

**COMPARATIVE STUDY
OF THE MORPHOLOGY AND ANATOMY
OF OCTOPUSES OF THE FAMILY OCTOPODIDAE**

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ATTESTATION OF AUTHORSHIP

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning,

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ABSTRACT

The objective of this research was to evaluate those morphological and anatomical characters and their states that have been conventionally described in systematic studies of octopuses, focussing on those of the family Octopodidae. Additional characters that may assist in determining both phylogenetic relationships between taxa, and differentiation of taxa in this family, were also examined.

To undertake this research, representatives of a variety of octopus genera were examined, primarily incirrate Antarctic eledonids (characterised by having a single row of suckers along each arm), such as species of *Adelieledone*, *Bentheledone*, *Graneledone*, *Megaleledone*, *Pareledone* and *Thaumeledone*, augmented with species with two rows of suckers, an Antarctic species of *Muusoctopus*, and non-Antarctic species of *Enteroctopus*, *Octopus* and *Pinnoctopus*; one cirrate, *Cirroctopus*, was also examined. The taxonomic and systematic status of a number of these genera, and even those species assigned to them, has not been completely resolved, or they have been the subject of recent debate.

For each species, conventional characters such as the alimentary canal, female and male reproductive systems, and upper and lower beaks, are described and figured, augmented with less conventional descriptions of the ink sac, such as the extent to which it is embedded within the digestive gland, its relative size, and, when possible, the major branches of the arterial system leading from the heart to the reproductive, renal and alimentary systems, and ink sac.

To assess the usefulness of morphological characters frequently used in octopodid classifications, multivariate statistical analyses were performed on data sets of measurements of external and internal anatomy. Four data sets were analysed separately, then collectively using Principal Component Analysis (PCA) and Multidimensional Scaling (MDS): 1) external characteristics, including those cited as basic to octopus descriptions (Roper & Voss 1983); 2) internal characters of the alimentary canal and mantle cavity configuration; and 3) lower, and 4) upper beak morphologies. As indicated by PCA and MDS, the use of external characteristics only groups taxa into intuitively unnatural groups of grounds on statistical similarity between measures, states and categorical characters. In contrast, PCA and MDS results for internal and external characters group taxa in an intuitively more natural manner. Descriptions of octopus taxa as a consequence

should describe both. Beak morphology is of more limited value for discriminating closely-related species; however, in some cases it does add information of taxonomic importance, so descriptions of these structures are recommended. A subset of those characters that best differentiate genera and species are identified. At the generic level these comprise arm sucker counts (ASC), arm length index (ALI) and head width and length indices (HWI, HdLI) for externals; oesophagus length index (OesTLI), anterior and posterior salivary gland length indices (ASGLI, PSGLI), intestine length index (IntLI) and anterior oesophagus index (AoesLI) for internals; beak length and crest height indices (BLI, CHI) for lower beak, and rostrum width and wing length indices (RWI, WLI) for upper beak. At the specific level these comprise free funnel and funnel length indices (FFI, FLI) for externals; anterior oesophagus length index (AoesLI), posterior salivary gland length index (PSGLI) and gill count (GilC) for internals; crest height index (CHI) for lower beak, rostrum beak length index (BLI), rostrum edge and width indices (REI, RWI) for both beaks, and Wing length index (WiLI) for the upper beak.

Phylogenetic relationships between the various taxa analysed herein are not assessed because the statistical techniques employed, PCA and MDS, are not appropriate tools to use for phylogenetic reconstruction. More studies about which characters are useful for phylogeny need to be undertaken to improve classification. Characters that have been used extensively to differentiate subfamilies of octopodids (ink sac and number of sucker rows) are of limited phylogenetic value, and as such their use to define subfamilies should be avoided, treated with extreme caution, or the concept of the subfamily should be avoided altogether until relationships are independently corroborated by independent molecular data.

INTRODUCTION **1**

Relationships between many octopus taxa are unclear, in part because those taxonomic characters that have been commonly employed for differentiating species, genera and families have been used without prior critical assessment; because authors have tended to work in isolation from each other over the course of several centuries; taxonomic and nomenclatural procedures were not always followed consistently between authors; the classification of these animals is based largely on rather-plastic soft-part morphology; taxa have been often described on the basis of a single or very few individuals or juveniles; descriptions generally have been biased toward males of species only (with the female anatomy often perceived to be too conservative to enable accurate identification); specimens have been damaged or poorly preserved; and parts of type specimens post-dissection have not always been retained with parent bodies, type specimens have not always been designated, have been unlocalised, or the condition of type materials is so poor, or that are no longer extant that their examination proves futile or impossible.

Since octopus descriptions have not been historically standardised, and single counts and indices can be of limited value for differentiating some taxa (Allcock *et al.* 2008), the use of molecular techniques provides an alternative and independent means to determine relationships between taxa. However, molecular phylogenies are not constructed without error. Relationships determined between taxa from them depend entirely on the accuracy of initial identifications of taxa, which are not always correct (given aforementioned difficulties with their identification), and it is absolutely critical that systematists continue to be trained to describe taxa on morphological grounds as well, particularly for poorly known groups (Wiens 2004). Therefore, it is necessary to critically evaluate the appropriateness of morphological and anatomical characters (and their states) that have been conventionally used in descriptions and systematic studies of octopuses in order to establish their utility for differentiating taxa at levels of species, genus, subfamily and family ranking, all of which have proven contentious in the systematics of the Octopoda in recent years. This thesis contributes to our understanding of the most appropriate characters (and their states) to employ in identifying and differentiating taxa at these levels.

1.1 CLASSIFICATION

ORDER OCTOPODA

The Order Octopoda contains taxa characterised by: a generally short and rounded body; 8 arms joined by a web or skin; sessile, rarely stalked suckers disposed in 1 or 2 rows along the arms, all lacking chitinous rings or hooks; a mantle that is always fused with the head in the occipital area and generally not fused with the funnel; and vestigial or absent internal shell (Brusca & Brusca 2003, Lamprell *et al.* 2001). Two suborders, Cirrata and Incirrata, are recognised, which have on morphological grounds been considered monophyletic (Young & Vecchione 1996, Voight 1997), but such monophyly has not always been supported using molecular information (Carlini *et al.* 2001).

