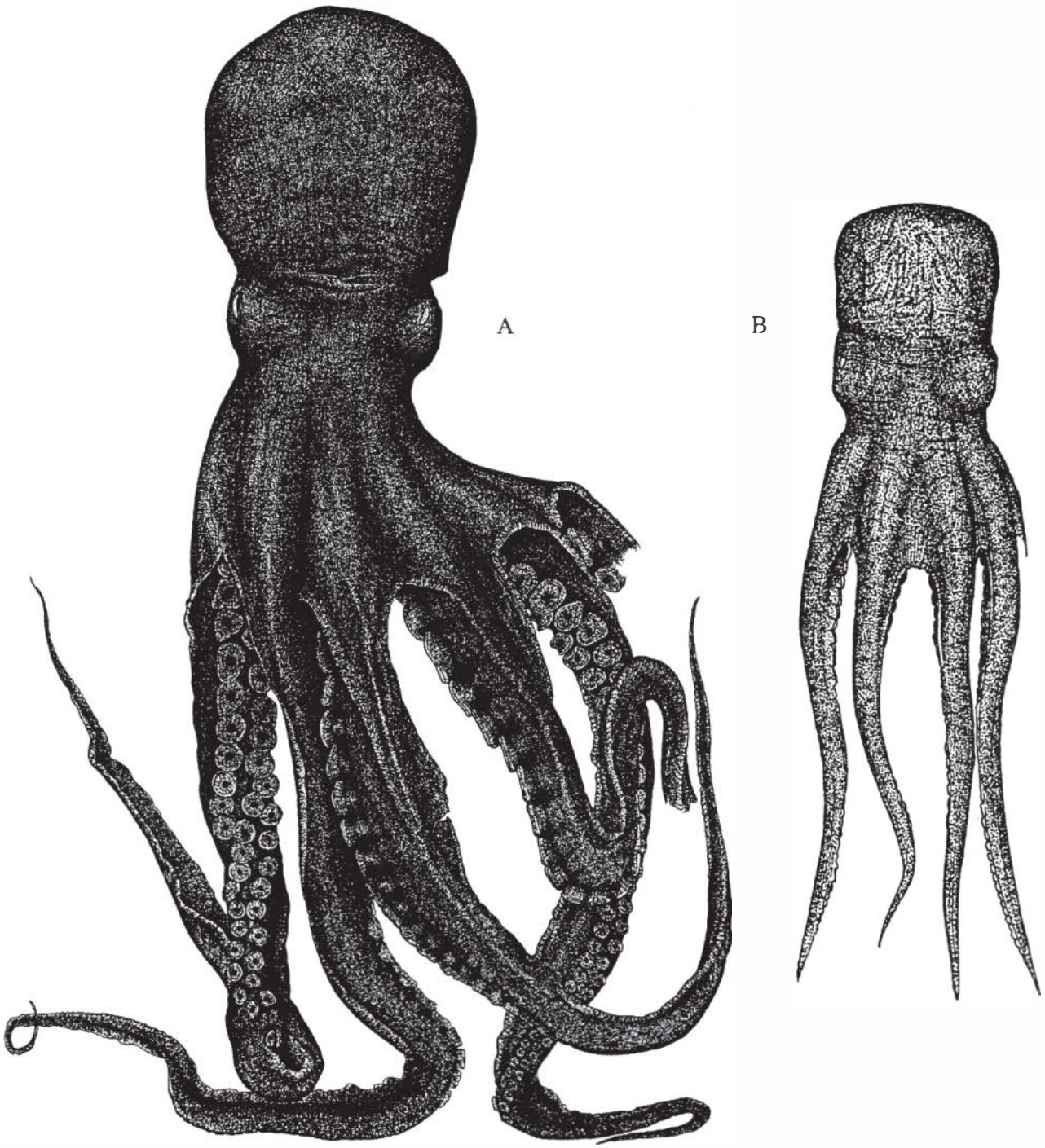


Figure 113. ***Enteroctopus zealandicus*** (Benham, 1944): **A**, NMNZ M.90301, female, ML 84 mm. **B**, NMNZ, M.90408, sex indet., ML 19.5 mm.

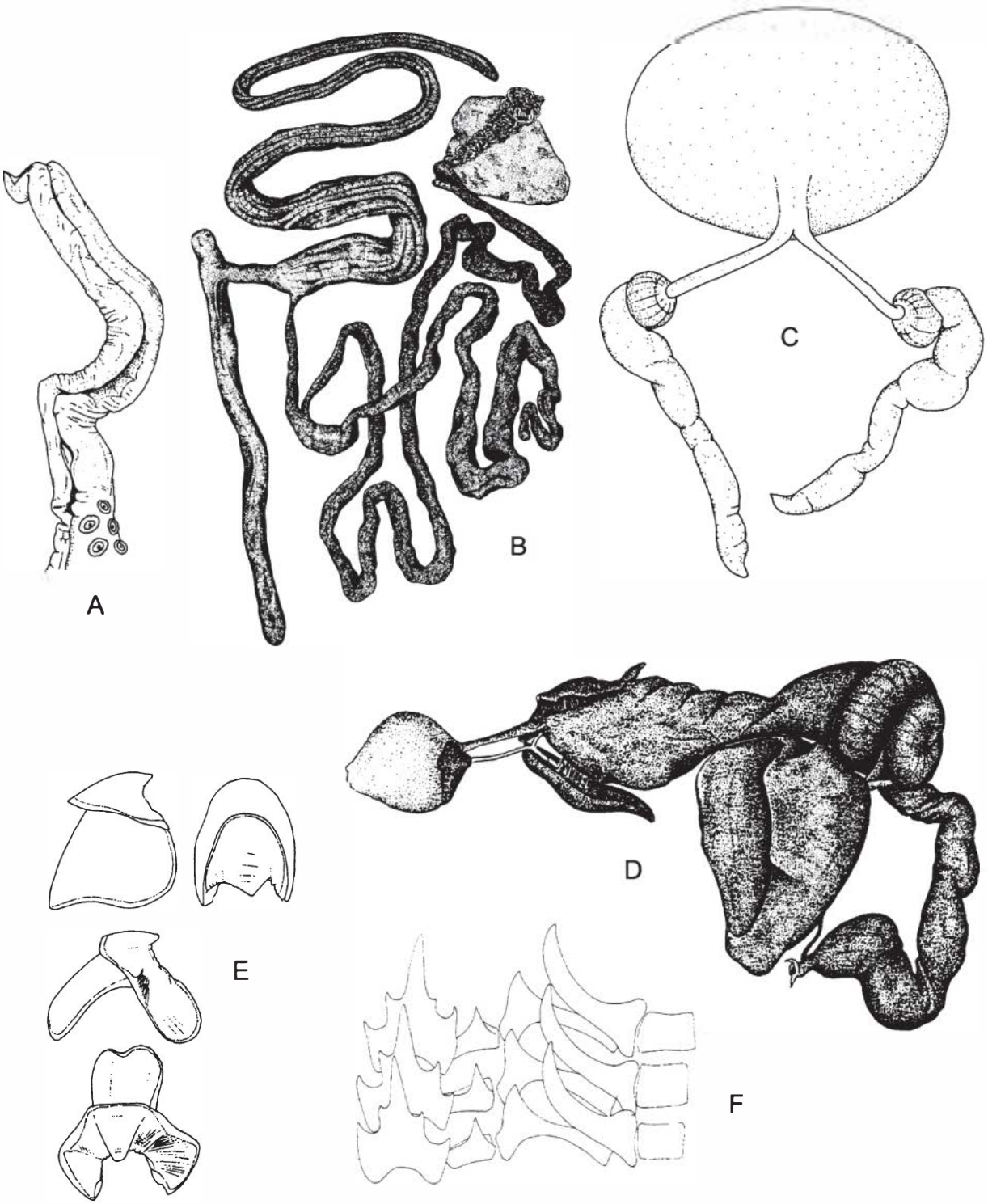


Figure 114. *Enteroctopus zealandicus* (Benham, 1944): Anatomy. **A**, NMNZ M.118251, male, Ml 155 mm. **B**, NMNZ M.118329, male, ML 250 mm. **C**, NZOI Stn Z8677, female, ML 165 mm. **D**, **F**, NMNZ M.90301, female, ML 84 mm. **E**, NMNZ M.95256, male, male, about 61 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 95. Raw measures for female *Enteroctopus zealandicus* (Benham) (* denotes damage, † denotes regrowth, # denotes terminal suckers difficult to count).

	NZOI Stn Z8677	NMNZ M.11015	NMNZ M.118251	NMNZ M. 110992
TL	937	540	550	407
ML	165.0	118.5	108.5	97.6
MW	203.0	74.0	81.5	45.2
HdL	45.0	28.2	26.5	29.5
HdW	126.0	46.0	52.0	39.8
EO	12.5	14.6	10.0	13.0
AL1R/L	727/754	243†/383	375/371	270*/234*
AL2R/L	701/627	402/372*	308/396	290*/300
AL3R/L	655/511*	278/386	373/320	257*/298
AL4R/L	691/705	392/346*	357/322	239*/231
WDA	137	42	75	57
WDBR/L	180/140	61/77	90/64	66/60
WDCR/L	177/167	84/83	94/63	72/63
WDDR/L	142/140	89/62	90/63	77/67
WDE	81	77	59	59
ASC1R	205	L238	179	*
ASC2R	194	240#	L196	L199
ASC3R	252	195#	202	L198
ASC4R	250	161#	187	L135
ASe1R	26.5	L13.5	12.8	11.0
ASe2R	28.0	13.1	11.0	11.0
ASe3R	28.0	13.1	13.5	11.5
ASe4R	26.5	13.1	14.0	10.0
GiLC	12	12	12	12
FuL	65.0	44.5	39.0	35.5
FFL	46.0	19.5	17.0	18.5
PA	123.0	46.7	50.0	34.5

many pointed warts, frequently connected with each other to form fleshy ridges, with dorsal mantle surfaces more warty, and 4 prominent tubercles arranged approximately in a diamond shape; with 3 or 4 superocular cirri, 1 larger than the others and assuming a quadrate shape; arms about 75% TL; web sectors A and E slightly shallower than B, C, and D, with web extending about 25% arm length; ASC about 250–300 per arm; proximal 8 to 9th through to 13 to 14th suckers larger than other sucker pairs, with a gradual reduction in sucker size towards arm tips; male third right arm hectocotylised, about 15% of the total arm length with a cylindrical, slender ligula ending in a blunt conical tip, a deep groove with numerous transverse striae; calamus small but with clear spermatophoric groove; total gill lamellae counts about 25; and with a slender prominent penis. As illustrated by Sasaki (1929) the mantle cavity of *Octopus dofleini* has a long penis diverticulum extending to the anteriormost end of the mantle. Although *Octopus dofleini* and *Enteroctopus zealandicus* are obviously similar in many respects, they differ fundamentally in skin sculpture, being smooth in the latter, papillose in the former, total arm sucker counts lower in *E. zealandicus*, and mature ligula length as a function of hectocotylised arm length, higher in *E. zealandicus*.

The recently described South African *Enteroctopus magnificus* is most similar to *E. zealandicus*. Without the benefit of examining any specimens of *E. magnificus*, however, one character state does serve to distinguish them (hectocotylised arm sucker count: 97–110 for *E. magnificus* (*fide* Villanueva *et al.* 1991: 42, Table 2), 80–91 for *E. zealandicus*).

Species of *Enteroctopus* are more similar to species of the Bathypolypodinae (see below), than to any species of *Octopus* (*s.s.*), *Octopus* Groups 1–3, or *Pinnoctopus*. Quite a number of character states are common to *Enteroctopus* and *Octopus* Group 4 species, although these two octopus morphologies differ in characters associated with the male reproductive system and hectocotylised arm.

A second species of *Enteroctopus* may occur in New Zealand waters, based on a single large female trawled off East Cape, North Island, at about 900 m depth. This specimen appears to differ from *E. zealandicus* in possessing smaller suckers and in having a comparatively slender body (one sucker from this specimen is illustrated in Fig. 155L). Additional material is required to resolve the status of this specimen.

Subfamily **BATHYPOLYPODINAE** Robson, 1932

Suckers biserial; ink sac absent; crop large, with diverticulum reduced or absent; radula octopus-like to degenerate; funnel organ W, VV, or IIII (after Voss 1988a: 269).

REMARKS: During the course of this research representatives of a number of species of *Benthoctopus*, *Bathypolypus*, and *Grimpella* have been examined. An abridged treatment of some of these species follows as interim justification for recognising the New Zealand species as *Benthoctopus* (*sensu lato*); a more detailed appraisal of relationships between the various species attributed to the genera *Bathypolypus* and *Benthoctopus* is currently in preparation. The relationship between these species and the New Zealand complement of species is discussed in respective remarks sections.

REFERENCE MATERIAL EXAMINED:

Bathypolypus arcticus (Prosch) (11 specimens, 3 male [M], 8 female [F]): NMNZ M.268578, M, ML 30.2 mm, 6F, ML 31.1, 29.5, 29.4, 29.0, 28.8, 24.0 mm, 24°N, 81°W, Straits of Florida, 146 m, -/11/1978, det. R. Toll, ex. UMML, pres.

Table 95. Raw measures for female *Enteroctopus zealandicus* (Benham) (* denotes damage, † denotes regrowth, # denotes terminal suckers difficult to count).

	NZOI Stn Z8677	NMNZ M.11015	NMNZ M.118251	NMNZ M. 110992
TL	937	540	550	407
ML	165.0	118.5	108.5	97.6
MW	203.0	74.0	81.5	45.2
HdL	45.0	28.2	26.5	29.5
HdW	126.0	46.0	52.0	39.8
EO	12.5	14.6	10.0	13.0
AL1R/L	727/754	243†/383	375/371	270*/234*
AL2R/L	701/627	402/372*	308/396	290*/300
AL3R/L	655/511*	278/386	373/320	257*/298
AL4R/L	691/705	392/346*	357/322	239*/231
WDA	137	42	75	57
WDBR/L	180/140	61/77	90/64	66/60
WDCR/L	177/167	84/83	94/63	72/63
WDDR/L	142/140	89/62	90/63	77/67
WDE	81	77	59	59
ASC1R	205	L238	179	*
ASC2R	194	240#	L196	L199
ASC3R	252	195#	202	L198
ASC4R	250	161#	187	L135
ASe1R	26.5	L13.5	12.8	11.0
ASe2R	28.0	13.1	11.0	11.0
ASe3R	28.0	13.1	13.5	11.5
ASe4R	26.5	13.1	14.0	10.0
GiLC	12	12	12	12
FuL	65.0	44.5	39.0	35.5
FFL	46.0	19.5	17.0	18.5
PA	123.0	46.7	50.0	34.5

many pointed warts, frequently connected with each other to form fleshy ridges, with dorsal mantle surfaces more warty, and 4 prominent tubercles arranged approximately in a diamond shape; with 3 or 4 superocular cirri, 1 larger than the others and assuming a quadrate shape; arms about 75% TL; web sectors A and E slightly shallower than B, C, and D, with web extending about 25% arm length; ASC about 250–300 per arm; proximal 8 to 9th through to 13 to 14th suckers larger than other sucker pairs, with a gradual reduction in sucker size towards arm tips; male third right arm hectocotylised, about 15% of the total arm length with a cylindrical, slender ligula ending in a blunt conical tip, a deep groove with numerous transverse striae; calamus small but with clear spermatophoric groove; total gill lamellae counts about 25; and with a slender prominent penis. As illustrated by Sasaki (1929) the mantle cavity of *Octopus dofleini* has a long penis diverticulum extending to the anteriormost end of the mantle. Although *Octopus dofleini* and *Enteroctopus zealandicus* are obviously similar in many respects, they differ fundamentally in skin sculpture, being smooth in the latter, papillose in the former, total arm sucker counts lower in *E. zealandicus*, and mature ligula length as a function of hectocotylised arm length, higher in *E. zealandicus*.

The recently described South African *Enteroctopus magnificus* is most similar to *E. zealandicus*. Without the benefit of examining any specimens of *E. magnificus*, however, one character state does serve to distinguish them (hectocotylised arm sucker count: 97–110 for *E. magnificus* (*fide* Villanueva *et al.* 1991: 42, Table 2), 80–91 for *E. zealandicus*).

Species of *Enteroctopus* are more similar to species of the Bathypolypodinae (see below), than to any species of *Octopus* (*s.s.*), *Octopus* Groups 1–3, or *Pinnoctopus*. Quite a number of character states are common to *Enteroctopus* and *Octopus* Group 4 species, although these two octopus morphologies differ in characters associated with the male reproductive system and hectocotylised arm.

A second species of *Enteroctopus* may occur in New Zealand waters, based on a single large female trawled off East Cape, North Island, at about 900 m depth. This specimen appears to differ from *E. zealandicus* in possessing smaller suckers and in having a comparatively slender body (one sucker from this specimen is illustrated in Fig. 155L). Additional material is required to resolve the status of this specimen.

Subfamily **BATHYPOLYPODINAE** Robson, 1932

Suckers biserial; ink sac absent; crop large, with diverticulum reduced or absent; radula octopus-like to degenerate; funnel organ W, VV, or IIII (after Voss 1988a: 269).

REMARKS: During the course of this research representatives of a number of species of *Benthoctopus*, *Bathypolypus*, and *Grimpella* have been examined. An abridged treatment of some of these species follows as interim justification for recognising the New Zealand species as *Benthoctopus* (*sensu lato*); a more detailed appraisal of relationships between the various species attributed to the genera *Bathypolypus* and *Benthoctopus* is currently in preparation. The relationship between these species and the New Zealand complement of species is discussed in respective remarks sections.

REFERENCE MATERIAL EXAMINED:

Bathypolypus arcticus (Prosch) (11 specimens, 3 male [M], 8 female [F]): NMNZ M.268578, M, ML 30.2 mm, 6F, ML 31.1, 29.5, 29.4, 29.0, 28.8, 24.0 mm, 24°N, 81°W, Straits of Florida, 146 m, -/11/1978, det. R. Toll, ex. UMML, pres.

N. Voss; NMNZ M.268576, 2M, ML 46.2, 28.3 mm, 2F, ML 28.3, 23.7, unlocalised, ex. Atlantic Reference Centre, Huntsman Marine Laboratory, Canada.

Bathypolypus faeroensis (Russell, 1909), det. R.B. Toll: neotype, USNM (not registered, on long-term loan), F, ML 74.5 mm, 67°21.5' N, 23°30' W, 480–485 m, 09/09/1973, FFS *Walter Herwig* Stn 630/73 (figs 115C–D).

Benthoctopus berryi Robson, 1924: holotype, BMNH 1924.9.9.23, F, ML 45.4 mm, S.W. of Cape Town, 2194 m (figs 117G–I, 154P); SAM S76, F, ML 95.0 mm, 28°37.8' S, 32°38.4' E, 1000–1200 m, 25/05/1976, R.S. *Meiring Nande* Stn SM 107 (figs 117G–I); SAM S2910, M, ML 128.2 mm, F, ML 106.3 mm, 32°22.0' S, 16°09.0' E, 1150 m, 14/01/1995, R.S. *Africana* Stn A17109-127-DT03; SAM S1951, M, ML 135.6 mm, 32°25' S, 16°17.6' E, 903 m, 10/02/1988, R.S. *Africana* Stn 6892/E011 (figs 118A–B).

Benthoctopus canthylus Voss & Pearcy 1990: holotype, USNM729993, F, ML 53.5 mm, 44°58.1' N, 126°35.8' W, 2795 m, 19/02/1971.

Benthoctopus januarii (Hoyle, 1885), det. R.B. Toll: UMML 31.1750, 2M, ML 51.3, 45.0 mm, 14°10' N, 81°55' W, 440–460 m, 21/05/1962.

Benthoctopus levis Hoyle, 1885: holotype, BMNH 1889.4.24.28–29, M, ML 46.0 mm, 52°59' S, 73°33' E, 137 m, 07/02/1874 (figs 117A–C, 154Q).

Benthoctopus magellanicus Robson, 1930: holotype, MNHN 1096, M, ML 56.8 mm, 49°00.30' S, 61°58.00' W, 146–145 m, 18/04/1927, NW of Falkland Islands (figs 117D–F, 154R).

Benthoctopus oregonae Toll, 1981: holotype, USNM 730015, M, ML 57.5 mm, 10°56'N, 67°38'W, 1080 m, 10/10/1963.

Benthoctopus oregonensis Voss & Pearcy 1990: holotype, USNM 729991, M, ML 92.0 mm, 44°37.0' N, 125°01.0' W, 1260 m, 06/08/1966.

Benthoctopus piscatorum (Verrill): Holotype, USNM 574641, F, ML *c.* 40 mm, off Nova Scotia, 219 m, -/10/1879 (figs 115A–B).

Benthoctopus robustus Voss & Pearcy 1990 (3 specimens, 2 male [M], 1 female [F]): holotype USNM 729994, M, ML 137.3 mm, 44°38.5' N, 126°03.8' W, 2800 m, 01/06/1963 (figs 116A–C); paratype USNM 730895, M, ML 114.0 mm, 52°27.42'N, 135°34.36'W, 3660 m, 16/10/1978. Additional material examined: SBMNH 42224, F, ML 115.0 mm, 30°57.9' N, 119°08.0' W, 3510 m, 17/12/1969 (det. F.G. Hochberg) (figs 116D–E).

Benthoctopus yaquinae Voss & Pearcy, 1991: holotype, USNM 729992, M, ML 88.5 mm, 44°48.8' N, 125°59.5' W, 2800 m, 12/01/1965.

Benthoctopus sp. A (Voss, MS idents. on labels) (2 specimens, 1 male [M], 1 female [F]): USNM 817339, M, ML 49.0 mm, 74°06' S, 175°05' W, 2350 m, 08/02/1968, r.v. *Eltanin*. USNM 817335, F, ML 74.5 mm, 72°27' S, 177°04' E, 1883–1890 m, 12/02/1968, r.v. *Eltanin* (figs 119A–C).

Benthoctopus sp.: USNM 817336, F, ML 46.0 mm, 75°03' S, 176°37' W, 801 m, 16/01/1968 (fig. 119D); USNM 817338, F, ML 64.0 mm, 72°27' S, 177°04' E, 1883–1890 m, 12/02/1969, r.v. *Eltanin* Stn 2121 (figs 119E–F).

Benthoctopus sp. SAM C.308690, *Benthoctopus* sp. nov., F, ML 75.0 mm, 35°28' S, 150°52–53' E, 933–978 m, 03/04/1984, f.r.v. *Kapala* Stn K84-4-1.

Grimpella thaumastocheir Robson (3 specimens, 1 male [M], 2 female [F]): SAM D17996, M, ML 32.5 mm, Sir Joseph Banks Group, Marum Island, N. Point, Sth Australia, in sand and rubble, 15–20 feet, 22/01/1985, coll. K. Gowlett-Holmes; SAM D17995, 2F, ML 30.2, 25.0 mm, 23/01/1986, Sir Joseph Banks Group, Reevesby Island, Sth Australia, in rocky rubble with *Posidonia*, 3–5 m, coll. N. Holmes, A. Horesfall.

The shallowest web sector in each of *Benthoctopus piscatorum*, *B. levis*, *B. berryi*, *B. magellanicus*, and *B. robustus* is moderately deep, whereas the deepest web sector is very deep. Whole-arm sucker counts in *B. piscatorum* and *B. robustus* are very low, while those of *B. levis*, *B. berryi* and *B. magellanicus* are low. Hectocotylised arm-sucker counts are unknown for *B. piscatorum*, but differ appreciably between two otherwise similar southern ocean species, *B. levis* (54) and *B. berryi* (62–69). The distinctive *B. magellanicus* has an arm-sucker count similar to that of *B. berryi* (60), but differs from this species most notably in skin papillation and pigmentation (blotched, reticulated pattern, and with the counter-pigmentation characteristic of *B. berryi* not apparent in *B. magellanicus*). The equally distinctive *B. robustus* has a very low hectocotylised arm-sucker count (42), which, along with a low total arm-sucker count and high gill-lamellae count, distinguish this species from all others. Suckers are small in all species other than *B. magellanicus*, which has moderately large suckers. It appears *B. robustus* and *B. piscatorum* are quite similar, and both are quite distinct from other described *Benthoctopus* species; the peculiar pigmentation and surface papillation of *B. magellanicus* renders this species quite unlike any other; *B. levis* and *B. berryi* are probably more closely related to each other than to any other described species.

Excluding *Bathypolypus faeroensis*, which has very low sucker counts similar to those of *B. piscatorum* and *B. robustus*, whole-arm sucker counts of *Benthoctopus* sp. A (herein) and *Benthoctopus* sp. (USNM 817338)

Table 97. Indices and formulas for *Benthoctopus berryi* Robson, 1924, additional material examined (* denotes damage, † denotes a character which was not measured).

	SAM S1951	SAM S2910	SAM S2910	SAM S76
ALI1–4[1]	55.5–72.4	60.4–76.6	66.9–72.4	†
WDIA–E	16.5–29.6	16.7–26.2	16.9–33.7	†
ASC1–4[2]	133–139	135*–142	139–154	137*–143*
ASC3R(M)	62	69	F	F
ASIn1–4	6.7–7.4	6.8–7.6	8.2–9.3	8.4–9.4
GiLC	8/8	9/8	9/8	9/9
CaLI	47.0	30.1	F	F
LLI	8.8	9.0	F	F

[1] Excludes AL3R male [2] Excludes ASC3E male

Table 96. Indices and formulas for *Benthoctopus* spp. (* denotes damage, † denotes a character which was not measured).

	B. piscatorum Holotype	*B. levis* Holotype	*B. berryi* Holotype	*B. magellanicus* Holotype	*B. robustus* Holotype[1]	*B. robustus* SBMNH
ALI1–4	49.3–60.7	†	†	57.4–73.0	†	55.3–61.6
WDIA–E	?25.3–33.0	19.3*–28.1*	20.0–29.7	26.2–42.2	†	22.6–38.7
ASC1–4	64–77	110–122	130–132	*–108	73–78	76–80
ASC3R(M)	F	54	F	60	42	F
ASIn1–4	5.0–6.3	6.5–8.0	7.3–7.9	11.3–12.3	†	5.1–5.7
GiLC	7/7	8/8	9/8	8/9	†	11/11
CaLI	F	63.0	F	30.9	†	F
LLI	F	8.8	F	9.5	†	F

[1] Holotype described by Voss and Percy (1996).

Table 98. Indices and formulas for *Benthoctopus* and *Bathypolypus* spp. (* denotes damage, † denotes a character which was not measured).

	Benthoctopus sp. A USNM 817339	*Benthoctopus* sp. USNM 817338	*Benthoctopus* sp. USNM 817336	*Benthoctopus* sp. A USNM 817335	*Bathypolypus faeroensis* Neotype
ALI1–4	55.1–74.9	60.6–72.0	58.4–73.4	†	†
WDIA–E	18.2–25.9	14.7–24.2	20.4–25.5	20.0–26.9	†
ASC1–4	99–103	104–110	118–161	99–108	70–79
ASIn1–4	8.2–9.6	7.8–9.4	6.5	6.2–6.7	†

Table 99. Raw measures for *Benthoctopus* spp. (REFERENCE MATERIAL EXAMINED: * denotes damage; † denotes character not measured/enumerated; ‡ denotes arm tip regrowth).

	B. piscatorum Holotype	*B. levis* Holotype	*B. berryi* Holotype	*B. magellanicus* Holotype	*B. robustus* Holotype[1]	*B. robustus* SBMNH
TL	150	†	†	256	†	302
ML	40.0	46.0	45.4	56.8	†	115.0
MW	34.5	40.6	49.4	61.0	†	96.0
HdL	18.0	18.4	21.0	16.0	†	20.0
HdW	29.0	32.9	42.5	49.5	†	63.0
EO	5.0	†	†	†	†	6.5
AL1R/L	88/88	116*/135*	146*/175	173/179	†	186/180
AL2R/L	74*/91	117/131	157*/175	164*/168*	†	184*/177
AL3R/L	83*/87	92/118	148/148	147/187	†	185/172
AL4R/L	77/74	126/113	138/138	95‡/170*	†	180/167
WDA	30	34	48	56	†	55
WDBR/L	*/30	38/35	50/47	62/68	†	67/63
WDCR/L	*/26	31/35	52/48	70/79	†	72/62
WDDR/L	*/23	38/35	40/40	60/61	†	64/63
WDE	12*	26	35	49	†	42
ASC1R	77	112	L132	108	‡/73	80
ASC2R	64*	110	L130	*	‡/74	69*
ASC3R	63*	54	132	60	42	76
ASC3LM	*	†	†	*	76	†
ASC4R	64	122	130	*	‡/78	76
ASn1R	2.5	3.3	3.6	6.8	†	5.9
ASn2R	2.0	3.7	3.4	6.5	†	6.1
ASn3R	2.5	3.2	3.3	7.0	†	6.5
ASn4R	2.5	3.0	3.3	6.4	†	6.1
GiLC	7/7	8/8	9/8	8/9	†	11/11
FuL	11.0	13.0	19.5	20.0	†	31.5
FFL	4.5	9.9	11.4	10.0	†	20.0
CaL	F	5.1	F	4.3	†	F
LL	F	8.1	F	13.9	†	F

[1] Holotype described by Voss and Percy (1996).

Table 100. Raw measures for *Benthoctopus berryi* Robson, 1924. (ADDITIONAL MATERIAL EXAMINED: * denotes damage; † denotes character not measured/enumerated; ‡ denotes arm tip regrowth.)

	SAM S1951	SAM S2910	SAM S2910	SAM S76
Sex	M	M	F	F
TL	537	593	492	452
ML	135.6	128.2	106.3	95.0
MW	105.0	94.5	115.0	106.5
HdL	40.5	32.0	38.0	32.5
HdW	75.2	56.0	81.5	80.1
EO	15.1	22.0	14.0	6.1
AL1R/L	389/120*	398*/445*	333*/356	302*/256*
AL2R/L	383/373	280*/454	349*/352*	334*/336*
AL3R/L	245/324	276/403	334/342	234*/330*
AL4R/L	324/298	358/402	329/310*	295/329*
WDA	86	88	87	70
WDBR/L	115/94	96/92	104/88	73/81
WDCR/L	98/101	87/119	120/94	80/88
WDDR/L	82/84	85/103	96/91	70/84
WDE	64	76	60	48
ASC1R	139	L135*	L150	143*
ASC2R	133	L142	*	143*
ASC3R	62	69	139	†
ASC3LM	†	†	†	137*
ASC4R	136	137*	154	136
ASn1R	9.2	8.7	9.9	L8.9
ASn2R	9.5	8.7	8.7	8.1
ASn3R	9.1	9.0	9.9	8.1
ASn4R	10.0	9.8	9.6	8.0
GiLC	8/8	9/8	9/8	9/9
FuL	46.2	45.8	45.7	48.2
FFL	31.5	34.6	32.8	38.2
CaL	10.1	7.5	F	F
LL	21.5	24.9	F	F

Table 101. Raw measures for *Benthoctopus* spp. (REFERENCE MATERIAL EXAMINED: * denotes damage; † denotes character not measured/enumerated; ‡ denotes arm tip regrowth).

	Benthoctopus sp. A USNM 817339	*Benthoctopus* sp. USNM 817338	*Benthoctopus* sp. USNM 817336	*Benthoctopus* sp. A USNM 817335	*Bathypolypus faeroensis* Neotype
TL	227	264	214	†	†
ML	49.0	64.0	46.0	74.5	74.5
MW	51.0	64.0	37.0	72.0	†
HdL	17.5	16.0	13.0	16.0	†
HdW	42.0	49.0	30.0	45.0	†
EO	5.5	4.0	3.5	3.0	†
AL1R/L	167/170	177/176	151/157	167/175	140*/156
AL2R/L	162/168	190/177	152/141	171/170	144/152
AL3R/L	125/149	174/167	148/152	162/165	132/141
AL4R/L	145/145	174/160	125/144	168/155	127/134
WDA	41	43	32	47	†
WDBR/L	36/38	40/42	38/33	47/47	†
WDCR/L	39/41	45/42	40/40	47/46	†
WDDR/L	44/37	46/35	36/36	40/40	†
WDE	31	28	32	35	†
ASC1R	103	109	161	106	L79
ASC2R	99	110	156	108	76
ASC3R	51	106	157	99	74
ASC3LM	93	†	†	†	†
ASC4R	93	104	118	99	70
ASn1R	4.0	5.0	3.0	5.0	†
ASn2R	4.6	5.5	3.0	5.0	†
ASn3R	4.5	5.5	3.0	4.6	†
ASn4R	4.7	6.0	3.0	5.0	†
GiLC	8/8	8/7	8/8	7/7	†
FuL	19.5	26.0	12.0	27.0	†
FFL	10.5	15.0	9.0	17.0	†
CaL	7.0	F	F	F	†
LL	16.5	F	F	F	†

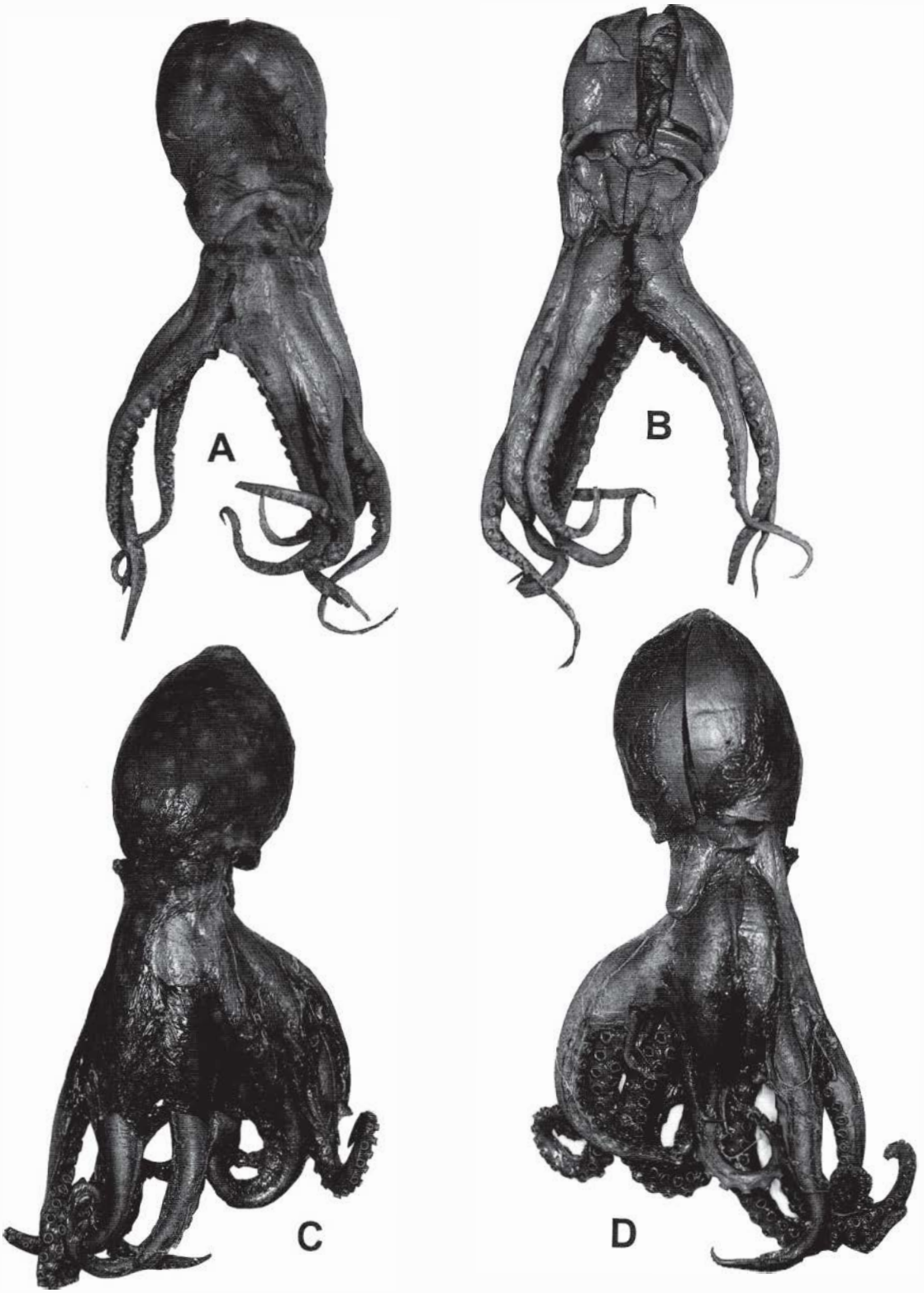


Figure 115. A, B, ***Benthoctopus piscatorum*** (Verrill, 1879): USNM 574641, holotype, female, ML about 40 mm. **C, D,** ***Bathypolypus faeroensis*** (Russell, 1909), neotype (USNM, not registered, on long-term loan), female, ML 74.5 mm.

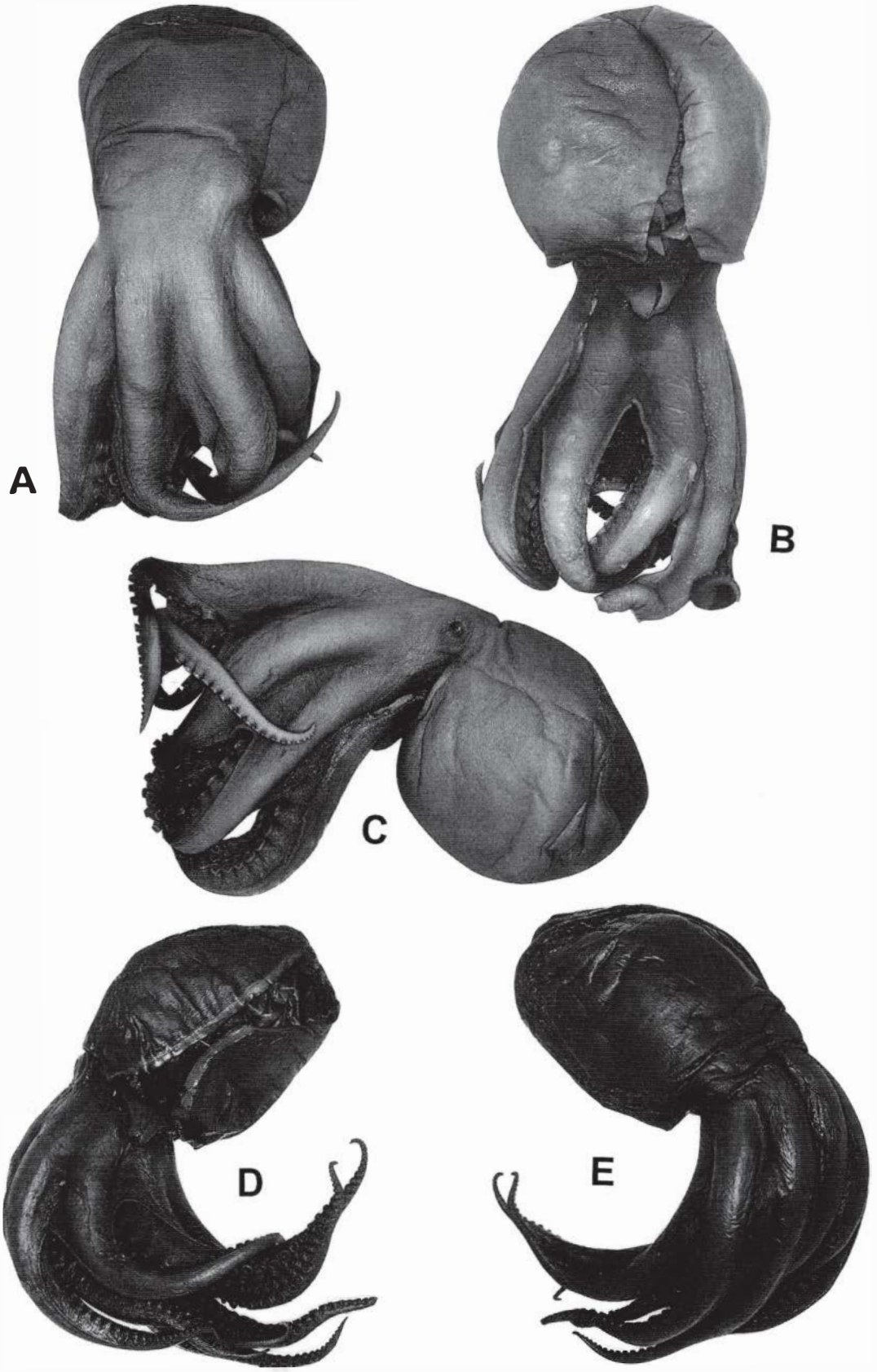


Figure 116. ***Benthoctopus robustus*** Voss & Pearcy, 1990: **A–C**, holotype, USNM 729994, male, ML 137.3 mm. **D, E**, SBMNH 42224, female, ML 115 mm.

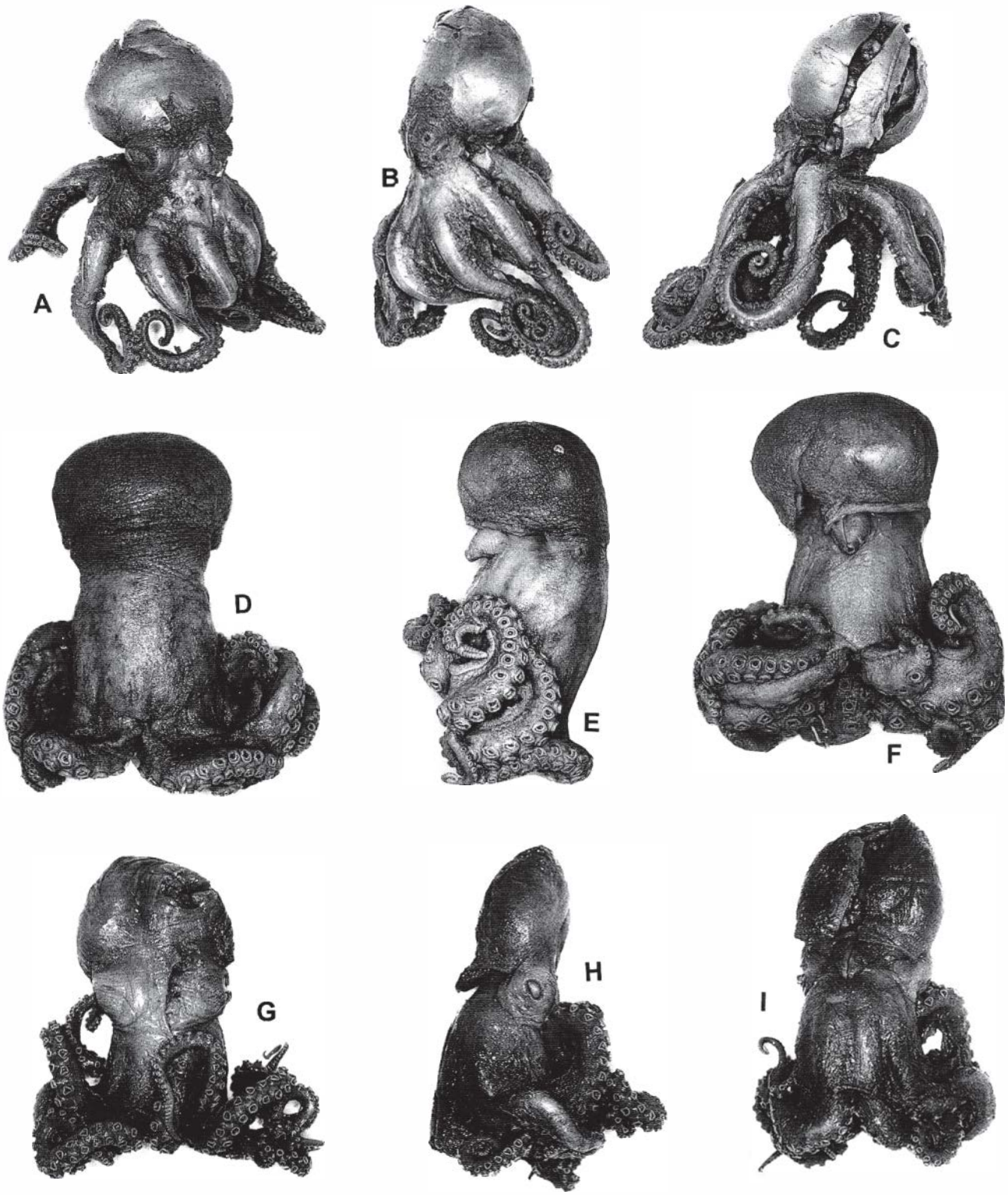


Figure 117. *Benthoctopus* spp.: **A–C**, ***B. levis*** (Hoyle, 1885), holotype, BMNH 1889.4.24.28–29, male, ML 46.0 mm. **D–F**, ***B. magellanicus*** Robson, 1930, holotype, MNHN 1096, male, ML 56.8 mm. **G–I**, ***B. berryi*** Robson, 1924, holotype, BMNH 1924.9.9.23, female, ML 45.4 mm.