SUBORDER CIRRATA

Cirrates are deep-water finned octopods, mostly pelagic or benthopelagic in habit (Nixon & Young 2003). They occur worldwide, from Arctic to Antarctic waters, and are found from at least 125 to 7500 m depth; a number of these taxa have considerable geographic ranges, possibly because of their pelagic nature (Voss 1988b, Nixon & Young 2003).

Cirrate octopuses are characterised by paired fins, possession of a row of cirri on either side of a single row of suckers, and an internal shell for fin support (Voight 1997, Lamprell *et al.* 2001), and secondarily by a narrow mantle aperture, well-developed web, lack of an ink sac, degenerate radula (usually absent), and presence of a single (left) oviduct in the female (Lamprell *et al.* 2001). The familial classification of this suborder is less than stable, and has been the subject of considerable debate over the past decade. The suborder in entirety was recently revised by O'Shea (1999) wherein two new families were described (Grimpoteuthidae O'Shea, 1999, and Luteuthidae O'Shea, 1999), although these families are not universally accepted; recently anywhere from 3 to 5 families have been recognised (Opisthoteuthidae, Stauroteuthidae and Cirroteuthidae, Sweeney & Roper (1998); Opisthoteuthidae, Grimpoteuthidae, Stauroteuthidae, Cirroteuthidae and Luteuthidae, O'Shea (1999); Opisthoteuthidae, Cirroteuthidae, Grimpoteuthidae and a new family (not described) to accommodate the genus *Cirroctopus* (Piertney *et al.* 2003); and ToL recognises three families only, Opisthoteuthidae, Cirroteuthidae and Stauroteuthidae, acknowledging that the classification of the suborder needs revision (Young *et al.* 2010)). It has recently been demonstrated that additional families of cirrate octopods likely exist, with one taxon, *Cirroctopus*, accommodated in the Opisthoteuthidae by both O'Shea (1999) and Collins (2003), consid-

ered to belong to a new family on the basis of molecular data, although a name for this family has yet to be proposed (Piertney *et al.* 2003).

Genera have been assigned to families largely on the bases of shell shape (Bizikov 2004), gill structure, and the structure of the interbrachial web (Voight 1997). There has been a similar level of debate as to the validity of genera described and/or assigned to each of these families, with those genera most recently considered valid not having been concordantly assigned to families (Collins 2003).

SUBORDER INCIRRATA

Incirrates comprise about 85% of all known octopus species. They occur from the intertidal zone to at least 4000 m, with bathypelagic forms found to at least 2000 m (Mangold & Young 2008). The familial classification of this group of octopuses is more stable than that of the cirrates, and 8 families are universally accepted.

Incirrates lack fins and cirri, and the shell vestige is either reduced or entirely absent (Voight 1997); suckers can be disposed in either single or double rows, the web generally does not extend to the arm tips, the mantle opening is usually wide to moderately wide (but can be represented by two apertures, one either side of the funnel, as is the case in Amphitretidae), the radula is present, as is the ink sac (which can also be reduced or absent), and both female oviducts are developed (Lamprell *et al.* 2001, Sweeney *et al.* 1992).

Phylogenetic relationships between incirrate families remain unclear. Naef (1923) divided this suborder into two groups, the Ctenoglossa (comprising Amphitretidae and Bolitaenidae — transparent pelagic octopuses), and the Heteroglossa (including Octopodidae and Argonautidae). These two were classified primarily on grounds of similarities in radular and hectocotylus morphology: the Ctenoglossa with a radula possessing a comb-like multicuspид rachidian, lateral and marginal teeth, and a hectocotylus lacking a longitudinal groove and canal derived from it, whilst only the rachidian tooth of the Heteroglossa radula is multicuspид (the teeth of adjacent rows never have more than 2 cusps) and the hectocotylised arm of the male is markedly modified (Naef 1923). On the basis of anatomical characters, Voight (1997) considered these two groups to be diphyletic and paraphyletic respectively; however, on the basis of molecular characters, Strugnell *et al.* (2009) demonstrate monophyly of the Ctenoglossa. Based on molecular evidence, the pelagic families Alloposidae, Tremoctopodidae, Argonautidae and Ocythoidae are united by their detachable hectocotylus and are considered to be a monophyletic clade (sometimes referred to as the superfamily Argonautoidae) (Strugnell *et al.* 2009). Taki erected a new family, Idiotoptodidae, for one

species (*Idioctopus gracilipes*) (Taki 1961), although this has recently been considered a junior synonym of *Amphitretus pelagicus* Hoyle, 1885 (Hochberg *et al.* 1992, O’Shea 1999). The most speciose family, Octopodidae, is united largely on the basis of hectocotylus morphology — either the third left or third right arm is distally modified into a longitudinal groove and spoon-shaped modified apex (Carlini *et al.* 2001) but is not considered to be monophyletic (Strugnell *et al.* 2009, Voight 1993b).

OCTOPODIDAE

The Octopodidae is the only exclusively benthic family in the order Octopoda. It is the largest in the Class Cephalopoda, is very diverse, and representative taxa can be found from the Arctic to the Antarctic, from the intertidal zone to depths greater than 3500 m (Lamprell *et al.* 2001, Nixon & Young 2003, Voight 1993a). In 2005 this family was considered to comprise 374 nominal species, of which about half (186 species) were considered to be valid; an additional, approximate 150 undescribed species were also recognised (Norman & Hochberg 2005).

The classification of octopodids is rather unstable, with the concept and status of the subfamilies conventionally applied to this family over the past century having been the subject of considerable debate and also conflicting opinion. Grimpe (1921) divided this family into two subfamilies, the Octopodinae and Eledoninae, separating taxa on the basis of their number of sucker rows (biserial or uniserial). Robson (1929) subsequently recognised three subfamilies: Bathypolypodinae (characterised by their deep-water habitat, absence of an ink sac, and lack or reduction of a crop), Eledoninae (with uniserial suckers and large eggs); and Octopodinae, including all the *Octopus*-like genera, possessing two rows of suckers and an ink sac. Several years later Robson (1932) was of differing opinion, and returned to recognition of two subfamilies only, although these differed from those of Grimpe (1921), the

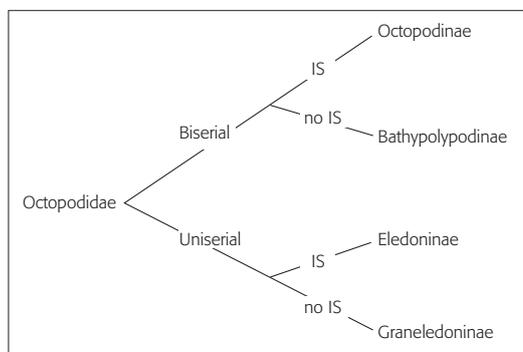


FIGURE 1. SUBFAMILY CLASSIFICATION (Voss 1988b).
IS. Ink Sac

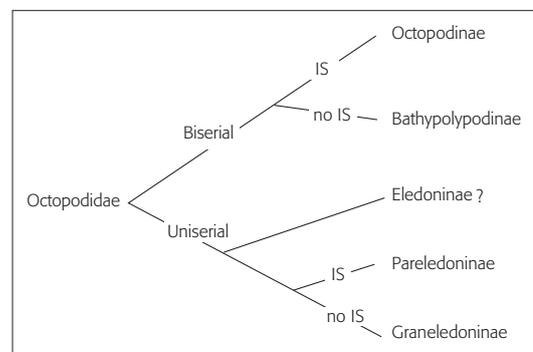


FIGURE 2. INFERRER SUBFAMILY CLASSIFICATION (Voss 1988a). If *Eledone* proves to be from Octopodinae.
IS. Ink Sac

TABLE I. OCTOPODIDAE CLASSIFICATION. Modified from Sweeney & Roper (1998) and Norman *et al.* (2009)

Family Octopodidae d'Orbigny, 1839–1842

- Subfamily Bathypolypodinae Robson, 1929
 - Genus *Bathypolypus* Grimpe, 1921
 - Genus *Muusoctopus* (Grimpe, 1921)
 - Genus *Grimpella* Robson, 1928
 - Genus *Teretoctopus* Robson, 1929
- Subfamily Eledoninae Grimpe, 1921
 - Genus *Adelieledone* Allcock, Hochberg, Rodhouse and Thorpe, 2003
 - Genus *Eledone* Leach, 1817
 - Genus *Pareledone* Robson, 1932
 - Genus *Tetracheledone* Voss, 1955
 - Genus *Vosseledone* Palacio, 1978
 - Genus *Velodona* Chun, 1915
- Subfamily Graneledoninae Voss, 1988
 - Genus *Bentheledone* Robson, 1932
 - Genus *Graneledone* Joubin, 1918
 - Genus *Microeledone* Norman, Hochberg and Boucher-Rodoni, 2004
- Genus *Thaumeledone* Robson, 1930
 - Subfamily Megaleledoninae Taki, 1961
 - Genus *Megaleledone* Taki, 1961
 - Subfamily Octopodinae Grimpe, 1921
 - Genus *Abdopus* Norman and Finn, 2001
 - Genus *Ameloctopus* Norman, 1992
 - Genus *Amphioctopus* Gleadall, 2002
 - Genus *Aphrodoctopus* Roper and Mangold, 1992
 - Genus *Callistoctopus* Taki, 1964
 - Genus *Cistopus* Gray, 1849
 - Genus *Galeoctopus* Norman, Boucher and Hochberg, 2004
 - Genus *Enteroctopus* Rochebrune and Mabile, 1889
 - Genus *Euaxoctopus* Voss, 1971
 - Genus *Hapalochlaena* Robson, 1929
 - Genus *Octopus* Cuvier, 1797
 - Genus *Pinnoctopus* d'Orbigny, 1845
 - Genus *Pteroctopus* Fischer, 1882
 - Genus *Robsonella* Adam, 1938
 - Genus *Sasakiopus* Jorgensen, 2009
 - Genus *Scaeurus* Troschel, 1857
 - ? Subfamily Vulcanoctopodinae González, Guerra, Pascual and Briand, 1998
 - Genus *Vulcanoctopus* González, Guerra, Pascual and Briand, 1998

Octopodinae and Bathypolypodinae; Robson (1932) recognised the loss of an ink sac to be an adaptation to depth, and the number of sucker rows to be an inappropriate taxonomic feature upon which to differentiate subfamilies. Subsequent to Robson's (1929 and 1932) seminal

works, few major changes were proposed to the subfamilial classification of the Octopodidae. The next major addition to the subfamilial classification was that of Taki (1961), wherein a new subfamily, the Megaleledoninae, was proposed for a new genus and species, *Megaleledone senoi* Taki, 1961; this subfamily was characterised by the large size of the only known species, and its lack of a crop diverticulum and simplicity in the form of its radula.

The status of the Megaleledoninae was relatively short-lived; Voss (in Palacio 1978) considered *Megaleledone* and *Pareledone* to be synonyms, and the Megaleledoninae to be invalid. Shortly the synonymy of these two genera was rejected (Kubodera & Okutani 1986, Lu & Stranks 1994) and *M. senoi* was redescribed, although neither Kubodera & Okutani (1986) nor Lu & Stranks (1994) accepted the subfamily Megaleledoninae. The next major review of subfamilial relationships was that of Voss (1988a), wherein one new subfamily, the Graneledoninae, was described, characterised by its uniserial suckers, lack of an ink sac, crop with reduced (or without) diverticulum, and reduced homodont radula. Voss (1988b) subsequently proposed another new subfamily, the Pareledoninae (Fig. 2), as a replacement name for the subfamily Eledoninae, for use in the event that *Eledone* subsequently was shown to belong in the Octopodinae (Voss 1988b). Allocation of genera to subfamilies recognised by Voss (1988b) was based on combinations of two characters, both of which Robson (1932) had earlier discounted as being of phylogenetic value: the loss of an ink sac and the number of sucker rows along the arms — the Octopodinae and Bathypolypodinae, with two rows of suckers, but with and without an ink sac respectively; the Eledoninae and Graneledoninae, with a single row of suckers, similarly with and without an ink sac respectively (Fig. 1). Voight (1993a) re-evaluated the classification of the Octopodidae and re-arranged genera, arguing that the families were formed by paraphyletic groups and that subfamily categories should be avoided.