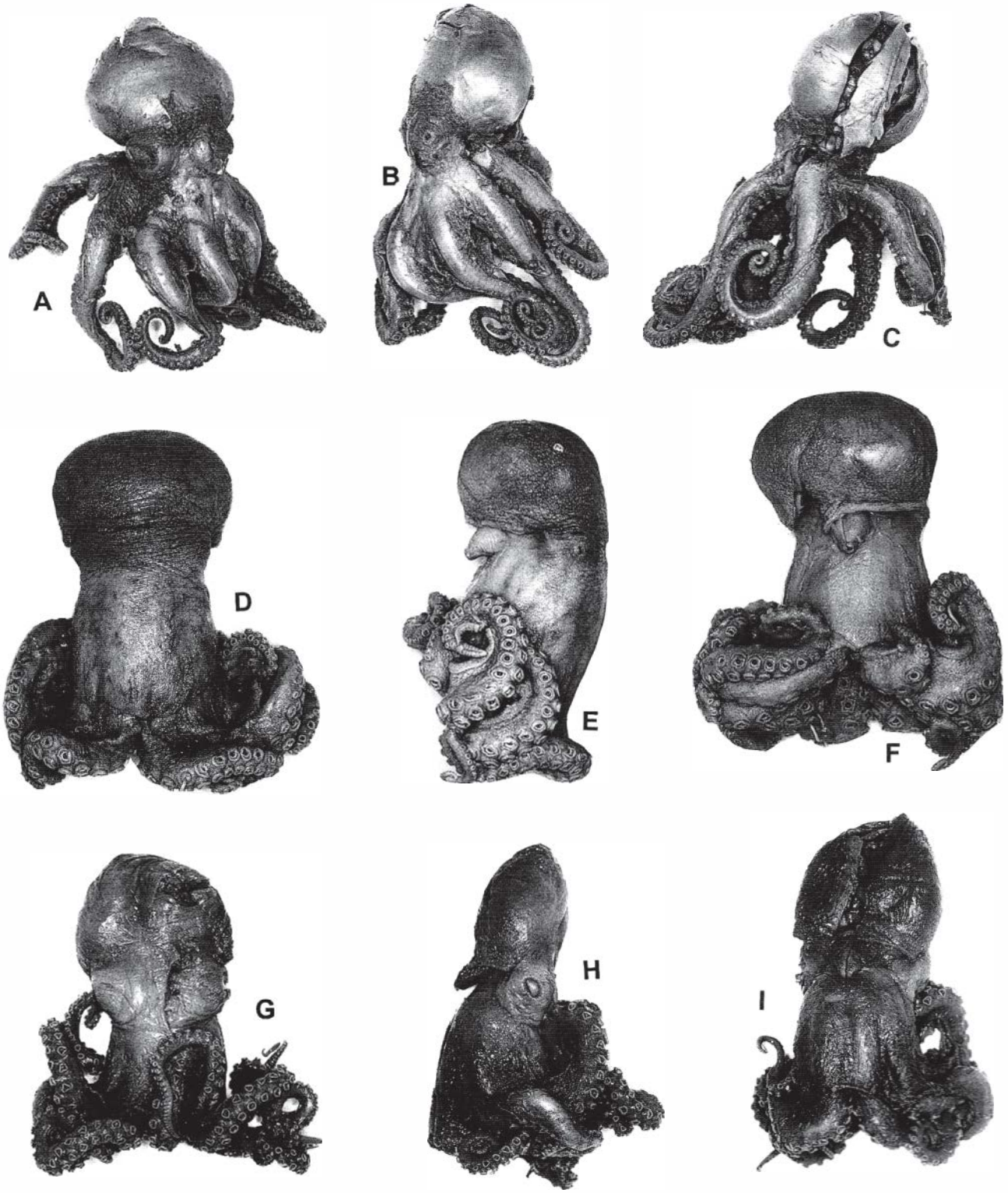


Figure 117. *Benthoctopus* spp.: **A–C,** ***B. levis*** (Hoyle, 1885), holotype, BMNH 1889.4.24.28–29, male, ML 46.0 mm. **D–F,** ***B. magellanicus*** Robson, 1930, holotype, MNHN 1096, male, ML 56.8 mm. **G–I,** ***B. berryi*** Robson, 1924, holotype, BMNH 1924.9.9.23, female, ML 45.4 mm.

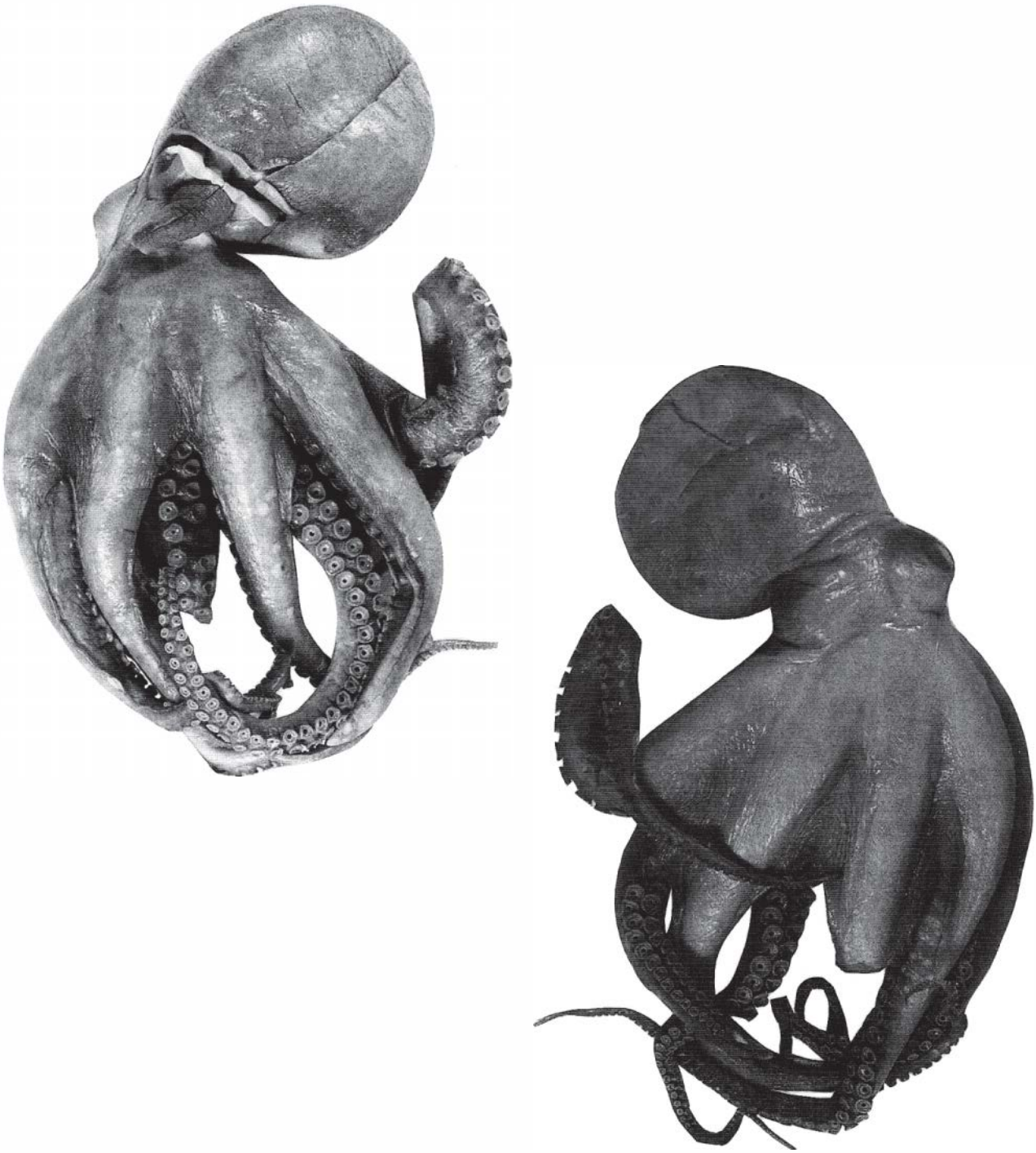


Figure 118. ***Bentoctopus berryi*** Robson, 1924: SAM S specimens.

are low while those of *Benthoctopus* sp. (USNM 817336) are moderate. The shallowest and deepest web sector in each of these two *Benthoctopus* species is shallower than in *B. piscatorum*, *B. levis*, *B. berryi*, *B. magellanicus*, or *B. robustus*. Sucker diameter is low but variable in all species. Refer to Tables 96–101, figures 115–119.

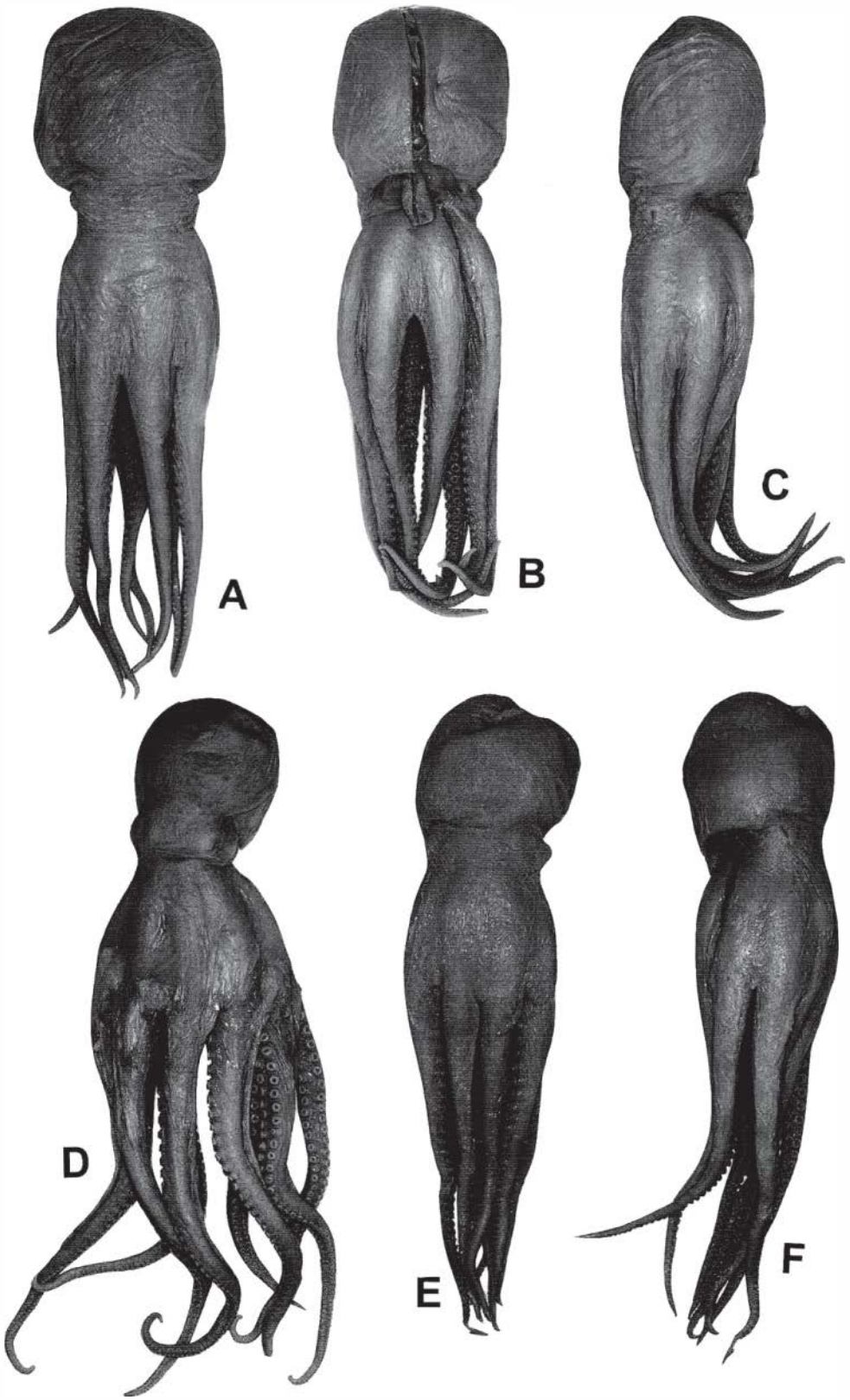


Figure 119. ***Benthoctopus*** spp.: **A–C**, ***Benthoctopus*** sp., USNM 817335, female, ML 74.5 mm. **D**, ***Benthoctopus*** sp., USNM 817336, female, 46 mm. **E, F**, ***Benthoctopus*** sp., USNM 817338, female, ML 64 mm.

Benthoctopus Grimpe, 1921

TYPE SPECIES: *Benthoctopus piscatorum* (Verrill, 1879)

DIAGNOSIS: With characters of subfamily; animal moderate sized, skin smooth; crop with or without diverticulum; posterior salivary glands vestigial (relative to mantle length) to large; rachidian tooth with or without lateral cusps (modified from Voss 1988a: 269).

Benthoctopus tegginmathae sp. nov. (Figs 121–123) (Tables 102–104)

TYPE MATERIAL (18 specimens, 9 male [M], 9 female [F]): Holotype: NZOI H-659, M, ML 64.5 mm, FPT, 39°57–00' S, 178°16–15' E, 1020–1250 m, 25/09/1995, f.v. *San Torshavn*, NZOI Stn Z8375. Paratypes: NZOI P-1092, F, ML 68.0 mm, FPT, 42°47.63–47.59' S, 176°40.76–42.78' W, 1000–1004 m, 12/07/1995, f.v. *San Waitaki* Stn SWA9501/11, NZOI Stn Z8332; NZOI P-1093, F, ML 73.0 mm, FPT, 40°03–05' S, 178°09–06' E, m, 24/09/1995, f.v. *San Torshavn*, NZOI Stn Z8376; NZOI P-1094, F, ML 69.0 mm, FPT, 39°50' S, 177°39' E, 1000–1100 m, 10/08/1995, f.v. *Peterson*, NZOI Stn Z8371; NZOI P-1119, F, ML 96.5 mm, FPT, 42°54.60–54.51' S, 178°54.90-56.94' E, 777–785 m, BT 6.5°C, 13/06/1996, f.r.v. *Tangaroa* Stn TAN9608/05, NZOI Stn Z8495.

ADDITIONAL MATERIAL EXAMINED: NZOI Stn F896, M, ML 54.0 mm, ?FL, 36°40.50' S, 176°19.20' E, 909 m, 06/10/1968; NMNZ M.90333, F, ML 31.0 mm, ?FL, 37°30' S, 179°22' E, 1240–1320 m, 07/02/1974, r.v. *Acheron*; NMNZ M.90332, M, ML 66.0 mm, 40°46.1' S, 176°59.4' E, 1035 m, 25/11/1981, f.v. *Kalinovo* Stn K01/24/81; NMNZ M.109069, 2F, ML *c.* 69.0 mm, 63.0, 41°22.8' S, 176°08.9' E, 924–1087 m, 16/10/1984, f.v. *James Cook* Stn J18/1/84; NMNZ M.95257, M, 62.0 mm, 41°24.7' S, 176°08.4' E, 1071–1103 m, 16/10/1984; NMNZ M.109070, M, ML 69.0 mm, 42°00.67' S, 174°36.44' E, 1000–1084 m, 28/09/1989; NZOI Stn E757 TAM, M, ML 52.0 mm, ?FL, 42°03.2' S, 174°27.2' E, 1081–1125 m, 30/03/1967; NMNZ M.90274, M, ML 29.0 mm, 42°41.7' S, 174°28.0' E, 1723–1549 m, 13/01/1979, r..v. *Tangaroa* (NZOI Stn R18), mud substratum; NMNZ M.90329, F, ML 61.0 mm, 42°51.7' S, 175°37.4' E, 990 m, 20/07/1985; NMNZ M.95300, M, ML 46.0 mm, 42°52.9' S, 175°19.2' W, 1050–1054 m, 28/07/1988, f.v. *Cordella* Stn C01/089/88; NZOI Stn E426, F, ML 45.0 mm, ?FL, 44°47' S, 172°48' E, 1130 m, 16/10/1965; NMNZ M.90383, M, ML 87.0 mm, 44°52' S, 173°12' E, 910–990 m, 01/12/1979.

RECOGNISED DISTRIBUTION (Fig. 120, p. 172): New Zealand, over about 8 degrees of latitude, 13 degrees of longitude, between 36°40.50–44°52' S, 175°19.2' W–172°48' E, off the east coast of North and South Islands, extending along the Chatham Rise; 777 to 1723(–1549) m.

DIAGNOSIS: Small to moderate-sized, smooth-skinned, short-armed *Benthoctopus* species; total arm-sucker counts moderate, 117–155; hectocotylised arm with 44–49 suckers; sucker lateral wall and suction pad musculature well developed; suckers small, ASIn 4.9–7.2; gills with 7 or 8 outer lamellae per demibranch; crop with anterior diverticulum; rachidian tooth of radula without lateral cusps; body counter-pigmented, dorsal surfaces of mantle, head, arms and web lighter than ventral and oral surfaces.

DESCRIPTION: Adult attaining small to moderate size (ML to 96.5 mm, TL to 328 mm); body stocky (Figs 121A–E, 122A–D). Mantle ovoid (MW about 75–95% ML), dorsoventral compression absent; lateral keel or fold of skin absent. Head large (HdL about 35–45% ML; HW about 55–75% ML), narrower than mantle, separated from mantle by well-developed preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head; eye apertures dorsolaterally oriented. Funnel large, well developed, attached entirely to ventral surface of head, free of brachial crown. Nuchal constriction well developed.

Brachial crown robust, wider than head. Arms slender, short to moderately long (about 55–80% TL), gradually tapering to fine non-filiform tips; arm lengths subequal, no consistent disparity in relative arm length apparent. Web shallow to deep, about 15–30% longest arm length, with narrow, poorly-developed membranous extension down basal half of each arm; web formula variable, sector E shallowest, other sectors variable, with no consistent disparity in relative sector depths. Distal 10–30 minute suckers frequently uniserial in specimens fixed post thaw; arm sucker counts moderate, 117–155; suckers extend to arm tips; dorsal arms with 15–18 suckers between beaks and web margin; suckers small, ASIn 4.9–7.2, not enlarged in male. Suckers with: small suction chamber, poorly constricted sucker aperture; small grasping ring with about 30 faint radial grooves; about 20 rounded beadlike crenulations lining sucker aperture; and well-developed suction pad and lateral- wall sucker musculature (Fig. 155S).

Skin entirely smooth over all body surfaces; supraocular cirrus absent. Animal counter-pigmented: dorsal surfaces of mantle, head, arms 1–3, and web sectors A–D dark red; ventral surfaces of mantle, head, funnel, arms 4, and web sector E, darker red; ventrolateral and oral surfaces of arms and web very dark red to maroon; spermatophoral groove cream coloured.

Third right arm of male hectocotylised, shorter than opposite member (OAI 56.2–75.6), with 44–49 suckers in total, none obviously enlarged. Spermatophoral groove well developed, with thickened margin, not continued onto or over oral surface of web sector D. Hectocotylised portion (Fig. 122F) small (immature) to large, ligula 4.0–23.7% arm length, with shallow

excavation, poorly marked lateral cheeks, with about 12 faint transverse rugae; calamus large, about 40--45% ligula length, well developed, with thick cheeks and central incomplete groove not extending entire calamus length to acute tip.

Pallial aperture slightly reduced, mantle attached to ventral surface of orbit; mantle margin proximal to mantle attachment points with small triangular lappet; funnel short, robust, distal aperture not inrolled or contracted; adsiphonal pouches mode-rately-well developed; ventral mantle musculature thin. Funnel collar well developed; funnel retractor muscles large; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; mem-branes connecting renal tissue to ventral and inner surface of mantle absent. Male penis and diver-ticulum disproportionately large; both penis and diverticulum extend along anteroposterior axis of mantle about 50% mantle length. Female with distal oviducts running parallel to anteroposterior axis of body, genital apertures open at anterior base of interpallial septum, not extending to anus; anal flaps absent. Gills well developed, with 7 or 8 lamellae per demibranch. Lateral muscles restraining digestive gland, visceral envelope, renal papilla and anal region with numerous small red chromatophores. Funnel organ W-shaped, with moderately thick inner and outer limbs of sub-equal length.

Male reproductive system (Fig. 123A) with short, thick, weakly convoluted proximal vas deferens; spermatophoral gland long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Accessory gland terminally expanded, incomplete terminal volution large. Spermatophore sac long, thin walled, containing up to 8 spermatophores. Distal vas deferens short, thick; penis diverticulum single, large, thick walled; penis large, genital aperture subterminal. Mature female (Fig. 123B) with large ovary sac (about 67% ML in greatest dimension); proximal oviducts short, narrow; oviducal gland large, brown, with single hemisphere, without radial striations; distal oviducts about 3.5 times longer than proximal ducts, with pronounced U-twist; genital aperture terminal, porelike, not secondarily modified. Mature eggs few in number (probably less than 40), very large, teardrop-shaped, to 22.0 x 7.0 mm, each with short stalk and about 18–20 longitudinal striations running the entire egg length; egg-capsules unknown.

Alimentary canal (Figs 123C–D) with large buccal bulb, length about 28% ML; anterior salivary glands large, length about 50% buccal bulb greatest dimension; anterior oesophagus short, narrow, enters crop dorsally; crop well developed, with or without ventral diverticulum (independent of crop distension). Posterior salivary glands large, length about 97% greatest buccal bulb dimension, about 28% ML; right gland larger than left, both broadly triangular. Posterior oesophagus muscular, thick walled. Stomach larger than buccal bulb, with thin-walled basal, thick-walled central, and thin-walled distal sections; stomach with undivided lumen. Spiral caecum with single complete volution, without apparent radial striations. Intestine long, about 2–2.7 times oesophagus length, thin walled, dilated for entire length, particularly proximal half; anal flaps absent. Digestive gland large, broadly ovoid, with neither apparent anterior peaks nor depressions imparted by stomach and crop; pancreas small; ink sac absent. Stomach contents comprise crustacean and polychaete remains.

Upper beak (Fig. 123E) moderately tall (height 100% length); hood and lateral walls dark brown, margins translucent; hood moderately deep (depth 37.8% beak length), with rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, very slightly deflected down; jaw without teeth. Lateral walls straight sided; crest broadly rounded, lateral wall fold weak. Lower beak (Fig. 123E) depressed (height 70.4% width); hood dark brown, lateral wall and wings lighter brown, margins translucent. Lateral wall with deep, acute angled V-shaped basal notch and keeled crest. Hood shallow (depth 28.3% beak length), with flattened chisel-like to weakly bifid rostrum; hood with shallow posterior notch; lateral wings very long (length 109.2% beak length); lateral wings with single weak fold.

Radular dentition simple (Fig. 123F); rachidian well developed, broad based, without lateral cusps; 1st lateral tooth with single cusp; 2nd lateral broad based, with single large cusp; marginal tooth robust; marginal block well developed.

REMARKS: Although a number of male specimens of this species are known, few are in a condition suitable for detailed morphometric analysis. Detailed measures of the holotype male alone are presented, with additional measures of less perfect males made to supplement descriptions of male characters, particularly hectocotylised arm characters. The specimen upon which the illustration of the radula is based lacked lateral cusps on the rachidian tooth. Since *B. tegginmathae* is certainly referable to *Benthoctopus*, at least as currently recognised, the generic diagnosis of Voss (1988a) has had to be modified to accommodate this species' unique attributes.

Benthoctopus tegginmathae differs from *B. magellanicus* in being totally smooth bodied and counter-pigmented, with the ventral surfaces of mantle, head, arms and web much darker than those of the dorsal

Table 102. Indices, formulas, and counts for *Benthoctopus tegginmathae* sp. nov. (* denotes damage).

	NZOI P-1119	NZOI P-1094	NZOI P-1093	NZOI P-1092	NZOI H-659
MWI	83.9	83.3	94.2	76.5	94.3
HdLI	46.3	41.3	44.2	34.7	46.5
HdWI	53.9	69.1	72.5	66.8	73.2
EOI	10.5	12.3	17.4	14.7	15.3
ALI1–4	62.8–67.7	54.2–69.7	68.4–78.1	62.3–68.6	69.2–76.7
AFR	1=2.3.4	1.3.4.2	*	1.3.4.2	*
AFL	3.1.2.4	1.2.3.4	1.3.4.2	1.2=3.4	1.3.2.4
WDIA–E	19.4–27.9	15.3–25.9	17.4–26.0	19.8–27.2	15.2–29.5
WFR	B.A.C.D.E	A.B.C.D.E	B=C.D.A.E	C=D.B.A.E	C.B.A.D.E
WFL	C.B.A.D.E	A.B.C.D.E	C.A.D.B=E	C=D.B.A.E	B.A.C.D.E
ASC1–4	131–135	134–153	146–155	117–125	133–145
ASIn1–4	6.0–6.2	4.9–5.1	7.1–7.2	6.6–7.1	6.4–6.8
FuLI	33.2	34.6	39.1	33.8	35.5
FFuI	21.8	10.1	18.8	20.6	21.7
PAI	48.2	52.2	57.2	46.8	52.7

Table 103. Indices and counts for male *Benthoctopus tegginmathae* sp. nov.

	NZOI Stn F896	NMNZ M.90332	NMNZ M.90274	NMNZ M.90383	NMNZ M.95257	NZOI H-659
OAI	59.4	56.2	75.6	60.0	66.2	64.2
ASC3R	49	48	47	47	46	44
CaLI	41.2	43.8	40.0	39.5	44.8	44.5
LLI	23.7	10.0	4.0	10.1	9.2	14.0

surfaces. *Benthoctopus magellanicus* has apparent skin papillation and a reticulated blotchlike surface pigmentation in which counter-pigmentation is not apparent. These two species also differ in total arm sucker counts, relative sucker diameters, and hectocotylised arm sucker counts. *Benthoctopus tegginmathae* differs from *B. levis* most notably in the hectocotylised arm-sucker count — 54 in the type of *B. levis*, 44–49 in *B. tegginmathae*. *Benthoctopus tegginmathae* differs from *B. berryi* in: absolute size, to 593 mm TL in *B. berryi*, 328 mm in *B. tegginmathae*; sucker diameter, ASIn *B. tegginmathae* 4.9–7.2, *B. berryi* 7.3–9.9; outer gill lamellae count (7 or 8 and 8 or 9 respectively); and hectocotylised arm sucker count, 62–69 in *B. berryi*, 44-49 in *B. tegginmathae*. *Benthoctopus tegginmathae* differs from all described southern ocean species in the muscularity of the suction cup and lateral wall of the suckers. In light of these differences I feel it appropriate to interpret the New Zealand species as new to science.

ETYMOLOGY: Named for my dear wife, Shoba Tegginmath, as the smallest of tokens for all of her perserverance and support during this study.

Benthoctopus tangaroa sp. nov. (Figs 125–127) (Tables 105–107)

Octopus sp. Kubodera 1990: 350, pl. 278.
Benthoctopus sp. (Kubodera): O'Shea & Kubodera 1996: 153, fig. 1.

TYPE MATERIAL (16 specimens, 6 male [M], 10 female [F]): Holotype: NZOI H-660, M, ML 97.0 mm, FPT, 44°06.99–06.23' S, 178°26.01–28.61' E, 936–999 m, BT 6.2°C, 11/10/1995, f.r.v. *Tangaroa* Stn TAN 9511/40, NZOI Stn Z8392. Paratype: NZOI P-1095, F, ML 78.5 mm, ?FL, 41°15.2' S, 167°07.2' E, 1463–1457 m, 23/04/1980, NZOI Stn P941; FSFRL EI219 (14–2–3), F, ML 120.5 mm, 48°58' S, 171°01.5' E, 644 m, 24/01/1976, f.v. *Shinkai Maru*.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.118239, 2F, ML 120.0, 74.0 mm, FPT, 40°00' S, 168°00' E, 900 m, -/08/1994, f.v. *San Manukau*; NMNZ M.118241, F, ML 91.0 mm, FPT, 40°00' S, 168°02' E, 900 m, 25/07/1994, f.v. *San Manukau*; NMNZ M.109082, F, ML 86.0 mm, 41°17.2' S, 176°21.3' E, 1211–1175 m, 05/04/1984, f.r.v. *James Cook* Stn J06/24/84; NMNZ M.91576, F, ML 48.0 mm, 41°27.5–25.2' S, 176°02.4–05.2' E, 1068–1042 m, 02/04/1984, f.r.v. *James Cook* Stn J6/7/84; NMNZ M.95252, F, ML 59.0 mm, 42°45.6' S, 177°24.8' W, 1072–1068 m, 13/07/1988, FRD

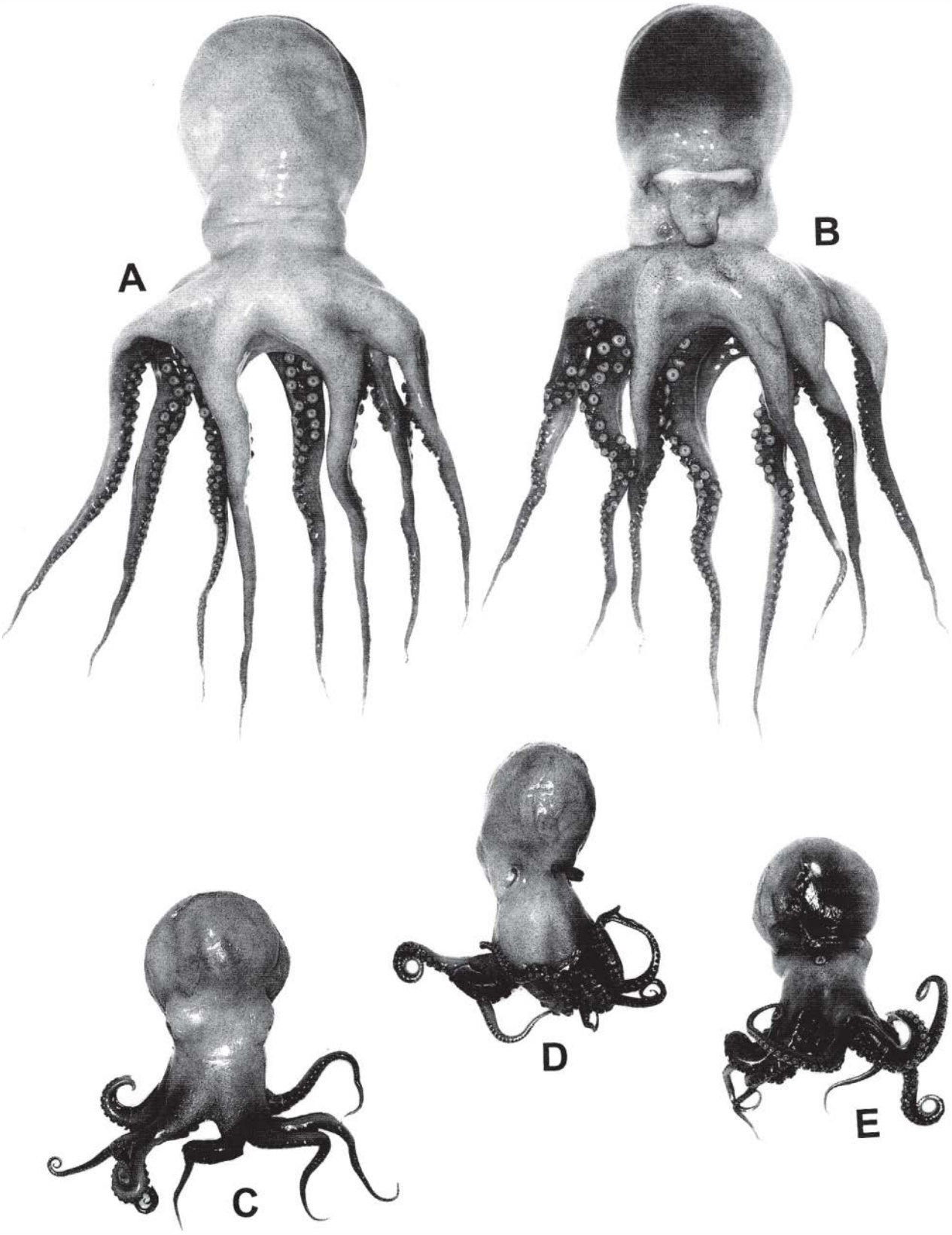


Figure 121. ***Benthoctopus teggimmathae*** sp. nov.: **A, B**, paratype, NZOI P-1092, female, ML 68.0 mm. **C–E**, NZOI Stn F895, male, ML 54.0 mm.

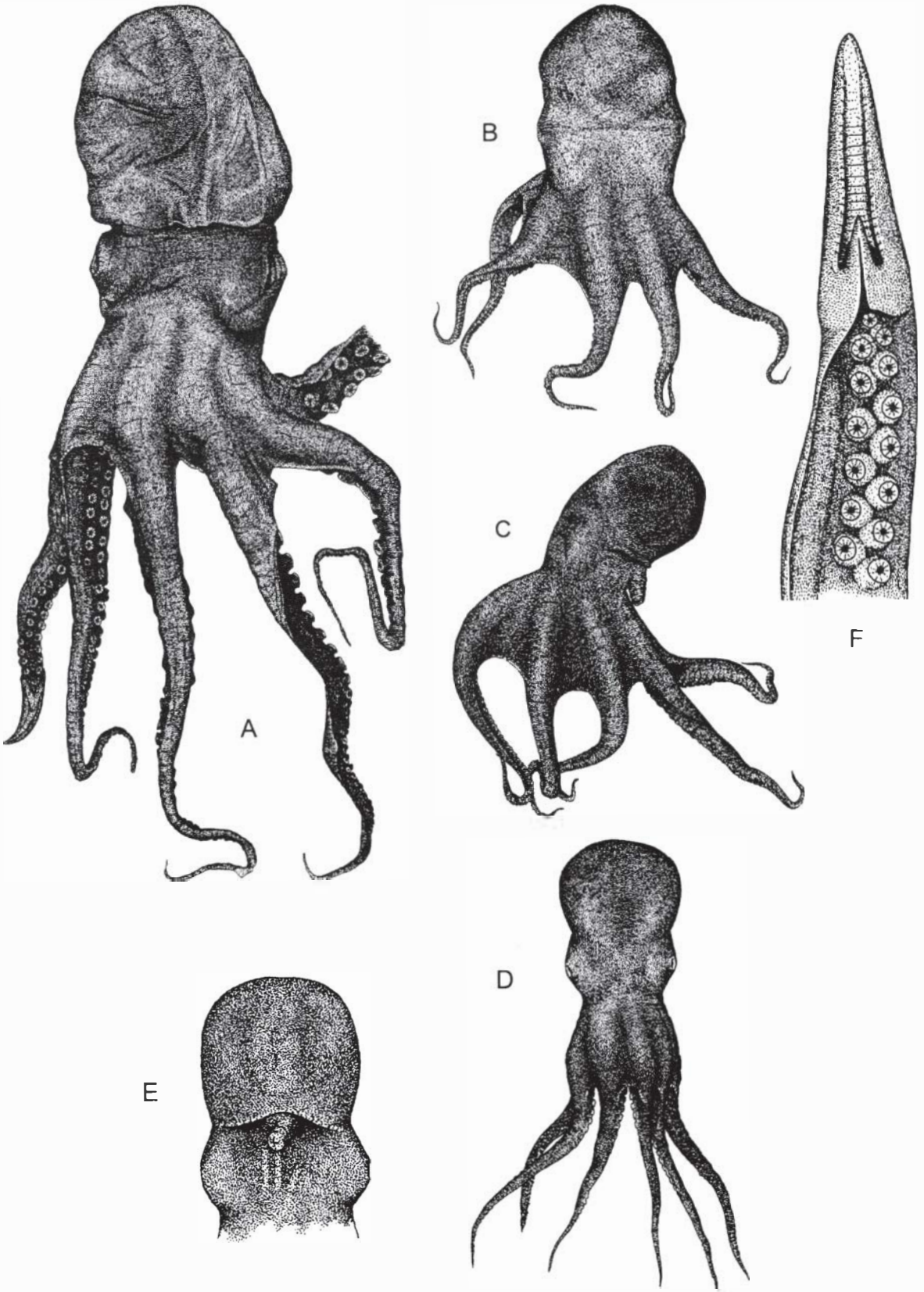


Figure 122. *Benthoctopus tegginmathae* sp. nov.: **A**, NMNZ M.90383, male, ML 87.0 mm. **B, C**, NMNZ M.90333, female, ML 31.0 mm. **D, E**, NMNZ M.90274, male, ML 29.0 mm. **F**, hectocotyl, NZOI Stn F896.

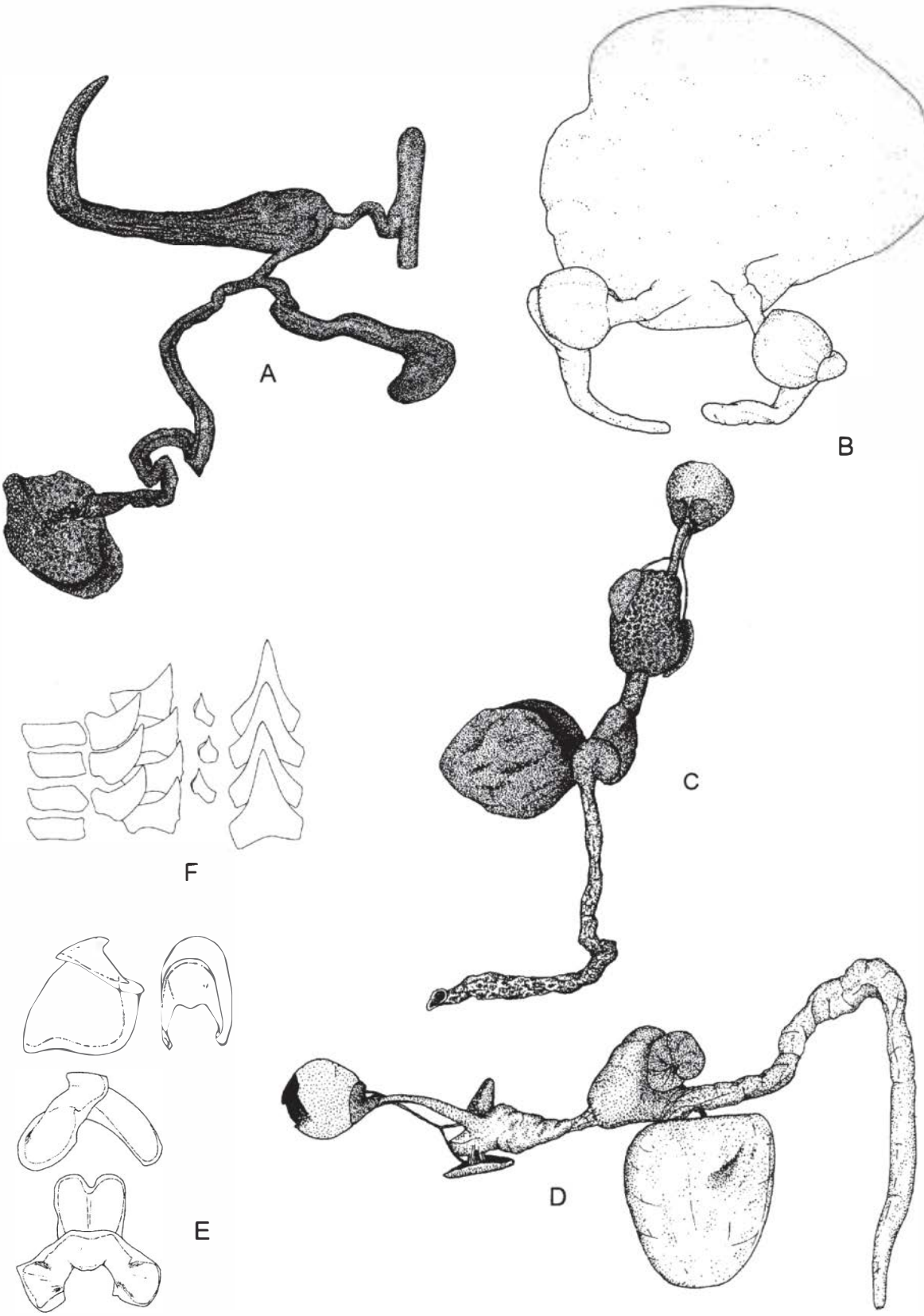


Figure 123. ***Benthoctopus teggimmathae*** sp. nov. Anatomy: **A, C, F**, NMNZ M.90383, male, ML 87 mm. **B**, paratype, NZOI P-1119, female, ML 96.5 mm. **D, E**, NMNZ M.90329, female, ML 61 mm. **A**, male reproductive system. **B**, female reproductive system. **C**, alimentary canal. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 104. Raw measures for *Benthoctopus tegginmathae* sp. nov. (* denotes damage).

	NZOI P-1119	NZOI P-1094	NZOI P-1093	NZOI P-1092	NZOI H-659
TL	328.0	271.0	310.0	236.0	292.0
ML	96.5	69.0	69.0	68.0	64.5
MW	81.0	57.5	65.0	52.0	60.8
HdL	37.5	28.5	30.5	23.6	30.0
HdW	52.0	47.7	50.0	45.4	47.2
EO	10.1	8.5	12.0	10.0	9.9
AL1R/L	220/219	186/189	237/242	162/154	147*/217
AL2R/L	220/202*	147/178	241/212	158/148	224/211
AL3R/L	212/222	178/162	87*/217	159/148	136/212
AL4R/L	200*/206	163/160	212/216	154/147	202/206
WDA	57	52	46	33	58
WDBR/L	62/60	46/49	63/42	41/40	65/62
WDCR/L	56/61	37/48	63/58	44/41	66/49
WDDR/L	42/53	32/46	48/43	44/41	48/41
WDE	43	29	42	32	34
ASC1	131	149	155	125	L144
ASC2R	105*	L146	148	125	145
ASC3R	135	153	L146	117	44M
ASC3LM	F	F	F	F	142
ASC4R	110*	134	146	110*	133
ASn1R	6.0	3.5	4.9	4.8	4.1
ASn2R	6.0	3.5	5.0	4.5	4.3
ASn3R	5.8	3.5	4.9	4.5	4.4
ASn4R	5.8	3.4	4.9	4.5	4.3
GiLC	7/7	8/8	8/7	7/7	8/8
FuL	32.0	23.9	27.0	23.0	22.9
FFL	21.0	7.0	13.0	14.0	14.0
PA	46.5	36.0	39.5	31.8	34.0
CaL	F	F	F	F	8.5
LL	F	F	F	F	19.1

C01/005/88; NMNZ M.117578, M, ML 96.0 mm, 46°55' S, 169°45' E, 550–600 m, 14/12/1977, f.r.v. *James Cook* Stn J9/9/77; NMNZ M.100854, M, ML 96.0 mm, 50°45.5' S, 167°36.5' E, 490 m, 01/01/1976, f.v. *Shinkai Maru* Stn 207; NMNZ M.100853, F, ML 110 mm, 51°19' S, 166°53' E, 585–576 m, 29/01/1977, f.v. *Shinkai Maru* Stn 310; NMNZ M.100852, M, ML 100.0 mm, 52°42' S, 168°02' E, 658–603 m, datNR, f.v. *Shinkai Maru* Stn 192; NMNZ M.100851, F, ML 122.5 mm, 53°04' S, 169°08' E, 503–498 m, 19/11/1976, f.v. *Shinkai Maru* Stn 171.

UNLOCALISED SPECIMENS (no further or reliable data available): NMNZ M.137779, M, ML 100.0 mm, f.v *Shinkai Maru* Stn 241; NMNZ M.100850, M, ML 75 mm, f.v. *Shinkai Maru*, net # 63, 03/82.

RECOGNISED DISTRIBUTION (Fig. 124, p. 208): New Zealand, spanning about 13 degrees of latitude, 16 degrees of longitude, 40°00– 53°04' S, 167°07.2' E–177°24.8' W, off both east and west coasts of North and South Islands, extending over Challenger and Auckland Plateaus and over the Chatham Rise; depth range 498(–503) to 1457(–1463) m. Southern specimens on Auckland Plateau encountered in shallower water than more northern specimens.

DIAGNOSIS: Large-sized, smooth-skinned, long-armed *Benthoctopus* species; total arm sucker counts moderately high, 153–215; hectocotylised arm with 70–74 suckers; sucker lateral wall and suction pad musculature well developed; suckers small to moderate-sized, ASIn 4.9–7.2; gills with 7–9 outer lamellae per demibranch; crop with anterior diverticulum; rachidian tooth of radula with 1 or 2 lateral cusps; body counterpigmented, dorsal surfaces of mantle, head, arms and web lighter than ventral and oral surfaces.

DESCRIPTION: Adult attaining large size (ML to 122.5 mm, TL to 721.0 mm); body slender (Figs 125A–B, 126). Male and female of similar gross morphology; female attaining greater size (to 122.5 mm ML; male to 100.0 mm ML). Mantle ovoid, broad (MW about 75–107% ML), dorsoventral compression and lateral keel

or fold of skin absent. Head moderately large to large, broad (HdL about 28–43% ML; HW about 44–82% ML), narrower than mantle; separated from mantle by moderate preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head, situated upon base of arm pairs 1 and 2; eye apertures large, dorsolaterally oriented. Funnel large, well developed (FuLI about 29–51), with base entirely free of brachial crown. Nuchal constriction little developed.

Brachial crown robust, equivalent to or slightly exceeding head width. Arms slender, very short to long, about 45–80% TL, gradually tapering to delicate tips; arm pairs 1 and 2 probably longer than arms 3 and 4, otherwise no consistent disparity in relative arm length. Web shallow to deep, about 11–26% longest arm length, little extended along dorsolateral face of each arm, with narrow, poorly developed extension along ventrolateral face of each arm to distal third arm length; web formula variable, sector E usually shallowest, sectors A and B deepest, with no consistent disparity in relative sector depths. Suckers biserial; non-hectocotylised arm tips of males not secondarily modified in any discernible way. Arm sucker counts moderately high, ASC 153–215; suckers extend to arm tips. Suckers small to moderate sized, ASIn 6.0–9.3, not enlarged in male; with small suction chamber, moderately constricted sucker aperture, moderately well-developed grasping ring with about 22 faint radial grooves, beaded crenulate sucker aperture with about 22 tooth-like structures, and thick, well-developed muscular suction pad (Fig. 155T).

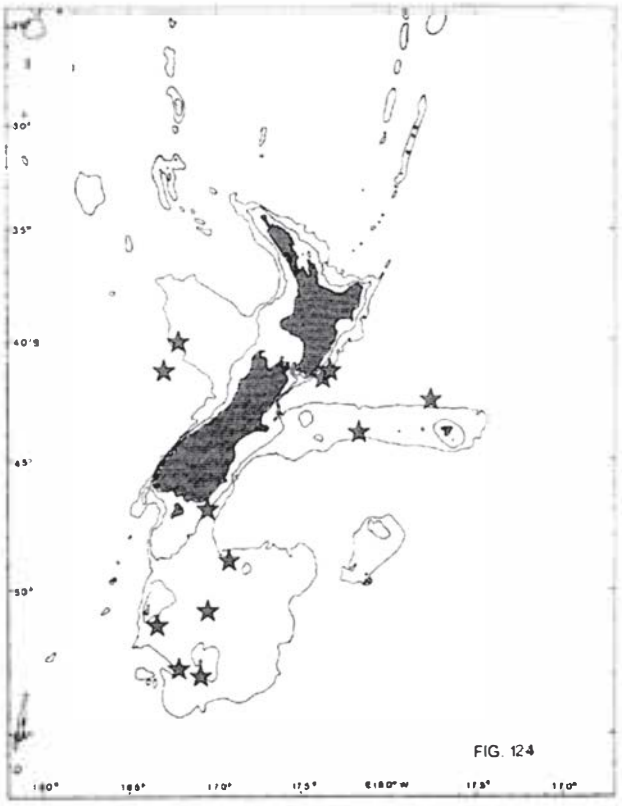
Third right arm of male hectocotylised, shorter than opposite member (OAI 66.9–70.5), with 70–74 suckers in total, none obviously enlarged. Spermatophoral groove shallow, slightly continued over adoral surface of web sector D; web extending down ventrolateral surface of arm 3 wide, web margin thickened, with 9 or 10 papillaelike ridges within recess formed by junction of spermatophoral groove and web sector D. Hectocotylised portion (Fig. 127A) small to moderate sized, ligula about 7–8% arm length, with raised, thickened lateral cheeks, with narrow, shallow central excavation and about 12 faint transverse rugae; calamus short, about 23–32% ligula length, well developed, with thick cheeks and central groove running entire calamus length to acute tip.

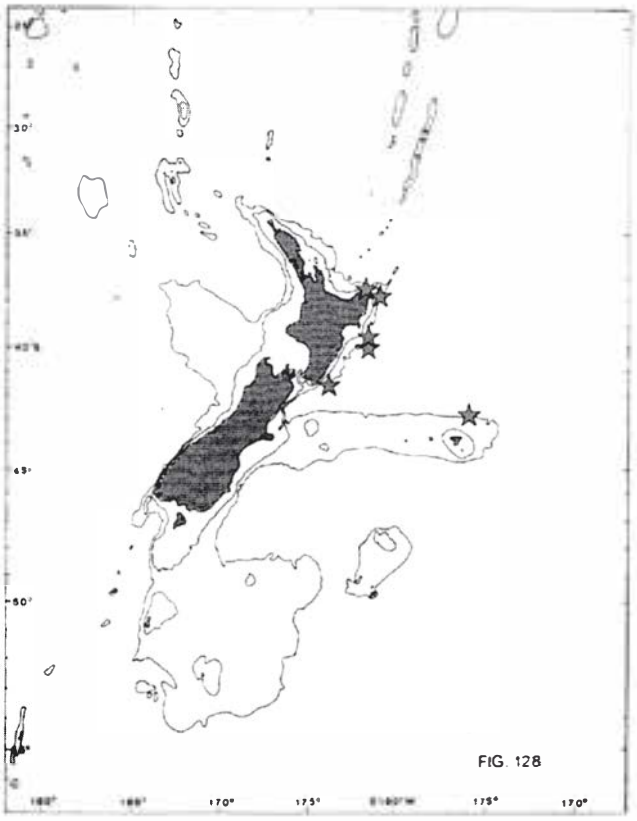
Skin smooth over entire surfaces of mantle, head, arms and web; superocular cirrus absent. Animal counter-pigmented: dorsal surfaces of mantle, head, arms 1–3 and web sectors A–D light pink to dark red; ventral surfaces of mantle, head, funnel, arms 4 and web sector E, slightly darker, red to maroon; ventrolateral and oral surfaces of arms and web, slightly darker still, red to maroon; spermatophoral groove cream coloured.

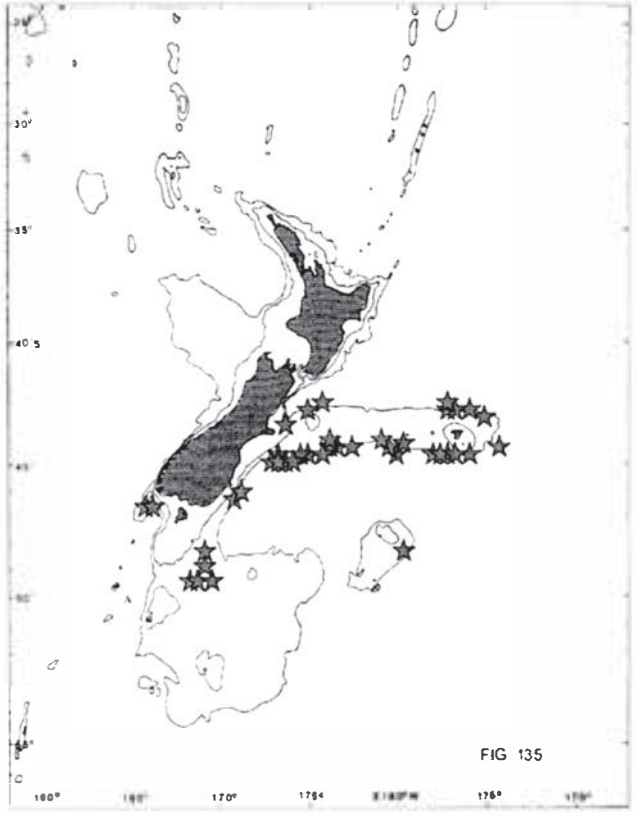
Pallial aperture wide, mantle attaches anterior to ventral surface of orbit; funnel moderately long, wide; adsiphonal pouches moderately well developed. Mantle musculature thin. Funnel collar well developed; funnel retractor muscles large; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting renal tissue to ventral and inner surface of mantle absent. Penis and diverticulum disproportionately large, oriented along anteroposterior axis of mantle. Ovary sac enormous, with weak fibrous connection to ventral inner surface of mantle musculature; genital apertures open at about 45° degree angle on face of viscera proximal to anterior interpallial musculature, not extending over interpallial musculature or to anus; anal flaps absent. Gills large, with 7–9 lamellae per outer demibranch. Visceral envelope and anal region densely pigmented with small to large red chromatophores; lateral muscles restraining digestive gland sparsely pigmented with small red chromatophores; renal papilla without apparent chromatophores. Funnel organ not apparent in any specimens.

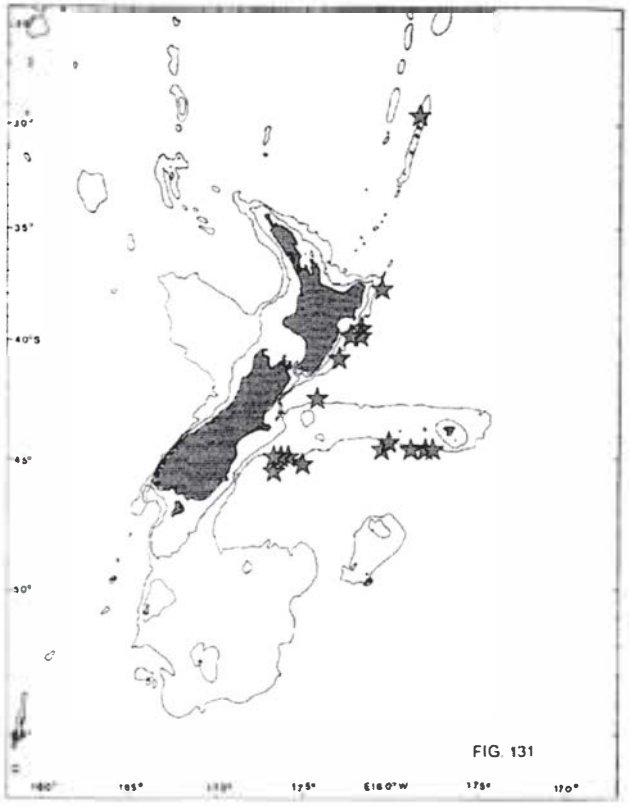
Male reproductive system (Fig. 127B) with short, thick, weakly convoluted proximal vas deferens; spermatophoral gland long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Accessory gland granular, distally thickened, expanded, with large, complete terminal volution. Spermatophore sac long, thin walled, containing up to 13 spermatophores of 120 mm total length; with anterior appendix. Distal vas deferens long, thin; penis diverticulum single, large, thick walled; penis large, about 50% longer than diverticulum, genital aperture subterminal (aperture not apparent). Mature female with large ovary sac (Fig. 127C); proximal oviducts depart sac from common base (ducts short, narrow, slightly swollen anterior to oviducal gland), oviducal gland large, black to brown, with single radially striate hemisphere; distal oviducts about 3 to 4 times longer than proximal ducts, with pronounced U-twist; genital aperture terminal, not secondarily modified. Mature eggs very large, teardrop-shaped, to 23.0 x 7.5 mm, each with short stalk and about 23 longitudinal striations running entire egg length; egg capsules unknown.

Alimentary canal (Figs 127D, E) with large buccal bulb, length about 32% ML; anterior salivary glands well developed, small, length about 31% greatest buccal bulb dimension; anterior oesophagus short









Recognised distribution. **Fig. 124**, *Benthoctopus tangaroa* sp. nov. **Fig. 128**, *Benthoctopus clyderoperi* sp. nov. **Fig. 131**, *Graneledone challengeri* (Berry, 1916). **Fig. 135**, *Graneledone taniwha taniwha* s.sp. nov.

narrow; crop with well-developed short anterior diverticulum of length about 15% total crop length. Left posterior salivary gland broader than right, both broadly triangular, large, length about 91% buccal bulb length, about 29% ML. Posterior oesophagus muscular, thick walled. Stomach with 3 apparent sections, basal thin walled, central thick walled, and distal thin walled; lumen continuous. Spiral caecum about 75% size of stomach, with incomplete volution and faint radial striations. Intestine long, length about 2.5 times that of oesophagus and crop, thin walled, dilated for proximal half, slightly constricted for next quarter and secondarily dilated for distal quarter; anal flaps absent. Digestive gland large, broadly ovoid, without apparent anterior peaks; pancreas not apparent; ink sac absent.

Upper beak (Fig. 127F) tall (height 106.0% length); hood dark brown to black, lateral walls dark brown, hood and lateral wall margins translucent; hood deep (depth 42.7% beak length), with broadly rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, slightly deflected down; with single broad tooth in jaw. Lateral walls straight sided; crest broadly rounded, lateral wall fold weak, directed to broad sinus in lateral wall margin. Lower beak (Fig. 127F) moderately tall (height 73.6% width); hood, lateral wall and wings dark brown to black, lateral wing and wall margins translucent. Lateral wall with deep, acute-angled basal notch and broadly keeled triangular crest. Hood moderately deep (depth 35.0% beak length), forward projecting, with flattened chisel-like, weakly bifid rostrum; hood with shallow posterior notch; lateral wings long (length 100% beak length) with single weak fold.

Radular dentition simple (Fig. 127G); rachidian well developed, as tall or taller than broad, with 1 or 2 asymmetric lateral cusps either side of central, 3 or 4 lateral cusps per tooth) 1st lateral tooth with pronounced inner heel, with or without inner cusp-like prominence, and larger outer cusp; 2nd lateral wider than tall, with large inner cusp; marginal tooth robust; marginal block elongate, wider than long.

Indices, formulas, and counts in Tables 105 and 106, and raw measures in Table 107.

REMARKS: This species differs from previously described southern ocean *Benthoctopus* species in the much higher arm-sucker counts (ASC 153–215), with potential overlap with only one undescribed species (*Benthoctopus* sp., USNM 817336). The shallowest web and deepest web sectors in *B. tangaroa* are much shallower than in any other recognised species. Another obvious character state differentiating *B. tangaroa* from other southern ocean species is the high hectocotylised arm sucker counts, closest to but higher than that in *B. berryi*. *Benthoctopus tangaroa* differs from all other *Benthoctopus* species in the well-developed sucker musculature (Fig. 155T), similar to that of *B. tegginmathae* from which it differs in total arm sucker counts, absolute size and higher than that in *B. berryi*. *Benthoctopus tangaroa* differs from all other *Benthoctopus* species in the well-developed sucker musculature (Fig. 155T), similar to that of *B. tegginmathae* from which it differs in total arm sucker counts, absolute size and hectocotylised arm sucker counts. In light of these differences it seems clear that *B. tangaroa* is a distinct species.

ETYMOLOGY: Named after the NIWA fisheries research vessel *Tangaroa* in acknowledgement of the excellent specimens this vessel has collected.

Table 106. Indices and counts for male *Benthoctopus tangaroa* sp. nov.

	NMNZ M.137779	NZOI H-667
OAI	66.9	70.5
ASC3R	70	74
CaLI	31.7	23.2
LLI	7.0	8.1

Benthoctopus clyderoperi sp. nov. (Figs 129, 130) (Tables 108–110)

TYPE MATERIAL (6 specimens, 4 male [M], 2 female [F]): Holotype: NZOI H-667, M, ML 80.0 mm, FPT, c. 39°58.55' S, 178°14.80' E, -/04/1994, 900 m, f.v. *San Manukau*, NZOI Stn Z8590. Paratype: NZOI P-1111, F, ML 85.0 mm, FPT, 37°24.21–24.76' S, 178°38.22–38.30' E, 783–1050 m, 19/05/1995, f.r.v. *Tangaroa* Stn TAN 9506/84, NZOI Stn Z8415.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.90384, M, ML 72.3 mm, 37°40.4' S, 179°11.4'E, 1123–1125 m, 10/12/1985, f.v. *Wanaka* Stn WK3/023/85; NMNZ M.118256, M, ML 89.0 mm, FPT, c. 39°58.55' S, 178°14.80'E, -/04/1994, 900 m, f.v. *San Manukau*; NMNZ M.90381, F, ML 34.0 mm, FPT, 41°25.2' S, 176°04.2' E, 1009–1013 m, 16/10/1994, f.r.v. *James Cook* Stn J18/2/84; NMNZ M.90272, M, ML 88.5 mm, 42°55.1' S, 175°56.6' W, 840 m, -/-/1972, f.v. *Kaltan* Stn KTN/32/82.

RECOGNISED DISTRIBUTION (Fig. 128, p. 208): New Zealand, 37°24.21–24.76' S to 42°55.1' S, 176°04.2' E–175°56.6' W; 840 to 1123–1125 m.

DIAGNOSIS: Small to moderate -sized, smooth-skinned, short-armed *Benthoctopus* species; pre- and post-ocular mantle constrictions well developed; total arm sucker counts moderate, 130–151; hectocotylised arm

Table 105. Indices, formulas, and counts for *Benthoctopus tangaroa* sp. nov. (* denotes damage).

	NMNZ M.137779	NZOI H-667	NMNZ M.118241	NMNZ M.109082	NMNZ M.118239	NZOI P-1095
MWI	74.7	84.5	84.1	86.6	106.5	91.7
HdLI	28.1	41.2	36.0	39.2	30.3	43.2
HdWI	44.2	66.0	61.5	70.2	70.9	82.5
EOI	15.1	17.5	12.6	8.0	14.1	7.9
ALI1–4	44.7–72.6	46.0–75.3	49.8–80.2	69.6–78.7	48.7–72.2	58.8–74.2
AFR	2.1.3.4	?2.1.4.3	*	*	*	1.2=3.4
AFL	*	*	*	2.3.4.1	*	1.2.3.4
WDI1–4	14.6–20.7	16.9–25.0	10.9–19.0	12.4–16.5	11.1–16.7	18.4–26.0
WFR	B.C.D.A.E	B.A.C.D.E	A=B.D.C.E	B.D.C.E.A	B.A.C.D.E	B.C.D.A.E
WFL	B.D.C.A.E	A.B.C.E.D	A.B.C.D=E	B.C.D.E.A	A.C.B.D.E	B.C.A.D.E
ASC1–4	153–161	177–179	187–215	191–210	176–202	155–162
ASIn1–4	6.0–6.9	6.2–6.6	7.7–7.8	8.1	8.6–9.3	7.0–7.8
FuLI	29.0	37.4	39.0	51.2	41.9	39.4
FFuI	16.0	19.6	30.8	31.4	23.2	16.3
PAI	36.3	50.7	56.6	57.0	61.5	56.7

Table 107. Raw measures for *Benthoctopus tangaroa* sp. nov. (‡ denotes arm tip as branched; † denotes regrowth; * denotes damage).

	NMNZ M.137779	NZOI H-667	NMNZ M.118241	NMNZ M.109082	NMNZ M.118239	NZOI P-1095
TL	452	494	616	431	637	388
ML	100.0	97.0	91.0	86.0	74.0	78.5
MW	74.7	82.0	76.5	74.5	78.8	72.0
HdL	28.1	40.0	32.8	33.7	22.4	33.9
HdW	44.2	64.0	56.0	60.4	52.5	64.8
EO	15.1	17.0	11.5	6.9	10.4	6.2
AL1R/L	322/270*	323*/270†	392/484	323/300‡	294*/262†	285/288
AL2R/L	328/233*	372/363	494/440	339/338	460/411*	256/260
AL3R/L	202/302	227/322	310*/307	328*/335	400/310	256/251
AL4R/L	276/262*	332/329	430/255*	336*/316	412/315*	228/232
WDA	54	84	94	42	73	62
WDBR/L	61/68	93/82	94/87	52/56	77/66	75/64
WDCR/L	60/58	81/80	74/63	48/53	64/70	71/63
WDDR/L	55/62	74/64	78/54	50/52	61/53	68/59
WDE	48	63	54	45	51	53
ASC1R	157*	*	187	191	*	155
ASC2R	161	179	207	214	176	159
ASC3R	70	74	L212	L210	176	162
ASC4R	153	177	215	L199	202	159
ASn1R	6.0	6.0	7.1	7.0	6.4	6.1
ASn2R	6.9	6.0	7.0	7.0	6.4	5.5
ASn3R	6.4	6.4	7.1	7.0	6.9	5.5
ASn4R	6.4	6.2	7.1	7.0	6.6	5.5
GiLC	8	9	9	9	8	7
FuL	29.0	36.3	35.5	44.0	31.0	30.9
FFL	16.0	19.0	28.0	27.0	17.2	12.8
PA	36.3	49.2	51.5	49.0	45.5	44.5
CaL	4.5	4.5	F	F	F	F
LL	14.2	18.5	F	F	F	F

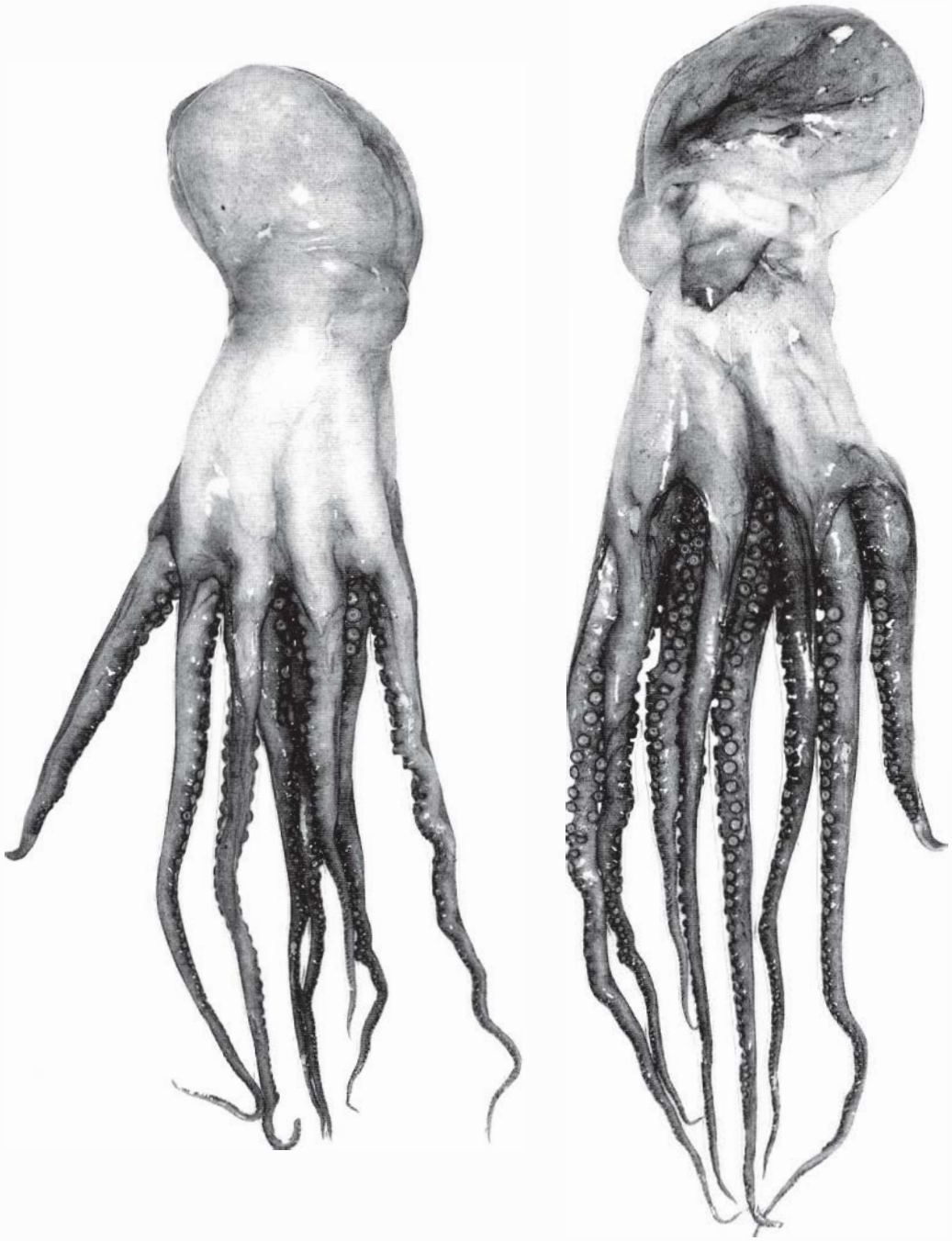


Figure 125. ***Benthoctopus tangaroa*** sp. nov.: Holotype, NZOI H-660, male, ML 97 mm.

with 50–55 suckers; sucker lateral wall and suction pad musculature well developed; suckers small to moderate sized, ASIn 4.5–8.8; gills with 8–9 outer lamellae per demibranch; crop without anterior diverticulum; rachidian tooth of radula with 1–2 lateral cusps; body counter-pigmented, dorsal surfaces of mantle, head, arms, and web lighter than ventral and oral surfaces.

DESCRIPTION: Adult attaining moderate size (ML to 89.0 mm, TL to 381.0 mm); body slender (Figs 129, 130A). Mantle ovoid (MW about 53–100% ML), dorsoventral compression and lateral keel or fold of skin absent. Head small to very large (HdL about 25–68% ML; HW about 36–90% ML), narrower than mantle, separated from mantle by pronounced preocular constriction. Orbits large, bulbous, situated

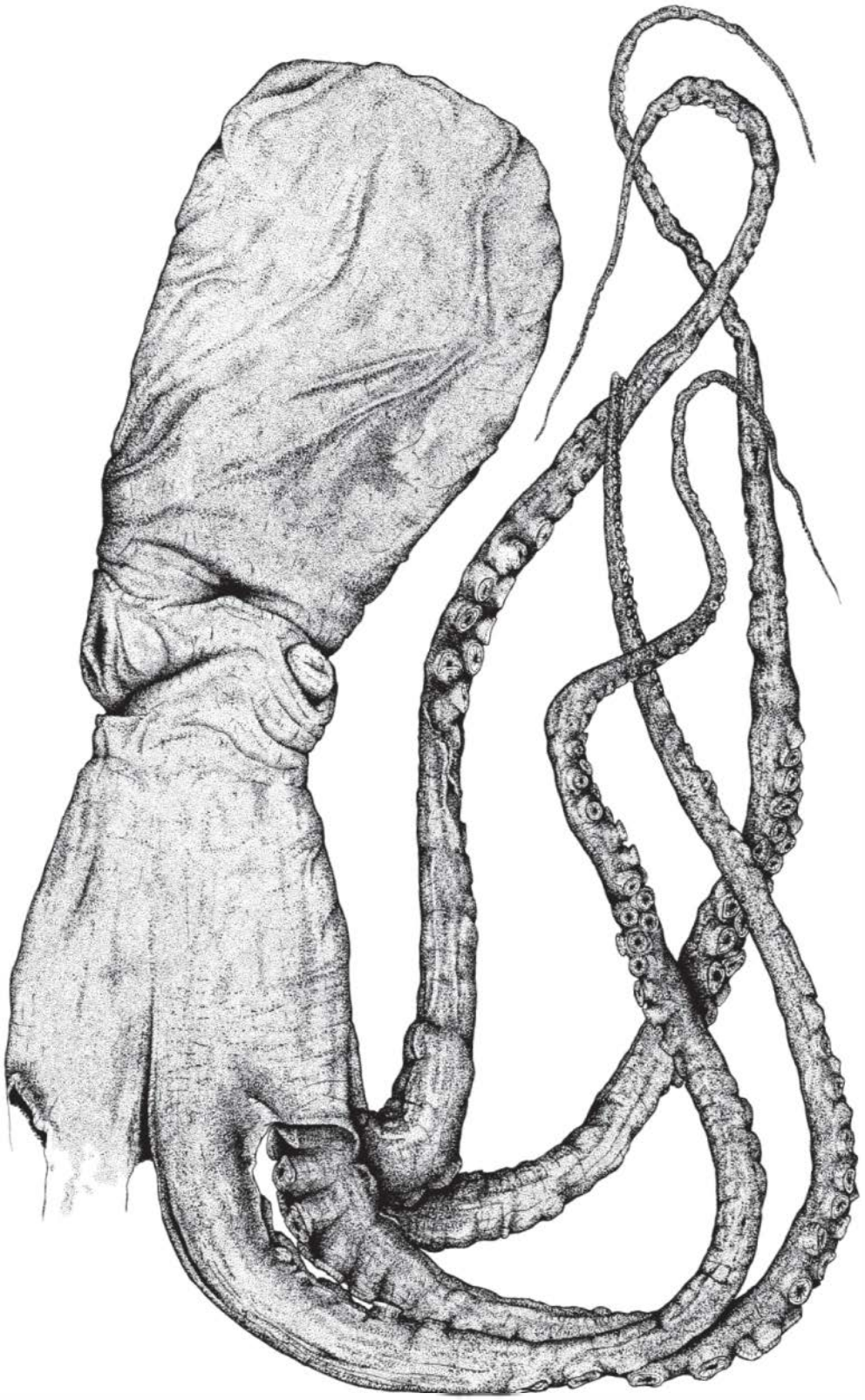


Figure 126. *Benthoctopus tangaroa* sp. nov.: NMNZ M.100851, female, ML 122.5 mm.

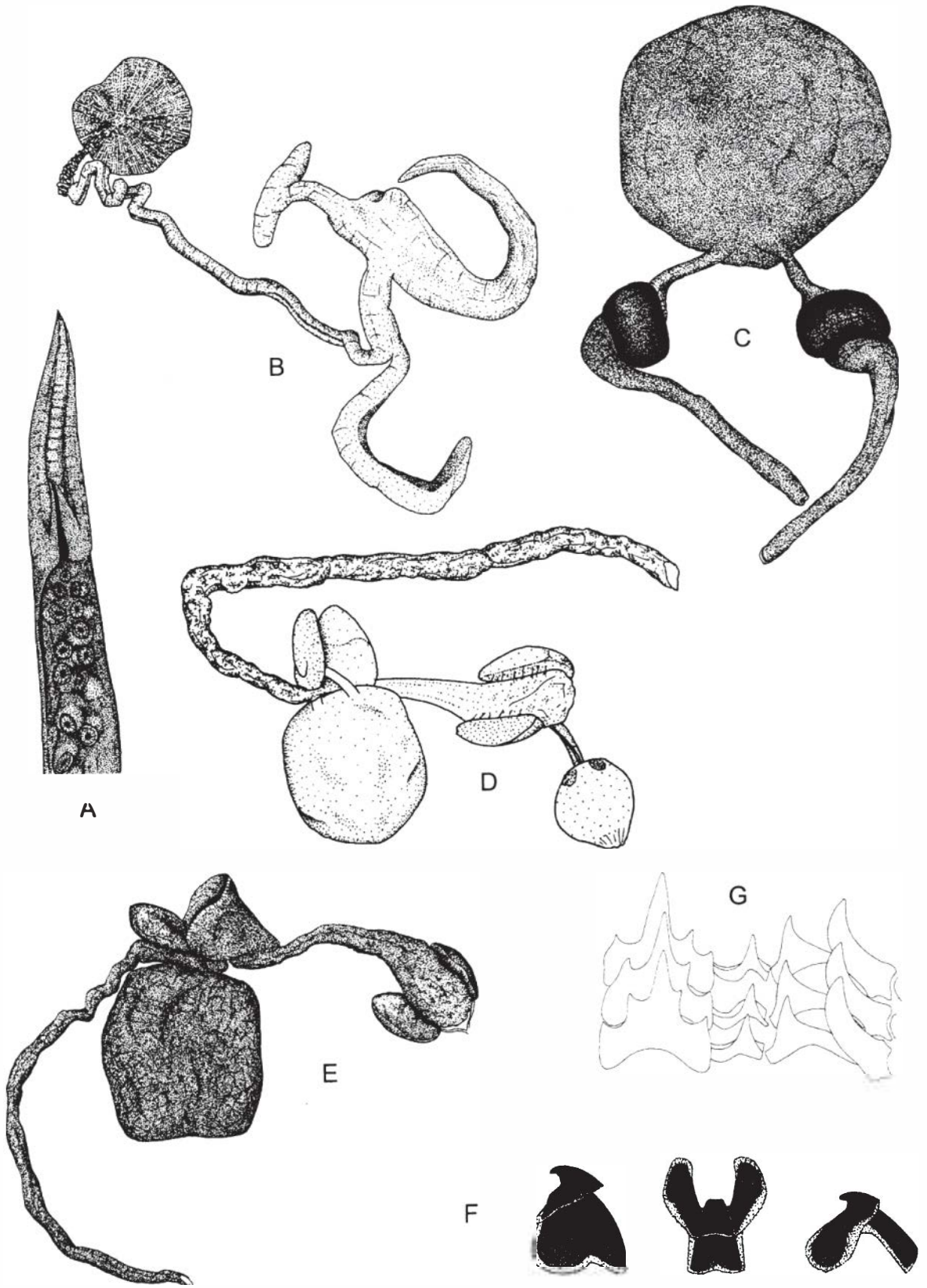


Figure 127. *Benthoctopus tangaroa* sp. nov. Anatomy: **A**, NMNZ M.100852, male, ML 100 mm. **B, D**, NMNZ M.100851, female, ML 122.5 mm. **C, E, G**, NMNZ M.100850, male, ML 75 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, alimentary canal (minus buccal bulb). **F**, beaks. **G**, radula.

above base of arm pairs 1 and 2, meeting across dorsal midline of head; eye apertures dorsolaterally oriented. Funnel large, well developed (FuL about 21–53% ML), base entirely free of brachial crown. Nuchal constriction well developed.

Brachial crown robust, equivalent to or slighter wider than head. Arms slender, very short to moderately long (male and female combined about 39–75% TL), gradually tapering to fine tips; arms 1 and 2 frequently longest, arms 3 and 4 shortest, without consistent disparity in relative arm length. Web shallow to moderately deep, about 12–25% longest arm length, with minimal membranous extension down either dorso- or ventrolateral faces of any arm; web formula variable, with no consistent disparity in relative sector depths. Suckers biserial; non-hectocotylised arm tips of males not secondarily modified in any discernible way. Non-hectocotylised arm sucker counts moderate, ASC 130–151; suckers extend to arm tips. Suckers small, ASIn 4.5–8.8, not enlarged in male; distal 5–10 suckers minute; suckers with: small suction chamber; poorly constricted sucker aperture; poorly developed grasping ring with about 18 faint radial grooves; and well-developed muscular suction pad (Fig. 155U).

Third right arm of male hectocotylised, shorter than opposite member (OAI 72.1–73.3), with 50–55 suckers in total, none obviously enlarged. Spermatophoral groove shallow, slightly continued over adoral surface of web sector D; web extending down ventrolateral surface of arm 3 narrow, web margin thickened, with 6 or 7 papillaelike ridges within recess formed by junction of spermatophoral groove and web sector D. Hectocotylised portion large (Fig. 130B), ligula about 11–16% arm length, with raised, thickened lateral cheeks, with narrow, shallow central excavation and about 15 faint transverse rugae; calamus large, about 37–50% ligula length, acute, with thick cheeks and incomplete groove not extending entire structure length.

Skin (post-thaw-fixed) entirely smooth; superocular cirrus absent. Colour over dorsal surfaces of mantle, head, dorsal and dorsolateral surfaces of arms 1–3, and web sectors A–D pinkish-red, surfaces of arms 4 and web sector E slightly darker red; spermatophoral groove pale yellow; ventral surfaces of mantle, head, funnel, ventrolateral faces of arms 1–3 and both dorso- and ventrolateral surface of arms 4, adoral surface of web sectors A–E, and oral surfaces of arms within web margins maroon. Dorsal surfaces of mantle, head and arms lighter than ventral and oral surfaces of arms and web.

Pallial aperture reduced, mantle attaches anterior to ventral surface of orbit; funnel moderately long, slender; adsiphonal pouches moderately well developed. Ventral mantle musculature thin. Funnel collar and funnel retractor muscles moderately well developed; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting renal tissue to ventral and inner surface of mantle absent. Male penile complex large; penis and diverticulum oriented along anteroposterior axis of mantle. Ovary sac large, with weak fibrous connection to ventral inner surface of mantle musculature; female genital apertures open proximal to anterior base of interpallial septum on face of digestive gland; 3 anal flaps (small lateral lappets aside an upper dorsal flap). Gills with 8 or 9 lamellae per outer demibranch. Lateral muscles restraining digestive gland, dorsolateral surface of visceral envelope, and anal region with small to large red chromatophores. Funnel organ not preserved in any specimens.

Male reproductive system (Fig. 130C) with short, thick, weakly convoluted proximal vas deferens; spermatophoral gland moderately long, with thickenings, glandular regions and constrictions, with small appendix proximal to junction with accessory gland. Accessory gland distally thickened, expanded, with incomplete terminal volution. Spermatophore sac long, thin walled, containing numerous (to 25) spermatophores of total length to 76 mm. Distal vas deferens short, thick; penis diverticulum single, about 3 times longer than penis, often containing single spermatophore; penis short, genital aperture subterminal. Neither well-preserved mature nor submature female known.

Alimentary canal (Fig. 130D) with moderate-sized buccal bulb about 20% ML; anterior salivary glands well developed; anterior oesophagus long, narrow; crop without ventral diverticulum. Left posterior salivary gland broader than right, both broadly triangular, vestigial (relative to ML, their absolute size is large), length about 70% buccal bulb length, about 13% ML. Posterior oesophagus muscular, thick walled. Stomach with three apparent sections, basal thin walled, central thick walled, distal thin walled; stomach with undivided lumen. Spiral caecum about 75% size of stomach, of single incomplete radially striate volution. Intestine short, length equivalent to oesophagus and crop; basal third thick walled, followed by short, thin-walled section, posterior third thin walled, dilated; 3 anal flaps, (2 small lateral lappets either side of central flap).

Digestive gland large, broadly triangular, with small anterior peaks and depressions to accommodate stomach and crop; pancreas small; ink sac absent.

Upper beak (Fig. 130E) tall (height 106.8% length);

hood dark brown to black, lateral walls dark brown, hood and lateral wall margins translucent; hood moderately deep (depth 38.1% beak length), with broadly rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, slightly deflected down, lateral margins strongly chiselled; with single broad tooth in jaw. Lateral walls straight sided; crest broadly rounded, lateral wall fold not apparent; with broad sinus in lateral wall basal margin. Lower beak (Fig. 130E) moderately tall (height 75.2% width); hood, lateral wall and wings dark brown to black, lateral wing and wall margins translucent. Lateral wall with deep, acute-angled basal notch and broadly keeled triangular crest. Hood moderately deep (depth 32.4% beak length), projecting forward, with flattened chisel-like to weakly bifid rostrum; hood with shallow posterior notch; lateral wings long (length 100% beak length); lateral wings with single weak fold.

Radular dentition simple; rachidian well developed, broad based with 1 or 2 asymmetrically disposed lateral cusps; 1st lateral tooth small, with pronounced upward-deflected inner heel, inner base with cusp-like prominence, outer base with short, acute cusp; 2nd lateral of equivalent length to rachidian, with single large broad-based cusp; marginal tooth robust, broad based, shorter than 2nd laterals, with comparable-sized cusp; marginal block well developed, broader than long (across transverse axis of radula ribbon).

REMARKS: This species differs from previously described southern ocean *Benthoctopus* species in its higher arm sucker counts (ASC 130–151), although there is potential overlap with *B. berryi* (ASC 130–132) in this feature. *Benthoctopus clyderoperi* can be differentiated from *B. berryi* by its shallower web (WDI in *B. clyderoperi* 12.0–25.0, in *B. berryi* 20.0–29.7), and smaller suckers (ASIn in *B. clyderoperi* 4.5–8.8, in *B. berryi* 7.3–7.9). These two species differ also in general morphology, with mantle constriction more strongly developed in *B. clyderoperi* (*B. berryi* being a far more robust-looking species). The two species also differ in the relative muscularity of the suction cup and lateral walls of the suckers (Figs 155P, U), being very weak in *B. berryi* and well developed in *B. clyderoperi.* In light of these differences I feel it advisable to describe the New Zealand species as new.

Whereas *B. tegginmathae* has a crop diverticulum but no lateral cusps on the rachidian tooth, *B. clyderoperi* lacks a crop diverticulum and has a rachidian with well-developed, asymmetric lateral cusps. The combination of character states in these two new species necessitates further revision of the generic diagnosis proposed by Voss (1988a) for *Benthoctopus*.

ETYMOLOGY: Named for Clyde Roper as a small token of appreciation for his many valued discussions and support throughout the duration of this research.

Table 109. Indices and counts for male *Benthoctopus clyderoperi* sp. nov. (* denotes damage).

	NMNZ M.118256	NMNZ M.90272	NZOI H-667	NMNZ M.90384
OAI	*	*	72.1	73.3
ASC3R	55	50	51	55
CaLI	49.7	37.4	41.5	49.5
LLI	11.2	15.6	13.6	12.7

Subfamily **GRANELEDONINAE** Voss, 1988a

Deep-sea octopods with uniserial suckers; ink sac absent; crop with diverticulum reduced or absent; radula reduced, degenerate; funnel organ V, VV, or paired pads; posterior salivary glands small to vestigial; spermatophores large and few (Voss 1988a: 270).

Graneledone Joubin, 1918

TYPE SPECIES: *Graneledone verrucosa* (Verrill, 1881)

DIAGNOSIS: Radula homodont, teeth narrow to broad; funnel organ VV; crop diverticulum absent; posterior salivary glands reduced; dorsal and ventral surfaces of mantle, head, arms and web variably covered with clusters of cartilagelike tubercles, each cluster comprising numerous smaller elements; diverticulum of penis coiled in spiral; gill lamellae number 6–9 per outer demibranch, inner demibranch not markedly reduced; ink sac absent (modified from Voss 1988a: 270).

Graneledone challengeri (Berry, 1916)

(Figs 132–134)
(Tables 111–116)

Eledone verrucosa (not Verrill, 1881): Hoyle 1886 (*partim*, specimen from Discovery Stn 170A): 104.
?*Moschites verrucosa* (not Verrill): Hoyle 1904: 201.
Moschites verrucosa (not Verrill): Oliver 1915: 559.
Moschites challengeri Berry, 1916: 49–50; Berry 1917: 4, pl. 2, fig. 2.

hood dark brown to black, lateral walls dark brown, hood and lateral wall margins translucent; hood moderately deep (depth 38.1% beak length), with broadly rounded crest, without posterior notch; rostrum triangular, rostral tip blunt, slightly deflected down, lateral margins strongly chiselled; with single broad tooth in jaw. Lateral walls straight sided; crest broadly rounded, lateral wall fold not apparent; with broad sinus in lateral wall basal margin. Lower beak (Fig. 130E) moderately tall (height 75.2% width); hood, lateral wall and wings dark brown to black, lateral wing and wall margins translucent. Lateral wall with deep, acute-angled basal notch and broadly keeled triangular crest. Hood moderately deep (depth 32.4% beak length), projecting forward, with flattened chisel-like to weakly bifid rostrum; hood with shallow posterior notch; lateral wings long (length 100% beak length); lateral wings with single weak fold.

Radular dentition simple; rachidian well developed, broad based with 1 or 2 asymmetrically disposed lateral cusps; 1st lateral tooth small, with pronounced upward-deflected inner heel, inner base with cusp-like prominence, outer base with short, acute cusp; 2nd lateral of equivalent length to rachidian, with single large broad-based cusp; marginal tooth robust, broad based, shorter than 2nd laterals, with comparable-sized cusp; marginal block well developed, broader than long (across transverse axis of radula ribbon).

REMARKS: This species differs from previously described southern ocean *Benthoctopus* species in its higher arm sucker counts (ASC 130–151), although there is potential overlap with *B. berryi* (ASC 130–132) in this feature. *Benthoctopus clyderoperi* can be differentiated from *B. berryi* by its shallower web (WDI in *B. clyderoperi* 12.0–25.0, in *B. berryi* 20.0–29.7), and smaller suckers (ASIn in *B. clyderoperi* 4.5–8.8, in *B. berryi* 7.3–7.9). These two species differ also in general morphology, with mantle constriction more strongly developed in *B. clyderoperi* (*B. berryi* being a far more robust-looking species). The two species also differ in the relative muscularity of the suction cup and lateral walls of the suckers (Figs 155P, U), being very weak in *B. berryi* and well developed in *B. clyderoperi*. In light of these differences I feel it advisable to describe the New Zealand species as new.

Whereas *B. tegginmathae* has a crop diverticulum but no lateral cusps on the rachidian tooth, *B. clyderoperi* lacks a crop diverticulum and has a rachidian with well-developed, asymmetric lateral cusps. The combination of character states in these two new species necessitates further revision of the generic diagnosis proposed by Voss (1988a) for *Benthoctopus*.

ETYMOLOGY: Named for Clyde Roper as a small token of appreciation for his many valued discussions and support throughout the duration of this research.

Table 109. Indices and counts for male *Benthoctopus clyderoperi* sp. nov. (* denotes damage).

	NMNZ M.118256	NMNZ M.90272	NZOI H-667	NMNZ M.90384
OAI	*	*	72.1	73.3
ASC3R	55	50	51	55
CaLI	49.7	37.4	41.5	49.5
LLI	11.2	15.6	13.6	12.7

Subfamily **GRANELEDONINAE** Voss, 1988a

Deep-sea octopods with uniserial suckers; ink sac absent; crop with diverticulum reduced or absent; radula reduced, degenerate; funnel organ V, VV, or paired pads; posterior salivary glands small to vestigial; spermatophores large and few (Voss 1988a: 270).

Graneledone Joubin, 1918

TYPE SPECIES: *Graneledone verrucosa* (Verrill, 1881)

DIAGNOSIS: Radula homodont, teeth narrow to broad; funnel organ VV; crop diverticulum absent; posterior salivary glands reduced; dorsal and ventral surfaces of mantle, head, arms and web variably covered with clusters of cartilagelike tubercles, each cluster comprising numerous smaller elements; diverticulum of penis coiled in spiral; gill lamellae number 6–9 per outer demibranch, inner demibranch not markedly reduced; ink sac absent (modified from Voss 1988a: 270).

Graneledone challengeri (Berry, 1916)

(Figs 132–134)
(Tables 111–116)

Eledone verrucosa (not Verrill, 1881): Hoyle 1886 (*partim*, specimen from Discovery Stn 170A): 104.
?*Moschites verrucosa* (not Verrill): Hoyle 1904: 201.
Moschites verrucosa (not Verrill): Oliver 1915: 559.
Moschites challengeri Berry, 1916: 49–50; Berry 1917: 4, pl. 2, fig. 2.

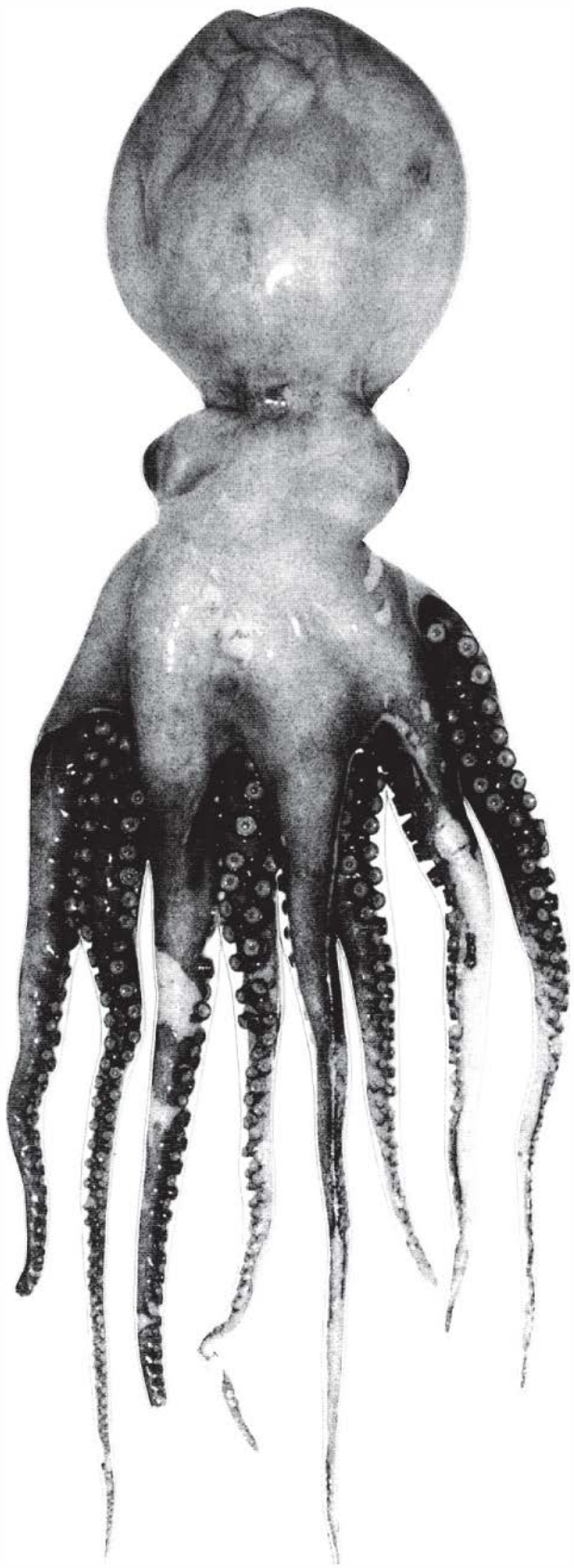


Figure 129. ***Benthoctopus clyderoperi*** sp. nov.: Paratype, NZOI P-1111, female, ML 85 mm.