The most recently proposed classification of Octopodidae (generic level), which is followed (somewhat uncritically) in this thesis, is presented in Table 1.

1.2 SYSTEMATICS

Prior to standardised measures, counts and characters being proposed for species descriptions by Roper & Voss (1983), numerous, often different characters and their states were described for cephalopods when being described, with descriptions often being incomplete, or focussing on single or very few characters and their states. This lack of standardised descriptions hindered di-

rect comparison of taxa described by different authors at different times and locations, a problem only exacerbated by historically described taxa on the basis of single or very few specimens, single sexes, juveniles, specimens being preserved in a variety of media or damaged specimens.

As the previous synopsis has shown, more recent subfamilial classifications of the Octopodidae have focussed on characters such as sucker arrangement (whether the suckers are disposed in one or two rows), and the presence or absence of an ink sac. Differentiation of genera and species typically has employed a different suite of characters and their states. At the generic level, frequently cited characters have included the nature of the crop, and whether or not it had a diverticulum; the size of the posterior salivary glands relative to either the buccal bulb or mantle length; the nature of the rachidian tooth of the radula, (uni- or multi-cuspid), or the number of teeth in a transverse row (Voss 1988b, O'Shea 1999, Allcock 2005), and for at least one genus, *Adelieledone*, lower beak morphology. Although subtle differences in squid beak morphology have been long used to differentiate squid taxa, or identify them where hard-part remains have been lost (typically in stomach content samples of predators), these have rarely been used to differentiate octopus taxa, although the shape, pigmentation, and various angles on the lower beak are recognised as being of some use for differentiating genera of octopuses (Roper & Voss 1983, Ogden *et al.* 1998). At the level of the species, beaks have been considered too conservative in morphology to assist much in the differentiation taxa (Allcock 2005, Ogden *et al.* 1998). The radula has been routinely used to differentiate octopus taxa, but these teeth can differ in number and in features, such as size, shape and form (Nixon 1998, Roper & Voss 1983) within species (Samuel & Patterson 2003), individuals, and even on the same individual (Clarke 1998). The presence or absence of stylets has been used as a character for differentiating genera of octopods, while its length is of potential value for discriminating species (Hochberg *et al.* 2005).

At species level, the texture of the skin has been recently, intensively used to differentiate species within a genus, particularly in the speciose, but anatomically conservative genus *Pareledone*, and to a lesser extent *Graneledone*; the former enables differentiation of species of *Pareledone* that are otherwise extremely similar in anatomical detail (Allcock 2005), and the latter, species of *Graneledone* that most obviously differ in the number and distribution of tubercles on the mantle, head and arms (Guerra *et al.* 2000). The component parts of the reproductive system in males and females have also been used for species identification (Vecchione 1994, Roper & Voss 1983), with the ligula and calamus morphology, and spermatophore length being extremely variable between taxa, and therefore useful for differentiating taxa at levels of both genus and species (Voight 2002).

Prior to the 2003 CIAC (Cephalopod International Advisory Council) meeting, a workshop was convened wherein the current state of generic and species-level taxonomy, and morphological, meristic and molecular characters that could be used for descriptions of octopus taxa, was discussed (Hochberg *et al.* 2005). As a consequence, a number of characters were proposed to augment those detailed by Roper & Voss (1983), although the two accounts differed little overall; characters included aspects of sucker morphology and number; arm and web lengths and depths, presence or absence of an ink sac (and associated anal flaps), in addition to the position of the ink sac opening relative to the anus; gill lamellae count, shape and ratio of inner to outer lamellae; presence or absence of stylets (and their composition); aspects of hectocotyliised arm shape and length; associated reproductive structures such as spermatophore and egg size, for the former microscopic detail; details of the radula; details of the skin (e.g., papillation, colour, spots, bars and bands); and attributes of species' distribution, behaviour, development and habitat. This account differed from Roper & Voss (1983), however, in defining those characters or states that might prove of value for differentiating genera separate from those of species. In short:

- The generic level, the number of rows of suckers was described as of systematic importance, followed by the presence or absence of enlarged suckers, and their individual modification, or modification at the arm tips; at the species level, total arm sucker counts, sucker shape and diameter, and their distribution along and between arms (their configuration) were recognised to be important.
- Arm-to-body ratio (long, medium or short), arm width, and arm formula were important for differentiating genera, with the relative lengths of these arms (to each other) important for differentiating species.
- Web depth formula proved valuable for differentiating genera, whereas individual web sector depths (relative to each other, i.e., web formula) proved valuable for differentiating species.
- Funnel shape was useful for differentiating genera, and its length relative to that observed in other taxa for differentiating species.
- The presence or absence of an ink sac and anal flaps were deemed to be of value for differentiating genera, and the size of the ink sac reservoir for differentiating species; the position of the ink duct opening was also valuable for differentiating genera.
- The range in number of gill lamellae, relative number of inner and outer lamellae, gill length and length of inner and outer lamellae relative to ML, were important for defining genera, whereas the specific number of lamellae and gill length were of value for differentiating species.
- Spermatophore size, number, armature and shape were of value for differentiating genera, while the length and number of sperm cord whorls were of value for differentiating species.

The variability of some of these characters has already been related to their depth of habitat, particularly those characters or states associated with the ink sac. This sac in shallow-water octopuses can vary in size or extent of embedding within the digestive gland, or it can be entirely absent; in slope-dwelling octopuses the ink sac can be of 'normal' size anywhere through to small, vestigial, or absent, and for some it is even deeply buried within the digestive gland; in the deepest-dwelling, true bathyal taxa the ink sac is almost always absent, its loss considered a modification to a lightless habitat in which it would serve no function at all. Additional modifications of the alimentary canal associated with depth include reduction of the size of the crop, or loss of its diverticulum; similarly, the radula, usually well developed in littoral forms and with seven teeth and two marginal plates per transverse row, is often reduced in deeper-dwelling taxa, either by way of loss of lateral cusps on the rachidian, or reduction in the number of teeth per transverse row; possibly associated with this is the concomitant reduction in the relative size of the posterior salivary glands with depth. The gills of deeper-dwelling octopus taxa are also usually smaller, with fewer lamellae per demibranch, than their more shallow-water relatives.