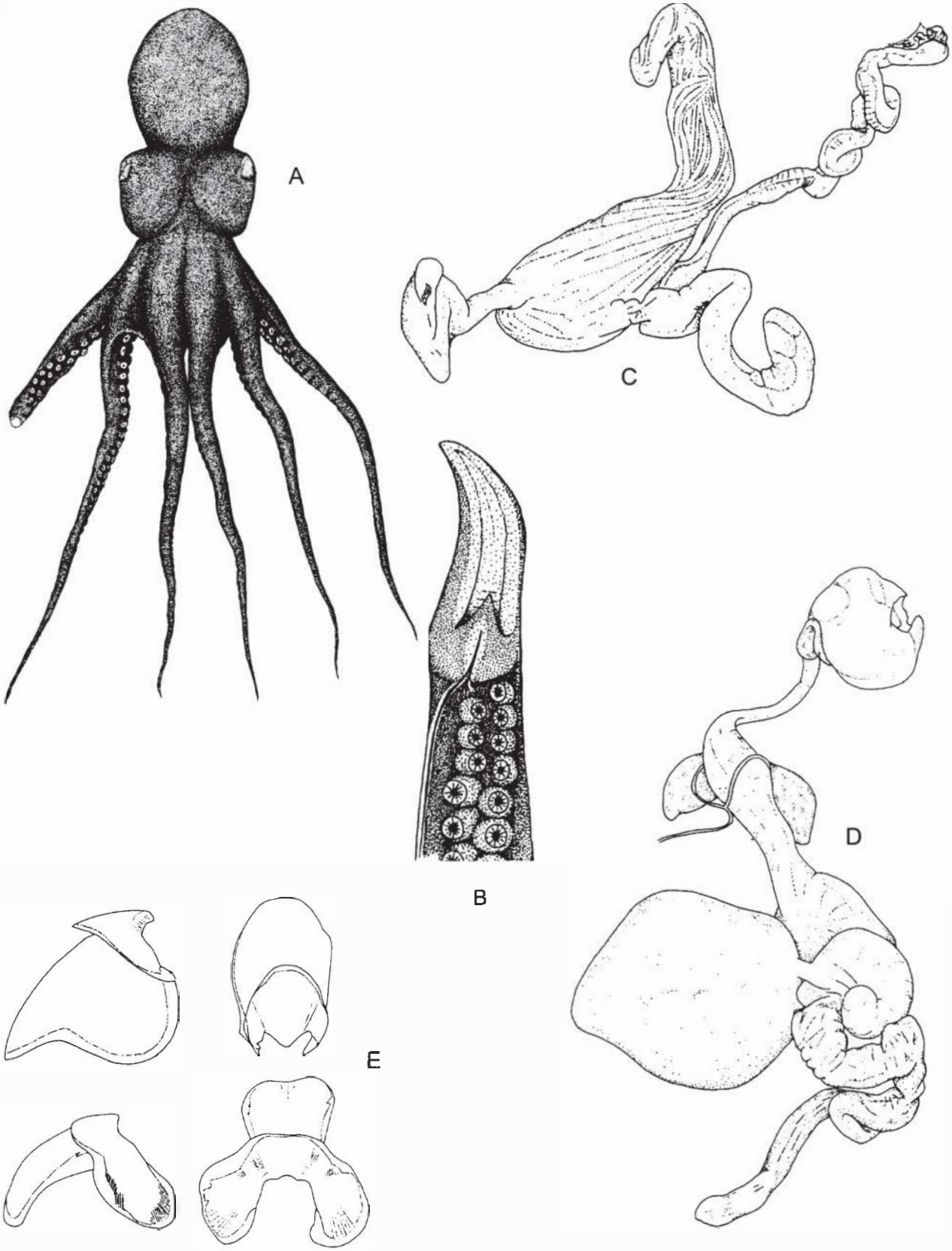


Figure 130. *Benthoctopus clyderoperi* sp. nov.: **A**, NMNZ M.90381, female, ML 34 mm. **B**, NMNZ M.90272, male, ML 88.5 mm. **C–D, F**, NMNZ M.118256, male, ML 89 mm. **E**, holotype NZOI H-667, male, ML 80 mm. **A**, whole animal. **B**, hectocotyl. **C**, male reproductive system. **D**, alimentary canal. E, beaks.

Table 108. Indices, formulas and counts for *Benthoctopus clyderoperi* sp. nov. (* denotes damage).

	NMNZ M.118256	NMNZ M.90272	NZOI H-667	NZOI P-1111	NMNZ M.90384	NMNZ M.90381
MWI	53.4	54.7	64.4	89.8	78.4	100.0
HdLI	32.6	24.9	36.4	33.6	37.3	67.6
HdWI	47.8	36.2	50.3	60.6	59.5	92.6
EOI	20.2	15.0	18.9	17.8	14.5	32.1
ALI1-4	42.9–74.5	51.1–*	39.4–71.9	*–68.0	49.0–73.3	64.5–72.7
AFR	2.1.4.3	*	1.2.4.3	*	2.4.1.3	*
AFL	*	*	*	*	2.1.3.4	1.4.3.2
WDIA–E	12.4–18.8	*	16.1–25.5	12.8–25.1	18.7–24.3	15.8–22.6
WFR	B.A.E.D.C	D.C.B.E.A	A.B.C.D.E	A.C.B.D.E	C=D.B.E.A	C.A.B=D.E
WFL	B.A.C=D.E	*	A.C.B.D.E	B.A.C.D.E	D.C.B.E.A	D.A.B.E.C
ASC1-4	42–*	*	149–*c.* 151	*	145–150	130–151
ASIn1-4	4.5–4.7	4.5–4.7	6.3–6.4	5.7–6.4	5.5–5.8	8.8
FuLI	21.0	25.4	31.3	34.8	33.2	52.9
FFuI	12.2	14.1	14.0	14.0	14.7	26.5
PAI	22.5	21.5	52.3	36.6	34.9	35.3

Table 110. Raw measures for *Benthoctopus clyderoperi* sp. nov. (* denotes damage).

	NMNZ M.118256	NMNZ M.90272	NZOI H-667	NZOI P-1111	NMNZ M.90384	NMNZ M.90381
TL	357	264	381	322	292	183
ML	89.0	88.5	80.0	78.5	72.3	34.0
MW	47.5	48.4	51.5	70.5	56.7	34.0
HdL	29.0	22.0	29.1	26.4	27.0	23.0
HdW	42.5	32.0	40.2	47.6	43.0	31.5
EO	18.0	13.3	15.1	14.0	10.5	10.9
AL1R/L	241/235*	144*/60*	274/272	183*/219	201/197	120/129
AL2R/L	244*/266	120*175*	246/252	168*/186*	214/210	133/118
AL3R/L	153/236*	135/150*	150/208	213*/208*	143/195	68*/126
AL4R/L	240/197*	165/166	228/190*	187*/157*	205/192	122/128
WDA	45	26	70	49	40	29
WDBR/L	48/50	32/30	63/67	41/55*	44/42	28/25
WDCR/L	33/43	33/38	52/69	43/48	52/47	30/21
WDDR/L	40/43	37/*	48/48	37/38*	52/48	28/31
WDE	42	30	44	28	41	23
ASC1R	*	*	*c.* 151	*	145	L151
ASC2R	*	*	149	*	150	L130
ASC3R	55	50	51	*	54	L131
ASC4R	*	*	118*	*	148	L137
ASn1R	4.2	4.0	5.1	5.0	4.2	3.0
ASn2R	4.0	4.2	5.0	5.0	4.0	3.0
ASn3R	4.1	4.2	5.0	5.0	4.1	3.0
ASn4R	4.0	4.0	5.0	4.5	4.0	3.0
GiLC	8	8	8	8	9	9
FuL	18.7	22.5	25	27.3	24	18
FFL	10.9	12.5	11.2	11.0	10.6	9
PA	20	19	41.8	28.7	25.2	12
CaL	8.5	7.9	8.3	F	9.0	F
LL	17.1	21.1	20.0	F	18.2	F

Moschites verrucosa var. *Challengeri* [*sic*]: Joubin, 1924: 13.
Eledone challengeri: Robson 1926: 1329.
Graneledone challengeri: Robson 1932: 311–313, fig. 71; Voss 1976: 454; O'Shea & Kubodera 1996: 153–163, fig. 1.

TYPE MATERIAL EXAMINED (27 specimens, 12 male [M], 15 female [F]): Holotype: BMNH 1889.4.24.49, M, ML *c.* 75 mm, *c.* 29°45'S, 178°11'W, 1151 m, 14/07/1874, HMS. *Challenger* Stn 170A.

ADDITIONAL MATERIAL EXAMINED: NZOI Stn Z8317, F, ML 91.0 mm, FPT, 37°48' S, 179°24–25' E, 1050 m, f.v. *San Torshavn*, 18/03/1995; NMNZ M.118288, M, ML 83.5 mm, FPT, *c.* 39°35.0' S, 178°24' E, 1000 m, -/04/1994, f.v. *Peterson*; NZOI Stn Z8316, M, ML 77.0 mm, FPT, 39°54–55' S, 178°17–16' E, 1050 m, f.v. *San Torshavn*, 17/06/1995; NZOI Stn Z8325, M, ML 121.5 mm, FPT, 39°56–54' S, 178°15–16' E, 960–1130 m, f.v. *San Torshavn*, 08/09/1995; NMNZ M.118254, F, ML *c.* 125 mm, FPT, *c.* 39°58.55' S, 178°14.80' E, -/04/1994, 900 m, f.v. *San Manukau*; NMNZ M.118250, F, ML 131.2 mm, FPT, *c.* 39°59.0' S, 178°13' E, 900 m, -/04/1994, f.v. *Peterson*; NMNZ M.118324, M, ML 88.0 mm, F, ML 73.2 mm, FPT, 39°59' S, 178°13' E, 940–1070 m, -/04/1994, f.v. *Peterson*; NMNZ M.118249, 2F, ML *c.* 119, 99.5 mm, FPT, 39°59.0' S, 178°13.0' E, 900 m, -/06/1994, f.v. *Peterson*; NMNZ M.109054, F, ML 81.6 mm, 40°28.5' S, 176°59.05' E, 1336–1340 m, 3/10/1990, f.v. *Willwatch* Stn WIL/070/89; NMNZ M.102561, F, ML 92 mm, 41°13' S, 177°02' E, 1458–1500 m, 02/10/1990, f.v. *Cordella* Stn 9003/060; NMNZ M.134146, M, ML 137.0 mm, F, ML 149.0 mm, FPT, 42°35' S, 175°29' E, 1440 m, 15/12/1996, coll. D. Pollock (956/152); NMNZ M.118162, F, ML *c.* 85 mm, 44°14.3' S, 179°59.2' E, 766–769 m, 25/11/1987; NZOI Stn Z8396, M, ML 101.5 mm, F, ML 113.0 mm, FPT, 44°21.06–21.66' S, 179°25.63–28.31' E, 1123–1134 m, BT 4.4°C, 13/10/1995, f.r.v. *Tangaroa* Stn TAN9511/49; NZOI Stn Z8403, M, ML 125.0 mm, FPT, 44°33.89–34.31' S, 177°43.82–41.07' W, 983–995 m, BT 4.5°C, 24/10/1995, f.r.v. *Tangaroa* Stn TAN9511/128; NMNZ M. 117198, M, ML 123.5 mm, FPT, 44°35' S, 178°46' W, 1218–1229 m, 05/06/1992, f.r.v. *Tangaroa* Stn 9206/13; NMNZ M.100356, F, ML *c.* 76 mm, 44°37.4' S, 178°04.1' W, 1167 m, 13/10/1988, f.v. *Otago Buccaneer*; NMNZ M.110531, M, ML 80.0 mm, FPT, 44°47.08' S, 173°10.15' E, 1061–1083 m, 31/10/1990; NZOI Stn Z8382, M, ML 133.0 mm, FPT, 44°54.19–55.91' S, 173°47.75–49.22' E, 1150–1167 m, BT 3.2°C, 06/10/1995, f.r.v. *Tangaroa* Stn TAN9511/003; NZOI Stn Z8385, F, ML 144.5 mm, FPT, 44°57.23–57.30' S, 173°55.89–58.72' E, 1174–1184 m, BT 3.1°C, 07/10/1995, f.r.v. *Tangaroa* Stn TAN9511/012; NMNZ M.109055, F, ML 92 mm, 45°10.2' S, 174°59.0' E, 1156–1162 m, 07/11/1986; NZOI Stn S153 SEB, F, ML 26.8 mm, ?FL, 45°21.1' S, 173°35.8' E, 1386 m, 27/10/1979.

RECOGNISED DISTRIBUTION (Fig. 131, p. 208): Kermadec Islands (type), east coast North Island, East Cape to Chatham Rise (*c.* 29°45' S, 178°11' W to 45°21.1' S, 173°35.8' E); 766–1500 m; recorded bottom temperature range 3.1–4.5°C (4 specimen lots).

DIAGNOSIS: Moderate to large-sized animal; arms with few suckers, ASC 73–114; hectocotylised arm sucker count 41–51; hectocotylised portion of arm short, about 4–6% arm length; suckers small, ASIn 5.0–8.0; mantle with about 30–40 cartilage-like clusters along dorsal midline, 20–30 in transverse line between orbits; clusters small, diameter 1.6–5.3% ML, with 1–18 individual processes within each (most frequently 4–10).

DESCRIPTION: Adult attaining moderate to large size (ML to 144.5 mm, TL to 607.0 mm); body slender to moderately robust (Figs 132A–B, 133A–D). Male and female of similar gross morphology; female attaining greater mantle and total length. Mantle ovoid, dorsoventral compression and lateral keel or fold of skin absent. Head large, broad, narrower than mantle (HdL about 28–42% ML, HdW about 71–107% ML), separated from mantle by poorly defined preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head, situated above base of lateral arm pairs 2 and 3; eye apertures large, dorsolaterally to laterally oriented. Funnel of moderate length, base almost entirely free of arm bases 4. Nuchal constriction little developed.

Head as wide as or wider than brachial crown; brachial crown robust. Arms short to moderately long, about 60–80% TL, gradually tapering to non-filiform tips; arm pairs 1 and 2 frequently longest, 3 and 4 shortest, with no consistent disparity in relative arm lengths. Web deep, about 20–35% longest arm length, little developed along both dorsal and ventral faces of arms; web formula variable, sectors A and E usually shallowest, sectors B and C deepest, with no consistent disparity in relative sector depths. Arm sucker counts greater in mature females than males, female ASC 77–114, male 73–96; suckers extend to arm tips; distal arm tips of male not modified in any discernible way. Suckers small, ASIn 5.0–7.3 (male), 5.5–8.0 (female); distal 15–30 suckers minute; not abruptly enlarged in male; suckers with: large suction chamber, little-constricted sucker aperture, mode-rately well-developed grasping ring with about 18–30 faint radial grooves, and simple development of muscular suction pad (Fig. 155V–W).

Third right arm of male hectocotylised, shorter than opposite member (OAI 77.4–87.9), with 41–51 suckers in total, none obviously enlarged; hecto-cotylised arm sucker with 41–51 suckers. Spermato-phoral groove moderately well developed, narrow, little flaring, with conspicuously thickened web margin. Hectocotylised portion (Fig. 134A) short, ligula about 4–6% hectocotylised arm length, calamus proportionally large, about 30–55% ligula length.

Skin over dorsal surfaces of mantle, head, arms 1 and 2, web sectors A–C, and dorsolateral surfaces of

arms 3 covered in clusters of cartilage-like processes. Individual clusters small, diameter 1.6–5.3% ML, with 1–18 individual processes within each, most frequently 4–10; about 30–40 clusters along dorsal midline, 20–30 in transverse line between orbits. Ventral surfaces of mantle, head, funnel, ventrolateral surfaces or arms 3, dorso- and ventrolateral surfaces of arms 4, and web sectors D and E smooth; superocular cirrus absent, however, 3 enlarged superocular platelike clusters are present on males; tissues with slight subcuticular gelatinous layer.

Colour variable: immature–submature individuals uniformly maroon over dorsal, ventral, and oral surfaces; mature specimens purplish-red over dorsal surface of mantle, head, dorso- and ventrolateral surface of arms 1 and 2, dorsolateral surface of arms 3, and web sectors A–C; ventral surface of mantle, web sectors D and E, ventrolateral surfaces of arms 3, both dorso- and ventrolateral surfaces of arms 4, and oral surfaces of arms and web darker coloured, maroon; spermatophoral groove white to cream coloured. Counter pigmentation marked in mature specimens, with dorsal surfaces of mantle, head and arms lighter than ventral and oral surfaces.

Pallial aperture reduced, mantle attaches to ventral surface of orbit; funnel moderately long, slender, distal aperture not inrolled or contracted; adsiphonal pouches poorly developed. Mantle musculature thick. Funnel collar not well developed; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting viscera to ventral inner surface of mantle absent. Male with large penis diverticulum oriented away from interpallial septum; female with genital apertures opening at about 45° angle on face of viscera, not extending over lateral interpallial musculature nor opening proximal to anus. Gills small, compact, with 6 or 7 lamellae per inner and outer demibranch. Lateral muscles restraining digestive gland and visceral envelope, renal papilla and region proximal to anus pigmented with small maroon chromatophores. Funnel organ comprising two narrow V-shaped pads in VV-formation, both inner and outer limbs of subequal length.

Male reproductive system (Fig. 134B) with short, thin proximal vas deferens; spermatophoral gland moderately long, with regional swellings, constrictions and glandular portions, and small appendix at junction with accessory gland. Accessory gland large, moderately long, granular, with terminal partial recurvature. Spermatophoric sac swollen proximal to spermatophoral gland and penis junctions, distally attenuated, thin walled, containing single spermatophore. Distal vas deferens short, thick; penis diverticulum large, single, with pronounced spiral; penis proper large, thick, genital aperture subterminal. Female (Fig. 134C) with short, stout proximal oviducts departing ovary sac singly; oviducal glands large, not chambered; distal oviducts short, stout, swollen. Mature eggs large (19.5 x 7.2 mm), each with short stalk.

Alimentary canal (Fig. 134D) with large buccal bulb about 28% ML in greatest dimension; anterior salivary glands very small, about 27% buccal bulb greatest dimension; anterior oesophagus moderately long, narrow; crop a pronounced thin-walled dilation of oesophagus without anterior diverticulum. Posterior salivary glands elliptical, vestigial (relative to ML, their absolute size is large), length about 36% buccal bulb greatest dimension or 9% ML. Posterior oesophagus almost non-existent. Stomach with three apparent external sections, basal thin walled, central thick walled, distal thin walled; stomach with undivided lumen. Spiral caecum of single incomplete radially striate volution. Intestine short, length equivalent to that of oesophagus and crop, thick walled, dilated for greatest length (slightly constricted proximal to anus); anal flaps absent. Digestive gland large, ovoid, without anterior peaks but with depressions imparted by stomach, crop and intestine; pancreas well developed; ink sac absent. Stomach contents comprise small crustaceans.

Upper beak (Fig. 134E) very tall (height 112.5% length); hood dark brown, lateral walls light brown, hood and lateral wall margins translucent; hood very deep (depth 50.0% beak length), with squared crest, shallow posterior notch and weak furrow running from notch to rostrum; rostrum triangular, rostral tip blunt, slightly deflected down. Lateral walls straight sided; crest squared, lateral-wall fold absent; jaw with single large tooth. Lower beak (Fig. 134E) moderately tall (height 74% width); hood dark brown, lateral wall and wings lighter brown, lateral wing and wall-margins translucent. Lateral wall with strong basal notch and broadly rounded triangular crest. Hood very deep (depth 42% beak length), projecting forward, with flattened chisel-like rostrum; hood without posterior notch; lateral wings moderately long (length 100% beak length); lateral wings with single weak fold.

Radular dentition (Fig. 134F, G) simple, variable; rachidian well developed, broad based, without lateral cusps; 1 or 2 first lateral teeth, with or without cusp; 2nd lateral with large broad-based cusp; marginal tooth robust; marginal blocks well developed.

REMARKS: The dorsal surfaces of mantle, head and arms 1–3 of the holotype of *G. challengeri* (Berry) are

Table 111. Indices and formulas for male *Graneledone challengeri* (Berry) (* denotes damage).

	NZOI Stn Z8382	NZOI Stn Z8403	NMNZ M.117198	NZOI Stn Z8325	NMNZ M.118288
MWI	101.5	120.0	104.5	107.0	101.8
HdLI	28.9	28.8	28.3	33.7	41.9
HdWI	76.7	83.2	76.0	80.7	91.0
EOI	11.7	11.2	14.3	10.7	15.0
ALI1–4	59.2–69.9	60.2–70.1	60.1–71.7	65.1–77.1	62.4–79.8
AFR	2.1.4.3	*c.* 1.2.4.3	*	2.1.4.3	2.1.4.3
AFL	1.2.4.3	*	3.2.1.4	*	*
WDIA–E	26.7–33.9	21.6–34.5	22.9–37.0	18.1–27.2	22.6–36.4
WFR	B=C=D.E.A	C.D.B=E.A	B.D.E.C.A	B.C.E.A.D	C.B.D.A.E
WFL	C.B.E.D.A	C.C.B.E.A	C.D.E.B.A	D.C.B.E.A	B.A.D.C.E
ASC1–4	79–86	73–86	76–81	95–96	93–96
ASIn1–4	5.3–6.0	5.6–7.2	5.0–5.7	5.8–6.5	6.0–7.3

Table 112. Indices and formulas for female *Graneledone challengeri* (Berry) (* denotes damage).

	NZOI Stn Z8385	NMNZ M.118250	NMNZ M.118254	NMNZ M.118249	NMNZ M.118249
MW	81.0	102.9	102.0	100.0	122.6
HdL	30.4	31.3	33.4	33.2	39.2
HdW	70.6	80.8	88.8	94.4	107.5
EO	10.7	9.4	16.0	*	13.9
ALI1–4	58.8–66.8	73.3–79.3	68.2–85.3	66.0–81.7	65.9–73.6
AFR	3.2.1=4	3.4.2.1	2.3.1.4	1.2=3.4	2.1.4.3
AFL	2.3.1.4	*	*	2.1.3.4	2.3.1.4
WDIA–E	24.9–32.2	15.7–28.1	21.8–32.0	14.5–25.4	21.7–31.9
WFR	C.D.B=E.A	C.B.D.A.E	B.D.E.C.A	B.A.C.D.E	C=D.B.A.E
WFL	C.B.D.E.A	B.C.D.A.E	E.C.B.A.D	B.C.A.D.E	C.B=D.A.E
ASC1–4	77–88	97–107	109–114	98–109	96–105
ASIn1–4	5.5–6.2	5.6–6.9	5.5–6.4	5.9–7.2	6.8–8.0

Table 113. Indices hectocotylised 3R for arm of male *Graneledone challengeri* (Berry) (* denotes damage).

	NZOI Stn Z8382	NZOI Stn Z8403	NMNZ M.117198	NZOI Stn Z8325	NMNZ M.118288
OAI	87.9	77.4	*	*	87.5
ASC3R	43	43	41	50	51
CaLI	31.5	32.6	49.3	28.6	56.7
LLI	4.9	5.2	5.9	4.7	3.9

Table 114. Cluster characteristics for *Graneledone challengeri* (Berry).

	NMNZ M.118324 (M)	NMNZ M.118324 (F)
clusters across mantle	39	34
cluster # interocular	24	22
# processes within cluster	range 1–6, av. 4, n=15	range 3–10, av. 6, n=16
cluster diameter (mm)	range 1.0–1.6, av. 1.4	range 1.7–2.7, av. 2.2
CDI	1.1–1.8	2.3–3.7

Table 115. Raw measures for male *Graneledone challengeri* (Berry) (* denotes damage).

	NZOI Stn Z8382	NZOI Stn Z8403	NMNZ M.117198	NZOI Stn Z8325	NMNZ M.118288
TL	412	475	396	501	372
ML	133.0	125.0	123.5	121.5	83.5
MW	135.0	150.0	129.0	130.0	85.0
HdL	38.5	36.0	35.0	41.0	35.0
HdW	102.0	104.0	93.8	98.0	76.0
EO	15.6	14.0	17.6	13.0	12.5
AL1R/L	286/272	324*/320	293*/271	330/350	286/256
AL2R/L	288/268	333/216*	316*/284	356/386	297/232
AL3R/L	225/256	257/332	239/284*	299/337*	231/264
AL4R/L	244/259	286/317	257/238	326/343	270/242*
WDA	79	72	65	82	91
WDBR/L	90/95	84/93	103/75	105/85	101/96
WDCR/L	90/97	115/105	67/105	93/101	108/88
WDDR/L	90/84	101/97	93/93	70/105	96/90
WDE	86	84	88	83	67
ASC1R	79	L80	L78	96	96
ASC2R	86	86	L81	95	94
ASC3R	43	43	41	50	51
ASC4R	81	73	76	96	93
ASn1R	7.0	7.0	6.5	7.0	5.5
ASn2R	7.0	7.0	6.2	7.0	5.0
ASn3R	7.3	7.8	6.3	7.0	5.4
ASn4R	8.0	9.0	7.1	8.0	6.1
GiLC	7	6	6	7	6
FuL	56.0	51.5	50.2	53.0	31.5
FFL	32.0	39.0	15.0	35.0	10.0
PA	72.5	73.5	72.0	68.0	53.0
CaL	3.5	4.4	6.9	4.0	5.1
LL	11.1	13.5	14.0	14.0	9.0

tan coloured, while the ventral surface of orbits, oral surface of arms and residual web sectors C, D, and E are darker madder-brown to purple. Although the skin over much of both dorsal and ventral surfaces of mantle, head, arms and web is abraded; cartilaginous clusters appear to have extended over the arms to at least the margin of the web, and are present in web sector C and on arm bases 1–3; about 20 small clusters are apparent around the left eye, while none is especially enlarged to form a supraocular cirrus. Web vestiges indicate the web extended along the ventrolateral face of at least some arms almost to the arm tips. All of alimentary canal, reproductive system, buccal bulb, and radula previously removed from the body are presumed lost. Voss (1976) described the radula of the type of *G. challengeri* as being more typically octopodan (p. 454) and more similar to that of *G. macrotyla* than *G. antarctica* (p. 457), but provided no further details or illustration.

Records of *Graneledone* from Cape Mala, Gulf of Panama (Hoyle 1904) and *Graneledone* sp. B (Voss 1988b) from the same location are of particular interest. Whether *Graneledone* sp. B (of Voss) from the Gulf of Panama is based on the same specimen referred to *Mochites verrucosa* (Verrill) by Hoyle (*l. c.*), a specimen included in the synonymy of *G. challengeri* (Berry) by Robson (1932), is not known given the location of Voss's material is unknown (pers. com. Hochberg 1996). Although I have not re-examined the specimen refer-red to *M. verrucosa* by Hoyle, a number of South Australian specimens similar to *G. challengeri* (Berry) (Figs 143A–E) have been examined. No attempt has been made to identify these specimens.

Graneledone taniwha taniwha ssp. nov.
(Figs 136, 137)
(Tables 117–122)

Graneledone sp. O'Shea & Kubodera 1996 (eggs and larvae): 153–163, figs 1–4.

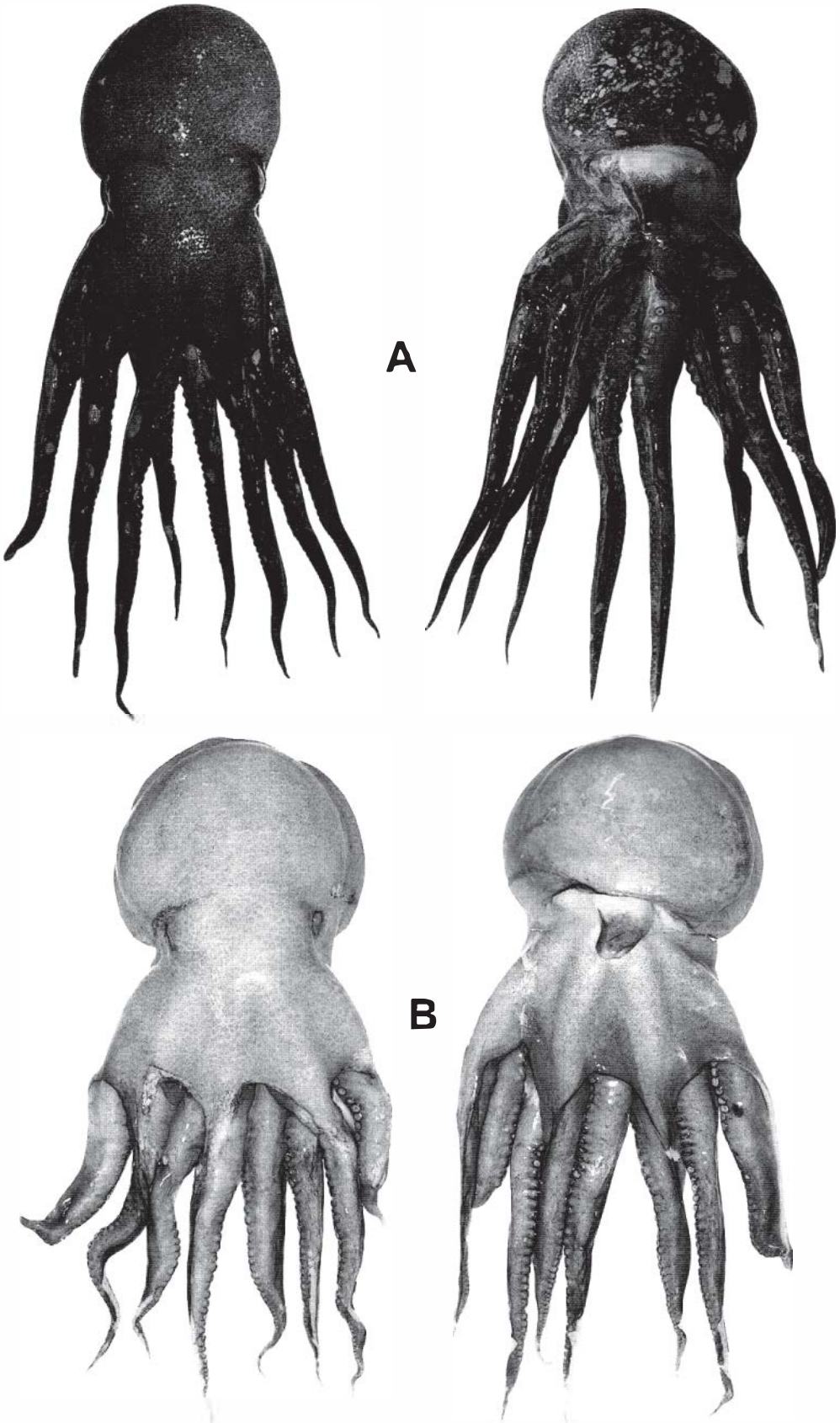


Figure 132. *Graneledone challengeri* (Berry, 1916): **A**, NMNZ M.11834, pre-fix, post-thaw, male, ML 88 mm. **B**, NZOI Stn Z8403, pre-fix, post-thaw, male, ML 125.0 mm.

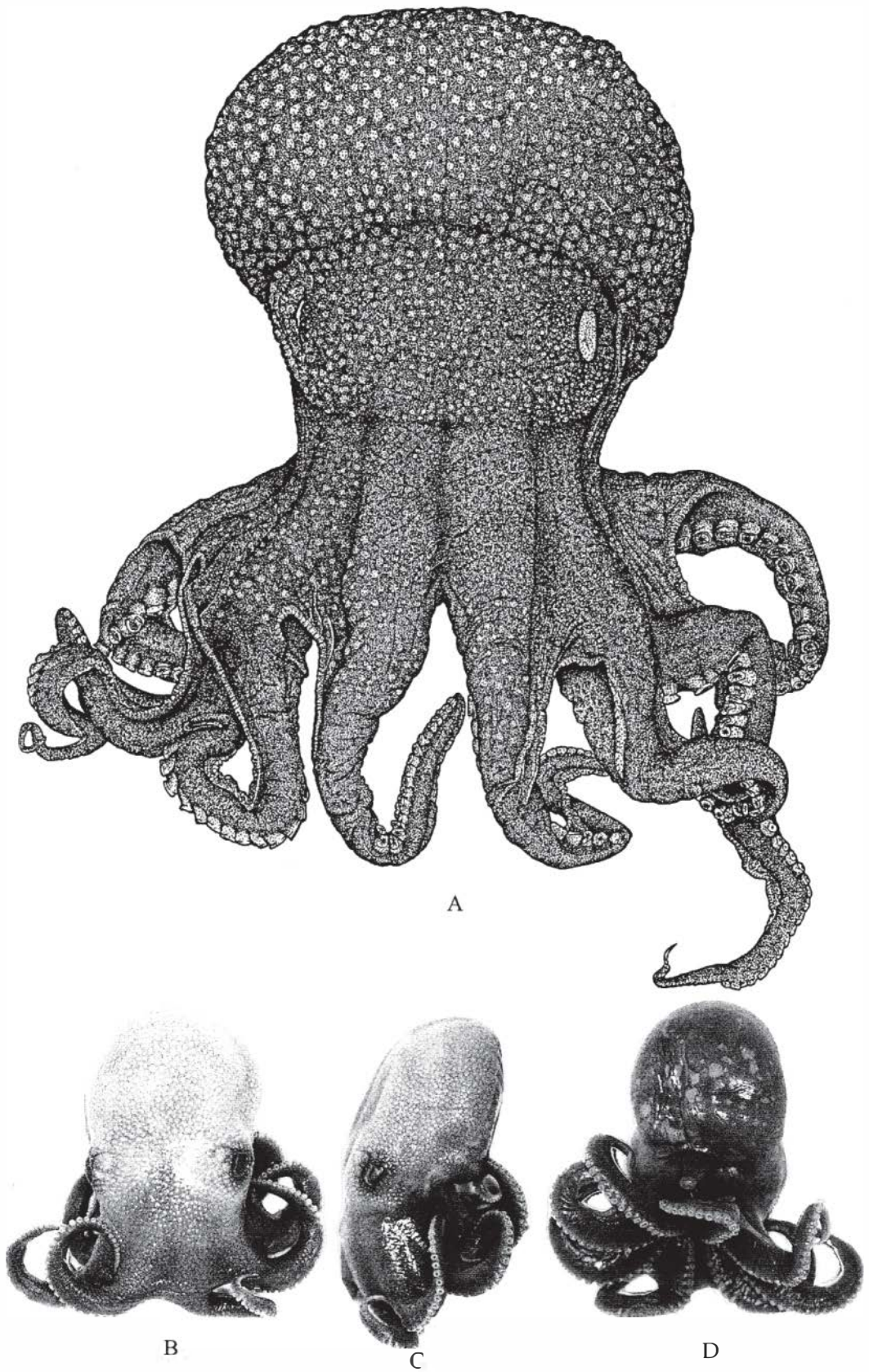


Figure 133. *Graneledone challengeri* (Berry, 1916): **A**. NMNZ M.110531, M, ML 80 mm. **B–D**. NZOI Stn S153 SEB, F, ML 26.8 mm.

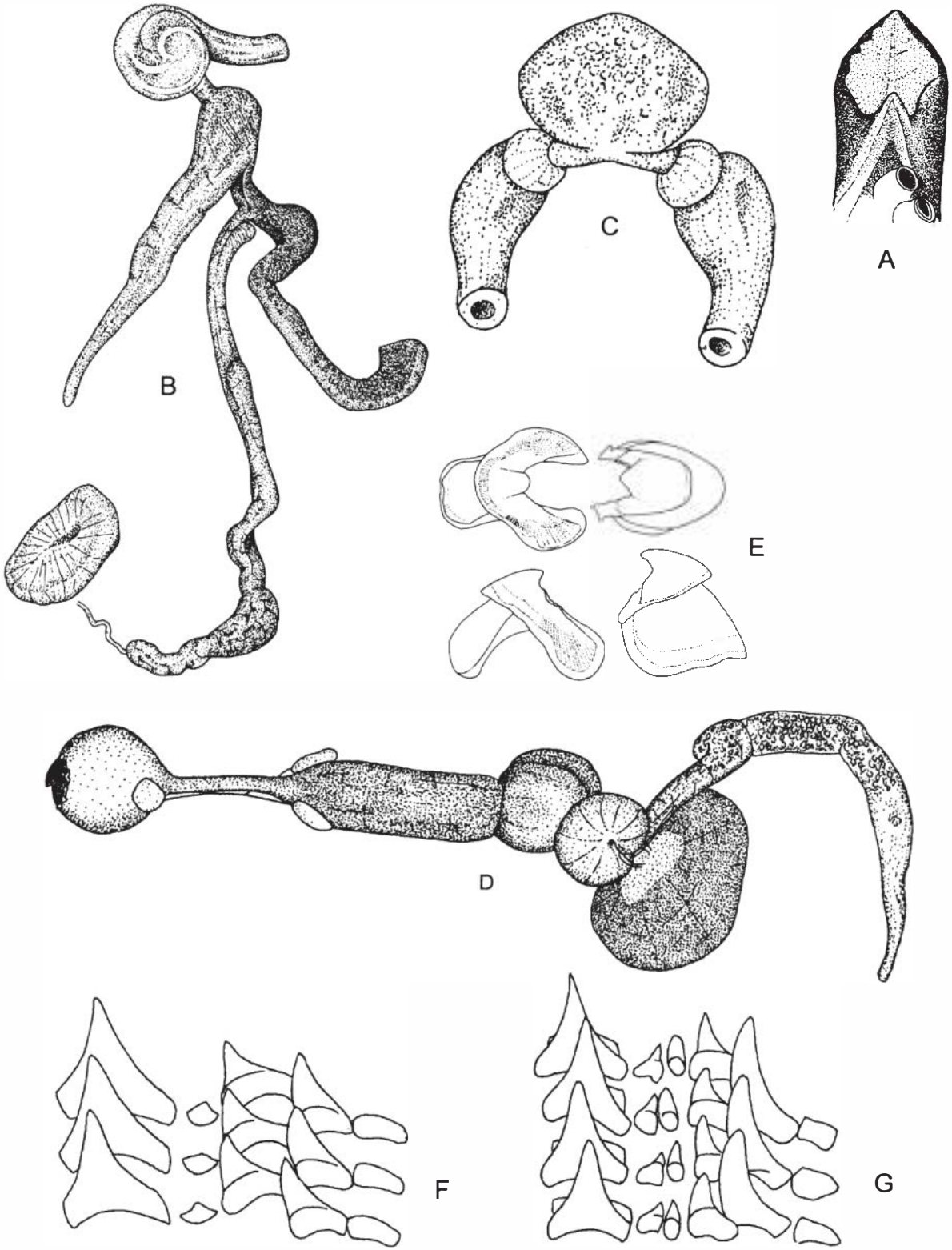


Figure 134. *Graneledone challengeri* (Berry, 1916). Anatomy: **A, B, F**, NMNZ M.110531, M, ML 80 mm. **C**, NMNZ M.102561, F, ML 92 mm. **D, E, G**, NMNZ M.109054, —, ML — mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula. **G**, radula.

Table 116. Raw measures for female *Graneledone challengeri* (Berry) (* denotes damage).

	NZOI Stn Z8385	NMNZ M.118250	NMNZ M.118254	NMNZ M.118249	NMNZ M.118249
TL	512	561	607	608	469
ML	144.5	131.2	*c.* 125.0	*c.* 119.0	99.5
MW	117.0	135.0	*c.* 127.5	*c.* 116.0	122.0
HdL	44.0	41.0	41.8	39.5	39.0
HdW	102.0	106.0	111.0	112.3	107.0
EO	15.5	12.3	20.0	*	13.8
AL1R/L	310/316	411/423	471/493	432/494	337/313
AL2R/L	321/342	426/411*	518/414	412/497	345/339
AL3R/L	330/317	445/442	482/404*	412/436	320/330
AL4R/L	310/301	428/425	438/417*	401/402	326/309
WDA	85	78	116	104	90
WDBR/L	88/106	105/98	166/123	126/126	102/100
WDCR/L	101/110	125/91	130/126	102/115	106/110
WDDR/L	100/92	102/97	165/113	92/100	106/100
WDE	88	70	135	72	75
ASC1R	87	97	109	100	98
ASC2R	88	107	114	101	105
ASC3R	86	100	112	109	99
ASC4R	77	103	109	98	96
ASn1R	7.9	7.3	6.9	7.0	7.0
ASn2R	8.3	7.5	7.3	7.0	6.8
ASn3R	8.1	8.5	7.5	8.0	7.4
ASn4R	9.0	9.0	8.0	8.6	8.0
GiLC	7	6	7	7	7
FuL	53.0	44.5	50.0	64.0	53.0
FFL	43.0	18.6	32.5	31.5	27.0
PA	72.0	88.0	72.0	90.5	82.0

TYPE MATERIAL (51 specimens, 18 male [M], 33 female [F]): Holotype: NZOI H-662, M, ML 121.0 mm, 44°41.90–42.06' S, 177°23.71–20.90' W, 1135–1157 m, BT 4.5°C, 17/10/1995, f.r.v. *Tangaroa* Stn TAN9511/075, NZOI Stn Z8398. Paratypes: NZOI P-1096, F, ML 97.0 mm, FPT, 44°28.52–29.44' S, 175°45.71–46.87' E, 755–769 m, BT 6.0°C, 08/10/1995, f.r.v. *Tangaroa* Stn TAN9511/021, NZOI Stn Z8387; NZOI P-1097, M, ML 87.0 mm, F, ML 86.0 mm, FPT, 44°37.99–38.77' S, 177°04.22–06.83' W, 927–965 m, BT 5.1°C, 23/10/1995, f.r.v. *Tangaroa* Stn TAN9511/122, NZOI Stn Z8402; NZOI P-1098, M, ML 72.5 mm, FPT, 44°38.26–38.21' S, 174°16.93–14.09' E, 882–924 m, BT 5.4°C, 06/10/1995, f.r.v. *Tangaroa* Stn TAN9511/010, NZOI Stn Z8384; NZOI P-1102, M, ML 55.0 mm, FPT, 44°45.73–46.47' S, 173°42.49–42.15' E, 942–969 m, BT 4.5°C, 03/11/1995, f.r.v. *Tangaroa* Stn TAN9511/159, NZOI Stn 8405.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.134148, F, ML 106 mm, FPT, 42°43' S, 175°44' E, 1040 m, 10/11/1996, coll. D. Pollock (956/16); NMNZ M. 100355, F, ML 76.0 mm, 42°44.8' S, 175°46.2' E, 896–894 m, 13/09/1988, f.v. *Cordella* Stn CO2/012/88; NZOI Stn Z8310, F, ML 129.0 mm, FPT, 42°45.58–45.48' S, 177°03.01–05.02' W, 1063–1069 m, BT 5.2°C, 10/07/1995, f.r.v. *Tangaroa* Stn TAN9508/003; NZOI Stn Z8306, M, ML 78.5 mm, FPT, 42°47.80–47.78' S, 176°41.06–43.12' W, 992–1003 m, BT 5.7°C, 12/07/1995, f.r.v. *Tangaroa* Stn TAN9508/020; NZOI Stn Z8305, F, ML 76.0 mm, FPT, 42°48.53–48.29' S, 176°59.39–177°01.41' W, 935–939 m, BT 5.4°C, 19/07/1995, f.r.v. *Tangaroa* Stn TAN9508/067; NMNZ M. 102469, F, ML 81.0 mm, 42°49.3' S, 177°09.9' W, 877 m, 01/07/1994; NZOI Stn Z8831, M, ML 53.2 mm, FPT, 42°50.69–49.18' S, 177°02.42' W, 806–867 m, BT 7.0°C, 01/08/1996, f.r.v. *Tangaroa* Stn TAN9609/20; NZOI Stn Z8312, M, ML 123.5 mm, FPT, 42°54.31–54.13' S, 176°07.00–09.04' W, 858–860 m, BT 6.0°C, 19/07/1995, f.r.v. *Tangaroa* Stn TAN9508/074; NMNZ M.118330, F, ML 121.5 mm, 42°55.00' S, 174°52.00' E, 715 m, f.v. *Labrador*, coll. W. Lyon; NMNZ M. 109061, F, ML 67.0 mm, 43°09.6' S, 175°10.4' W, 770–768 m, 28/07/1988, f.v. *Cordella* Stn CO1/82/88; NMNZ M.102562, M, ML 76.0 mm, F, ML 48.0 mm, 43°15.74' S, 173°47' E, 903–938 m, 26/09/1990; NZOI Stn Z8633, M, ML 140.0 mm, FPT, 44°00.24–43°57.67'S, 176°09.43–07.30'E, 477–492 m, 16/01/1997, f.r.v. *Tangaroa* Stn TAN9701/73; NZOI Stn Z8394, M, ML 104.0 mm, F, ML 122.6 mm, FPT, 44°04.39–04.94' S, 178°55.93–58.61' E, 788 m, BT 5.5°C, 12/10/1995, f.r.v. *Tangaroa* Stn TAN9511/045; NZOI Stn Z8395, F, ML 89.5 mm, FPT, 44°09.38–09.45' S, 179°15.57–12.78' E, 830–841 m, BT 5.5°C, 12/10/1995, f.r.v. *Tangaroa* Stn TAN9511/048; NMNZ M.117829, M, ML 82.1 mm, 44°10.00' S, 174°30.00' W, *c.* 800 m, 28/01/1993, f.v. *San Rangitoto*, trip 578, tow 65; NZOI Stn Z8632, F, ML 138.0 mm, FPT, 44°13.68–11.64' S, 176°17.10–20.21' E, 484–579 m, 16/01/1997, BT 7.8°C, f.r.v. *Tangaroa* Stn TAN9701/75; NZOI Stn

8407, F, ML 80.5 mm, FPT, 44°14.48–13.94' S, 177°10.43–13.15' E, 940–977 m, 05/11/1995, BT 4.6°C, f.r.v. *Tangaroa* Stn TAN9511/167; NZOI Stn Z8389, 2M, ML 122.0, 109.5 mm, FPT, 44°15.63–15.21' S, 176°45.58–48.30' E, 810–846 m, 09/10/1995, BT 6.2°C, f.r.v. *Tangaroa* Stn TAN9511/025; NMNZ M.109060, F, ML 108.0 mm, 44°21' S, 179°48.7' W, 852–688 m, 27/05/1979, f.v. *Wesermunde* Stn W03/17/79; NZOI Stn Z8397, F, ML 126.0 mm, FPT, 44°22.52–22.59' S, 178°12.94–10.14' W, 820–855 m, BT 5.4°C, 15/10/1995, f.r.v. *Tangaroa* Stn TAN9511/063; NMNZ M.118331, F, ML 94.4 mm, 44°25.72' S, 178°56.89' W, 940 m, 11/11/1990; NZOI Stn Z8383, M, ML 70.7 mm, F, ML 119.5 mm, FPT, 44°32.21–31.58' S, 174°54.50–57.16' E, 801–820 m, 06/10/1995, BT 5.6°C, f.r.v. *Tangaroa* Stn TAN9511/006; NZOI Stn Z8409, F, ML 80.5 mm, FPT, 44°34.61–34.86' S, 177°52.15–54.94' W, 960–977 m, BT 4.0°C, 11/11/1995, f.r.v. *Tangaroa* Stn TAN9511/201; NZOI Stn Z8408, F, ML 65.0 mm, FPT, 44°35.07–35.71' S, 175°50.88–53.56' W, 948–954 m, BT 5.8°C, 09/11/1995, f.r.v. *Tangaroa* Stn TAN9511/189; NMNZ M.119219, 1 egg cluster, 23 eggs, 22 larvae, 44°37.30' S, 173°31.6' E, 784 m, 23/9/1989, f.v. *Oyang 76*; NZOI Stn Z8399, M, ML 99.7 mm, FPT, 44°37.67–38.04' S, 176°53.16–55.92' W, 802–856 m, BT 5.9°C, 17/10/1995, f.r.v. *Tangaroa* Stn TAN9511/080; NMNZ M.90434, M, ML 71.0 mm, 44°39.5' S, 174°00' E, 886 m, 18/11/1987, f.v. *Oyanga 7* tow 35; NZOI Stn Z8386, M, ML 48.0 mm, FPT, 44°39.88–39.94' S, 174°53.57–51.20' E, 800–825 m, BT 5.6°C, 08/10/1995, f.r.v. *Tangaroa* Stn TAN9511/018; NZOI Stn Z8404, F, ML 70.0 mm, FPT, 44°39.91–39.40' S, 173°37.30–37.23' E, 932–938 m, 03/11/1995, BT 5.3°C, f.r.v. *Tangaroa* Stn TAN9511/158; NMNZ M.118962, F, ML 62.0 mm, 44°40.0' S, 174°02.0' E, 852 m, 18/08/1994; NZOI Stn Z8401, F, ML 124.0 mm, FPT, 44°40.64–38.67' S, 176°57.71–58.30' W, 965–990 m, 23/10/1995, BT 5.0°C, f.r.v. *Tangaroa* Stn TAN9511/121; NMNZ M.109062, M, ML 87.0 mm, 44°41.5' S, 173°38.6' E, 870–986 m, 29/11/1982, f.r.v. *James Cook* Stn J19/006/82; NZOI Stn Z8406, F, ML 90.0 mm, FPT, 44°43.40–43.12' S, 173°45.83–43.04' E, 930–992 m, 03/11/1995, BT 4.7°C, f.r.v. *Tangaroa* Stn TAN9511/160; NMNZ M.102563, F, ML 98.0 mm, 44°43.8' S, 173°09.73' E, 922–937 m, 10/09/1990, f.r.v. *James Cook* Stn J15/3/90; NZOI Stn Z8414, F, ML 88.4 mm, FPT, 46°00.2' S, 171°14.7' E, 1018 m, 13/10/1995, f.v. *Otakou*; NMNZ M.117418, F, 74.5 mm, 46°15.34–20.00' S, 170°54.81–54.63' E, 811–1051 m, BT 7.0°C, 27/06/1992, f.v. *Giljanes* Stn GIL 9201/029; NMNZ M.117570, M, ML 81.2 mm, 46°37.05' S, 166°29.01' E, 884 m, 09/12/1992; NMNZ M.117201, F, ML 102.1 mm, 46°38.3' S, 166°09.0' E, 678 m, 12/07/1992, f.v. *Klara Birting*, trip 534, tow 116; NMNZ M.117551, 2F, ML 164.0, 154.5 mm, 48°14.77' S, 169°12.48' E, 602–615 m, 29/09/1992; NMNZ M.117417, M, ML 125 mm, 48°20.08' S, 169°15.84' E, 636–650 m, 29/09/1982, f.r.v. *Tangaroa* Stn TAN9209/51; NMNZ M.117872, F, ML 69.0 mm, 48°20.75' S, 179°53.72' W, 538–541 m, 15/11/1993, f.r.v. *Tangaroa* Stn 9310/02; NMNZ M.109064, M, ML 70.0 mm, F, ML *c.* 108 mm, 48°47' S, 169°15' E, 757–734 m, 21/03/1982, f.v. *Shinkai Maru* Stn 63; NMNZ M.117699, F, ML 50.0 mm, 49°11.0' S, 168°40.0' E, 806 m, 01/08/1992, f.v. *Nororn* Stn 524/193; NMNZ M.117574, 2F, ML 97.0, 90.0 mm, 49°17' S, 168°44' E, 763 m, 23/08/1992; NMNZ M.118238, F, ML 136.5 mm, 49°17' S, 168°46' E, 766–688 m, 03/03/1994; NMNZ M. 109058, F, ML 50.0 mm, 49°21.1' S, 168°36.7' E, 730 m, 19/10/1990; NMNZ M.117416, F, ML 141.5 mm, 49°25.55' S, 168°28.82' E, 700–708 m, 09/10/1992.

REFERENCE MATERIAL: USNM 332971, *Graneledone verrucosa* (Verrill), Syntype, F, ML ?100 mm[1], 39°50.30' N, 70°11.00' W, 852 m, 01/07/1880, *Blake* Stn 312; *Graneledone verrucosa* (Verrill).

ADDITIONAL MATERIAL EXAMINED: USNM 731131, M, ML 32.0 mm, 39°33.00' N, 71°16.15' W, 2153 m, 21/08/1884, r.v. *Albatross*; USNM 730989, M, ML 84.0 mm; USNM 574996, F, ML 24.0 mm, 41°09.40' N, 66°02.20' W, 2294 m, 04/09/1883, *Albatross*; USNM 730995, 2F, ML 42.5, 15.0 mm, 39°44.54' N, 70°43.12' W, 1885–1967 m, 10/07/1975, r.v. *Chain*; USNM 730996, F, ML 45.0 mm, 39°44.12' N, 70°28.36' W, 1830–1912 m, 08/07/1975, r.v. *Chain*. *Graneledone verrucosa media* Joubin: Holotype, M, ML 83.0 mm, 42°40' N, 62°49.30' W, 1458 m, 26/08/1913. *Graneledone pacifica* Voss & Pearcy: Holotype, USNM 730716, M, ML 84.0 mm, 44°52.0' N, 125°32.8' W, 2706 m, 16/07/1969; Paratypes: UMML 31.2541, F, ML 52.0 mm, 45°21' N, 125°37.3' W, 2500 m, 05/10/1969; UMML 31.2539, M, ML 38.0 mm, F, ML 99.0 mm, 45°59.6' N, 125°44.0' W, 2500 m, 01/08/1965; UMML 1959, M, ML 75.0 mm, 44°52' N, 125°32.8' W, 2706 m, 16/07/1969. *Graneledone antarctica* Voss, 1976, Paratypes, UMML 31.1667, M, ML 35.0 mm, F, ML 41.0 mm, 74°05.6' S, 175°05.2' W, 2273–2376 m, 08/02/1968, r.v. *Eltanin* Stn 2110. *Graneledone* cf. *challengeri* Berry, 1916: NMV F76888, F, 41°53.6–48.9' S, 144°24.6–21.6' E, 1364–1416 m, 18/05/1986; NMV F76887, F, 40°55.7–58.3' S, 143°40.5–42.2' E, 1280–1264 m, 15/05/1986. *Graneledone* sp. nov: NMV F66840, F, 52°42.72–42.22' S, 74°26.37–28.74' E, 185–204 m, 26/01/1992.

RECOGNISED DISTRIBUTION (Fig. 135, p. 208): New Zealand, off the Wairarapa coast, Chatham Rise to Auckland and Campbell Islands, 42°43-49°25.55' S, 168°28.82' E–175°44' E, 477–1157 m, bottom temperature range (recorded) 4.0–7.8°C.

DIAGNOSIS: Moderate to large-sized animal; arms with few suckers, ASC 58–97; hectocotylised arm sucker count very low, 39–45; hectocotylised portion of arm short, about 3–7.6% arm length; suckers small, ASIn 3.8–8.6; mantle with about 24–29 cartilagelike clusters along dorsal midline, 12–15 in transverse line between orbits; clusters of small to moderate diameter, 0.5–7.5% ML, with 1–37 individual processes within each (most frequently 12–17); well-developed, triangular superocular cirrus almost invariably present.

DESCRIPTION: Adult attaining moderate to large size (ML to 170.0 mm, TL to 660.0 mm); animal robust bodied (Fig. 136). Male and female with similar gross morphology; female attaining greater mantle and total length. Mantle ovoid, dorsoventral compression and lateral keel or fold of skin absent. Head large,

[1] *Fide* Roper and Sweeney (1978), specimen now mutilated

narrower than equivalent width of mantle (HdLI about 30-43, HdWI about 63–102), separated from mantle by poorly defined preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head; eye apertures large, dorsolaterally oriented. Funnel of moderate length, free almost entire length but for slight attachment to arm bases 4. Nuchal constriction little developed.

Brachial crown and arms robust. Arms short to moderately long, about 50–73% TL, gradually tapering to non-filiform tips; arm pairs 1 and 2 most frequently longest, arms 2 and 4 shortest, with no consistent disparity in relative arm lengths. Web deep, about 15–35% longest arm length, with moderate development along both dorso- and ventrolateral faces of each arm; web formula variable, sector A usually shallowest, sectors C and D deepest, with no consistent disparity in relative sector depths. Arm sucker counts greater in mature females than males, female ASC 71–97, male 58–88; suckers extend to arm tips; arm tips of male not secondarily modified in any discernible way. Suckers small, ASIn 3.8–7.4 (male), 5.3–8.6 (female), relative size seemingly inversely proportional to mantle length; distal 5–10 suckers minute; no suckers abruptly enlarged in male. Suckers with: large suction chamber; little-constricted sucker aperture; moderately well-developed grasping ring with about 14 faint radial grooves; and simple development of muscular suction pad (Fig. 155Y).

Indices, formulas, and counts for male and female *G. taniwha taniwha* in Tables 117, 118; raw measures in Tables 121, 122.

Skin over dorsal surfaces of mantle, head, arms 1 and 2, web sectors A–C, and dorsolateral surfaces of arms 3 beset with irregular-sized clusters of cartilage-like processes; processes not extending along arms. Individual clusters of small to moderate size, diameter 0.5–7.5% ML (CDI), with 1–37 processes within each (average 14); with 24–29 clusters along dorsal midline, 12–15 between orbits. Ventral surfaces of mantle, head, funnel, ventrolateral surfaces or arms 3, dorso- and ventrolateral surfaces of arms 4, and web sectors D and E, smooth; superocular cirrus large, single, triangular, lappetlike.

Third right arm of male hectocotylised, shorter than opposite member (OAI about 75–90), with 39–45 not-obviously enlarged suckers. Spermatophoral groove well developed, wide; web margin conspicuously thickened; junction of web sector D and spermatophoral groove with 5 or 6 fleshy ridges on adoral web surface. Hectocotylised portion short (Fig. 137A), ligula 3.0–7.6% hectocotylised arm length, increasing with maturity, with 7 or 8 fleshy faint transverse rugae; calamus proportionately large, about 32–68% ligula length.

Colour uniformly rose pink to light red with small darker-red chromatophores over dorsal surfaces of mantle, head, and arms 1 and 2; ventral surfaces of mantle, head, funnel, arms 3 and 4, and oral surfaces or arms and web slightly darker pink to red. Counter-pigmentation apparent, with dorsal surfaces of mantle, head and arms lighter than ventral and oral surfaces of arms and web.

Pallial aperture reduced, mantle attaches to ventral surface of orbit; funnel moderately long, broad, distal aperture not inrolled or contracted; adsiphonal pouches well developed. Mantle musculature thick. Funnel collar not well developed; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting viscera to ventral inner surface of mantle absent. Gills small, compact, with 7 or 8 lamellae per inner and outer demibranch. Male with massive spiral penis diverticulum on left side, oriented away from interpallial septum; female with genital apertures opening at about 45° on face of viscera, not extending over lateral face of septal musculature nor extending to anus. Ventrolateral and dorsal surfaces of visceral envelope densely pigmented with large dark-red chromatophores; renal papilla sparsely pigmented with minute red chromatophores; lateral muscles restraining digestive gland and region proximal to anus variably pigmented with small red chromatophores (often absent). Funnel organ comprising 2 narrow V-shaped pads in VV-formation, with limbs of subequal length.

Male reproductive system (Fig. 137B) with short, thick proximal vas deferens; spermatophoral gland moderately long, with regional swellings, constrictions and glandular regions, with small appendix at junction with accessory gland. Accessory gland large, moderately long, granular, with terminal partial recurvature. Spermatophore sac long, thin walled, swollen proximal to spermatophoral gland and penis junctions, distally attenuated, in one specimen containing a single spermatophore of TL 118 mm. Distal vas deferens short, very thick; penis diverticulum large, single, with pronounced spiral; penis large, thick, genital aperture subterminal. Female (Fig. 137C) with short, stout proximal oviducts appearing to depart ovary sac singly; oviducal glands large, with single hemisphere; distal oviducts about 5 times longer than proximal ducts, stout, swollen proximally, narrowing towards genital apertures. Mature eggs large (24.0 x 9.0 mm), each with short stalk.

Alimentary canal (Fig. 137D) with large buccal bulb, about 25% ML in greatest dimension; anterior

Table 117. Indices, formulas, and counts for male *Graneledone taniwha taniwha* ssp. nov. (* denotes damage).

	NZOI Stn Z8389	NZOI H-662	NZOI Stn Z8389	NZOI Stn Z8394	NMNZ M.109062	NZOI P-1097	NZOI P-1098	NZOI Stn Z8831
MWI	115.6	86.1	117.8	98.7	121.6	85.2	94.6	88.3
HdLI	36.1	33.6	39.3	43.2	37.9	42.5	41.7	41.4
HdWI	82.0	69.3	83.3	84.6	83.7	65.5	82.8	63.0
EOI	13.5	13.4	18.3	15.4	16.1	14.9	17.8	13.3
ALI1–4	48.3–70.4	57.9–70.4	55.7–68.1	52.4–66.8	49.3–69.7	55.3–66.3	57.0–67.5	47.9–63.7
AFR	1.4.2.3	1.2.4.3	2.1.4.3	*	1.2.4.3	?2.4.3.1	2.4.1.3	1.2.4.3
AFL	1.2.3.4	1.2.3.4	?1=2.3.4	3.2.4.1	3.1=2.4	?1=2.4.3	1.2.3.4	2.1.3.4
WDIA–E	14.6–30.5	23.3–28.1	24.6–37.2	21.2–29.0	18.9–28.5	21.8–34.2	20.6–34.4	20.4–31.2
WFR	C.D.B.A.E	D.C.B.E.A	C.D.B.E.A	D.E.C.B.A	D.C.B.E.A	D.E.C.B.A	C.D.A.E.B	B.D.A=C.E
WFL	C.D.B.A.E	D.C.E.B.A	B.D.C=E.A	D.E.B.C.A	C.E.B.D.A	C.E.B.D.A	C.B.D.A.E	B.A.C.E.D
ASC1–4	84–88	83–86	75–76	79–83	77–81	66–79	68–73	58–62
ASIn1–4	5.4–6.7	5.0–6.4	5.3–6.3	6.3–7.4	5.7–7.0	4.1–4.6	5.5	3.8–3.9
FuL	36.9	43.0	44.7	37.1	44.8	42.5	39.9	30.1
FFL	15.2	23.1	30.1	22.5	13.8	25.7	22.2	19.0
PA	66.1	52.5	60.1	63.7	72.5	50.6	55.9	45.1

Table 118. Indices, formulas, and counts for female *Graneledone taniwha taniwha* ssp. nov. (* denotes damage).

	NMNZ M.117531	NZOI Stn Z8310	NZOI Stn Z8513	NZOI Stn Z8514	NZOI P-1096	NZOI Stn Z8395
MWI	127.6	99.2	110.4	145.7	88.7	131.3
HdLI	29.7	30.4	37.1	36.9	42.6	38.6
HdWI	83.8	76.7	77.5	101.7	74.0	90.9
EOI	10.0	10.8	11.3	13.8	14.2	11.9
ALI1–4	50.6–67.4	49.1–65.4	59.9–69.1	58.7–72.3	57.1–66.1	66.5–73.2
AFR	*c.* 1.2.3.4	1.4.3.2	3.4.2.1	1.2.3.4	3.1.2.4	2.3.1.4
AFL	*	1.4.3.2	*	2.1.4.3	2.1=3.4	2.3.1.4
WDIA–E	19.6–36.0	21.5–30.2	21.3–28.4	23.8–31.9	20.9–31.8	25.7–32.8
WFR	C.B.D.A.E	C.B.E=A=D	C.B=D.A.E	C.B.A.D=E	B.C.A=D.E	D.C=E.A=B
WFL	C.D.B.A.E	D.C=A=E.B	A.B=C=D.E	D.C.A.E.B	C.D.A=B=C	C=D.B.E.A
ASC1–4	84–97	80–88	84–87	78–85	74–78	71–82
ASIn1–4	5.9–7.3	5.3–5.9	6.7–7.5	6.9–8.6	5.2–6.3	5.7–6.8
FuL	35.0	42.3	35.4	48.3	47.6	43.2
FFL	12.9	13.4	13.3	27.6	25.1	16.5
PA	62.0	62.5	60.4	78.4	52.5	71.0

Table 119. Cartilaginous cluster distribution for *Graneledone taniwha taniwha* ssp. nov.

	NZOI P-1098	NZOI H-662	NZOI P-1102	NZOI P-1097(F)	NZOI P-1096
clusters across mantle	27	27	24	24	29
cluster # interocular	12	13	13	15	13
# processes within cluster	1–32, av. 12, n=12	1–30, av. 14, n=12	4–24, av. 13, n=12	1–37, av. 17, n=12	1–29, av. 13, n=12
cluster diameter (mm)	0.5–5.4	1.2–8.0	0.7–3.9	1.0–6.5	0.5–5.0
CDI	0.7–7.4	1.0–6.6	1.3–7.1	1.1–7.5	0.5–5.2

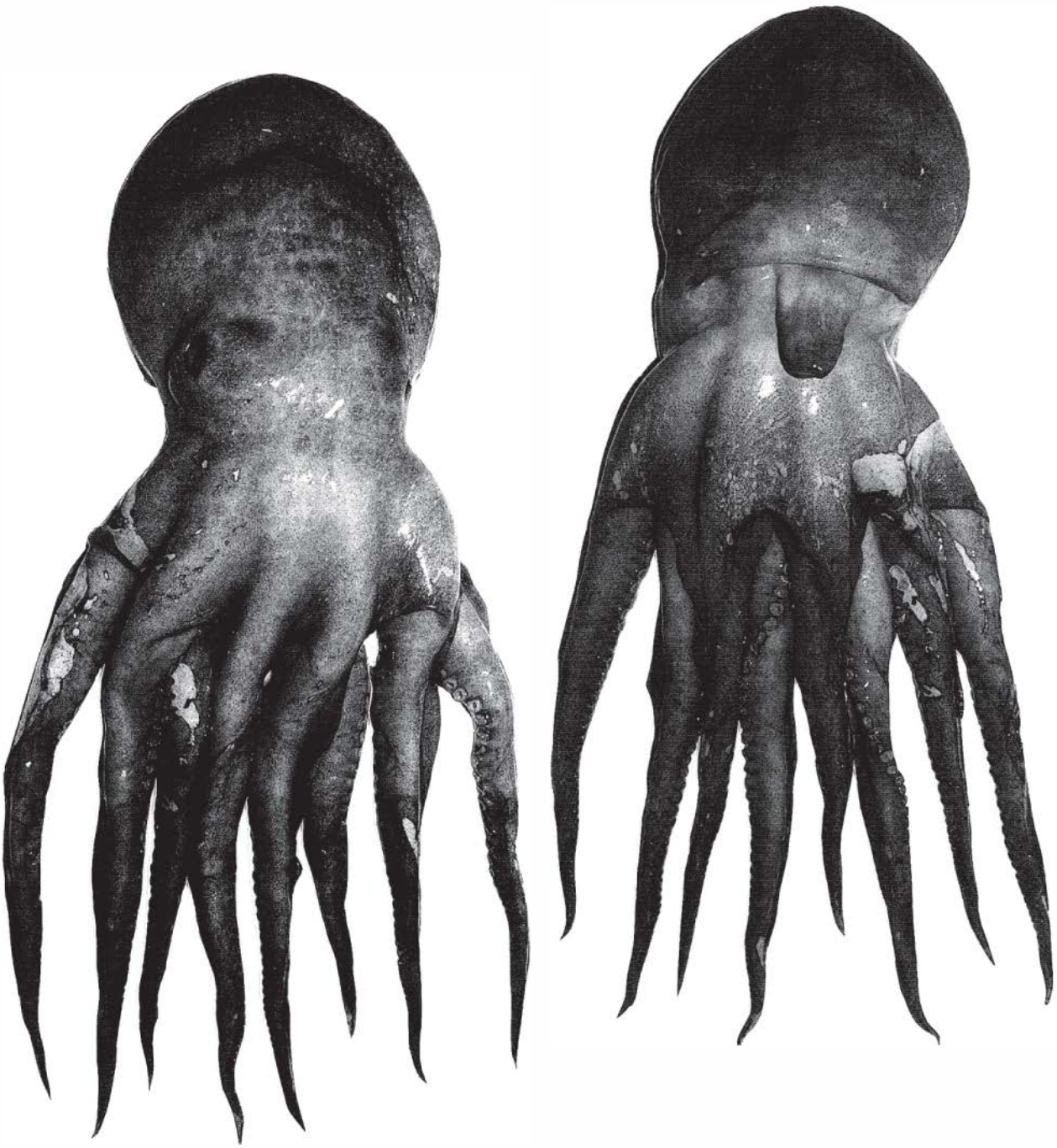


Figure 136. ***Graneledone taniwha taniwha*** ssp. nov.: NMNZ M.118330, female, ML 121.5 mm.

salivary glands well developed; anterior oesophagus moderately long, narrow, about 32% total crop and oesophagus length; crop large, thin walled, without anterior diverticulum. Posterior salivary glands elliptical, vestigial (relative to ML, their absolute size is large), of length about 38% buccal bulb greatest dimension, about 10% ML. Posterior oesophagus almost non-existent. Stomach with three apparent external sections, basal thin walled, central thick walled, distal largest, thin walled; stomach with undivided lumen. Spiral caecum with single incomplete radially striate volution. Intestine long, length twice that of oesophagus and crop, thick walled, dilated for greatest length, slightly constricted for distal third, particularly proximal to anus; anal flaps absent. Digestive gland large, ovoid, with weak

Figure 137. *Graneledone taniwha taniwha* ssp. nov. Anatomy: **A, B**, NMNZ M.117417, male, ML 125 mm. **C–F**, NMNZ M.118238, female, ML 136.5 mm. **A**, hectocotyl. **B**, male reproductive system. **C**, female reproductive system. **D**, alimentary canal. **E**, beaks. **F**, radula.

Table 120. Indices of hectocotylised 3R arm male for *Graneledone taniwha taniwha* ssp. nov. (* denotes damage).

	NZOI Stn Z8389	NZOI H-662	NZOI Stn Z8389	NZOI Stn Z8394	NMNZ M.109062	NZOI P-1097	NZOI P-1098	NZOI Stn Z8831
OAI	74.5	86.8	84.0	78.4	76.5	*	90.0	84.3
ASC3R	42	42	39	42	42	45	42	42
CaLI	47.1	54.0	47.5	31.7	51.3	68.3	65.0	42.9
LLI	7.6	6.3	5.7	5.1	6.5	3.7	4.4	3.0

Table 121. Raw measures for male *Graneledone taniwha taniwha* ssp. nov. (* denotes damage).

	NZOI Stn Z8389	NZOI H-662	NZOI Stn Z8389	NZOI Stn Z8394	NMNZ M.109062	NZOI P-1097	NZOI P-1098	NZOI Stn Z8831
TL	466	409	442	382	357	291	237	146
ML	122.0	121.0	109.5	104.0	87.0	87.0	72.5	53.2
MW	141.0	104.2	129.0	102.6	105.8	74.1	68.6	47.0
HdL	44.0	40.6	43.0	44.9	33.0	37.0	30.2	22.0
HdW	100.0	83.9	91.2	88.0	72.8	57.0	60.0	33.5
EO	16.5	16.2	20.0	16.0	14.0	13.0	12.9	7.1
AL1R/L	306/328	282/288	297/295	230/234	249/220	161/193	141/163	89/90
AL2R/L	296/307	270/284	301/295	230/236	232/220	189†/193	144/160	88/93
AL3R/L	225/302	237/273	246/293	200/255	176/230	163/142†	135/150	70/83
AL4R/L	300/271	242/272	294/248*	135*/235	208/201	193/183	142/142	80/82
WDA	60	67	74	54	47	42	37	26
WDBR/L	75/85	75/71	84/92	66/69	60/59	50/58	33/44	29/27
WDCR/L	92/100	79/80	112/75	67/66	66/74	55/60	55/51	26/25
WDDR/L	76/65	80/81	93/78	74/72	71/49	66/53	54/42	28/19
WDE	48	74	75	70	56	56	34	22
ASC1R	84	86	76	79	81	66	73	62
ASC2R	88	83	75	83	77	L79	71	58
ASC3R	42	42	39	42	42	45	42	42
ASC4R	84	85	75	L79	79	74	68	59
ASn1R	6.6	6.0	6.0	6.5	5.0	3.6	4.0	2.0
ASn2R	7.1	6.0	5.8	6.9	5.0	3.6	4.0	2.0
ASn3R	7.9	7.0	6.0	7.0	5.6	4.0	4.0	2.1
ASn4R	8.2	7.7	6.9	7.7	6.1	4.0	4.0	2.1
CaL	8.0	8.1	6.6	3.2	5.9	4.1	3.9	0.9
LL	17.0	15.0	13.9	10.1	11.5	6.0	6.0	2.1
GiLC	7	7	7	7	7	8	7	7
FuL	45	52	49	38.6	39.0	37.0	28.9	16.0
FFL	18.5	27.9	33.0	23.4	12.0	22.4	16.1	10.1
PA	80.6	63.5	65.8	66.2	63.1	44.0	40.5	24.0

anterior peaks and central depression to accommodate stomach; pancreas well developed; ink sac absent. Stomach contents comprise small crustaceans, with numerous sand grains present in faecal matrix suggesting benthic food sources.

Upper beak (Fig. 137E) moderately tall (height 94.7% length); hood and lateral walls dark brown, margins light brown to translucent. Hood very deep (depth 48.4% beak length), with rounded crest, without posterior notch; rostrum triangular, margins strongly chiselled, rostral tip blunt, strongly deflected down. Lateral walls parallel sided; crest squared, lateral wall fold absent; jaw with single large tooth. Lower beak (Fig. 137E) tall (height 76.2% width); hood, lateral wall and wings dark brown, lateral wing and wall margins light brown to translucent. Hood very deep (depth 40.8% beak length), forward projecting, with flattened chisel-like rostrum; hood with faint trace of posterior notch. Lateral wall with strong basal notch and broadly rounded triangular

Table 122. Raw measures for female *Graneledone taniwha taniwha* ssp. nov. (* denotes damage).

	NMNZ M.117531	NZOI Stn Z8310	NZOI Stn Z8513	NZOI Stn Z8514	NZOI P-1096	NZOI Stn Z8395
TL	660	456	469	477	319	287
ML	170.0	126.5	120.0	116.0	97.0	88.0
MW	217.0	125.5	132.5	169.0	86.0	115.5
HdL	50.5	38.5	44.5	42.8	41.3	34.0
HdW	142.5	97.0	93.0	118.0	71.8	80.0
EO	17.0	13.6	13.5	16.0	13.8	10.5
AL1R/L	445/410	298/282	307/302	343/337	208/202	197/204
AL2R/L	427161*	224/264	316/270*	338/345	206/210	205/210
AL3R/L	423/405*	277/265	324/281	321/280	211/202	201/207
AL4R/L	311*/334	296/267	321/319	287/289	201/182	191/202
WDA	96	70	78	87	55	54
WDBR/L	140/116	78/64	83/73	97/82	62/55	54/65
WDCR/L	160/135	90/70	92/73	110/95	58/67	61/69
WDDR/L	130/125	69/77	82/72	85/99	44/65	67/69
WDE	87	71	69	85	55	61
ASC1R	97	88	87	79	78	80
ASC2R	96	80	85	78	76	82
ASC3R	*	85	87	85	74	82
ASC4R	84	82	84	84	74	71
ASn1R	11.0	6.7	8.0	8.0	5.0	5.0
ASn2R	10.0	6.9	8.5	8.0	5.5	5.0
ASn3R	11.3	6.8	8.5	8.0	5.6	5.0
ASn4R	12.4	7.5	9.0	10.0	6.1	6.0
GiLC	8	7	8	8	7	7
FuL	59.5	53.5	42.5	56.0	46.2	38.0
FFL	22.0	17.0	16.0	32.0	24.3	14.5
PA	105.4	79.0	72.5	91.0	50.9	62.5

crest; lateral wings very long (length 104.0% beak length), with single weak fold.

Radular dentition (Fig. 137F) simple; rachidian robust, broadly triangular, taller than wide, with 1 or 2 symmetrically disposed small lateral cusps beside large central cusp; 1st lateral tooth small, with single outer cusp, inner heel upturned, with blunt promi-nence; 2nd lateral with large, massive-based cusp, without inner heel or with heel marked by slight prominence only; marginal tooth robust, cusp more delicate than that of either rachidian or 2nd lateral; marginal blocks short, rectangular.

ETYMOLOGY: Named after *Taniwha*, a legendary Maori monster, for its grotesque looks.

REMARKS: See under *Graneledone taniwha kubodera* sp. nov.

Graneledone taniwha kubodera ssp. nov.
(Figs 139, 140)
(Tables 122–126)

Pareledone sp. Kubodera 1990: 351, pl. 279.
Graneledone sp. O'Shea & Kubodera 1996: 153.

TYPE MATERIAL (10 specimens, 5 male [M], 5 female [F]): Holotype: NMNZ M.109068, M, ML 79.5 mm, 48°25.25' S, 179°27.03' E, 541–548 m, 20/11/1989, f.v. *Alex* Stn 8902/18. Paratypes: NMNZ M.118332, M, ML 108.5 mm, 47°40.68' S, 178°00.72' E, 840 m, 09/12/1990; NMNZ M.109059, M, ML 82.1 mm, F, ML 147 mm, 48°26' S, 179°50' E, 556–557 m, 10/01/1977, f.v. *Shinkai Maru* Stn 234.

ADDITIONAL MATERIAL EXAMINED: NMNZ M.90271, F, ML 89.1 mm, 48°28–27.5' S, 179°50–36.5' E, 552–565 m, 26/05/1976; NMNZ M.95292, M, ML 58.5 mm, 48°04.5–14.5' S, 178°50.5–179°46.5' E, 547–502 m, 17/11/1975; FSFRL EI 259 (14–2–3), F, ML 76.0 mm, 48°15.5' S, 179°48.5' E, 512 m, 17/11/1975, f.v. *Shinkai Maru*; NMNZ M.117874, F, ML 147.0 mm, 48°27.30' S, 179°27.56' E, 565–599 m, 15/11/1993; NMNZ M.109064, M, ML 70.0 mm, F, ML 93 mm, 48°47' S, 169°15' E, 757–734 m, 21/03/1982, f.v. *Shinkai Maru* Stn 63.

RECOGNISED DISTRIBUTION (Fig. 138, p.236): Southern New Zealand, Campbell Rise, Bounty Plateau, between co-ordinates 47°40.68–48°47' S, 169°15–179°50' E, bathymetric range 502–547 to 840 m.

DIAGNOSIS: Moderate to large-sized animal; arms with few suckers, ASC 71–99; hectocotylised arm sucker count low, 44–48; hectocotylised portion of arm short, about 3–7.6% arm length; suckers small, ASIn 4.3–5.5; mantle with about 23–25 cartilage-like clusters along dorsal midline, 11–14 in transverse line between orbits; clusters of small to moderate size, 1.0–5.5% ML, with 4–13 processes within each (most frequently 9); well-developed, triangular superocular cirrus almost invariably present.

DESCRIPTION: Adult attaining moderate to large size (ML to 147.0 mm, TL to 683.0 mm); body slender (Figs 139A–B). Male and female of similar gross morphology; female probably attaining greater mantle and total length. Mantle ovoid, narrower to wider than mantle (MW about 66–105% ML), dorsoventral compression and lateral keel or fold of skin absent. Head large, narrower than equivalent width of mantle (HdL about 35–44% ML, HdW about 58–79% ML), separated from mantle by poorly defined preocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head; eye apertures large, dorsolaterally oriented. Funnel length moderate, funnel free for almost entire length with exception of short attachment to arm bases 4. Nuchal constriction little developed.

Brachial crown and arms slender. Arms short to moderately long, about 50–80% TL; arms 1 and 2 frequently longest, arms 2 and 3 shortest, with arm formula 1.2.3.4 frequent; arms gradually tapering to non-filiform tips. Web shallow to deep, about 15–35% longest arm length, with broad, well-developed membranous extension along each arm, particularly widest along terminal half to third of arm; web formula variable, with no consistent disparity in relative sector depths. Arm sucker counts greater in females than males, female ASC 79–99, male 71–83; suckers extend to arm tips; arm tips of males not modified in any discernible way. Suckers small, ASIn 5.1–6.3 (male), 4.5–7.1 (female); distal 15–20 suckers minute; suckers not obviously enlarged in male. Suckers with: large suction chamber; little-constricted sucker aperture; moderately well-developed grasping ring with about 14 faint radial grooves; and simple development of muscular suction pad (Fig. 155Z).

Third right arm of male hectocotylised, shorter than opposite member (OAI about 80–90%), with 44–48 suckers in total, none obviously enlarged. Spermatophoral groove well developed, wide, little flaring, with conspicuously thickened web margin. Hectocotylised portion (Fig. 140A) short, ligula deep, with 3 or 4 faint transverse rugae upon the floor, about 4–6% hectocotylised arm length; calamus proportionally large, triangular, of feeble construction (Fig. 140A) or about 40–60% ligula length.

Table 124. Indices and counts of hectocotylised 3R arm for male *Graneledone taniwha kubodera* ssp. nov.

	NMNZ M.118332	NMNZ M.109059	NMNZ M.109068
OAI	79.3	83.0	91.5
ASC3R	44	44	48
CaLI	52.0	59.5	38.0
LLI	4.3	4.5	5.5

Skin over dorsal surfaces of mantle, head, arms 1 and 2, web sectors A–C, and dorsolateral surfaces of arms 3, covered in small clusters of cartilage-like processes; processes not extending along arms. Individual clusters small, diameter 1.0–5.5% ML (CDI), with 4–13 processes within each (average 9); with about 23–25 clusters along dorsal midline, 11–14 in transverse line between orbits. Ventral surfaces of mantle, head, funnel, ventrolateral surfaces of arms 3, dorso- and ventrolateral surfaces of arms 4, and web sectors D and E smooth; superocular cirrus large, single, triangular, lappetlike.

Animal typically uniform pale pink over dorsal, ventral, and oral surfaces, slightly darker on ventral mantle and oral surfaces of arms and web; spermatophoral groove white to cream coloured. Counter pigmentation apparent, not pronounced: dorsal surfaces of mantle, head and arms lighter than ventral and oral surfaces of arms and web.

Pallial aperture wide; mantle attaches to ventrolateral margin of orbit; funnel short to moderately long, slender; adsiphonal pouches moderately well developed. Mantle musculature thick. Funnel collar well developed; interpallial septum moderately long, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting viscera to ventral inner surface of mantle absent. Male with large penis and diverticulum; diverticulum with pronounced spiral oriented away from interpallial septum. Female with genital apertures opening at about 45° on face of viscera proximal to anterior margin of interpallial musculature, not extending over lateral face of septal musculature nor extending to anus. Gills small, compact, with 7 or 8 lamellae per demibranch. Lateral muscles restraining digestive gland, visceral envelope and renal papilla sparsely pigmented with small maroon chromatophores. Funnel organ poorly preserved in all available material.

Male reproductive system (Fig. 140B) with short, thin proximal vas deferens; spermatophoral gland moderately long, with regional swellings, constrictions

Table 123. Indices, formulas, and counts for female *Graneledone taniwha kubodera* ssp. nov.

	NMNZ M.117551	NMNZ M.117874	NMNZ M.118332	NMNZ M.109059	NMNZ M.109068
MWI	65.7	104.8	99.5	80.4	95.0
HdLI	35.6	38.1	35.0	43.8	40.9
HdWI	58.3	74.8	72.8	70.8	79.2
EOI	11.5	16.3	11.1	11.6	17.0
ALI1–4	56.0–64.6	58.7–80.5	51.7–73.5	57.1–75.6	51.4–71.9
AFR	1=2=3.4	*c.* 1.2.3.4	1.2.4.3	1.2.4.3	1.2.4.3
AFL	2.1.3.4	1.4.3.2	1.2.3.4	1=2.3.4	1.2.4.3
WDIA–E	22.3–36.2	14.9–27.8	22.6–26.6	19.2–26.9	15.6–23.8
WFR	D.C.E.B.A	B.D.E.C.A	A.B.C.D.E	C=D.B.E.A	B.C.A.E.D
WFL	C.E.D.B.A	C.E.D.B.A	A=B.D.C.E	D.B=E.C=A	B.C.A.E.D
ASC1–4	79–88	81–99	79–83	75–82	71–85
ASC3R M	F	F	44	44	48
ASIn1–4	4.5–5.5	6.5–7.1	5.1–5.5	6.1	5.7–6.3

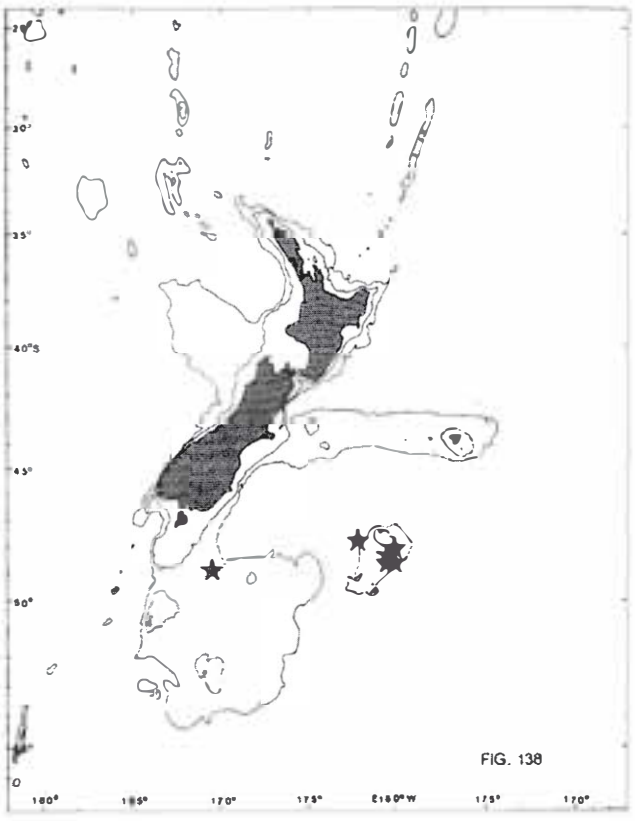
Table 125. Cartilaginous cluster distribution for *Graneledone taniwha kubodera* ssp. nov.

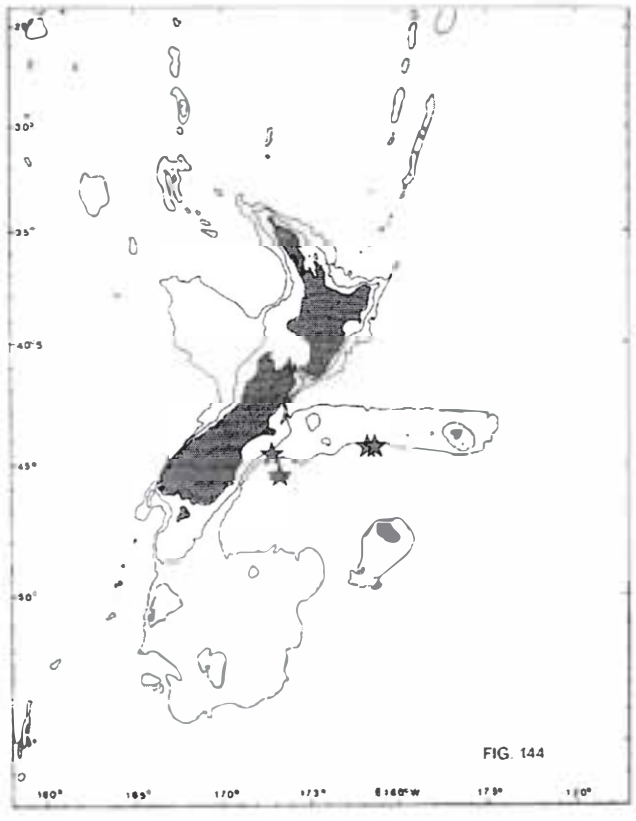
	NMNZ M.117874	NMNZ M.118332	NMNZ M.109059	NMNZ M.109068
clusters across mantle	25	23	24	25
cluster # interocular	13	14	11	12
# processes within cluster	range 5–12, av. 9	range 4–13, av. 9	range 6–13, av. 9	range 4–11, av. 9
cluster diameter (mm)	range 2.0–6.5	range 1.0–3.0	range 0.8–4.5	range 1.0–2.0
CDI	1.4–4.4	1.0–2.8	1.0–5.5	1.3–2.5

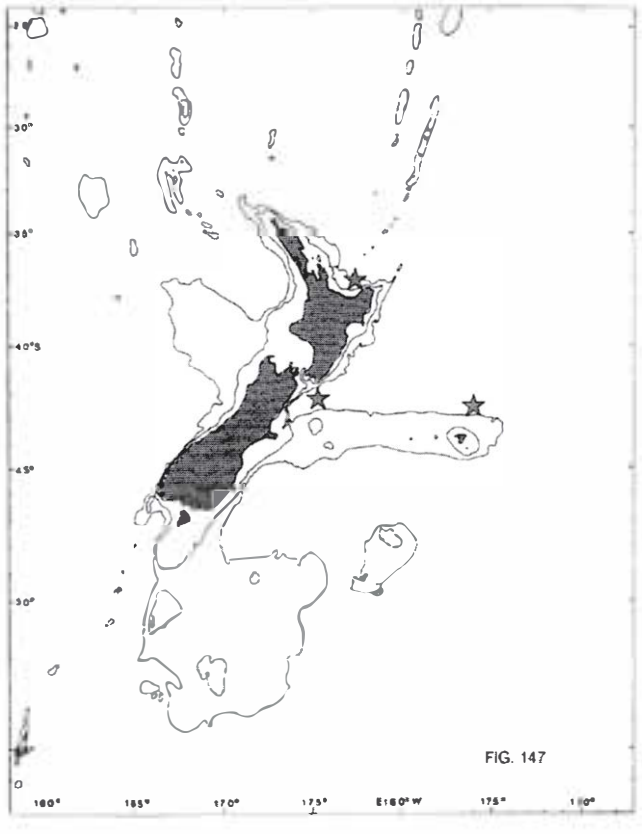
and glandular portions, and small appendix at junction with accessory gland. Accessory gland large, moderately long, granular, with terminal partial recurvature. Spermatophore sac swollen proximal to spermatophoral gland and penis junctions, distally attenuated, thin walled, containing single spermatophore. Distal vas deferens short, thick; penis diverticulum large, single, with pronounced spiral; penis large, thick, genital aperture subterminal. Female (Fig. 140C) with short, stout proximal oviducts appearing to depart ovary sac separately; oviducal glands large, non-chambered; distal oviducts about 9 times longer than proximal ducts, stout, swollen proximal to oviducal ball, narrowing towards genital aperture. Mature eggs large, 20.5–22.0 mm dimension, each with short stalk.

Alimentary canal (Fig. 140D) with large buccal bulb, length about 31% ML; anterior salivary glands ovoid, very small, length about 39% buccal bulb greatest dimension; anterior oesophagus moderately long, narrow; crop without anterior diverticulum. Posterior salivary glands elliptical to acutely triangular, vestigial (relative to ML their absolute size is large), length about 45% buccal bulb greatest dimension 14% ML. Posterior oesophagus short, thick. Stomach with 3 apparent sections, basal thin walled, central thick walled, and distal thin walled; stomach with undivided lumen. Spiral caecum forming single complete radially striate spiral volution. Intestine short, length equivalent to oesophagus and crop, thin walled, dilated for greatest length; anal flaps absent. Digestive gland large, ovoid, with small anterior peaks and weak depression imparted by stomach; pancreas not apparent; ink sac absent. Stomach contents identify a diet comprising small crustaceans, particularly pagurid crabs.

Upper beak (Fig. 140E) very tall (height 112.5% length); hood black, lateral walls dark brown to black, hood and lateral wall margins translucent; hood very deep (depth 53.6% beak length), with squared crest, very shallow posterior notch and weak furrow running from notch to rostrum; rostrum broadly triangular, rostral tip blunt, chisel-like, without apparent downward deflection. Lateral walls parallel sided; crest squared, lateral wall fold absent; jaw with single low-profile broad tooth. Lower beak







Recognised distribution. **Fig. 138**, *Graneledone taniwha kubodera* s.sp. nov. **Fig. 144**, *Thaumeledone zeiss* sp. nov. **Fig. 147**, *Thaumeledone marshalli* sp. nov.

Table 126. Raw measures for *Graneledone taniwha kubodera* ssp. nov. (* denotes damage).

	NMNZ M.117551	NMNZ M.117874	NMNZ M.118332	NMNZ M.109059	NMNZ M.109068
TL	500.0	683.0	445.0	324.0	356.0
ML	154.5	147.0	108.5	82.1	79.5
MW	101.5	154.0	108.0	66.0	75.5
HdL	55.0	56.0	38.0	36.0	32.5
HdW	90.0	110.0	79.0	58.1	63.0
EO	17.7	24.0	12.0	9.5	13.5
AL1R/L	317/291	550/532	301/327	245/244	256/235
AL2R/L	317/323	546/401	284/323	236/244	240/226
AL3R/L	316/286	455*/458	230/290	185/223	183/200
AL4R/L	292/280	435/470	265/275	211/200	203/203
WDA	72	82	87	47	47
WDBR/L	91/91	153/105	84/87	58/52	59/61
WDCR/L	105/110	94/145	82/78	66/47	52/52
WDDR/L	117/95	123/108	76/84	66/57	42/40
WDE	98	114	74	52	44
ASC1R/L	88/*	98/99	79/80	79/82	80/71
ASC2R/L	87/*	99/81	80/83	82/81	85/75
ASC3R/L	82/*	*/97	44/79	44/81	48/77
ASC4R/L	79/*	96/96	73/75	78/75	75/72
ASe1R	8.5	9.6	5.5	5.0	5.0
ASe2R	7.0	9.9	6.0	5.0	4.5
ASe3R	7.5	10.4	6.0	5.0	5.0
ASe4R	7.5	10.4	6.0	5.0	5.0
GiLC	8	7	7	8	7
FuL	58.0	70.0	52.5	47.0	25.7
FFL	27.0	48.0	35.0	31.5	17.2
PA	61.0	83.5	57.0	34.5	48.0
CaL	F	F	5.2	5.0	3.8
LL	F	F	10.0	8.4	10.0

(Fig. 140E) moderately tall (height 72% width); hood dark brown, lateral wall and wings lighter brown, lateral wing and wall margins translucent. Lateral wall with strong basal notch and broadly rounded triangular crest. Hood deep (depth 38% beak length) forward projecting, with flattened chisel-like to weakly bifid rostral tip; hood with strong posterior notch; lateral wings very long (length 102% beak length); lateral wings with single weak fold.

Radular dentition simple (Fig. 140F); rachidian well developed, broad based, with small basal prominences; 2nd lateral with large broad-based cusp; marginal tooth robust; marginal blocks well developed.

ETYMOLOGY: Named for Tsunemi Kubodera, to mark his recognition of these specimens in the first place, and for his assistance in resolving some of the systematic complexities amongst species of *Graneledone*.

REMARKS: Differentiating species of *Graneledone* has proved difficult. In order to conduct this review of New Zealand species, representatives of all named species have been examined, with the exception of *G. boreopacifica* Nesis and *G. macrotyla* Voss. It is apparent that several additional southern ocean species await description. As characters herein considered valuable for differentiating described species have not earlier been described, a brief re-description of some species is made for comparison with New Zealand taxa. Future descriptions of *Graneledone* species must provide more detail on cartilaginous cluster distribution and composition, and hectocotylised and non-hectocotylised arm sucker counts.