The instability in the subfamilial classification of the Octopodidae is due largely to the fact that many of the characters and their states that have been used to characterise subfamilies, and have been proposed recently to differentiate genera, appear to vary with depth, thus potentially obscuring true phylogenetic relationships between littoral and deep-sea forms; this relationship has been long recognised (Robson 1929, 1932).

A major objective of this current research is to evaluate critically the usefulness of morphological and anatomical characters and their states that have been conventionally used in systematic and phylogenetic studies of octopuses by Roper & Voss (1983), such as that undertaken by Allcock *et al.* (2008), and to further critique a subset of those proposed by Hochberg *et al.* (2005) for this same purpose. Additional characters (and their states) that may assist in determining phylogenetic relationships between genera and families or assist in differentiating taxa for the purposes of taxonomic description are also considered.

METHODS²

2.1 MATERIAL EXAMINED

In order to undertake this research, representatives of many different genera of octopodids were examined: one cirrate, *Cirroctopus*, and 10 genera within the incirrate family Octopodidae, *Adelieledone*, *Bentheledone*, *Benthooctopus*, *Enterooctopus*, *Graneledone*, *Megaleledone*, *Octopus*, *Pareledone*, *Pinnoctopus*, and *Thaumeledone*. Collections available were largely from Antarctic waters, made available from two main repositories of cephalopods in New Zealand, the National Institute of Water & Atmospheric Research Ltd (NIWA), and National Museum of New Zealand *Te Papa Tongarewa* (NMNZ). Specimens were received preserved in alcohol, or frozen, then subsequently fixed and preserved in a 4% buffered formalin solution at Auckland University of Technology (AUT). All specimen lots examined are detailed in Table 3.

For the majority of species treated herein, additional material is recognised in museum collections. Only a subset of specimens available were examined for the purposes of this thesis; generally, given that specimens were to be extensively dissected in order to recover as much anatomical information as possible, the best specimens available of a given taxon were not dissected. These could therefore later be designated type specimens in the event any proved novel. One exception is the single known specimen herein attributed to the genus *Bentheledone*.

DESCRIPTION, MEASUREMENTS, INDICES AND COUNTS

Species descriptions and external specimen measurements, indices and counts mostly follow the guidelines proposed by Roper & Voss (1983). External terminology and measurements are based on Roper & Voss (1983) [referred as R&V characters hereafter] and are depicted in Figure 3 and described in Tables 4 and 5. Terminology and measurements of internal organs and beaks are depicted in Figures 9–11 and described in Table 8. Generic diagnoses presented herein take into consideration the most recent accounts of taxa within them, augmented with information discerned from specimens described herein.

When the specimens were slightly damaged, an estimate of their measure was carefully determined. For descriptions and multivariate analysis (see below) any obviously missing suckers were counted as if present; in the event that the extreme tip of the arm was lacking, the number of suckers and the length of the arm were estimated by comparing its narrowness and number of suckers along a comparable length of arm from the opposite (if intact) arm tip. Features too damaged to be reliably estimated are identified with an asterisk (*); features that were absent are denoted with a dash (–).

To obtain external and anatomical measures, each specimen was extensively dissected. Descriptions and drawings of some important anatomical features were prepared, such as the alimentary canal (Fig. 5), extent to which the ink sac was embedded within the digestive gland (Fig. 6), female and male reproductive systems (Figs 7, 8), and upper and lower beaks (Figs 9–11). With regard to the ink sac, the extent to which the sac was embedded within the digestive gland has been further qualified into types: type 1, where both the sac and duct are exposed; type 2, where part of the sac was exposed; and type 3, where the sac was not exposed on the surface of the digestive gland at all.

The beaks and the radula were removed from the buccal bulb. For descriptions and measurements of the beaks, the lower beak was placed with the wings and the corners of the walls resting on a flat surface, and the upper beak with the corners of the wall and the crest similarly on a flat surface (Fig. 9). For the radula, the tissue was cleaned using weak NaOH solution gently heated with a Bunsen burner from 3 to 30 minutes depending on the size and delicacy of the radula. Radulae were illustrated using light-compound microscopy with an attached drawing tube, with the scale drawn using a 1-mm micrometer slide. Following Nixon (1998), at least one transverse row of teeth was drawn, usually (whenever possible) from the region prior to the active cutting edge of the radula (thus undamaged); some radulae were photographed using Environmental Scanning Electron Microscopy (ESEM) after being critical-point dried and coated in platinum.

Partway into this research it became apparent that the circulatory system of these octopuses might contain information of both systematic and phylogenetic importance. For a selection of taxa the major arterial branches from the heart then were also dissected, with branches leading to reproductive, renal and alimentary systems, particularly the ink sac, detailed; generalised depictions of the arterial system are presented for each sex and species (Figs 12, 13). Those that were not examined included: *Pareledone* sp. nov. 3 (NMNZ M.160553), *Cirroctopus hochbergi* (NMNZ M.100327) and *Muusoctopus* sp. (NIWA 44151).

TABLE 2. ACRONYMS.

NIWA	National Institute of Water & Atmospheric Research Ltd, Wellington, New Zealand
NMNZ	Museum of New Zealand <i>Te Papa Tongarewa</i> , Wellington, New Zealand
SAM	South African Museum, Cape Town, South Africa
SAuM	South Australian Museum, Adelaide, Australia
OMNZ	Otago Museum, Dunedin, New Zealand
FByc	Fisheries Bycatch

TABLE 3. DISSECTED SPECIMENS. Information available from collections.