Graneledone spp. (Figs 141–143) (Tables 127–133)

Representatives of the following species have been examined:

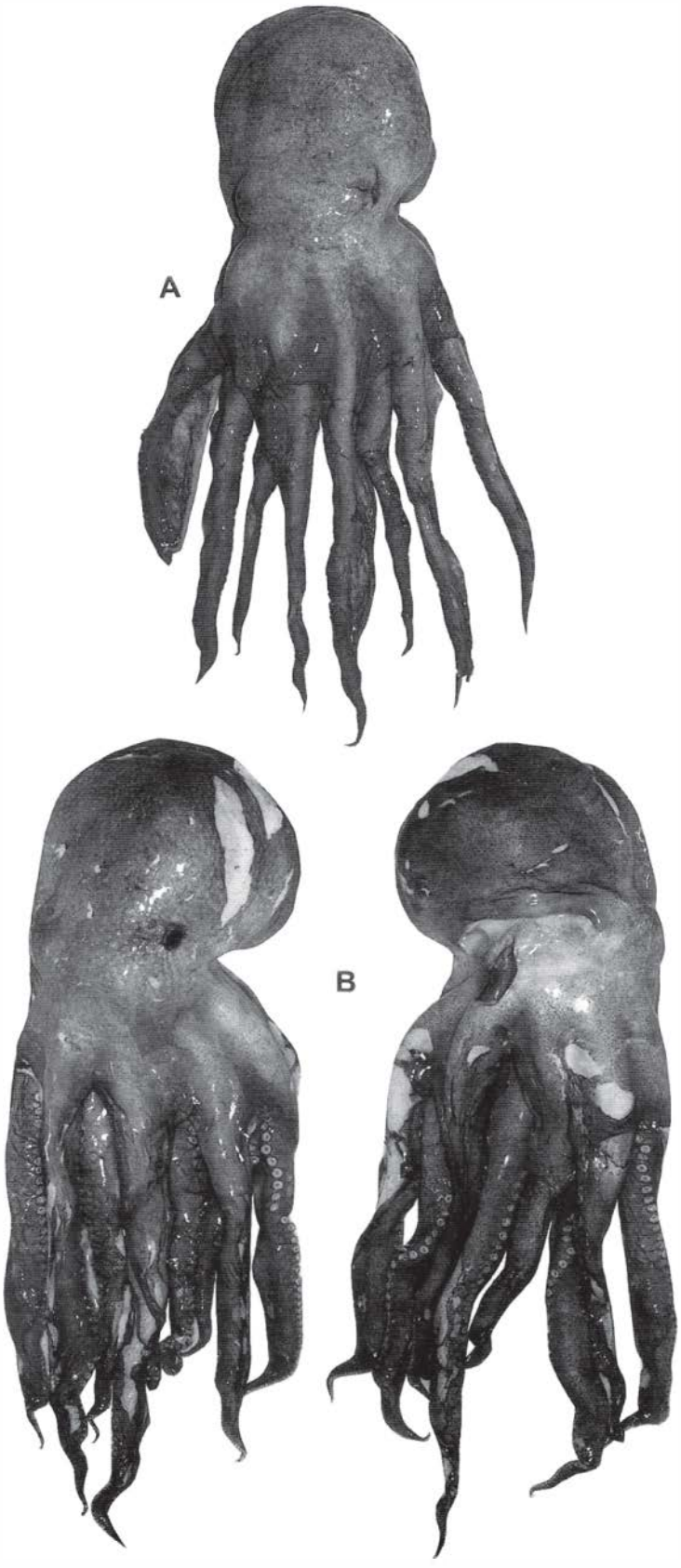


Figure 139. *Graneledone taniwha kubodera* ssp. nov.: **A**, NMNZ M.118332, male, ML 108.5 mm. **B**, NMNZ M.117874, female, ML 147 mm, both specimens pre-fix, post-thaw.

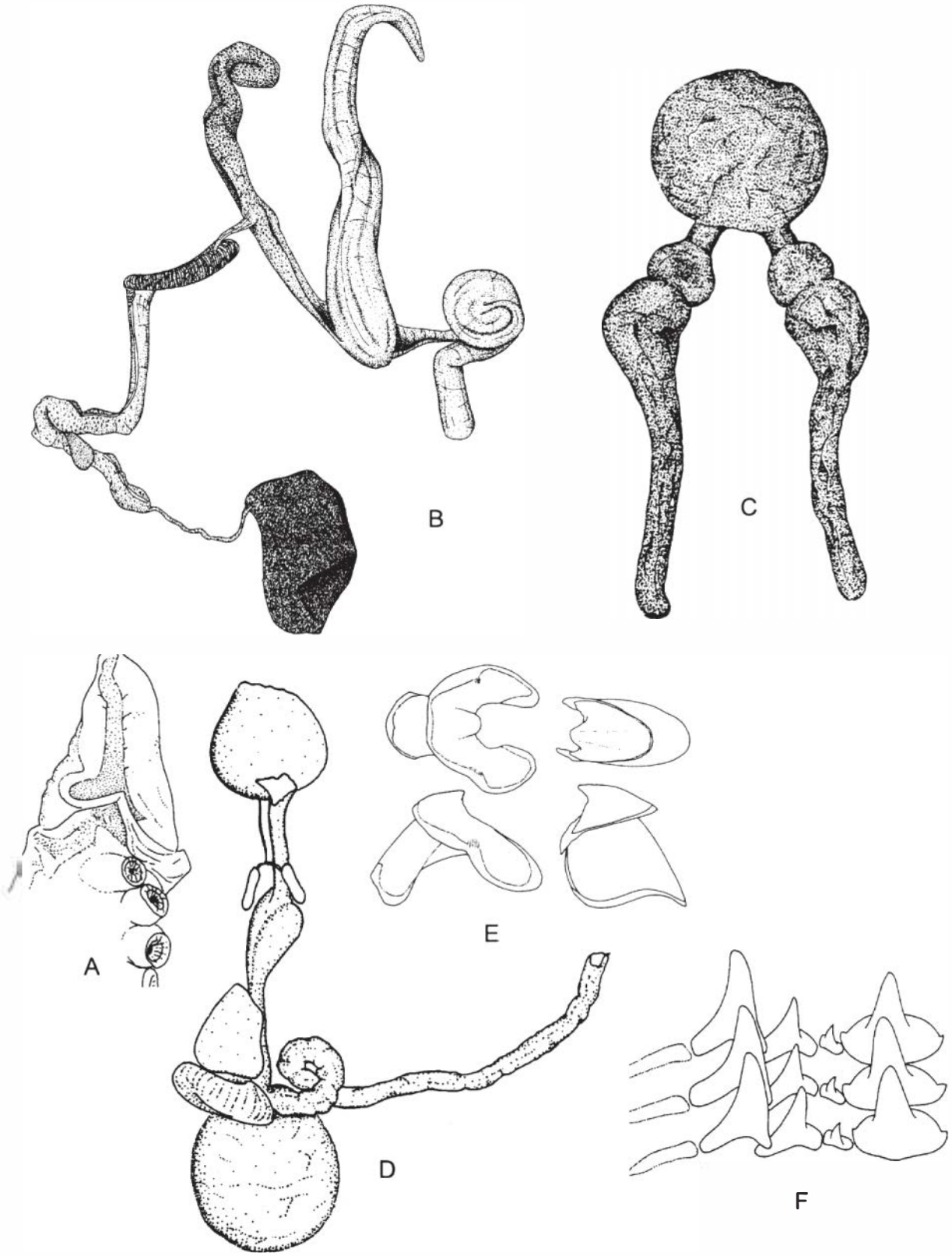


Figure 140. *Graneledone taniwha kubodera* ssp.nov.: **A**, holotype, NMNZ M.109068, male, ML 79.5 mm. **B, D–F**, NMNZ M.109064, male, ML 70 mm. **C**, NMNZ M.109059, female, ML 82.1 mm. **A**, hectocotylus. **B**, male reproductive system. **C**, female reproductive sysytem. **D**, alimentary canal. **E**, beaks. **F**, radula.

Graneledone verrucosa media Joubin, 1918: holotype, M, ML 83.0 mm, 42°40'N, 62°49.30'W, 1458 m, 26/08/1913 (fig. 141A–B).

Graneledone verrucosa (Verrill): USNM 332971, syntype, F, ML? 100 mm[1], 39°50.30' N, 70°11.00' W, 852 m, 01/07/1880, *Blake* Stn 312 (figs 141C); USNM 731131, M, ML 32.0 mm, 39°33.00' N, 71°16.15' W, 2153 m, 21/08/1884, r.v. *Albatross* (fig. 141D); USNM 730989, M, ML 84.0 mm; USNM 574996, F, ML 24.0 mm, 41°09.40' N, 66°02.20' W, 2294 m, 04/09/1883, r.v. *Albatross*; USNM 730995, 2F, ML 42.5, 15.0 mm, 39°44.54' N, 70°43.12' W, 1885–1967 m, 10/07/1975, r.v. *Chain*; USNM 730996, F, ML 45.0 mm, 39°44.12' N, 70°28.36' W, 1830–1912 m, 08/07/1975, r.v. *Chain*.

Graneledone antarctica Voss, 1976: paratypes, UMML 31.1667, M, ML 35.0 mm, F, ML 41.0 mm, 74°05.6' S, 175°05.2' W, 2273–2376 m, 08/02/1968, r.v. *Eltanin* Stn 2110 (figs 142A–C).

Graneledone sp. nov.: NMV F66840, female, 52°42.72–42.22' S, 74°26.37–28.74' E, 185–204 m, 26/01/1992 (figs 142D–E).

Graneledone pacifica Voss & Pearcy, 1990: holotype, USNM 730716, M, ML 84.0 mm, 44°52.0' N, 125°32.8' W, 2706 m, 16/07/1969. Paratypes: UMML 31.2541, F, ML 52.0 mm, 45°21' N, 125°37.3' W, 2500 m, 05/10/1969 (fig. 142F–G); UMML 31.2539, M, ML 38.0 mm, F, ML 99.0 mm, 45°59.6' N, 125°44.0' W, 2500 m, 01/08/1965; UMML 31.1959, M, ML 75.0 mm, 44°52' N, 125°32.8' W, 2706 m, 16/07/1969; UMML 31.2542, 2F, ML 51.0, 36.0 mm, 45°57.6' N, 125°46.2' W, 2265 m, 20/07/1970; UMML 31.1957, M, ML 77.0 mm, 45°37.9' S, 125°46.5' W, 2450 m, 19/03/1970.

Graneledone cf. *challengeri* Berry, 1914: NMV F76888, 2 female, 41°53.6–48.9' S, 144°24.6–21.6' E, 1384–1416 m, 18/05/1986; NMV F76887, female, 40°55.7–58.3' S, 143°40.5–42.2' E, 1280–1264 m, 15/05/1986 (Fig. 143A–E).

Neither web depth, arm-sucker count, nor relative arm length prove valuable for differentiating *G. verrucosa*, *G. verrucosa media*, *G. antarctica*, *G. taniwha taniwha*, or *G. taniwha kubodera*, although *G. challengeri* attains higher arm-sucker counts than other species.

Web depth, arm-sucker count, and relative arm length prove of no value for differentiating *G. pacifica* from *G. challengeri*, *G. taniwha taniwha*, or *G. taniwha kubodera*; for that matter it is difficult to distinguish between species of *Graneledone* and those provisionally identified as *Bentheledone* on the basis of these indices, although *Bentheledone* spp. have a slightly lower ASC value relative to mantle length.

Cartilaginous cluster distribution for *Graneledone pacifica* and *G. antarctica* are given in Table 129; for *G. verrucosa media* and *G. verrucosa* these are detailed in Table 131. Indices of hectocotylised arms of male *Graneledone* species are detailed in Table 130; raw measures are given in Tables 132 and 133.

[1] *Fide* Roper and Sweeney (1978), specimen now mutilated.

Both *Graneledone pacifica* and *G. antarctica* have similar counts of cartilaginous clusters along the anteroposterior mantle axis to the three New Zealand species, *G. pacifica* (24–29), *G. antarctica* (34–36), *G. challengeri* (34–39), *G. taniwha taniwha* (24–29), and *G. taniwha kubodera* (23–25). The number of processes in each cartilaginous cluster is also similar between 4 of these 5 species, with overlapping ranges for *G. pacifica* (2–12), *G. antarctica* (1–11), *G. challengeri* (1–10), and *G. taniwha kubodera* (4–13). *Graneledone taniwha taniwha*, however, is clearly distinguished from other species, with 1–37 processes per cluster. Cluster diameter (relative to mantle length) is similar in *G. pacifica* (2.0–2.9), *G. antarctica* (0.9–2.2) and *G. challengeri* (1.0–2.7) but greater in both *G. taniwha kubodera* (1.0–5.5) and *G. taniwha taniwha* (0.7–7.5). One means by which the New Zealand species can be differentiated from *G. antarctica* and *G. pacifica* is hectocotylised arm-sucker count: *G. antarctica* with 39 suckers only (in the single paratype available for study), which is below the recognised range for *G. challengeri* (41–51) and *G. taniwha kubodera* (44–48), and at the lowest recognised range for *G. taniwha taniwha* (39–45) — the latter already distinguished on the basis of cartilaginous-cluster characteristics. *Graneledone challengeri* and *G. taniwha kubodera* differ from *G. pacifica* (with 36–38 hectocotylised arm suckers), while *G. taniwha taniwha* again differs most notably in cartilaginous-cluster characteristics.

Both *Graneledone verrucosa* and *G. verrucosa media* have fewer cartilaginous clusters along the anteroposterior axis of the mantle (12–15) than *G. challengeri*, *G. taniwha taniwha* sp. nov. and *G. taniwha kubodera*. The number of processes within each cluster is also variable, with overlapping ranges for *G. verrucosa* (2–7), *G. verrucosa media* (1–12), *G. challengeri*, and *G. taniwha kubodera*, but *G. taniwha taniwha* is clearly distinguished with 1–37 processes per cluster.

Given the value of cartilaginous-cluster distribution and composition for differentiating species, the immature female *Graneledone* sp. specimen reported from Namibia by Villanueva and Sánchez (1993) differs from New Zealand taxa by: having less than 20 clusters along the anteroposterior axis of the mantle, and about 10 in a transverse line between the orbits; the clusters phase out over the brachial crown, scarcely reaching the web margin on any dorsal or dorsolateral arm; the number of processes in any cluster appears to be 10 or less. As Villanueva and Sánchez (1993) suggest, this species appears more similar to *G. pacifica* Voss & Pearcy, or *G. boreopacifica* Nesis, than to *G. challengeri*, *G. taniwha taniwha* or *G. taniwha kubodera*.

Table 127. Indices and formulas *Graneledone* spp. (* denotes damage, † denotes a character which was not measured; [1]*G. verrucosa media*, [2]*G. verrucosa verrucosa*, [3]*G. antarctica*).

	[1]MNHN 29-5353	[2]USNM 730989	[2]USNM 730996	[2]USNM 730995	[2]USNM 574996	[2]USNM 730995	[3]UMML 31.1667	[3]UMML 31.1667
ALI1–4	†	65.7–78.5*	63.5–75.5	60.6–73.3	49.4–63.0	53.1–62.5	56.0–71.4	57.1–80.7
WDIA–E	17.2–31.3	20.4–32.7*	19.2–27.8	22.3–30.6	*	†	20.8–32.0	19.2–27.7
ASC1–4	81–87	88–91	67–74	64–73	43–51	50–54	56–64	53–63
ASIn1–4	7.2	5.4–6.5	5.8–6.7	4.7	4.2	5.3	5.6–6.8	5.7–6.6

Table 128. Indices and formulas for *Graneledone* and ?*Bentheledone* spp. ([1]*G. pacifica*, [2]*Bentheledone* sp.).

	[1]UMML 31.2539	[1]UMML 31.1957	[1]UMML 35.2541	[1]UMML 31.2542	[1]UMML 31.2539	[1]UMML 31.2542	[2]UMML 31.2584	[2]UMML 31.2585
ALI1–4	64.3–77.8	64.8–79.7	60.1–77.3	60.3–72.3	60.3–72.2	59.8–67.2	65.0–72.6	62.1–72.6
WDIA–E	17.9–25.0	15.4–25.8	15.7–24.8	24.8–34.6	15.6–25.7	26.8–34.1	19.6–29.6	16.5–29.4
ASC1–4	75–82	72–78	76–79	79–83	59–62	64–70	60–62	63–71
ASIn1–4	5.6–6.6	6.5–7.4	4.6–5.2	4.3–5.1	4.5–4.7	4.4–5.0	8.0–8.7	6.3–6.9

Table 129. Cartilaginous cluster distribution for [1]*G. pacifica* Voss & Pearcy and [2]*G. antarctica* Voss († denotes a character not enumerated).

	[1]UMML 31.2542[1]	[1]UMML 31.2540	[1]UMML 31.1957	[2]UMML 31.1667 (F)	[2]UMML 31.1667 (M)
clusters across mantle	21	29	24	36	34
cluster # interocular	15	17	18	23	23
# processes within cluster	†	range 3–10, av. 5, n=6	range 2–12 av. 8, n=13	range 1–10 av. 6, n=16	range 1–11 av. 5, n=19
cluster diameter (mm)	1.0–1.5	2.0–3.0	1.0–2.5	0.5–0.9	0.3–0.7
CDI	2.0–2.9	2.3–3.4	1.3–3.3	1.2–2.2	0.9–2.0

[1] Female ML 51.0 mm.

Table 130. Indices of hectocotylised 3R arm for male *Graneledone* spp.: [1]*G. verrucosa media*, [2]*G. verrucosa verrucosa*, [3]*G.antarctica*, [4]*G. pacifica*.

	[1]MNHN 29-5353	[2]USNM 730989	[3]UMML 31.1667	[4]UMML 31.1957	[4]UMML 31.2539
OAI	85.1	84.4	98.0	93.5	87.5
ASC3R	42	44	39	36	38
CaLI	50.8	55.2	47.6	25.0	57.1
LLI	5.4	7.1	4.2	3.7	3.8

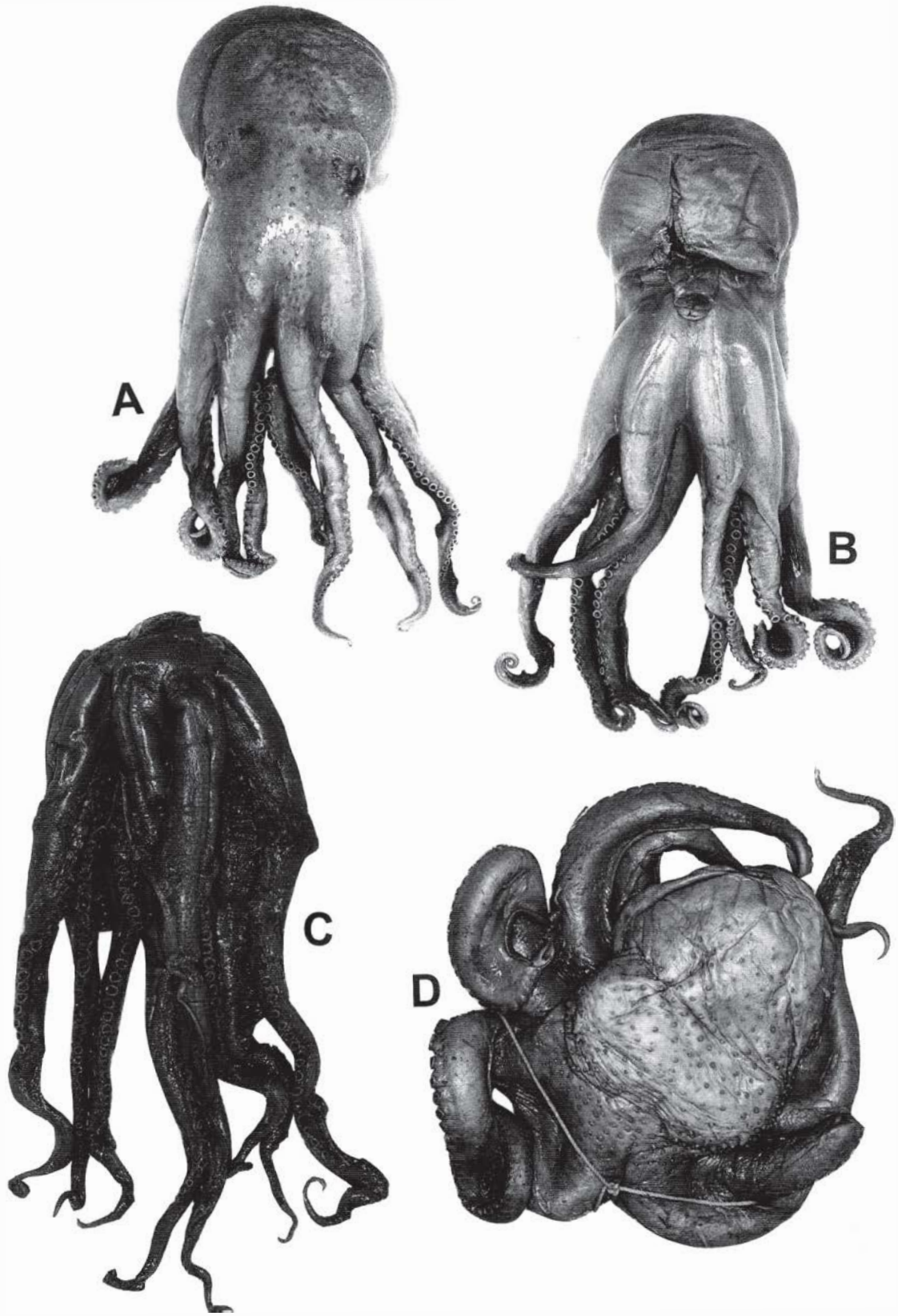


Figure 141. *Graneledone* spp.: **A, B**, *Graneledone verrucosa media* (Joubin, 1918), holotype, MNHN29-5353, male, ML 83 mm. **C**, *Graneledone verrucosa verrucosa* Verrill, 1881, syntype, USNM 577583. **D**, *Graneledone verrucosa verrucosa* Verrill, USNM 731131, male, ML 32 mm.

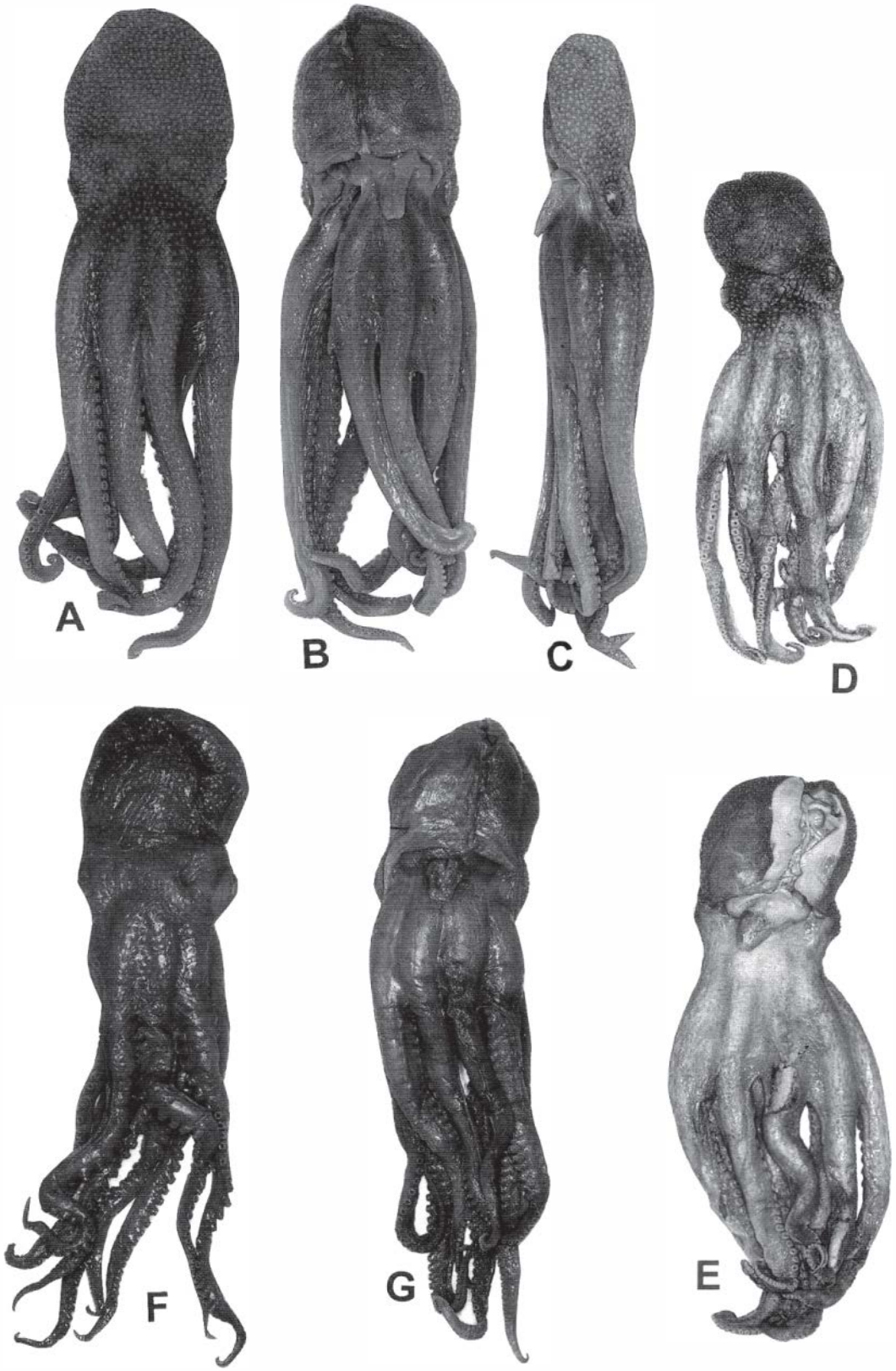


Figure 142. *Graneledone* spp.: **A–C**, *Graneledone antarctica* Voss, 1976, paratype, UMML 31.1667, female, ML 41 mm. **D, E**, *Graneledone* sp. nov., NMV F66840, female (note cartilage-like clusters on ventral surface of mantle). **F, G**, *Graneledone pacïfica* Voss & Pearcy, 1990, paratype, UMML 31.2541, female, ML 52 mm.

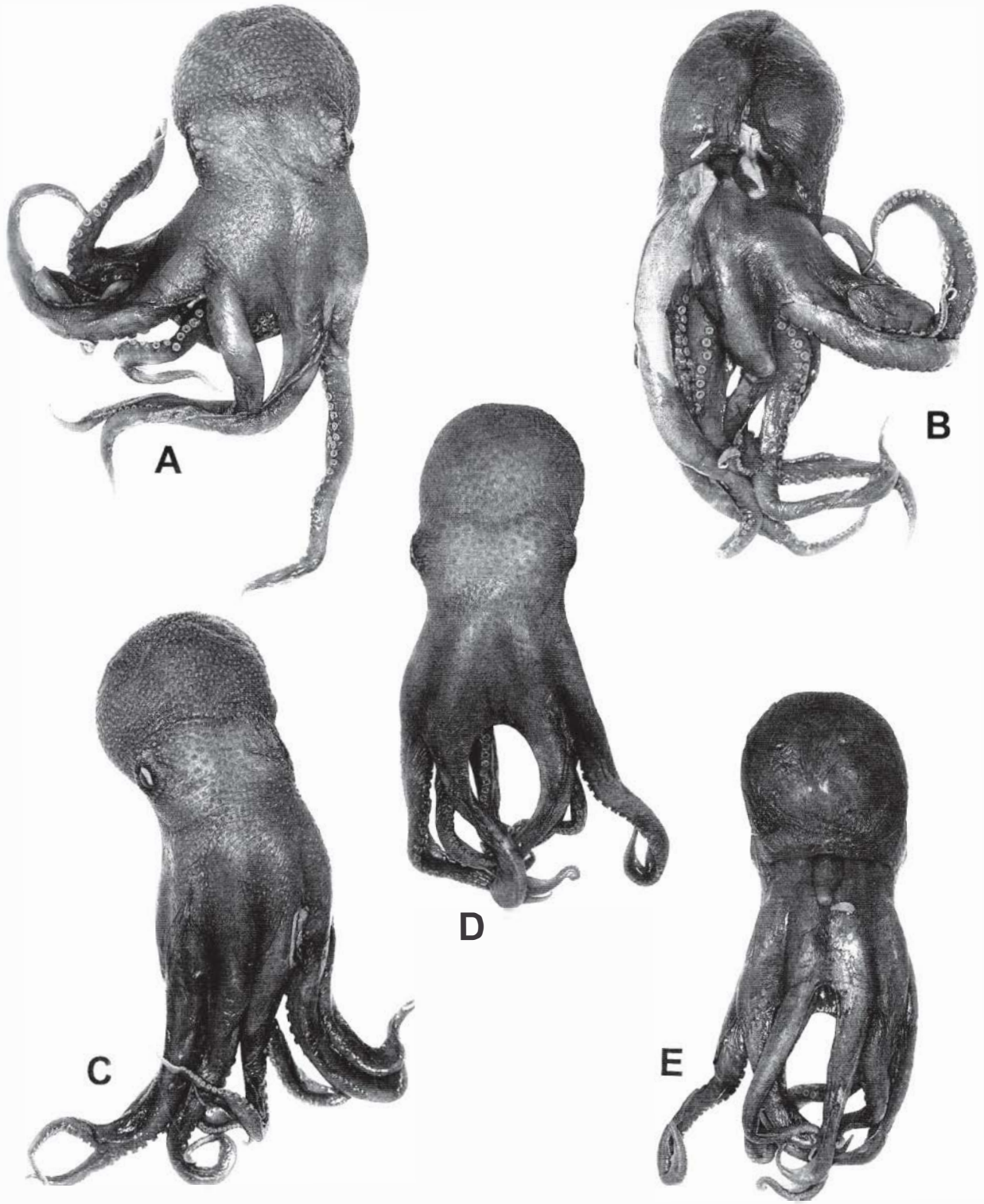


Figure 143. *Graneledone* cf. *challengeri* (Berry, 1914), South Australian specimens: **A, B**, NMV 76888, female; **C**, NMV 76888, female. **D, E**, NMV 76887, female.

Table 131. Cartilaginous cluster distribution for [1]*G. verrucosa media* and [2]*G. verrucosa*.

	[1]MNHN 29-5353	[2]USNM 730995	[2]USNM 730996	[2]USNM 574996
clusters across mantle	12	15	15	*
cluster # interocular	12	15	16	*
# processes within cluster	range 1–12 av. 5, n=15	range 2–6 av. 4, n=9	range 3–7 av. 5, n=12	range 1–6 av. 4, n=12
cluster diameter (mm)	0.3–3.2	0.8–1.2	1.0–1.1	†
CDI	0.4–3.9	1.9–2.8	2.2–2.4	†

Table 132. Raw measures for *Graneledone* spp. (* denotes damage; † denotes character not measured/enumerated; [1]*G. verrucosa media*, [2-5]*G. verrucosa verrucosa*, [6]*G. antarctica*.

	[1]MNHN 29-5353	[2]USNM 730989	[3]USNM 730996	[4]USNM 730995	[5]USNM 574996	[4]USNM 730995	[6]UMML 31.1667	[6]UMML 31.1667
TL	†	312	200	165	81	64	175	161
ML	83.0	84.0	45.0	42.5	24.0	15.0	41.0	35.0
MW	95.5	84.0	49.0	39.0	22.5	11.5	40.0	37.0
HdL	38.0	42.0	26.0	23.0	23.5	7.0	18.0	16.0
HdW	81.0	84.0	48.0	37.5	20.0	12.5	37.0	32.0
EO	8.0	6.5	6.0	8.0	4.0	3.0	6.5	6.5
AL1R/L	247/241	237/225	147/142	110/121	51/48	41/40	121/125	130/126
AL2R/L	252/252	245*/105*	151/143	104/102	41/48	35/40	118/124	117/115
AL3R/L	223/262	205/243	137/136	121/101	40/48	34/39	109/112	99/101
AL4R/L	225/194	216/221	127/132	113/100	41/48	39/38	107/98	92/99
WDA	65	50	42	37	*	†	26	25
WDBR/L	79/70	55/65	42/42	27/36	*/*	†	37/35	36/34
WDCR/L	82/79	60/80	38/37	26/36	*/*	†	40/40	34/34
WDDR/L	78/68	71/55*	29/36	30/31	*/*	†	35/34	33/34
WDE	45	65	31	27	*	†	28	27
ASC1R/L	81/82	91/†	69/†	64/†	51/†	50/†	56/†	56/†
ASC2R/L	85/87	*/†	74/†	73/†	49/†	54/†	64/†	63/†
ASC3R/L	42/85	44/†	70/†	69/†	43/†	43/†	64/†	39/†
ASC4R/L	81/83	88/†	67/†	69/†	45/†	†/†	59/†	53/†
ASn1R	6.0	4.5	2.6	2.0	1.0	0.8	2.3	2.0
ASn2R	6.0	5.5	2.7	2.0	1.0	0.8	2.8	2.3
ASn3R	6.0	5.5	3.0	2.0	1.0	0.8	2.8	2.3
ASn4R	6.0	5.2	3.0	2.0	1.0	0.8	2.8	2.3
CaL	6.1	8.0	F	F	F	F	F	2.0
LL	12.0	14.5	F	F	F	F	F	4.2
GiLC	7/7	†	7/6	7/7	7/6	8/7	removed	6/6
FuL	38	21.0	20.0	16.0	11.0	7.5	16.0	14.0
FFL	13	20.0	13.0	10.0	6.0	4.5	7.0	5.0
PA	54	62.0	37.0	†	†	†	29.0	18.0

Table 133. Raw measures for *Graneledone* and ?*Bentheledone* spp. (* denotes damage; † denotes character not measured/enumerated; [1]*G. pacifica*, [2]?*Bentheledone* sp.).

	[1]UMML 31.2539	[1]UMML 31.1957	[1]UMML 35.2541	[1]UMML 31.2542	[1]UMML 31.2539	[1]UMML 31.2542	[2]UMML 31.2584	[2]UMML 31.2585
TL	437	335	198	184	151	122	317	351
ML	99.0	77.0	52.0	51.0	38.0	36.0	69.0	80.0
MW	82.0	88.0	43.5	63.0	32.0	37.0	73.0	79.0
HdL	36.0	27.0	22.5	26.0	19.0	16.0	25.0	29.0
HdW	63.0	71.0	44.0	54.0	35.0	31.5	59.0	64.0
EO	18.0	10.5	8.5	7.5	8.5	4.0	5.0	12.0
AL1R/L	340/320	262/240	153/145	124/126	107/111	76/78	223/226	168*/240
AL2R/L	337/336	267/260	140/134	133/130	109/107	79/82	218/230	248/255
AL3R/L	315/316	217/232	131/136	129/121	91/104	79/77	221/222	231/247
AL4R/L	290/281	223/222	119/119	111/112	100/97	73/73	220/206	218/230
WDA	62	51	24	35	21	22*	45	42
WDBR/L	80/61	58/64	36/35	43/40	28/25	23/24	62/52	61/58
WDCR/L	85/79	62/69	38/36	46/42	23/24	25/27	66/62	68/65
WDDR/L	72/*	65/63	32/36	38/42	21/24	25/28	64/68	54/75
WDE	64	41	25	33	17	23*	47	60
ASC1R/L	82/78	78/78	79/†	83/†	60/†	69/†	62/†	*/67
ASC2R/L	75/†	78/77	78/†	80/†	62/†	70/†	60/†	71/
ASC3R/L	79/†	36/76	76/†	81/†	38/†	66/†	60/†	63/
ASC4R/L	75/†	72/73	77/†	79/†	59/†	64/†	†/†	66/
ASn1R	5.5	5.0	2.5	2.2	1.7	1.6	6.0	5.0
ASn2R	6.0	5.4	2.4	2.4	1.8	1.7	5.5	5.0
ASn3R	6.5	5.4	2.4	2.6	1.8	1.8	5.7	5.5
ASn4R	6.0	5.7	2.7	2.5	1.7	1.8	5.6	5.5
CaL	F	2.0	F	F	2.0	F	F	F
LL	F	8.0	F	F	3.5	F	F	F
GiLC	7/7	6/6	7/7	8/8	7/7	7/8	7/7	6/6
FuL	48.0	34.0	18.5	26.0	15.0	16.0	28.0	28.0
FFL	30.0	23.0	10.0	12.5	7.5	7.0	20.0	24.5
PA	53.0	†	36.0	†	22.5	†	58.0	51.0

Thaumeledone Robson, 1930

TYPE SPECIES: *Eledone brevis* Hoyle, 1885

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

REMARKS: Re-examination of type lots of *Thaumeledone brevis* (Hoyle) and *T. gunteri* Robson indicates the recent diagnosis afforded this genus by Voss (1988a) is not entirely satisfactory. Most important is the relative size of the posterior salivary glands in *T. brevis*, for which only those of the smaller syntype remain. Nevertheless, the size of these glands in this syntype (about 22% ML) and the New Zealand species differs considerably, being disproportionately large in the former and small in the latter. The glands in some peculiar *Eltanin* specimens attributed to *T. brevis* by Voss (1988a) are vestigial relative to mantle length.

Thaumeledone zeiss sp. nov. (Figs 145, 146) (Tables 134, 135)

Thaumeledone sp. O'Shea & Kubodera 1996: 153–164; O'Shea 1997a: 167, figs 1-4.

TYPE MATERIAL (4 specimens, 1 male [M], 3 female [F]): Holotype, NZOI H-657, M, ML 45.5 mm, FPT, 44°13.43–14.00' S, 178°41.59-44.29' E, 1066–1073 m, BT 4.5°C, 12/10/1995, f.r.v. *Tangaroa* Stn TAN9511/042, NZOI Stn Z8393. Paratypes: NMNZ M.117828, F, ML 54.9 mm, FPT, 44°12.86' S, 178°34.20' E, 1072–1076 m, 08/11/1993, f.r.v. *Tangaroa* Stn 9309/198; NZOI P-1099, F, ML 43.5 mm, FPT, 44°49.14–48.97' S, 173°02.81-02.33' E, 1053–1052 m, 13/04/1997, f.r.v. *Tangaroa* Stn TAN9705/003, NZOI Stn Z8789; NZOI P-1090, F, ML 37.2 mm, ?FL, 45°21.1' S, 173°35.8' E, 1386 m, 27/10/1979, NZOI Stn S153.

REFERENCE MATERIAL: BMNH 1889.4.24.50–51, *Thaumeledone brevis*, Syntypes, 2F, ML 17.0, 8.1 mm, 37°17' S, 53°52' W, *c.* 1096 m, 14/02/1876 (*Challenger* Stn 320, off Montevideo); BMNH 1951.4.26.50, *Thaumeledone gunteri*, Holotype, F, ML 37.7 mm, 53°48.30' S, 35°57' W, 21/01/1927, *c.* 409–400 m (*Discovery* Stn 158, NE of South Georgia); UMML 31.2584, ?*Bentheledone* sp. (det. *T. brevis*, F.G.Hochberg; det. *Pareledone polymorpha*, G.L. Voss), F, ML 69.0 mm, 59°08' S, 36°57.02' W, SE Scotia Sea, 2815–2818 m, 09/04/1964, *Eltanin* Stn 1070 (Figs 150D, E); UMML 31.2585, cf. ?*Bentheledone* sp. (det. cf. *T. brevis*, F.G. Hochberg), F, ML 80.0 mm, 55°01' S, 39°59' W, 2886–3040 m, 08/02/1966, *Eltanin* Stn 1537 (Figs 150A, B); AMS C40888, *Bentheledone albida* (Berry) holotype, ML indet., 64°34' S, 127°17' E, 3109 m, 14/01/1914 (fig. 150C); cf. *Thaumeledone* sp. (det. *T. brevis*, F.G. Hochberg), UMML (figs 151A–E); NMNH 00817370, *Thaumeledone* sp. (det. *T. brevis*, G.L. Voss), F, ML 41.0 mm, Ross Sea, Antarctica, 73°02' S, 176°54' E, 864–870 m, 12/01/1968 (Figs 151F–H).

RECOGNISED DISTRIBUTION (Fig. 144, p.236): New Zealand, 44°12.86-45°21.1' S, 173°02.81E–178°34.20' E, 1052–1386 m.

DESCRIPTION: Adult animal of small size (ML to 54.9 mm, TL to 120.0 mm); body squat (Figs 145A–D). Mantle profile semicircular, wide (MW about 82–95% ML); dorsoventral compression and lateral keel or fold absent. Head large, narrower than mantle, separated from mantle by well-developed preocular constriction (HdL about 33–41% ML, HdW about 51–76% ML); orbits massive, situated over base of arm pairs 1 and 2, raised from dorsal surface of head, almost confluent across dorsal midline; eye apertures large, dorsolateral in orientation. Funnel length moderate to long, length about 19–26% ML; funnel entirely free of arm bases 3 and 4. Nuchal constriction moderately well developed.

Brachial crown robust, narrower than head. Arms robust, short, length about 43–57% TL; cross-section triangular (live preserved) to ovoid (fixed post-thaw); arms rapidly taper to blunt tips; arm lengths subequal, with no consistent disparity in relative length apparent. Web moderately deep to very deep, WD about 21–53% longest arm length; web little extending along arms on either dorso- or ventrolateral surfaces; web formula variable, with no consistent disparity in relative sector depths apparent. Suckers uniserial; non-hectocotylised arm tips of male not modified in any discernible way. Arm sucker counts very low in mature specimens, ASC 29–33; suckers extend to arm tips. Suckers small, ASIn 3.6–5.3%, not enlarged in male; suckers with: small suction chamber, constricted sucker aperture, moderately well-developed grasping ring with about 10 faint radial grooves, and well-developed muscular suction pad (Fig. 155ZC).

Third right arm of male hectocotylised, shorter than opposite member (OAI 88.9), without obvious sucker enlargement. Spermatophoral groove well developed, wide; web margin conspicuously thickened; junction of web sector D with spermatophoral groove without apparent ridges or papillae. Hectocotylised portion (Fig. 146A) proportionally very long, ligula 17.0% hectocotylised arm length, with 8 faint transverse rugae; calamus proportionately very large, 63.2% ligula length.

External body surfaces off-white to light pink, papilla on dorsal surfaces of arms 1 and 2 and web sectors A–C red. Ventral surfaces of mantle, head, funnel and external surfaces of arms 3 and 4, light to dark red, associated papilla similarly darker in pigmentation than surrounding skin; subcuticular layer deep purple. Counter-pigmentation apparent, dorsal surfaces of mantle head, arms 1 and 2 and web sectors A–C, variably D, paler than ventral surfaces of same, arms 3 and 4 and web sector E (variably D). Oral surfaces of arms 1–4 and web sectors A–E deep red to maroon; oral surface of spermatophoral groove distinctly paler, yellow coloured.

Dorsal mantle skin anterior to orbits beset with approximately 12 large low-profile papillae; other mantle dorsal and ventral surfaces and dorsal, ventral and lateral surfaces of head, external surfaces of web sectors A–E, and arms 1–4, papillose. Oral surfaces of arms 1–4 and web sectors A–E smooth. Individual papilla large, low in profile, blisterlike, without secondary branching. Two superocular cirri situated on dorsal surface of orbits, anteriormost cirrus largest, hornlike, erect, without secondary branching; posteriormost cirrus similarly erect, also unbranched.

Pallial aperture wide (PAI 47.4–56.7), mantle attaching to ventrolateral surface of orbit. Funnel collar well developed; funnel organ comprising 2 narrow V-shaped elements in close VV-formation, both inner and outer limbs of subequal length (damaged in single specimen in which organ present). Gills compact, with 4 or 5 inner and outer lamellae, the inner demibranch not demonstrably reduced. Renal papillae erect, tubular. Interpallial septum short, muscular, attached to inner ventral surface of mantle, extending to anteromost portion of viscera;

Table 134. Indices, formulas, and counts for *Thaumeledone zeiss* sp. nov.

	NMNZ M.117828	NZOI Stn Z8393	NZOI Stn Z8789	NZOI Stn S153
MWI	82.1	94.9	92.0	94.6
HdLI	33.2	34.0	34.0	41.1
HdWI	51.0	63.4	60.9	75.8
EOI	16.2	16.0	10.8	10.8
ALI1–4	50.9–55.7	46.7–56.7	43.4–55.6	43.9–46.3
AFR	4.3.2.1	4.1.2.3	3.2.1.4	*
AFL	4.1=2=3	2.4.3.1	1.4.2.3	4.1=3.2
WDIA–E	45.8–52.5	20.6–38.2	27.3–50.9	35.9–48.7
WFR	D.E.A=B.C	C.D.A.B.E	A=C=D.B.E	D.C.E.A=B
WFL	D.E.B.A.C	A.D.B.E.C	A.B.C=E.D	C=D.E.B.A
ASC1–4[1]	30–31	31–33	29–31	32–33
ASC3R[2]	F	19	F	F
ASIn1–4	3.6–4.0	4.5–5.3	4.6	4.3–5.1
OAI	F	88.9	F	F
LLI	F	17.0	F	F
CaLI	F	63.2	F	F
FuLI	27.3	38.3	30.3	30.1
FFI	25.3	25.5	20.7	18.8
PAI	47.4	48.9	52.9	56.7

[1] Excludes arm 3R of male.
[2] Male only.

membranes connecting viscera to ventral inner surface of mantle absent. Funnel retractor muscles well developed. Penis diverticulum large, long, oriented towards but not extending around base of left gill; diverticulum not developed into spiral. Female with genital apertures opening on visceral face at anterior base of interpallial musculature; distal oviducts short, thick, swollen, the genital aperture marked by a small, pronounced, central pimplelike process opening on the duct's terminal concave face. Visceral envelope enclosing the digestive gland, interpallial muscles, base of renal papilla, adsiphonal pouches and inner-mantle aperture musculature densely pigmented with large wine-red chromatophores.

Single male not dissected; penis diverticulum large, thin walled, not forming spiral but pronounced in curvature. Mature female (Fig. 146B, C) with ovary sac distended by about 40 eggs, each ~ 9.3 x 5.0 mm (NMNZ M.117828, egg length 17% ML), with a stalk of comparable length to that of the egg capsule; eggs with 9–13 longitudinal striations running entire length. Proximal oviducts short, narrow, departing ovary sac singly; oviducal ball large, with single green axially striate hemisphere; distal oviducts inordinately short and swollen relative to proximal ducts; genital aperture rosettelike, with numerous papilla within concave face.

Alimentary canal (Fig. 146D–E) with small buccal bulb, about 20% ML; anterior salivary glands ovoid, vestigial, length about 29% buccal bulb greatest dimension; anterior oesophagus short, narrow; crop without anterior diverticulum, constituting no more than a pronounced, abrupt, thin-walled dilatation of oesophagus. Posterior salivary glands slender, elliptical, small, length about 72% buccal bulb greatest dimension, or 15% ML. Posterior oesophagus shorter than anterior, thick walled. Stomach of equivalent size to buccal bulb, with 3 apparent sections, basal small, thin walled, central large, thick walled, distal small, thin walled; stomach with undivided lumen. Spiral caecum saclike, without coiling, with faint radial striations. Intestine short, about 33% longer than oesophagus, thin walled, dilated for greatest length, constricted near anus; anal flaps absent. Digestive gland heart-shaped, with 2 broadly rounded anterior peaks and depressions to accommodate stomach, crop and intestine; pancreas well developed; ink sac absent. Crop contents comprise primarily polychaete remains.