Genus	Species	Sex	Specimen	Museum	Survey	Station
<i>Adelieledone</i>	<i>polymorpha</i>	M	44133	NIWA	Oceans Survey 2020, IPY, CAML2010	TAN0802/41
<i>Muusooctopus</i>	sp.	F	44151	NIWA	Oceans Survey 2020, IPY, CAML	TAN0802/121
<i>Cirroctopus</i>	<i>hochbergi</i>	F	M.100327	NMNZ		J9/41/89
<i>Enterootopus</i>	<i>zealandicus</i>	M		NIWA	Oceans Survey 2020, IPY, CAML2016	TAN0317/63
<i>Bentheledone</i>	<i>albida</i>	M	44160	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/189
<i>Graneledone</i>	sp. 2	M	S3569	SAM		
<i>Graneledone</i>	sp. 2	M	S3569	SAM		
<i>Graneledone</i>	<i>antarctica</i>	F	44051	NIWA	Oceans Survey 2020, IPY, CAML2015	TAN0802/167
<i>Graneledone</i>	<i>taniwha taniwha</i>	M		NIWA	Oceans Survey 2020, IPY, CAML2017	TAN0317/30
<i>Graneledone</i>	sp. 1	M	2735	SAM		
<i>Graneledone</i>	<i>antarctica</i>	M	44052	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/167
<i>Megaleledone</i>	cf. <i>setebos</i>	F	44147	NIWA	Oceans Survey 2020, IPY, CAML2009	TAN0802/77
<i>Octopus</i>	<i>kaurna</i>	F	D17989			
<i>Octopus</i>	<i>oliveri</i>	M	A 54.82	OMNZ		
<i>Pareleledone</i>	sp. nov. 1	F	44067	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/94
<i>Pareleledone</i>	sp. nov. 1	F	44091	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/100
<i>Pareleledone</i>	sp. nov. 1	F	44060	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/031
<i>Pareleledone</i>	sp. nov. 1	F	44070	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/66
<i>Pareleledone</i>	sp. nov. 1	M	44067	NIWA	Oceans Survey 2020, IPY, CAML2009	TAN0802/94
<i>Pareleledone</i>	sp. nov. 1	M	44066	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/081
<i>Pareleledone</i>	sp. nov. 1	M	44069	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/061
<i>Pareleledone</i>	sp. nov. 1	M	44074	NIWA	Oceans Survey 2020, IPY, CAML2009??	TAN0802/94
<i>Pareleledone</i>	sp. nov. 1	M	44066	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/081
<i>Pareleledone</i>	sp. nov. 1	M	44059	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/26
<i>Pareleledone</i>	sp. nov. 2	M	44097	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/123
<i>Pareleledone</i>	sp. nov. 3	F	44073	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/084
<i>Pareleledone</i>	sp. nov. 3	M	44113	NIWA	Oceans Survey 2020, IPY, CAML2009	TAN0802/94
<i>Pareleledone</i>	sp. nov. 3	F	44122	NIWA	Oceans Survey 2020, IPY, CAML2012	TAN0802/17
<i>Pareleledone</i>	sp. nov. 3	M	44120	NIWA	Oceans Survey 2020, IPY, CAML2014	TAN0802/117
<i>Pareleledone</i>	sp. nov. 3	F	M.160553	NMNZ	MFish SOP	1430/3R
<i>Pareleledone</i>	sp. nov. 4	F	44258	NIWA	Oceans Survey 2020, IPY, CAML2008	TAN0802/167
<i>Pareleledone</i>	sp. nov. 4	F	44258	NIWA	Oceans Survey 2020, IPY, CAML2011	TAN0802/167
<i>Pareleledone</i>	sp. nov. 4	F	44258	NIWA	Oceans Survey 2020, IPY, CAML2013	TAN0802/167
<i>Pareleledone</i>	sp. nov. 5	F	M.287686	NMNZ	MFish SOP	2332/34
<i>Pinnooctopus</i>	<i>cordiformis</i>	M	not-accessioned specimens (fisheries bycatch)			
<i>Thaumeledone</i>	<i>zeiss</i>	F	M.299399	NMNZ		trip1693 tow89
<i>Thaumeledone</i>	sp. nov.	F	44145	NIWA	Oceans Survey 2020, IPY, CAML2011	TAN0802/167

TABLE 3 (cont.). DISSECTED SPECIMENS. Information available from collections.

Species	Specimen	Longitude	Latitude	Depth (m)	Date	State
<i>A. polymorpha</i>	44133	74°43.8' E	167°0.58' S	916–930	12/02/2008	Frozen
<i>Muusoctopus</i> sp.	44151	175°31.93–34.58'E	72°20.37–21.05'S	945–950	21/02/2008	
<i>C. hochbergi</i>	M.100327	178°44.2'E	38°37.2'S	929–1067	25/09/1989	Frozen
<i>E. zealandicus</i>						
<i>B. albida</i>	44160	178°19.75–20.92'E	68°33.87–33.36'S	3203–3210	01/03/2008	Frozen
<i>Graneledone</i> sp. 2	S3569	unlocalised, collection details unknown				
<i>Graneledone</i> sp. 2	S3569	unlocalised, collection details unknown				
<i>G. antarctica</i>	44051	174° 1.8' E	1°51.6' S	1954–1990	25/02/2008	Frozen
<i>G. taniwha taniwha</i>						
<i>Graneledone</i> sp. 1	2735					
<i>G. antarctica</i>	44052	174° 1.8' E	1°51.6' S	1954–1990	25/02/2008	Frozen
<i>M. cf. setebos</i>	44147	179°57' E	76°49.8' S	663–664	16/02/2008	Frozen
<i>O. kaurna</i>	D17989	137°45.42'E	35.06.66'S	0–5	17/02/2008	?Relaxed
<i>O. oliveri</i>	A 54.82	177°56.57' W	29°16.20'S	0		Live fixed
<i>Pareledone</i> sp. nov. 1	44067	176°17.77–14.63'E	76°11.58–12.30'S	447	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44091	176°14.88–14.46'E	76°12.12–12.24'S	447–451	18/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44060	170°16.54–16.15'E	74°35.43–35.32'S	283	02/11/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44070	167°19.27–18.70'E	75°37.45–36.51'S	474–480	14/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44067	176°17.77–14.63'E	76°11.58–12.30'S	447	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44066	176°49.68–45.30'E	76°35.64–35.94'S	365–369	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44069	169°48.27–48.68'E	75°37.30–37.23'S	520–522	14/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44074	176°49.68–45.30'E	76°35.64–35.94'S	369–365 m	17/02/2008	
<i>Pareledone</i> sp. nov. 1	44066	176°49.68–45.30'E	76°35.64–35.94'S	365–369	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 1	44059	170°14.99–17.58'E	74°34.90–34.83'S	285	02/11/2008	Frozen
<i>Pareledone</i> sp. nov. 2	44097	175°28.2'E	72°19.8'S	915–936	2/21/2008	Frozen
<i>Pareledone</i> sp. nov. 3	44073	176°48.12–47.65'E	76°36.14–36.13'S	360	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 3	44113	176°17.77–14.63'E	76°11.58–12.3'S	447	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 3	44122	176°48.12–47.65'E	76°36.14–36.13'S	321	17/02/2008	Frozen
<i>Pareledone</i> sp. nov. 3	44120	175°20.54–20.55'E	72°35.42–35.58'S	475–479	21/02/2008	Frozen
<i>Pareledone</i> sp. nov. 3	M.160553	174°36.00'E	73°7.20'S	343	15/01/2001	Frozen
<i>Pareledone</i> sp. nov. 4	44258	174°01.98–06.59'E	71°51.34–53.40'S	1954–1990	25/02/2008	Frozen
<i>Pareledone</i> sp. nov. 4	44258	174°01.98–06.59'E	71°51.34–53.40'S	1954–1990	25/02/2008	Frozen
<i>Pareledone</i> sp. nov. 4	44258	174°01.98–06.59'E	71°51.34–53.40'S	1954–1990	25/02/2008	Frozen
<i>Pareledone</i> sp. nov. 5	M.287686	177°0.00'E	71°25.80'S	966 m	10/01/2007	Frozen
<i>P. cordiformis</i>						Frozen
<i>T. zeiss</i>	M.299399	164°59.9'E	48°00.9'S	1004–1179	30/11/2002	Frozen
<i>Thaumeledone</i> sp. nov.	44145	174°01.98–06.588'E	71°51.342–53.40'S	1954–1990	2/25/2008	Frozen

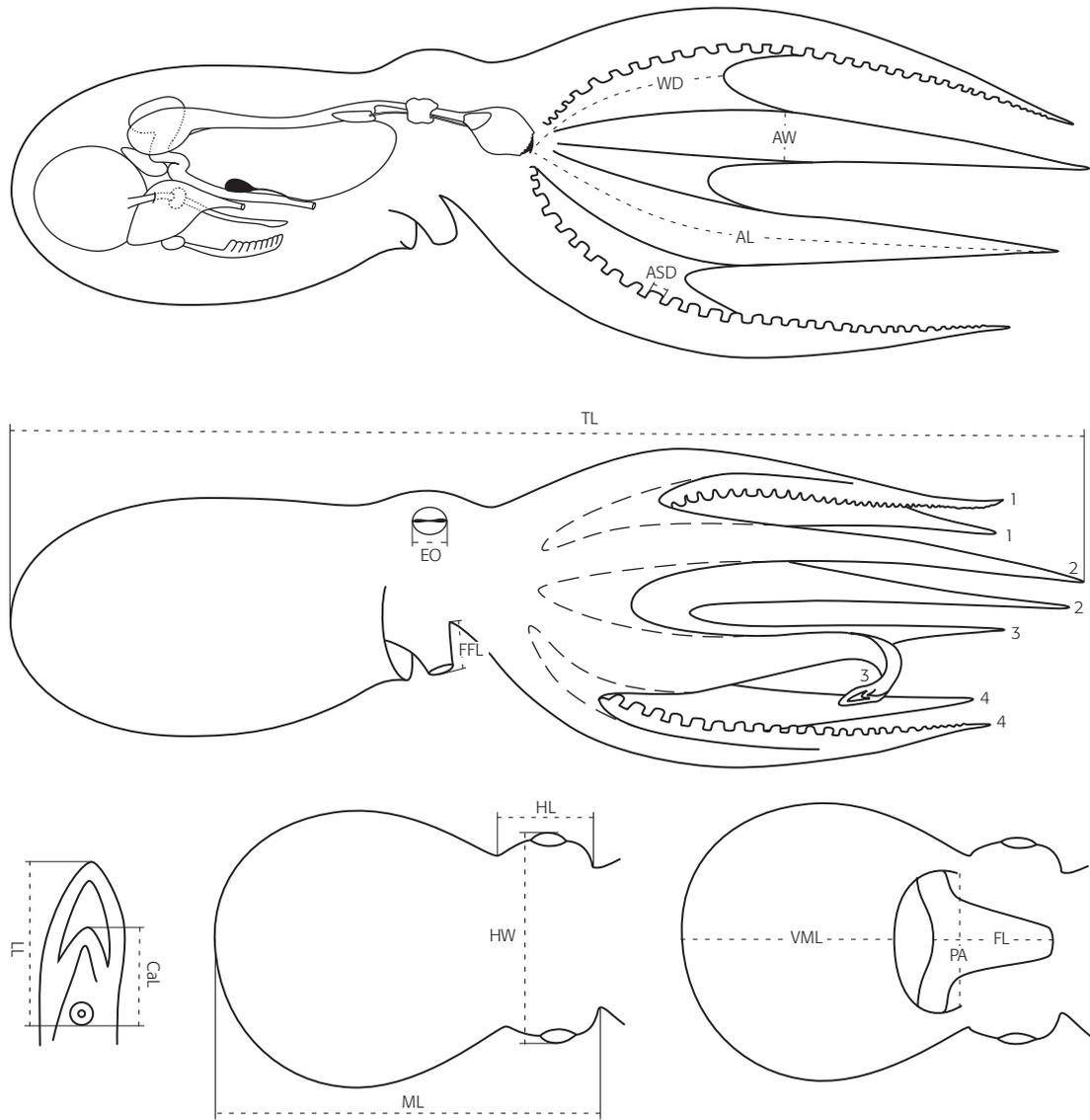


FIGURE 3. EXTERNAL MEASUREMENTS. AL. Arm Length; AW. Arm Width; ASD. Arm Sucker Diameter; CaL. Calamus Length; HL. Head Length; HW. Head Width; EO. Eye Opening; FL. Funnel Length; FFL. Free Funnel Length; LL. Ligula Length; ML. Mantle Length; PA. Pallial Aperture; TL. Total Length; VML. Ventral Mantle Length; WD. Web Depth