Upper beak (Fig. 153F) tall (height 104.4% length); hood black, lateral walls dark brown to black, hood and lateral wall margins lightly pigmented to translucent; hood very deep (depth 50.0% beak length), with squared crest, shallow posterior notch and weak furrow running from notch to rostrum; rostrum broadly triangular, rostral tip acute, lateral margins strongly chiselled, without apparent downward

Table 135. Raw measures for *Thaumeledone zeiss* sp. nov. (* denotes damage).

	NMNZ M.117828	NZOI H-657	NZOI Stn Z8789	NZOI Stn S153
TL	106.0	120.0	99.0	84.3
ML	54.9	47.0	43.5	37.2
MW	45.1	44.6	40.0	35.2
HdL	18.2	16.0	14.8	15.3
HdW	28.0	29.8	26.5	28.2
EO	8.9	7.5	4.7	4.0
AL1R/L	54/58	65/62	51/52	22*/38
AL2R/L	55/58	6368	53/46	38/37
AL3R/L	57/58	56/63	55/43	39/38
AL4R/L	59/59	66/64	48/48	39/39
WDA	28	23.0	28	14
WDBR/L	28/29	21/19	21/24	14/15
WDCR/L	27/27	26/14	28/17	1819
WDDR/L	31/31	24/22	28/15	19/19
WDE	30	16	17	16
ASC1R/L	30/30	32/30*	30/29	22*/32
ASC2R/L	31/31	33/32	30/30	32/33
ASC3R/L	30/31	19/31	30/31	32/32
ASC4R/L	30/31	33/33	31/30	32/32
ASn1R	2.1	2.1	2.0	1.9
ASn2R	2.0	2.1	2.0	1.6
ASn3R	2.2	2.5	2.0	1.7
ASn4R	2.2	2.5	2.0	1.9
GiLC	5/5	4/4?	4/4	5/5
FuL	15.0	18.0	13.2	11.2
FFL	13.9	12.0	9.0	7.0
PA	26.0	23.0	23.0	21.1
CaL	F	6.0	F	F
LL	F	9.5	F	F

deflection. Lateral walls parallel sided; crest rounded, lateral wall fold absent; jaw without apparent tooth. Lower beak (Fig. 153F) moderately tall (height 74% width); hood dark brown, lateral wall and wings lighter brown, lateral wing and wall margins translucent. Lateral wall with weak basal notch and broadly rounded crest. Hood very deep (depth 44% beak length) projecting forward, with flattened chisel-like to weakly bifid rostral tip; hood without apparent posterior notch; lateral wings very long (length 103% beak length), with single weak fold.

Radula (Fig. 153G) degenerate, reduced to well-developed, broad-based rachidian without lateral cusps, and three rows of poorly developed lateral and marginal teeth, in addition to a row of small, block-like marginal plates.

REMARKS: Voss (1988a) considered *Thaumeledone gunteri* (Robson) possibly synonymous with *T. brevis* (Hoyle). The holotype of *T. gunteri* is in excellent condition, although both buccal bulb and radula have been removed and are presumed lost; the beaks, however, remain. Both the type and syntype of *T. brevis* are in poor condition, with the more mature female reproductive system, buccal bulb, beaks, and radula evidently lost also. Nevertheless, *Thaumeledone zeiss* differs from *T. gunteri* in beak shape, relative length of the distal oviducts, and arm-sucker counts (Figs 151D, F), and from *T. brevis* in female reproductive characters and alimentary canal configuration, particularly the relative size of the posterior salivary glands to mantle length and crop detail (Figs 151A, B).

ETYMOLOGY: After Carl Zeiss Ltd, for their generous provision of microscopic equipment used while completing this revision of the New Zealand octopod fauna.

Thaumeledone marshalli sp. nov. (Figs 148, 149) (Tables 136–139)

Thaumeledone sp. O'Shea, 1990: 132, pl. 9, figs 12.1–12.4; O'Shea & Kubodera 1996: 152, 159.

TYPE MATERIAL (6 specimens, 4 male [M], 2 female [F]): Holotype: NZOI H-658, M, ML 43.5 mm, 42°14.7–16.6' S, 175°08.6–10.6' E, 2476–2542 m, 02/11/1979, NZOI Stn S202. Paratype: NZOI P-1091, 2M, ML 42.0, 13.0 mm, 42°14.7–16.6' S, 175°08.6–10.6' E, 2476–2542 m, 02/11/1979, NZOI Stn S202; NMNZ M.90340, F, ML 31.0 mm, 37°00.5–00.9' S, 177°35.7–36.0' E, White Island Trench, 2142–2202 m, 18/01/1979, mud and pumice substrate, r.v. *Tangaroa* (NZOI Stn R50); NMNZ M.109378, M, ML 37.7 mm, F, ML 28 mm, 42°36.79' S, 176°09.81' W, 1999–2002 m, 02/03/1992, r.v. *Tangaroa*.

REFERENCE MATERIAL: As for *Thaumeledone zeiss* sp. nov.

RECOGNISED DISTRIBUTION (Fig. 147, p. 236): New Zealand, between coordinates 37°00.5–00.9' S, 177°35.7–36.0' E to 42°36.79' S, 176°09.81' W, bathymetric range 1999 (–2002) m.

DESCRIPTION: Adult animal small (ML to 43.5 mm, TL to 102 mm), squat bodied (Figs 148A–E). Mantle ovoid, slightly narrower than or as broad as mantle length (MW about 75–101); dorsoventral compression and lateral keel or fold of skin absent. Head massive, broad, narrower than mantle (HdL about 42–52% ML, HdW about 71–81), separated from mantle by poorly defined preocular constriction; orbits massive, bulbous, raised from dorsal surface of head, confluent across dorsal midline of head, situated on base of arm pairs 1 and 2; eye apertures large, dorsolaterally oriented. Funnel length moderate, free for almost its entire length but for points of attachment to arms bases 3 and 4; adsiphonal pouches

Figure 145. ***Thaumeledone zeiss*** sp. nov.: **A, B**, holotype, NZOI H-657, male, ML 45.5 mm. **C**, NMNZ M.117828, female, ML 54.9 mm; **D**, NZOI Stn S153, female, ML 37.2 mm.

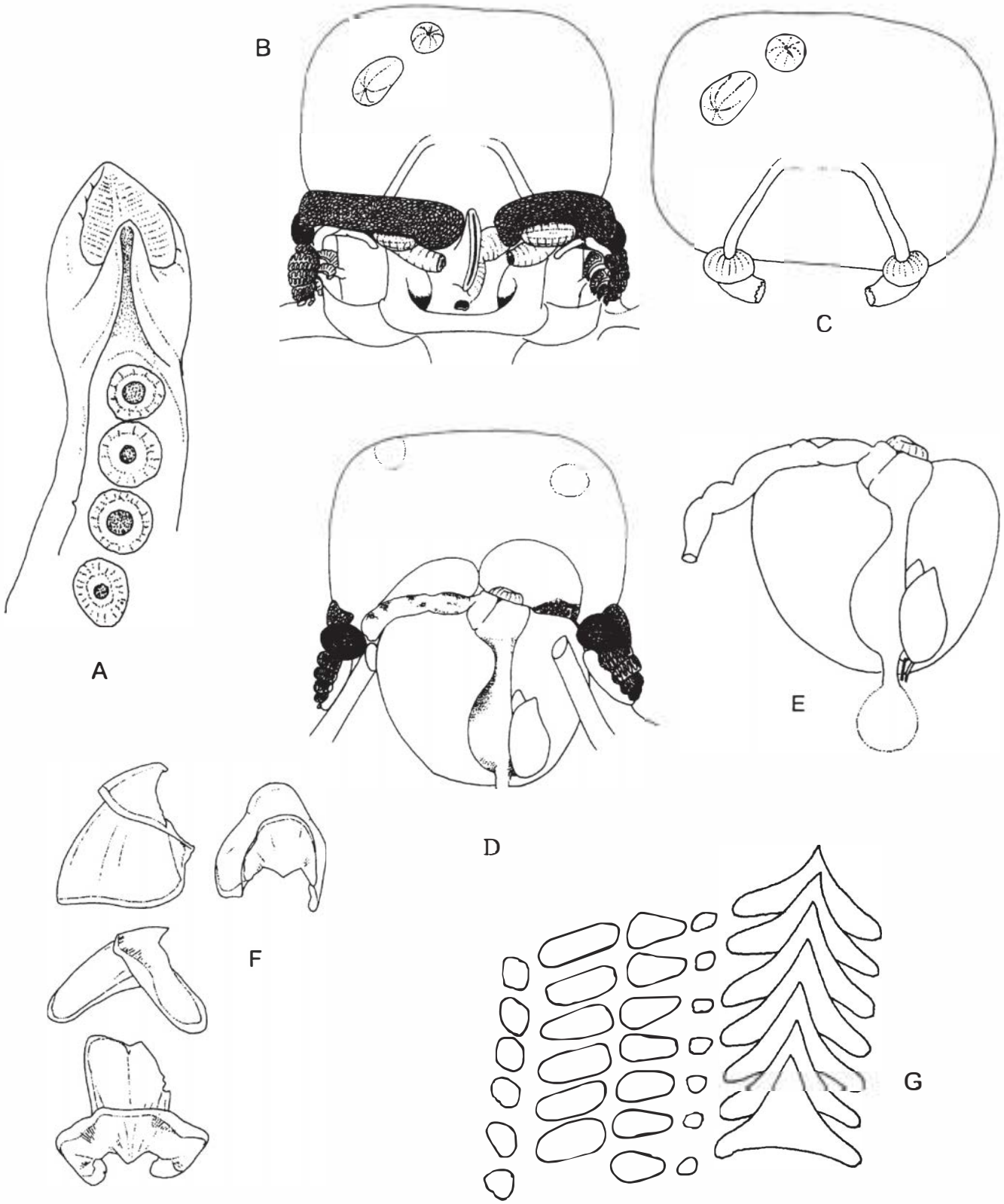


Figure 146. ***Thaumeledone zeiss*** sp. nov. Anatomy: **A, F, G**, Holotype, male, NZOI H-657. **B–E**, NMNZ M.117828, female, ML 54.9 mm. **A**, hectocotylus. **B, C**, ventral and dorsal perspectives of female reproductive system *in situ*. **D, E**, dorsal and reconstructed alimentary canal *in situ*. **F**, beaks. **G**, radula.

poorly developed. Nuchal constriction poorly developed.

Brachial crown robust, narrower than head. Arms short (AL about 41–61% TL), thick, rapidly attenuating to blunt tips; arm formula variable, arms of subequal length with no consistent disparity in relative length apparent. Web very deep (WD about 33–65% longest arm length), little developed along both dorsal and ventral faces of each arm; web formula variable, no consistent disparity in relative sector depth apparent. Suckers biserial, not enlarged in male; non-hectocotylised arm tips of males not modified in any discernible way; non-hectocotylised arm sucker counts on mature specimens very low, ASC 28–31 (excluding juvenile from NZOI Stn S202, ASC 19–23); suckers extend to arm tips; suckers small (ASIn 3.6–6.9), distal 4 or 5 suckers reduce rapidly in diameter; suckers with: large suction chamber, constricted sucker aperture, poorly developed grasping ring with about 18 faint radial grooves, and poorly developed muscular suction pad (Fig. 155ZD).

Third right arm of male hectocotylised, shorter than or equivalent in length to opposite member (OAI about 74–100), without obvious sucker enlargement. Spermatophoral groove well developed, wide; web margin conspicuously thickened; junction of web sector D with spermatophoral groove without apparent ridges or papillae. Hectocotylised portion (Fig. 149A) of moderate length in mature specimens; ligula 9.4–11.3% hectocotylised arm length, increasing with maturity (3.4% arm length in single juvenile), with 6 or 7 faint, fleshy transverse rugae; calamus proportionately large, 30.8–47.5% ligula length.

Skin over entire animal smooth or with extremely faint traces of papillation, with 2–4 small node-like structures along arms 1–3 and in web sectors A–D; superocular cirrus absent; tissues with thick subcuticular gelatinous layer.

Dorsal surface of mantle, head, arms 1 and 2 to web margin, web sectors A–C and oral surface of sucker rims, off-pink; ventral surface of mantle, web sectors D and E, dorso- and ventrolateral surfaces of arms 3 and 4, oral surface of arms and web, and dorso- and ventrolateral surface of arms 1–4 outside web margin, maroon; spermatophoral groove light red. Counter-pigmentation marked with dorsal surfaces of mantle, head, arms, and web lighter than ventral and oral surfaces.

Pallial aperture moderately wide, mantle attached directly to ventral surface of orbits; mantle musculature thick. Funnel collar well developed; interpallial septum short, muscular, attached to inner ventral surface of mantle, extending to anteriormost portion of viscera; membranes connecting viscera to ventral inner surface of mantle absent. Gills small,

Table 137. Indices and counts for male *Thaumeledone marshalli* sp. nov. (* denotes damage).

	NZOI Stn S202	NMNZ M.109378	NZOI Stn S202	NZOI Stn S202
ASC3R	18	18	17	20
OAI	100.0	82.5	74.1	80.0
CaL	*	47.5	30.8	41.7
LL 3.4	11.3	9.4	10.9	

compact, with 5 lamellae per inner and outer demibranch. Interpallial septum, lateral muscles restraining the digestive gland and visceral envelope, and inner mantle musculature pigmented with large dark red chromatophores. Funnel organ 2 V-shaped elements in VV formation (Fig. 149B).

Male reproductive system (Figs 149C, D) with short, loosely coiled, thin proximal vas deferens; spermatophoral gland similarly short, with small appendix at junction with accessory gland. Accessory gland short, straight, without terminal volution or modification. Spermatophore sac long, thin walled, containing 3 spermatophores; penis diverticulum containing single spermatophore. Distal vas deferens short, thick; penis diverticulum large, single, with pronounced spiral; penis large, thick, genital aperture subterminal. Single submature female known, (Fig. 149E) with short, stout proximal oviducts departing ovary sac singly; oviducal glands large, non-chambered; distal oviducts short, stout, swollen. Eggs small (2.5 x 0.7 mm), each with short stalk (immature).

Alimentary canal (Figs 149F, G) with small buccal bulb, about 21% ML in greatest dimension; anterior salivary glands ovoid, small, length about 40% buccal bulb greatest dimension; anterior oesophagus short, narrow; crop a pronounced, abrupt, thin-walled dilatation of oesophagus, anterior diverticulum absent. Posterior salivary glands slender, elliptical, granular, large, length about 72% buccal bulb greatest dimension or 15% ML. Posterior oesophagus short, thick. Stomach with three apparent sections, basal largest, thin walled, central thick walled, muscular, distal thinwalled, small; stomach lumen undivided. Spiral caecum of single radially striate incomplete volution. Intestine short, length equivalent to that of oesophagus and stomach, thick walled, dilated for greatest length but slightly constricted near anus; anal flaps absent. Digestive gland large, ovoid, of granular composition, with 2 anterior peaks and depressions imparted by stomach, crop, and intestine; pancreas well developed; ink sac absent. Stomach contents comprise amphipod remains.

Table 136. Indices and formulas for *Thaumeledone marshalli* sp. nov. (* denotes damage).

	NZOI Stn S202	NMNZ M.109378	NMNZ M.109378	NZOI Stn S202	NZOI Stn S202
MWI	92.3	100.0	100.8	77.4	75.4
HdLI	46.2	45.0	42.4	52.4	44.1
HdWI	78.5	78.6	74.3	81.0	71.3
EOI	11.5	17.9	19.4	13.8	18.4
ALI1–4	50.9–56.1	45.1–53.4	41.3–52.3	45. 1–60.9	43.1–55.9
AFR	1.2.3.4	4.1.2.3	1.2=4.3	4.1=2.3	4.1=2.3
AFL	*	4.1.2.3	4.3.2.1	3=4.2.1	1.4.3.2
WDIA–E	44.3–57.0	45.1–64.8	33.3–60.0	37.5–50.0	36.8–50.9
WFR	A=B.C.D.E	D.B.C.A.E	E.A.B.C.D	A.B=D.C=E	B.D.A=E.C
WFL	A.B=D=E.C	A.B.E.C.D	D.E.A.B.C	A=C.B.D.E	C.B.A=E.D
ASC1, 2, 4	19–23	28–31	28–29	29–31	27–32
ASIn1–4	6.9	3.6–3.9	4.0–5.0	5.0–5.2	4.6–5.1

Table 138. Raw measures for *Thaumeledone marshalli* sp. nov. (* denotes damage).

	NZOI Stn S202	NMNZ M.109378	NMNZ M.109378	NZOI Stn S202	NZOI Stn S202
TL	28.5	66.5	86	92	102
ML	13.0	28.0	37.7	42.0	43.5
MW	12.0	28.1	38.0	32.5	32.8
HdL	6.0	12.6	16.0	22.0	19.2
HdW	10.2	22.0	28.0	34.0	31.0
EO	1.5	5.0	7.3	5.8	8.0
AL1R/L	15.8/16	35.0/34.0	44.0/41.0	49.0/53.0	53.0/57.0
AL2R/L	15.5/9.8*	34.5/31.5	43.0/42.0	49.0/55.0	53.0/53.0
AL3R/L	14.8/14.8	32.0/30.0	35.5/43.0	41.5/56.0	44.0/55.0
AL4R/L	14.5/15.2	35.5/35.0	43.0/45.0	52.0/56.0	55.0/56.0
WDA	9.0	20.0	22.0	28.0	25.0
WDBR/L	9.0/7.9	22.0/17.5	19.0/18.0	25.0/27.0	27.0/26.0
WDCR/L	8.8/7.0	21.0/16.5	16.0/17.0	21.0/28.0	22.0/29.0
WDDR/L	8.3/7.9	23.0/16.0	15.0/27.0	25.0/26.0	26.0/21.0
WDE	7.9	17.0	25.0	21.0	25.0
ASC1R/L	22/22	29/29	29/29	30/29	30/27
ASC2R/L	23/11*	28/29	29/29	31/30	32/31
ASC3R/L	18/23	29/31	18 (M)/28	17/30	20/30
ASC4R/L	19/22	28/28	29/29	31/31	31/30
ASe1R	0.9	1.1	1.5	2.1	2
ASe2R	0.9	1	1.9	2.2	2.1
ASe3R	0.9	1.1	1.9	2.2	2.2
ASe4R	0.9	1.1	1.9	2.1	2.1
GiLC	5/5	5/5	5/5	5/5	5/5
FuL	5.1	15	10.5	15	15
FFL	2.9	6.2	10	6.1	8.1
PA	5.1	15	21	22.2	20.6
CaL	*	F	1.9	1.2	2
LL	0.5	F	4	3.9	4.8

Table 139. Raw measures for *Thaumeledone marshalli* sp. nov. (* denotes damage).

	T. cf. *brevis* USNM 817370	*T. brevis* (S)	*T. brevis* (T)	*T. brevis* (T)
TL	108	28.5	48	82
ML	41.0	8.1	17	37.7
MW	42.0	9.2	16	38.4
HdL	16.5	5.1	9.1	16.4
HdW	30.5	9.6	16.1	31
ED	16.0	5.1	9.8	15.9
EO	6.6	1.1	1.7	3.4
AL1R	50.0	12	25	49
AL2R	52.5	12	25	48
AL3R	55.5	10.5	25	51
AL4R	58.0	12.5	24	52
AL1L	51.0	12.2	25	49
AL2L	52.0	12	25.5	49
AL3L	53.0	12	23.5	51
AL4L	60.0	12	23*	51
AFR	4.3.2.1	4.1=2.3	1=2=3.4	4.3.1.2
AFL	4.3.2.1	1.2=3=4	2.1.3.4	3=4.1=2
WDA	26.5	8	*	26
WDBR	26.0	*	*	25
WDCR	29.0	7	16	28
WDDR	31.0	*	*	27
WDE	23.0	*	*	24
WDBL	28.5	*	*	25
WDCL	29.0	7	15	27
WDDL	32.5	*	*	25
WFR	D.C.A.B.E	*	*	C.D.A.B.E
WFL	C.D.B.A.E	*	*	C.A.B=D.E
ASC1R	31	24	29	35
ASC2R	31	24	28	35
ASC3R	33	21	26	36
ASC4R	32	23	25	37
ASC1L	31	23	26	36
ASC2L	31	23*	26	36
ASC3L	32	22	26	35
ASC4L	32	24	26	35
ASe1R	*	0.8	1	2.6
ASe2R	*	0.8	1	2.6
ASe3R	*	0.8	1	2.9
ASe4R	*	0.8	1	2.9
GiLC	*	4/5	5/5	5/5
FuL	15.6	2.5	7	14
FFL	6.5	*	*	*
PA	22.0	*	14	27
CaL	F	*	F	F
LL	F	*	F	F

Upper beak (Fig. 149H) very depressed (height 80.7% length); hood dark brown, with rounded crest; hood margins translucent; hood very deep (depth 49.0% beak length); jaw without teeth; rostral tip sharp, slightly deflected down. Lateral walls parallel sided; crest rounded, lateral wall fold weak. Lower beak (Fig. 149H) tall (height 78.3% width), dark brown, lateral wing and wall margins light brown to translucent. Lateral wall with strong basal notch and broadly convex crest. Hood deep (depth 39.2% beak length), forward projecting, pointed, without posterior notch; lateral wings very long (length 107% beak length); with single weak fold.

Radula (Fig. 149I, J) reduced to well-developed, broad-based rachidian without lateral cusps and single blocklike marginal.

ETYMOLOGY: Named for Bruce Marshall (Museum of New Zealand Te Papa Tongarewa) as a token of gratitude for his valued assistance during the years when this research was conducted.

REMARKS: Specimens referred to *Thaumeledone* sp. by O'Shea & Kubodera (1996) are here referred to *T. marshalli*. In proof (O'Shea & Kubodera, *loc. cit.*), sucker diameter was cited in error as ASIn (% ML) — the cited figures are, however, absolute measures of sucker diameter (mm), with correct details provided in Table 136.

In sucker morphology *T. marshalli* closely resembles the large female syntype of *T. brevis* (with its poor muscular development) (Fig. 155 ZB), the genus *Benth-octopus* (*s.s.*) (*fide* Robson 1932), and the New Zealand *Octopus* (*s.l.*) *mernoo*. Sucker morphology is different from that of *T. zeiss*, which has a well-developed muscular suction pad and grasping ring, similar to that of the holotype of *T. gunteri* (Fig. 155 ZA).

In external facies *T. marshalli* is most similar to specimens of *Thaumeledone* attributed to *T. brevis* by Voss (unpublished, ref. labels USNM specimens; Figs 151A–C), particularly with respect to extensive subgelatinous deposits and nodelike structures over the surfaces of mantle, arms and web. Radular dentition in *T. marshalli* sp. nov. differs from that described for both *T. brevis* and *T. gunteri* in that the lateral rows of teeth are more pronounced than described or illustrated for the types by Hoyle (1886) or Robson (1930). As the radula is absent from both type lots of *T. brevis* and *T. gunteri*, direct comparison is not possible.

GENERAL REMARKS: Voss (1988a) rediagnosed both *Thaumeledone* and *Bentheledone*, including a new character state — the relative size of the posterior salivary glands. *Thaumeledone* (in part) was rediagnosed with vestigial glands and *Bentheledone* with small glands, although a standard against which these glands could be measured was not given. The posterior salivary glands in holotypes of neither *T.*

brevis nor *T. gunteri* are particularly small, but they are certainly not vestigial (Figs 153A, D). Voss (1988b) subsequently alluded to two undescribed southern ocean species of *Bentheledone*, suggested that *T. gunteri* was synonymous with *T. brevis*, and indicated that *T. brevis* probably was circumpolar in distribution, south of the Antarctic Convergence.

Type material of *T. brevis* is in too poor a condition to evaluate alleged synonymy with the comparatively well-preserved type of *T. gunteri*. Additional *Thaumeledone* material from both respective type localities is required to fully evaluate the systematic status of these two species. Neverthless, Voss (1988b) records *T. brevis* off Antarctica, due south of New Zealand.

Although variation in any species cannot be assessed with the limited comparative material available, amongst those specimens identified as *T. brevis* by Voss in Miami collections it appears that several species and/or genera were confused. Two species are large bodied and long armed, and have comparatively high arm-sucker counts; one is smooth bodied, the other papillose (with general facies of a species of *Graneledone* lacking cartilagelike processes on any body surface). Both appear to have been subject to the same preservation history, and may be two species to which Voss (1988b) referred.

Although subject to ontogenetic change, arm-sucker count is quite stable in mature New Zealand *Thaumeledone* specimens. Mature and submature New Zealand *T. zeiss* are distinguished from the submature female *T. gunteri* by total arm-sucker count — 29–33 in *T. zeiss*, 35–37 in *T. gunteri*. The similar-sized mature Antarctic female referred to *T. brevis* by Voss (1988a) also differs from *T. gunteri* in having a lower arm-sucker count, 31–33. Mature *T. zeiss* females differ from the similar, mature Antarctic female in the relative length and shape of the distal oviducts, which are inordinately short, thick walled and tubular in *T. zeiss*, and longer, proximally swollen, distally constricted and thin walled in the Antarctic female. *Thaumeledone zeiss* differs further from the holotype of *T. brevis* in the relative development of basal-cup sucker musculature (Figs 155ZB, ZC). *Thaumeledone zeiss* is most obviously distinguished from *T. marshalli* by general sculpture, smooth in the former with several small, glandlike processes in the web sectors and over the mantle and head, and densely papillose on both dorsal and ventral surfaces of the mantle, head, arms and web in the latter. *Thaumeledone marshalli* and *T. zeiss* also differ in relative development of basal-cup sucker musculature (Figs 155ZC, ZD).

Thaumeledone marshalli differs from the unlocalised male referred to *T. brevis* by Voss by: hectocotylised arm sucker count (24 in the former, 18–20 in the latter); shape of the hectocotylised portion of calamus and ligula (club-like and robust in the former, less massive and not deeply excavated in the latter); and in whole-animal body facies (Figs 148A–E, 151A–C). *Thaumeledone zeiss* differs most notably from this unlocalised male in the extent of papillation of the mantle, head, arms and web, in hectocotylised arm sucker count (19), and in hectocotyl and total body shape (Figs 145A–D, 151A–C).

The male and female referred to *T. brevis* by Voss (1988a) are not particularly alike in general facies, and both can be differentiated from the holotype (only recorded specimen to date) of *T. gunteri* in total arm-sucker count. The two small-bodied Antarctic *Thaumeledone* specimens, and *T. zeiss* and *T. marshalli*, differ most obviously from specimens here referred to *Bentheledone*, in total arm sucker count, 60–71 in *?Bentheledone* (Tables 128, 133; Fig. 150). Posterior salivary gland size in the unlocalised male attributed to *T. brevis* by Voss is very small, and, without the benefit of an index, could have been construed as vestigial, leading Voss (1988a) to rediagnose the genus as he did.

Both New Zealand species differ sufficiently from each other and from previously described *Thaumeledone* species to allow recognition of each as novel. Moreover, there appears to be greater potential for recognising additional species of *Thaumeledone* than there does for synonymy of species. The Antarctic *Thaumeledone* female (USNM 817370) is similar to, but not conspecific with, New Zealand *T. zeiss*. On the other hand, the southern ocean *Thaumeledone* male, for which exact locality data are not available, is more similar to, but again not conspecific with, the second New Zealand species, *T. marshalli*. As *T. zeiss* and *T. marshalli* are not particularly alike, and because equally dissimilar species are found in southern oceans, it is possible that two genera exist amongst this complex of small-bodied, short-armed species (with low total arm-sucker counts): one group smooth bodied with few low-profile, dome-shaped blisterlike processes on the mantle and head; the other densely and finely papillose.

INCERTAE SEDIS

?Pareledone sp. indet. (Fig. 154)

MATERIAL EXAMINED: 1 specimen, F, ML 90 mm, TL 240 mm, unlocalised.

REFERENCE MATERIAL: *Eledone palari* Lu & Stranks, 1991: NZOI Stn Z8668, 4M, ML 65(2), 62, 55 mm, 5F, ML 80(2),

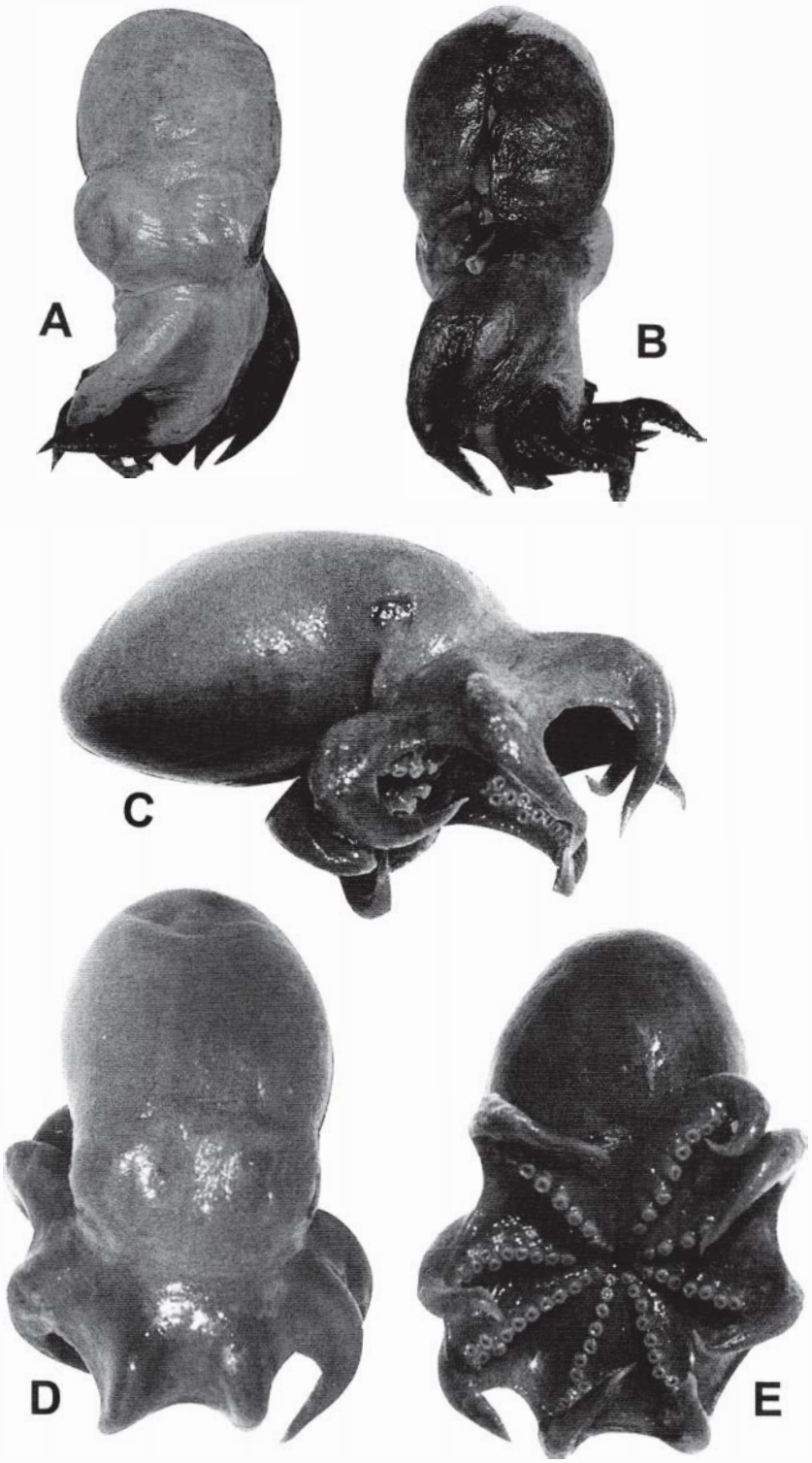


Figure 148. *Thaumeledone marshalli* sp. nov.: **A, B**, holotype, NZOI H-658, male, ML 43.5 mm. **C–E**, NMNZ M.90340, female, ML 31.0 mm.

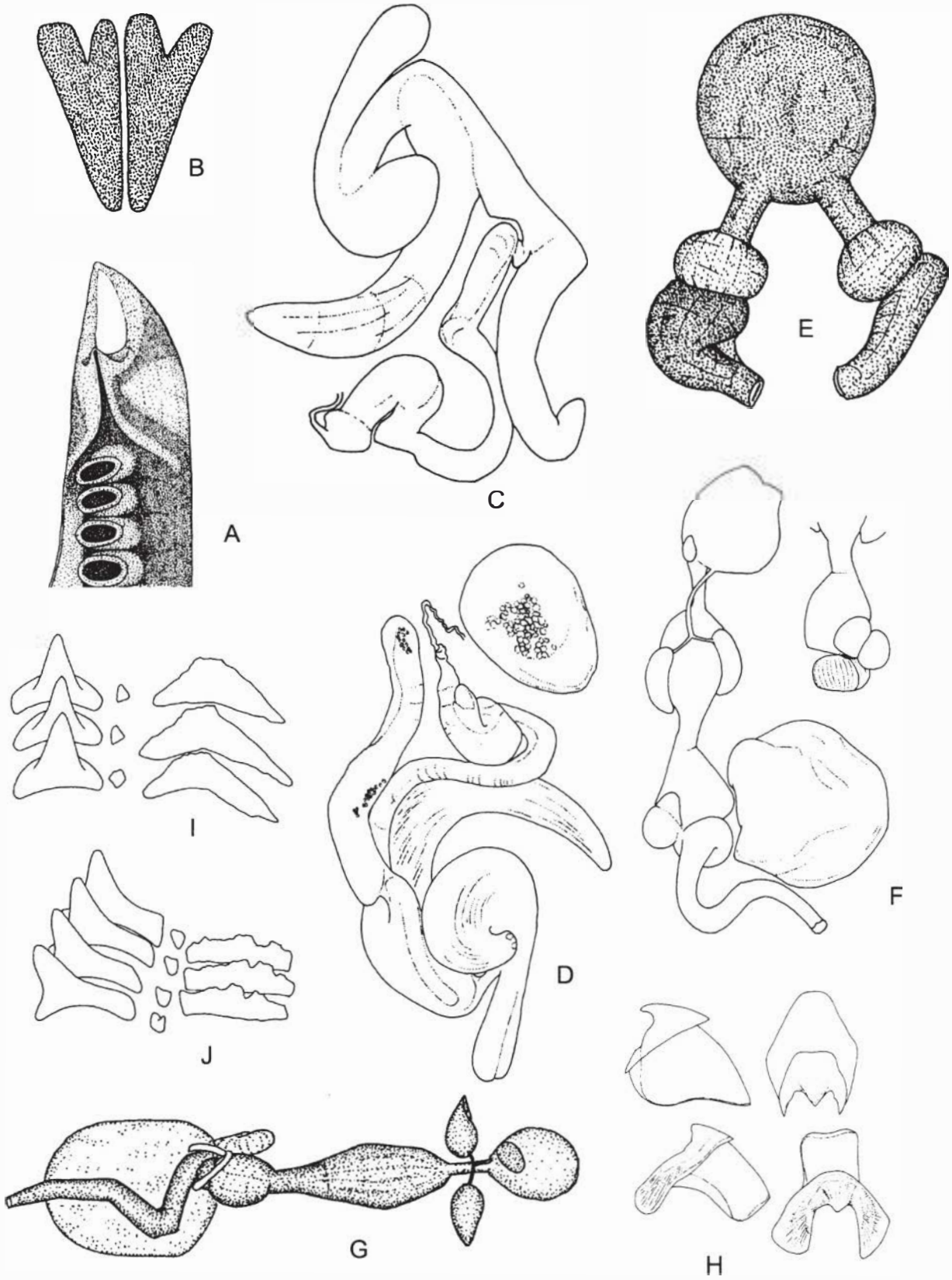


Figure 149. ***Thaumeledone marshalli*** sp. nov. Anatomy: **A, C, G, J,** NMNZ M.109378, female, ML 28 mm. **B, E, I,** NMNZ M.90340, female, ML 31 mm. **F,** NZOI Stn S202 (paratype), male, ML 42 mm. **A,** hectocotylus. **B,** funnel organ. **C,** male reproductive system. **D,** male reproductive system. **E,** female reproductive system. **F,** alimentary canal. **G,** alimentary canal. **H,** beaks. **I,** radula. **J,** radula.

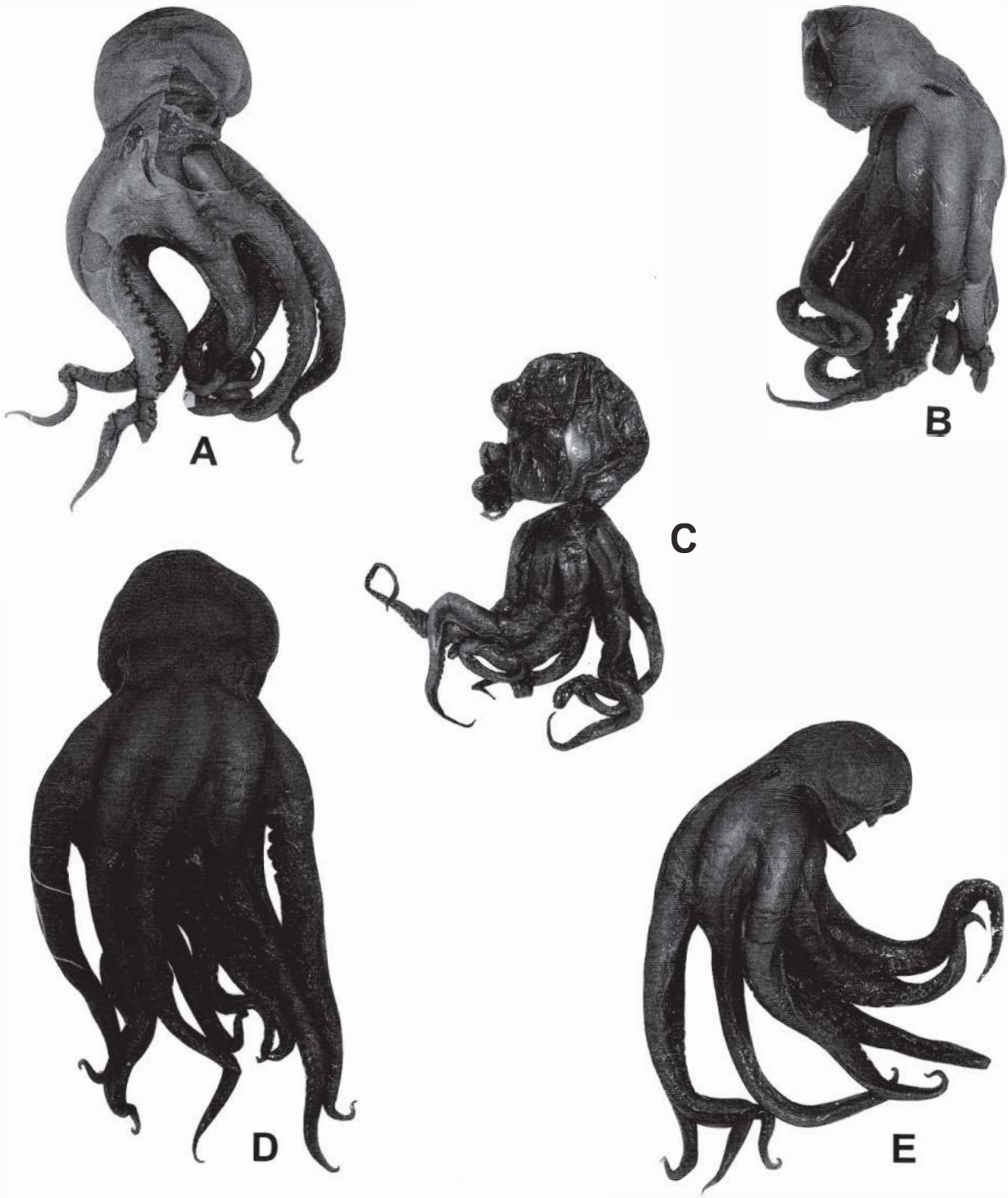


Figure 150. *Bentheledone* spp.: **A, B**, ?*Bentheledone* sp., UMML 31.2585, female, ML 80 mm. **C**, holotype, AMS C40888, *Bentheledone albida* (Berry). **D, E**, ?*Bentheledone* sp. UMML 31.2584, female, ML 69 mm.

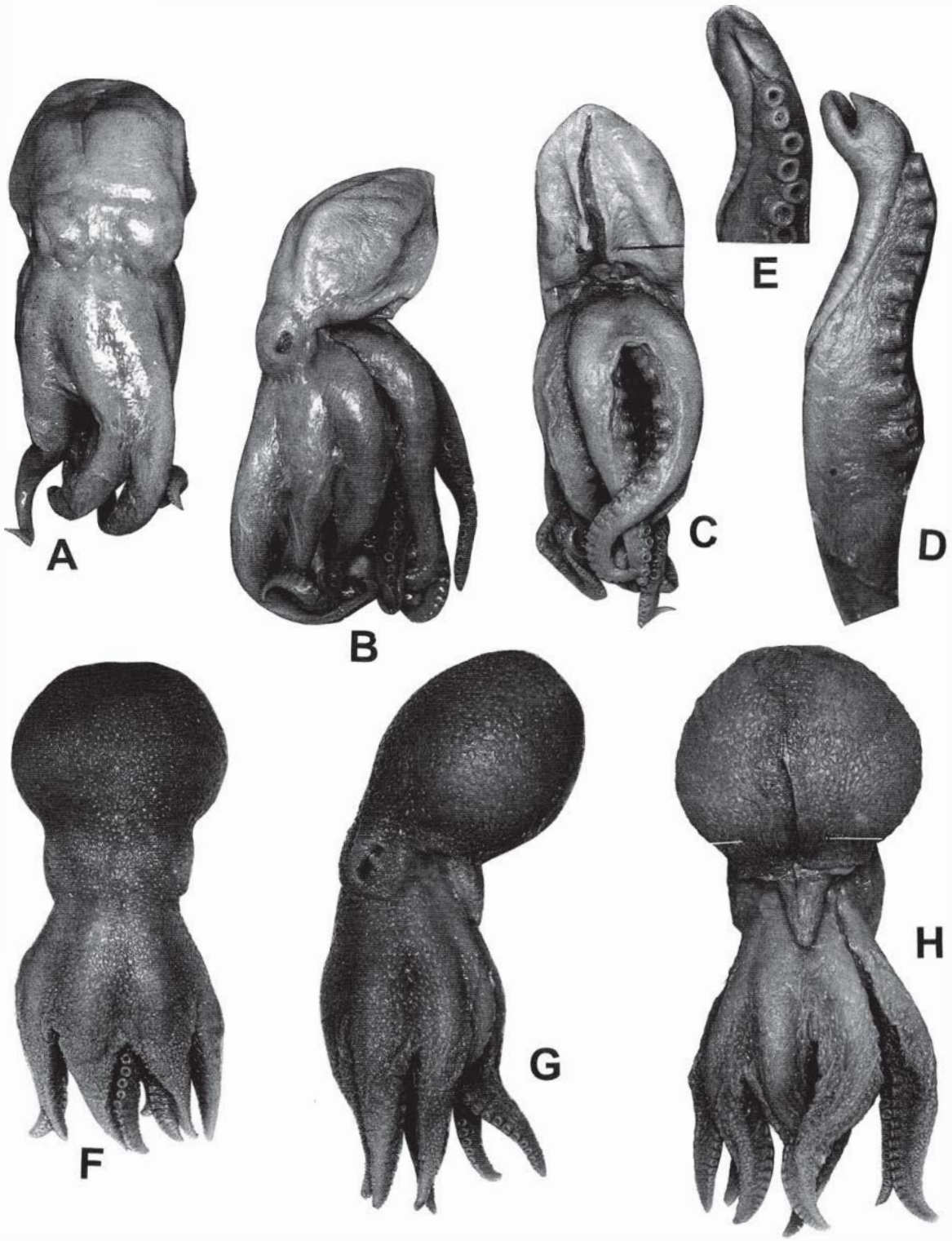


Figure 151. ***Thaumeledone (s.l.)*** spp.: **A–E**, ***Thaumeledone*** cf. ***brevis*** (Hoyle), male, ML 45 mm; UMML, no data. **F–H**, ?*Thaumeledone* sp., USNM 817370, female, ML 41 mm.

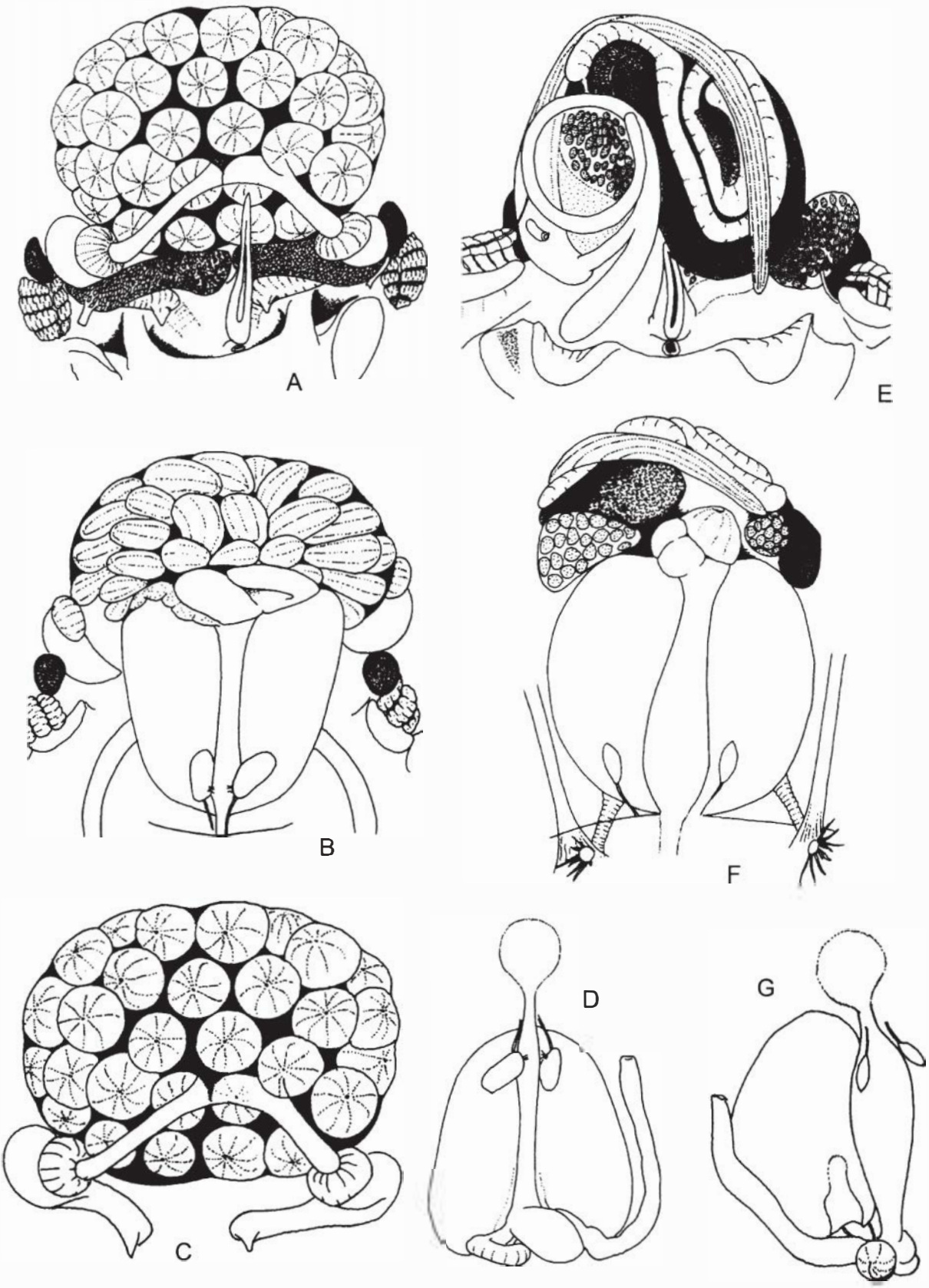


Figure 152. ***Thaumeledone (s.l.)*** spp. Anatomy: **A–D**, ***Thaumeledone*** cf. ***brevis*** (Hoyle), USNM 817370, female, ML 41 mm, USNM 817370. **E–G**, ?***Thaumeledone*** sp., UMML, data not available, male, ML 45 mm.

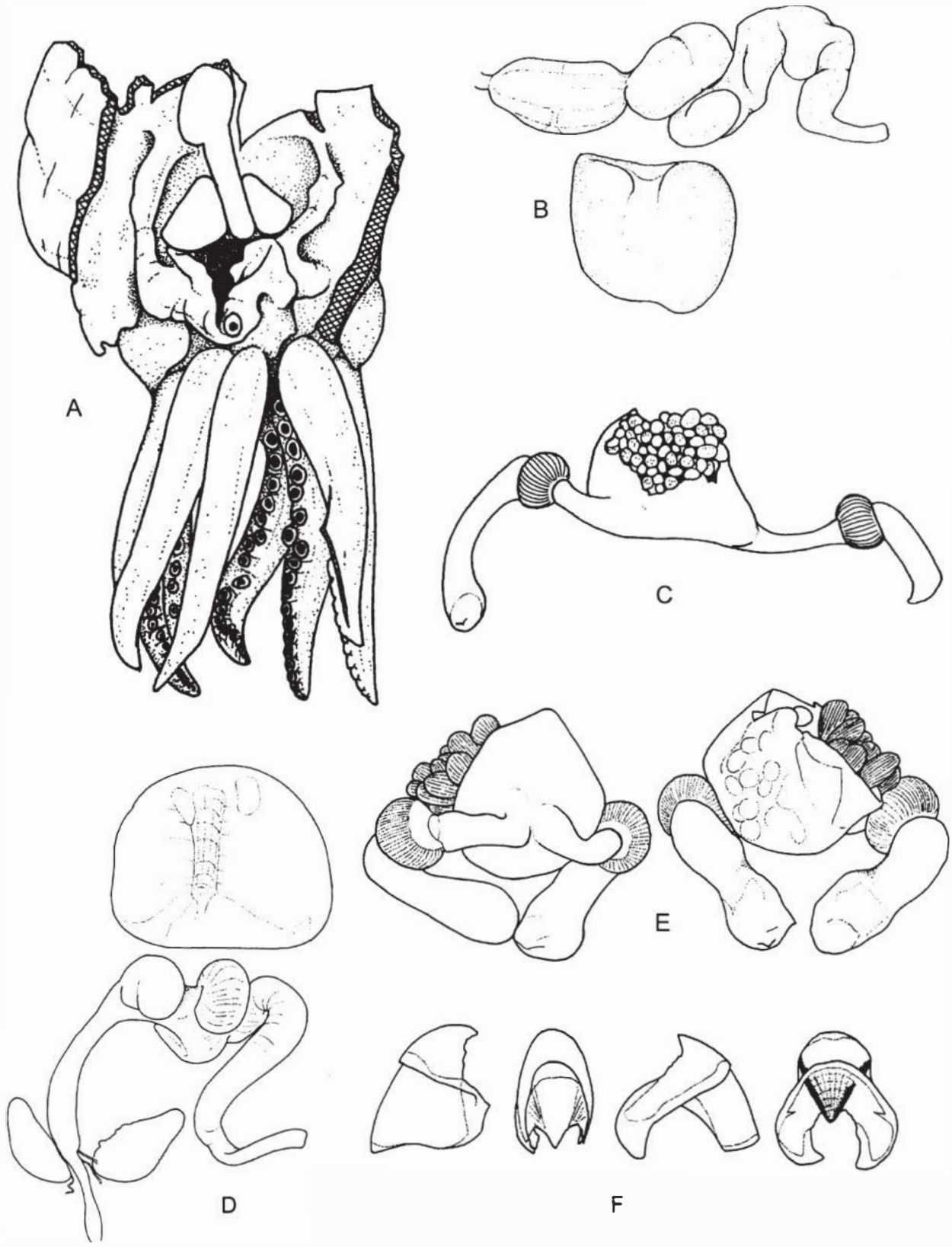


Figure 153. *Thaumeledone* spp., Anatomy: **A–C**, *Thaumeledone brevis*: **A**, syntype, female, ML 8.1 mm (note large posterior salivary glands). **B**, syntype, female, alimentary canal (buccal mass, salivary glands, and hepatic ducts removed). **C**, holotype, reproductive system. **D–F**, *Thaumeledone gunteri* holotype, female. **D**, alimentary canal (buccal mass and hepatic ducts removed). **E**, reproductive system. **F**, beaks.

73, 59, 55 mm, 22°14.58–21°57.68' S, 153°12,3301,70' E, 172–179 m, 15/02/1997, f.v. *Nelecia J.*

REMARKS: The anatomical condition and unlocalised nature of the present specimen renders it of limited scientific value. Nevertheless, this species is quite unlike any Antarctic *Pareledone* species reported by Lu and Stranks (1994), indicating it to be of non-Antarctic origin. Moreover, the specimen is in a condition comparable to that of many *Shinkai Maru Graneledone* and *Benthoctopus* specimens collected from the Campbell and Bounty Plateaus, and the Museum of New Zealand has no other Antarctic octopods in their collections. Figures provided by O'Shea (1990) are here duplicated. If this specimen is correctly assigned to *Pareledone*, it will be the only New Zealand species thus far recognised with both an ink sac and a single row of suckers, and represents an additional Antarctic biogeographic link. Those specimens assigned to the genus *Pareledone* by Kubodera (1990) are now recognised to belong to a new species and subspecies of *Graneledone, G. taniwha kubodera.*

As the presence or absence of the ink sac could not be ascertained in the single specimen available, it was compared with specimens of the geographically closest-known *Eledone* species, *E. palari* Lu & Stranks. The ?New Zealand female is quite dissimilar in body facies to *E. palari* and could not be mistaken for it in any state of preservation; *E. palari* also appears quite dissimilar to all other described species of *Eledone.*

DISCUSSION

Owing to inadequate sampling at depths greater than 1400 metres, knowledge of the octopod fauna is restricted primarily to littoral, continental shelf, slope, and seamount environments. More than 50% of the seafloor and waters surrounding New Zealand have not been sampled for octopods, and over 50% (19 species) of the fauna herein described are known from 10 or fewer specimens, 30% (11 species) from fewer than 5 specimens, and 14% (5 species) from 1 specimen only. There are probably many additional species, particularly cirrates, in our waters than are currently recognised.

CIRRATA

The problem with deep-sea cirrates is not recognition of species, but in attaching names to them. Of 29 cirrate species cited by Voss (1988b), 10 were described prior to 1900, 13 prior to 1920, and six between 1921 and 1988 (added subsequently: *Opisthoteuthis vossi* Sanchez & Guerra, 1989, *Grimpoteuthis tuftsi* Voss & Pearcy, 1990, and *G. bathynectes* Voss & Pearcy, 1990). Many authors have contributed towards a catalogue of this diversity, 16 authors describing 32 species, and only eight authors describing more than one. Since there has been no monographic treatment of these 32 species (although urgently required), and as descriptions of new taxa generally allude only to differences between previously described taxa, many of these based on fragmentary material or juvenile specimens, it is extremely difficult to identify any existing species, let alone justify the naming of new ones. Given that in many instances type specimens have deteriorated, have been lost, or had parts removed, their re-examination frequently proves to be of limited value. To overcome this problem, wherever possible, types were examined together with additional specimens likely to be conspecific. In a few cases this was not possible (e.g., abyssal species of the genus *Grimpoteuthis*), so original descriptions had to be relied upon for comparative purposes.

The five-family classification of the Cirrata proposed here is based on a similar suite of characters to that utilised by Voss (1988a). However, the present classification differs from Voss's in further defining : optic-lobe structure; white-body size, shape and position; and shell shape; and includes additional character states associated with the alimentary canal, specifically the relative length of the intestine to the oesophagus, presence or absence of radular and palatine teeth, and the nature of the digestive gland. Increased morphological resolution from the addition of new and redefined characters and character states has enabled recognition of two new families and two new genera of cirrates, and further identified *Cirroctopus* as manifestly so distinct from *Grimpoteuthis* that its removal from synonymy is deemed necessary. Moreover, it was apparent that by reclassifying several species previously assigned to *Grimpoteuthis* to either the new genus *Enigmatiteuthis, Cirrothauma*, or the reinstated *Cirroctopus*, each of these genera became markedly distinct from each other. In rediagnosing each of these genera it was also apparent that *Cirroctopus* is far more similar to *Opisthoteuthis* anatomically than to *Grimpoteuthis*, for which or which *Cirroctopus* and *Opisthoteuthis* are reclassified in a rediagnosed Opisthoteuthididae. *Grim-*

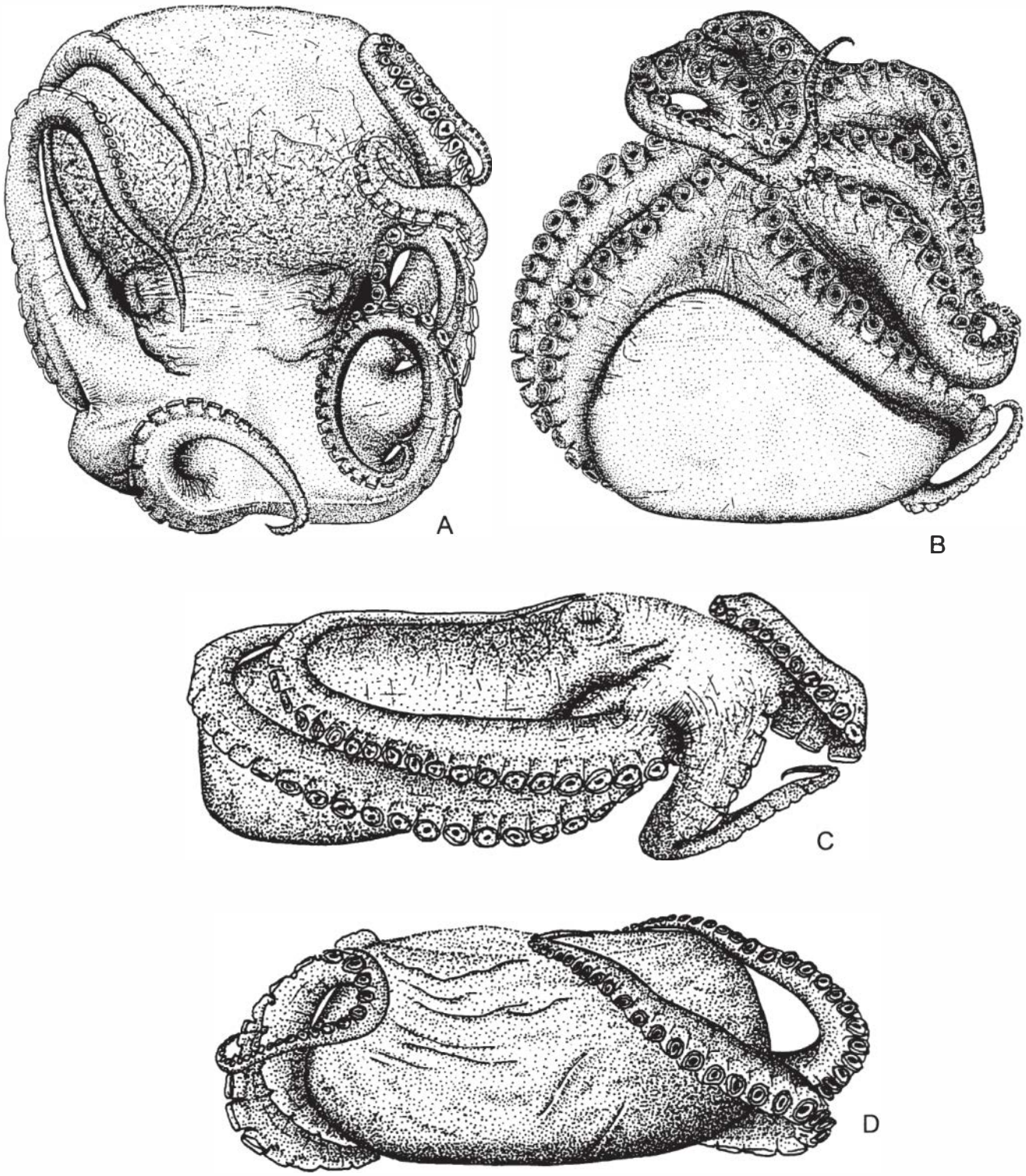


Figure 154. ***?Pareledone*** sp.: **A–D**, NMNZ, female, ML 90 mm, unlocalised.

Figure 155.
Legend, sucker morphology in family Octopodidae.

A *Pinnoctopus cordiformis*, NMNZ M.5640.

B *Pinnoctopus kermadecensis*, NMNZ M.256374.

C *Pinnoctopus* sp. indet., NMNZ M.

D *Octopus* (*s.s.*) *gibbsi* sp. nov., NZOI Stn Z8917.

E *Octopus* (*s.l.*) cf. *rugosus*, NZOI Stn Z8468.

F *Octopus* (*s.s.*) *oliveri*, NMNZ M.256372.

G *Octopus* (*s.l.*) *huttoni*, NMNZ M.117687.

H *Octopus* (*s.l.*) *kaharoa* sp. nov., NZOI Stn Z8567, paratype P-1115.

I *Octopus* (*s.l.*) *campbelli*, enlarged sucker, NMNZ M.8961.

J *Octopus* (*s.l.*) *campbelli*, normal sucker, NMNZ M.8961.

K *Enteroctopus zealandicus*, NMNZ M.11015.

L *Enteroctopus* sp. indet., NIWA, unregistered.

M *Octopus* sp. indet., NMNZ M.90363.

N *Octopus* sp. indet., NMNZ M.90289.

O *Octopus* (*s.l.*) *mernoo* sp. nov., holotype.

P *Benthoctopus berryi*, holotype.

Q *Benthoctopus levis*, holotype.

R *Benthoctopus magellanicus*, holotype.

S *Benthoctopus tegginmathae* sp. nov.

T *Benthoctopus tangaroa* sp. nov., NMNZ M.109082.

U *Benthoctopus clyderoperi* sp. nov., holotype.

V *Graneledone challengeri*, NMNZ M.110531.

W *Graneledone challengeri*, NMNZ M.117198.

X *Graneledone challengeri*, NMNZ M.118324.

Y *Graneledone taniwha taniwha* ssp. nov., NZOI Stn Z8399.

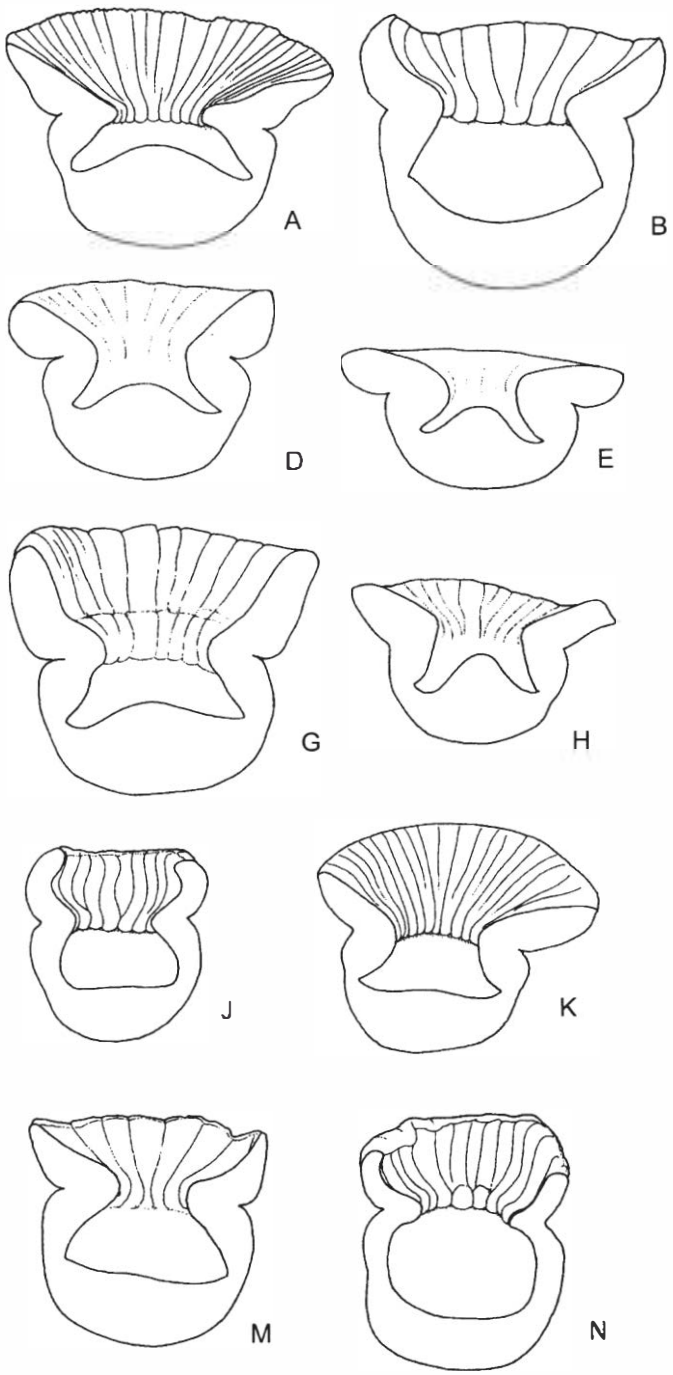
Z *Graneledone taniwha kubodera* ssp. nov., NMNZ M.109068.

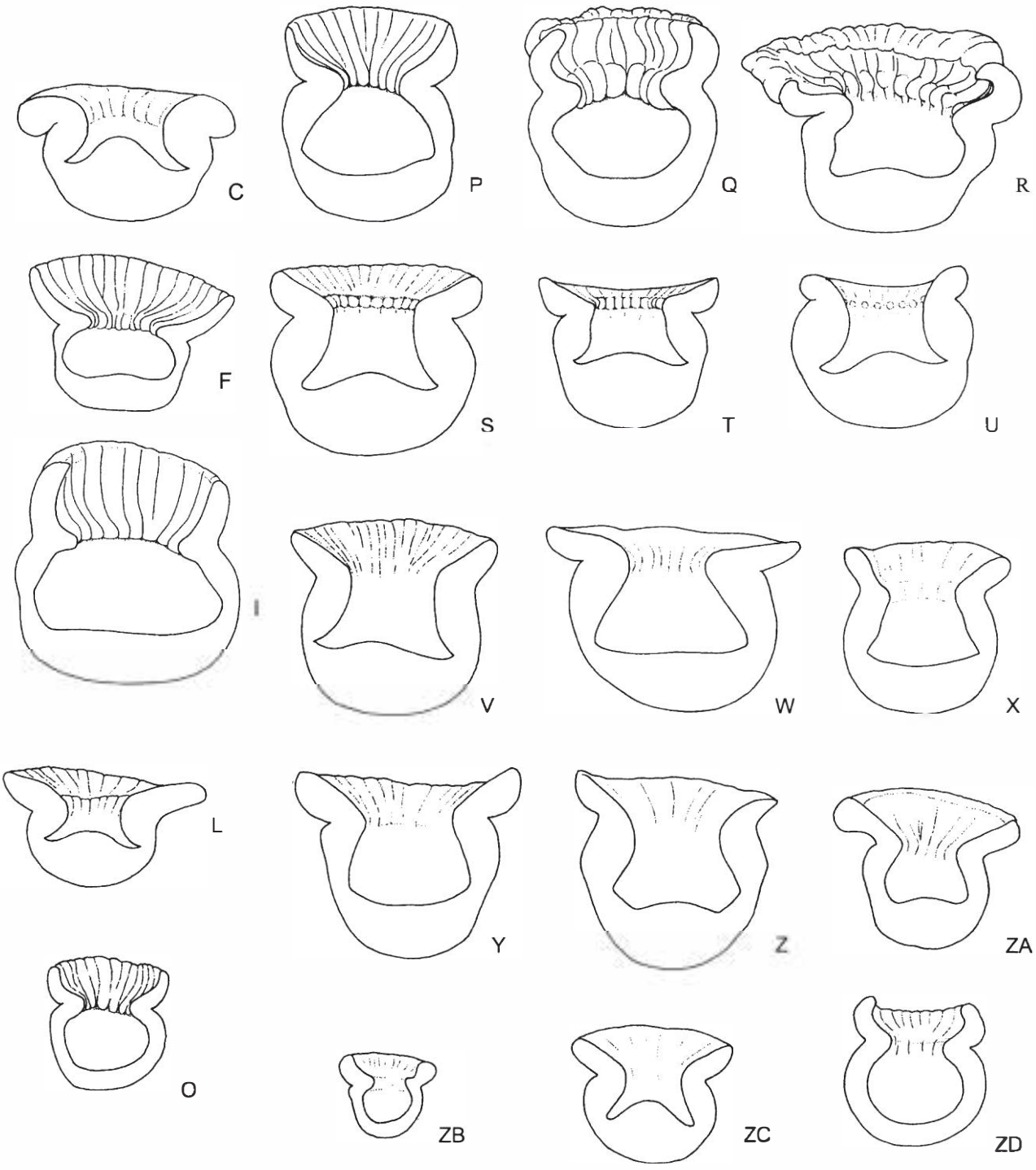
ZA *Thaumeledone gunteri*, holotype.

ZB *Thaumeledone brevis*, syntype.

ZC *Thaumeledone zeiss* sp. nov., NMNZ M.117828.

ZD *Thaumeledone marshalli* sp. nov., paratype NZOI P-1091.





poteuthis is transferred from the Opisthoteuthididae to the Grimpoteuthididae fam. nov., together with *Enigmatiteuthis* gen. nov. The Luteuthididae, based solely on *Luteuthis dentatus*, accommodates a species with a unique combination of anatomical characters and character states. Insufficient comparative material was available to evaluate genera assigned to the Cirroteuthididae, a family uncritically retained for *Cirroteuthis* and *Cirrothauma*, by Voss (1988a).

Opisthoteuthis and *Cirroctopus* have similar optic lobe and nerve configurations, shell structure, alimentary canal, and female reproductive systems. In these characters they resemble *Grimpoteuthis* (*s.s.*) and *Enigmatiteuthis* species. *Luteuthis* presents a problem in that it shares some characters not only with Grimpoteuthididae and Cirroteuthididae (particularly optic lobe and nerve configurations and the length of the intestine relative to the oesophagus), but also with the Opisthoteuthididae, particularly *Opisthoteuthis* (Groups 1 & 2) (bilobate digestive gland). Unlike any other group, however, *Luteuthis* has a unique shell and sucker morphology and both radular and palatine teeth. *Cirroteuthis* and *Cirrothauma* species are quite dissimilar (if *Cirroteuthis* cf. *magna* in fact belongs to *Cirrothauma*), and a closer relationship is possible between *Luteuthis* and *Cirrothauma* than between *Cirrothauma* and *Cirroteuthis*. Crop detail and relative oesophagus and intestine length are similar in *Cirroteuthis*, *Cirrothauma*, *Grimpoteuthis*, and *Luteuthis*, and it is only the comparable size of the spiral caecum and stomach and presence of anterior salivary glands (or their positional homologue) that presently unite *Cirroteuthis* and *Cirrothauma* in the one family. The systematic status of both *Stauroteuthis* and *Chunioteuthis* requires re-evaluation.

Ascertaining relationships between cirrate families is more difficult, although on the basis of shared similarities the Opisthoteuthididae and Grimpoteuthididae would appear to be more closely related, while the Luteuthididae and Cirroteuthididae appear to be closely related to each other but distantly related to the *Opisthoteuthis* and *Grimpoteuthis* groups. The systematic position of the Stauroteuthididae is problematic, although it appears closer to *Opisthoteuthis* and/or *Grimpoteuthis* than to either *Luteuthis*, *Cirroteuthis* or *Cirrothauma*.

Several species cannot presently be accommodated in the current classification. A new genus may be required to accommodate *Opisthoteuthis medusoides* (in the Opisthoteuthididae), a species certainly more closely related to *Opisthoteuthis* than to *Grimpoteuthis*. The systematic status of *Chunioteuthis gilchristi* (Robson, 1924a: 204–205, as *Cirrhoteuthis gilchristi*) will continue to cause problems until additional specimens are identified and redescribed; no specimen remotely similar to the type specimen or description was identified amongst extensive cirrate collections in the South African Museum (pers. obs.). Four character states described for this species preclude generic placement in the scheme advocated here: cirri commence at the first sucker and are of exceptional length; the digestive gland is entire; and the intestine is of the same length as the oesophagus. On the basis of this combination of character states, *C. gilchristi* should be treated as *incertae sedis*, though likely to belong in Grimpoteuthididae. Neither *Cirroteuthopsis massayae* Robson nor *Frokenia clara* Hoyle, 1904 are sufficiently well described to enable any family placement.

Presently, with the exception of *Cirroctopus*, no cirrate genus shows a clear pattern of biogeographic distribution. All well-established genera appear to be nearly cosmopolitan in distribution (although few extend into polar waters). *Cirroctopus* has a mostly circum-Antarctic distribution, broken by the single species in New Zealand waters. (*Pareledone*, another genus with a circum-Antarctic distribution, may be represented in New Zealand waters by a single species, the record of which rests on a single unlocalised specimen. *Thaumeledone*, previously considered restricted to Antarctic waters (Voss 1988b), is also represented in New Zealand waters by two species. It is possible that the incidence of *Cirroctopus*, ?*Pareledone*, and *Thaumeledone* in New Zealand waters identifies a biogeographic link with Antarctica, although it is also possible, given the general rarity of deep-sea taxa in collections, that all three genera have much wider distributions than presently recognised.)

INCIRRATA

With the exception of the Octopodidae, the classification employed by Robson (1932) is followed uncritically for other incirrate families. Altogether six non-octopodid incirrate families are represented in New Zealand waters, the Bolitaenidae, Amphitretidae, Argonautidae, Ocythoidae, Tremoctopodidae, and Vitreledonellidae. Additional material of species in pelagic families mentioned herein is either juvenile or adds only to already known local distributions of the well-known species: *Japetella diaphana*, *Eledonella pygmaea*, *Argonauta argo*, *A. nodosa*, and *Vitreledonella richardi*. The systematic status of New Zealand *Tremoctopus* specimens is changed from *T. violaceus gracilis* to *T. robsonianus*. Two further species are for the first time recorded from New Zealand waters — *Amphitretus thielei*, for which the distri-

bution is extended to include local waters as well as the type locality (off South Africa), although probably it is circumglobal south of the Subtropical Convergence; and the very poorly known *Bolitaena microtyla*.

In contrast to benthic octopods, pelagic or bathypelagic species appear to have widespread to near-cosmopolitan distributions. Nine species, *Japetella diaphana*, *Bolitaena microtyla*, *Eledonella pygmaea*, *Amphitretus pelagicus*, *Argonauta argo*, *A. nodosa*, *Ocythoe tuberculata*, *Tremoctopus robsonianus*, and *Vitreledonella richardi*, appear north of the Subtropical Convergence, whilst only one pelagic or bathypelagic species (*Amphitretus thielei*) is known from the water column south of this convergence. *Tremoctopus robsonianus* is rather unusual in that it is the only pelagic currently recognised as endemic.

The greatest contribution made in this report is in increasing the recognised diversity of New Zealand octopuses of the family Octopodidae. Whereas 6 species were recorded by Dell (1952), 18 species and 1 subspecies are now recognised (including the fauna of the Kermadec Islands) from collections far more representative of continental shelf and slope environments, and seamounts off the New Zealand mainland. Nevertheless, many of these new bathyal and abyssal taxa are known from few specimens, and many additional taxa are expected with increased collection effort, particularly at depths exceding 1400 m. Several additional species in the genera *Pinnoctopus* (Fig. 155C), *Enteroctopus* (Fig. 155L), and *Octopus* (*s.l.*) (Figs 155 M, N) probably exist in our waters, although none is described here given that apparent differences could be attributed to preservation history.

New records are made for species in the genera *Octopus* (*s.s.*), *Benthoctopus*, *Graneledone*, and *Thaumeledone*. The distribution of *Enteroctopus* is expanded to include one previously described New Zealand species, *Pinnoctopus* is formally rediagnosed for another, and three groups of *Octopus* (*s.l.*) are proposed based on distinctive morphology. The systematic status of littoral species assigned to any group of *Octopus* (*s.l.*) presently cannot be resolved given a general poor understanding of *Octopus* comparative anatomy and diversity worldwide. It is anticipated that some of these *Octopus* groups may prove to represent valid genera.

Whereas several littoral species have wide distributions, from either South Australia or Japan, most deep-water genera appear to have restricted bathymetric and geographic distributions, although certainly for a number of the deeper-water genera the full bathymetric and geographic ranges of species are far from known.

Of genera and species now known from New Zealand, those referable to *Octopus* (*s.s.*) and *Octopus* (*s.l.*) Group 2 indicate a tropical to subtropical biogeographic link between the northeast coast of North Island, Kermadec Islands, and the central and warm-temperate Pacific. *Octopus oliveri*, *O. gibbsi*, and *O.* sp. cf. *rugosus* are all restricted to comparatively warm Northland waters; *O. oliveri* is recorded also off the coast of Japan (Sasaki 1929). However, the littoral fauna of the Kermadec Islands is distinct from that of mainland New Zealand.

Of species assigned to *Pinnoctopus*, *P. cordiformis* has a distribution that includes both the New Zealand mainland and South Australia (as *O. flindersi*), while *P. kermadecensis* is presently known only from the Kermadec Islands. *Pinnoctopus cordiformis*, unlike *O. huttoni*, is not recorded from the Auckland, Campbell, and Bounty Islands. *Octopus huttoni*, the New Zealand representative of *Octopus* (*s.l.*) Group 2, has a distribution similar to *P. cordiformis*, occurring also in South Australia (as *O. warringa*), but is recorded not only from mainland New Zealand, but also the southern Auckland and Bounty Islands (but not the southernmost Campbell Island). The Subtropical Convergence appears to determine the distribution of *P. cordiformis*, a species with small eggs and anticipated planktotrophic long-lived larvae, but somewhat anomalously not that of *O. huttoni*, a species similarly with small eggs, planktotrophic young and anticipated long larval life.

The two species assigned to *Octopus* (*s.l.*) Group 3, *O. campbelli* and *O. "fontanianus"* appear to be of cold-water origin, identifying a biogeographic link between southern New Zealand and South America. Whereas *O. campbelli* is recorded intertidally from the Auckland, Campbell, and Bounty Islands, it is known only from bathyal depths off the New Zealand mainland, with a recognised distribution ending south of Chatham Rise. Those species assigned to *Octopus* (*s.l.*) Group 4, *O. mernoo* and *O. kaharoa*, are large-egged species; *O. kaharoa* is very similar to *O. australis* (as redefined by Stranks & Norman 1992), which may indicate a further biogeographic link with Australia. Whereas *Pinnoctopus cordiformis* and *O. huttoni* are common to both New Zealand and Australia, this may indicate recent or continuing larval dispersal rather than historic faunal relationships; the Chatham Rise and/or Subtropical Convergence also play an important role in limiting the distribution of these two species.

The genus *Enteroctopus* has an unusual cold-water bipolar distribution. There is tremendous potential for dispersal of species in this genus, with larvae travelling enormous distances as long-lived planktotrophic young (Kubodera 1991); the type species of this genus, *E. megalocyathus*, has large eggs and

benthic hatchlings (Re 1984). Like *O. campbelli*, *E. zealandicus* is encountered intertidally at the Auckland, Campbell, and Bounty Islands, although adult specimens are known only from the lower continental shelf and slope off mainland New Zealand. The distribution of this species appears to end on the northern Chatham Rise.

The distribution of seven New Zealand deep-sea octopodids appears to be largely influenced by the Chatham Rise (*Graneledone challengeri*, *G. taniwha taniwha*, *Benthoctopus tegginmathae*, *B. tangaroa*, *B. clyderoperi*, *Thaumeledone zeiss*, and *T. marshalli*). For only one, a subspecies of *Graneledone*, is the distribution evidently limited by some other factor, viz. *Graneledone taniwha kubodera*, a subspecies restricted to the Bounty Plateau.

Excluding near-cosmopolitan pelagic or bathypelagic species, biogeographic relationships are evident between New Zealand, South Australia, and South America, with present-day larval dispersal probably accounting for other species known from northern New Zealand (the Kermadec Islands) and Japan, and New Zealand and South Australia. The most significant local feature affecting the present-day distribution of east coast littoral species is the Subtropical Convergence, while for east coast continental shelf and slope species it is the Chatham Rise. The fauna from the west coast of New Zealand is poorly known.

The discussion now focuses on evaluating systematic relationships between deep-sea octopodid genera based on findings reported herein, with particular emphasis on subject matter that affects our present understanding of the subfamilial classification of the Octopodidae. Much has already been discussed in individual remarks sections in the systematic section of this work. This is a synopsis of these individual statements.

Two significantly different systematic treatments of relationship between genera in the Octopodidae are available, those of Robson (1929b, 1932), and Voss (1988a, b). In the classification provided by Robson (1932) the genera are accommodated in one of two subfamilies, the Octopodinae and Bathypolypodinae. Little regard was paid to the presence or absence of an ink sac, or number of sucker rows. His concept of Octopodinae included *Octopus*, *Benthoctopus*, *Eledone*, *Pareledone*, and *Velodona*, and the Bathypolypodinae, *Bathypolypus*, *Graneledone*, *Bentheledone*, and *Thaumeledone*.

Voss, alternatively, recognised four subfamilies: Octopodinae, Bathypolypodinae, Eledoninae, and Graneledoninae. In contrast to Robson's classification, Voss emphasised the presence or absence of an ink sac and number of sucker rows: thus the subfamilies were defined as follows: the Octopodinae, with 2 sucker rows and an ink sac; Bathypolypodinae, with 2 sucker rows and no ink sac; Eledoninae, with 1 sucker row and an ink sac; and Graneledoninae, with 1 sucker row and no ink sac.

Variability in ink sac size is apparent amongst octopodid genera, with this structure 'normally' developed in *Octopus*, small in *Megaleledone* (Taki 1961), "exceedingly small" in *Hapalochlaena* (Robson 1929b: 208), and degenerate in *Velodona* (Robson 1932: 283). The ink sac is variable in position, e.g., in *Pteroctopus* it lies superficially on the surface of the digestive gland in *Hapalochlaena* it is only partially buried in the digestive gland surface; whilst in *Cistopus* and *Vosseledone*, it is deeply embedded in the digestive gland (Robson 1929; Palacio 1978). Ink sac relative size and position are thus variable character states. Presence or absence of an ink sac has possibly been attributed a significance beyond its real systematic value.

Although the ink sac supposedly is absent in the genus *Graneledone*, it is now known to occur in some species lying superficially on the surface of the digestive gland, albeit appearing non-functional. It is most well developed in an undescribed South African species, in which it differs in no appreciable way from that of *Velodona togata* Chun (pers. obs.). In the New Zealand *Graneledone* species a structural and positional homologue of this sac is apparent, although it is so reduced as to resemble a blood vessel. In Voss's classification *Velodona* was in the subfamily Eledoninae (or Pareledoninae Voss, 1988b), and *Graneledone* in the Graneledoninae Voss, 19880 (Robson (1932) included *Graneledone* in the Bathypolypodinae, and *Velodona* in the Octopodinae). Neither classification recognised the apparent relationship between species in these two genera. In light of this, it appears that the Pareledoninae of Voss (1988b) differs in superficial characters only from the earlier proposed Graneledoninae (Voss 1988a).

A close relationship is also apparent between *Enteroctopus* and *Benthoctopus*, or at least between *Enteroctopus* and many species attributed to the genus *Benthoctopus*. Large eggs, orientation of the female genital apertures on the face of the viscera, swollen distal oviducts, a weakly developed anterior diverticulum of the crop, radular dentition, and the lack of membranous or connective tissue membranes between renal tissue and the ventral inner surface of the mantle cavity musculature, are characters or character states common to *Enteroctopus megalocyathus* (with the exception of egg size), *E. zealandicus* (Benham, 1944), and many *Benthoctopus* species. These two genera differ, however, in male characters of penis diverticulum and ligula shape. Nevertheless,

more shared character states appear to exist between these two genera than exist between both and *Octopus* (*s.s.*) or *Bathypolypus* (*s.s.*) (of type *B. arcticus*). Despite this, species attributed to *Benthoctopus* (given the absence of an ink sac) are placed in the Bathypolypodinae, while those in *Enteroctopus* presently are accommodated in the Octopodinae. As observed in some species of *Graneledone*, a non-functional vestigial ink sac has also been observed in one female *Benthoctopus* species — *B. robustus* Voss & Pearcy, 1990 (SBMNH 42224, Figs 116D, E, pers. obs.). It may be that *B. robustus* was incorrectly assigned to *Benthoctopus*; it may represent an extraordinary deep-water species of *Octopus* (*s.l.*). However, in general body facies and total arm sucker count, it is very similar to the type species of *Benthoctopus*, *B. piscatorum* (Tables 96, 99).

Description of additional *Benthoctopus piscatorum* material is required to evaluate the systematic status of this species, specifically whether or not it is referable to *Bathypolypus* as alluded to by Voss (1988a). The condition of the type specimen (Fig. 115A, B) is now too poor to determine this relationship, particularly given the abrasion of all dermal sculpture. Only when this species has been redescribed can the status of the genera *Bathypolypus* and *Benthoctopus* be evaluated to determine whether sufficient differences exist to warrant retention of these two generic names. The most recent diagnoses of *Benthoctopus* and *Bathypolypus* (Voss 1988a) differentiate them on the basis of skin sculpture, presence or absence of a diverticulum of the crop, and lateral cusps on the rachidian tooth of the radula. *Benthoctopus* included smooth-bodied species with a crop diverticulum and lateral cusps on the rachidian tooth of the radula, *Bathypolypus* included papillose species without a crop diverticulum or lateral cusps on the rachidian tooth. However, two New Zealand *Benthoctopus* species are described with and without a diverticulum of the crop, and with and without lateral cusps on the rachidian tooth of the radula, while *B. januarii* (Hoyle, 1885) was also re-described lacking a crop diverticulum, but with lateral cusps on the rachidian tooth (Toll 1981). According to Voss's most recent diagnoses of these genera, the distinction between them now rests on mantle papillation, although several *Benthoctopus* species are known to manifest this (*B. magellanicus* Robson, *B. karubar* Norman, Hochberg & Lu, 1997). Although the diagnoses of these two genera are clearly inadequate to accommodate all species, synonymy is premature given that *Bathypolypus arcticus* is manifestly different from the greatest majority of species presently attributed to *Benthoctopus* — so much so that additional genera undoubtedly would be required to accommodate them. Rather than the simple act of synonymy, what is required is detailed examination of many species in each genus, including the type species, and detailed anatomical and biogeographic analysis to evaluate and redefine genera.

The presence of an ink sac in species of *Graneledone* and *Benthoctopus*, and variation in size and position in many genera, suggest that presence or absence of an ink sac is of little value for differentiating suprageneric categories among octopodids. However, synonymy of Bathypolypodinae with Octopodinae, or Graneledoninae with Eledoninae, are not preferred courses of action since this would mean that genera would have to be differentiated on the basis of the number of sucker rows, which is equally uncertain (Voight 1993b).

Given the uncertain status of *Bathypolypus* and *Benthoctopus*, and the assignment of *Benthoctopus piscatorum* to *Bathypolypus*, the confusion in both nomenclatural and systematic status of many species attributed to *Benthoctopus*, and uncertainty as to whether *Bathypolypus* is more closely related to genera now accommodated in the Graneledoninae (*fide* Robson 1932), or Octopodinae (*fide* Voss 1988a), this discussion is limited to what it can meaningfully hope to resolve.

My personal preference is to favour Robson's systematic interpretation, where a closer relationship is drawn between *Bathypolypus* and genera such as *Graneledone*, *Thaumeledone*, and *Bentheledone* (to which would also be added genera such as *Pareledone*, *Tetracheledone*, and *Velodona*), than between *Bathypolypus* and *Benthoctopus*. Such a course of action would, however, significantly affect the classification, including prioritising the Bathypolypodinae over Graneledoninae and Pareledoninae.

With regard to the systematic status of *Benthoctopus* and *Bathypolypus*, Robson (1932: 249) commented "it must be borne in mind that the distinctions between these genera are difficult to draw". Despite this, he placed them in different subfamilies. Furthermore, Robson (1932: 51) stated "among the forms placed in the genus *Benthoctopus* are some so closely resembling ordinary forms of *Octopus*, that, were it not for the lack of the ink sac, one would place them in that genus. Moreover, some species of this genus tend to resemble shallow-water forms of *Octopus* that live in the same locality. Thus *B. magellanicus* and *B. eureka* are very like the local species of *Enteroctopus*. ... It looks as though some at least of these forms were independently derived from known littoral forms". This relationship appears to hold true for New Zealand species, where those assigned to *Benthoctopus* appear phylogenetically closer to *Enteroctopus* and *Octopus* (*s.l.*) Group 4 than they do

to, say, *Octopus* (*s.s.*) or *Pinnoctopus*. *Enteroctopus*, *Octopus* (*s.l.*) Group 4, and *Benthoctopus* species may then best be accommodated in a subfamily distinct from the Octopodinae and Bathypolypodinae. The systematic position of *Eledone* and the Eledoninae, however, remains to be resolved.

An independent molecular-systematic study is required to appraise relationships amongst the various deep-sea forms in the Octopodidae. Although I do not entirely agree with the definitions and resulting division of the family Octopodidae into the four subfamilies proposed by Voss (1988a), in the absence of independent corroboration his (1988a) classification is employed (with minor modification by including a single specimen of ?*Pareledone* in the Graneledoninae) in preference to that of Voss (1988b) or those classifications of Robson (1929, 1932), or the alternative, abandonment of the subfamilies entirely.

It may be argued that a cladistic analysis of those characters herein deemed important in the classification would contribute towards better understanding of proposed relationships. This, I feel, is premature as this study is largely a regional revision, with not all genera, particularly type species of genera, having been available for examination to enable any comprehensive revision.

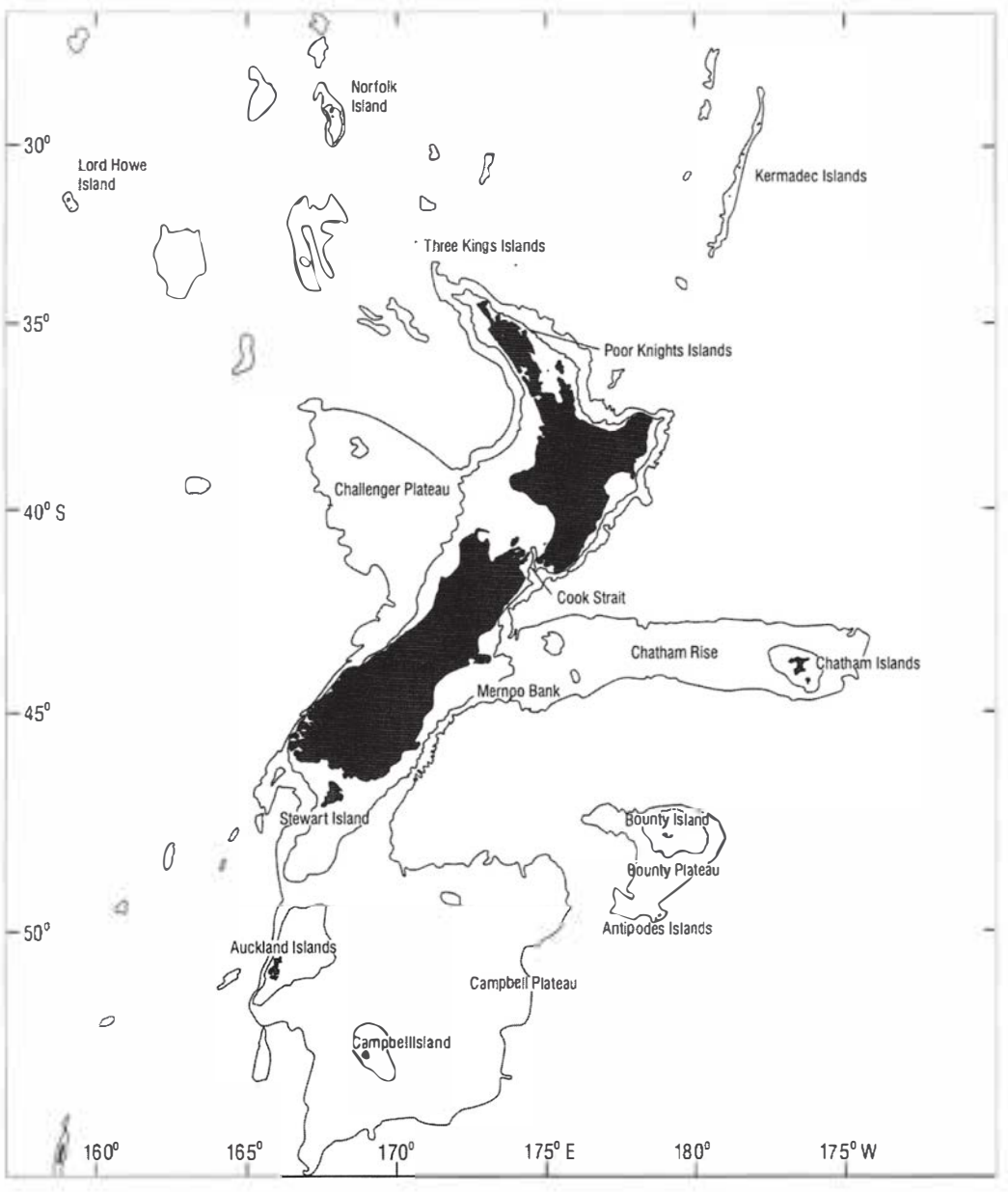


Figure 156. The New Zealand region showing named features as described and included in recognised distribution maps.

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TAXONOMIC INDEX

This index has been collated from the introduction, systematics, and remarks sections. Major illustration references are indicated in **bold** type.