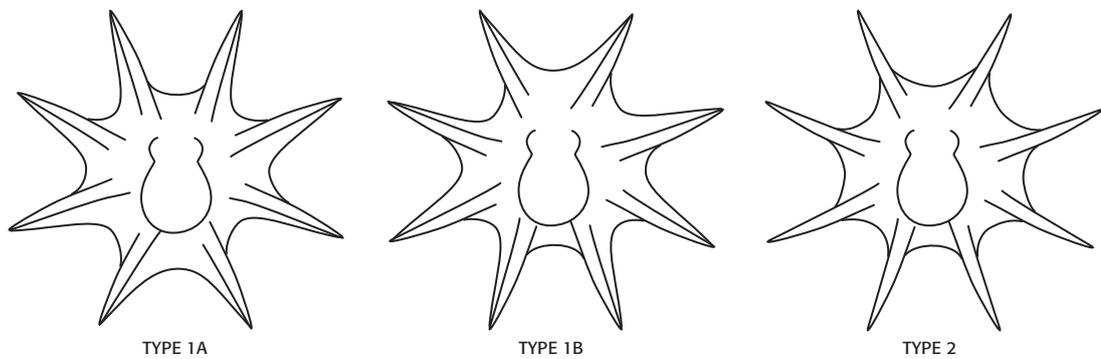


FIGURE 4. TYPE OF ARM-TO-WEB ATTACHMENT (wat). TYPE 1A. Sector A joins arm pairs I at mid-arm and web sector E joins arm pairs IV close to the tip of the arms. TYPE 1B. Web sector E joins arm pairs I at mid-arm and web sector A joins arm pairs IV close to the tip of the arms. TYPE 2. All web sectors join the arm at similar level.

TABLE 4. DEFINITION OF EXTERNAL CHARACTER MEASURES AND COUNTS (based on Roper & Voss, 1983) (Figs 3,4).

<p>AF-ARM FORMULA. Comparative length of arms (see AL) expressed in Roman numerals in decreasing order (e.g. I.III.IV.II, IV.III.II=I).</p> <p>AL-ARM LENGTH. Length of arm measured from beak to tip of arms. ALI-ARM LENGTH INDEX. AL expressed as a percentage of ML.</p> <p>ASC¹-ARM SUCKER COUNT. Number of suckers along each entire arm to tip; for the hectocotyliised arm (ASCIIIR), to calamus. (e.g., ASCIR 54).</p> <p>ASD²-ARM SUCKER DIAMETER. The diameter of largest normal (not enlarged) arm sucker (ASDn). ASI-ARM SUCKER INDEX. The measures of ASDn on each designated arm as a percentage of ML.</p> <p>AW-ARM WIDTH. Width of the thickest arm, measured at its widest point (excluding webs and membranes). AWI-ARM WIDTH INDEX. AW as a percentage of ML.</p> <p>CAL-CALAMUS LENGTH. Measured from the last (distal-most) sucker to tip of calamus. CALI-CALAMUS LENGTH INDEX. CaL as a percentage of LL.</p> <p>EO-EYE ORIFICE. Diameter of the opening of the eye. EOI-EYE ORIFICE INDEX. EO as a percentage of ML.</p> <p>FFuL-FREE FUNNEL LENGTH. Length of the funnel portion free from ventral attachment to the head or arm bases, measured from the distal aperture to the point of funnel attachment to the ventral surface of the head. FFLI-FREE FUNNEL LENGTH INDEX. FFuL as a percentage of ML.</p> <p>FuL-FUNNEL LENGTH. Length of the funnel measured from the distal to proximal apertures. FuLI-FUNNEL LENGTH INDEX. FuL measured as a percentage of ML.</p> <p>HdL³-HEAD LENGTH. Dorsal length of head measured from pre-orbital to post-orbital constriction. HdLI.-HEAD LENGTH INDEX. HL as a percentage of ML.</p> <p>HdW-HEAD WIDTH. Greatest width of head at level of eyes. HdWI-HEAD WIDTH INDEX. HW measured as a percentage of ML.</p> <p>LL-LIGULA LENGTH. Measured from the last (distal-most)</p>	<p>sucker to tip of arm. LLI-LIGULA LENGTH INDEX. LL as a percentage of hectocotyliised AL.</p> <p>ML-MANTLE LENGTH. Measured from mid-point between eyes to posterior end of mantle.</p> <p>MW-MANTLE WIDTH. Greatest straight-line (dorsal) width of mantle. MWI-MANTLE WIDTH INDEX. MW as a percentage of ML.</p> <p>OAI-OPPOSITE ARM LENGTH INDEX. Hectocotyliised AL as a percentage of its fellow arm on opposite side.</p> <p>PA-PALLIAL APERTURE. Measurement 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.</p> <p>TL-TOTAL LENGTH. Measured from end of longest arm to posterior end of mantle.</p> <p>WAT-ARM TO WEB ATTACHMENT. Type of attachment of web sector to the arms. Type 1A: web sector A joins arm pairs I at mid-arm and web sector E joins arm pairs IV close to the tip of the arms. Type 1B: web sector E joins arm pairs I at mid-arm and web sector A joins arm pairs IV close to the tip of the arms. Type 2: All web sectors join at similar level to the arm.</p> <p>WD-WEB DEPTH. Measurement of each sector of web, from beak to mid-point of sector between arms. (Web sectors: A = dorsal to dorsal arm, B = dorsal to dorso-lateral, C = dorso-lateral to ventro-lateral, D = ventro-lateral to ventral, E = ventral to ventral). WDI-WEB DEPTH INDEX. Measurement of the most extensive WD as a percentage of longest AL.</p> <p>WF-WEB FORMULA. Comparative WD of each sector expressed alphabetically in decreasing order. (e.g., B.C.D=A.E). WFR and WFL refer to the right-side and left-side sectors respectively.</p>
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1. Differs in complete sucker count instead of half-arm sucker count.
2. Not previously defined.
3. Clarifies limits of measures, which are ambiguously defined.

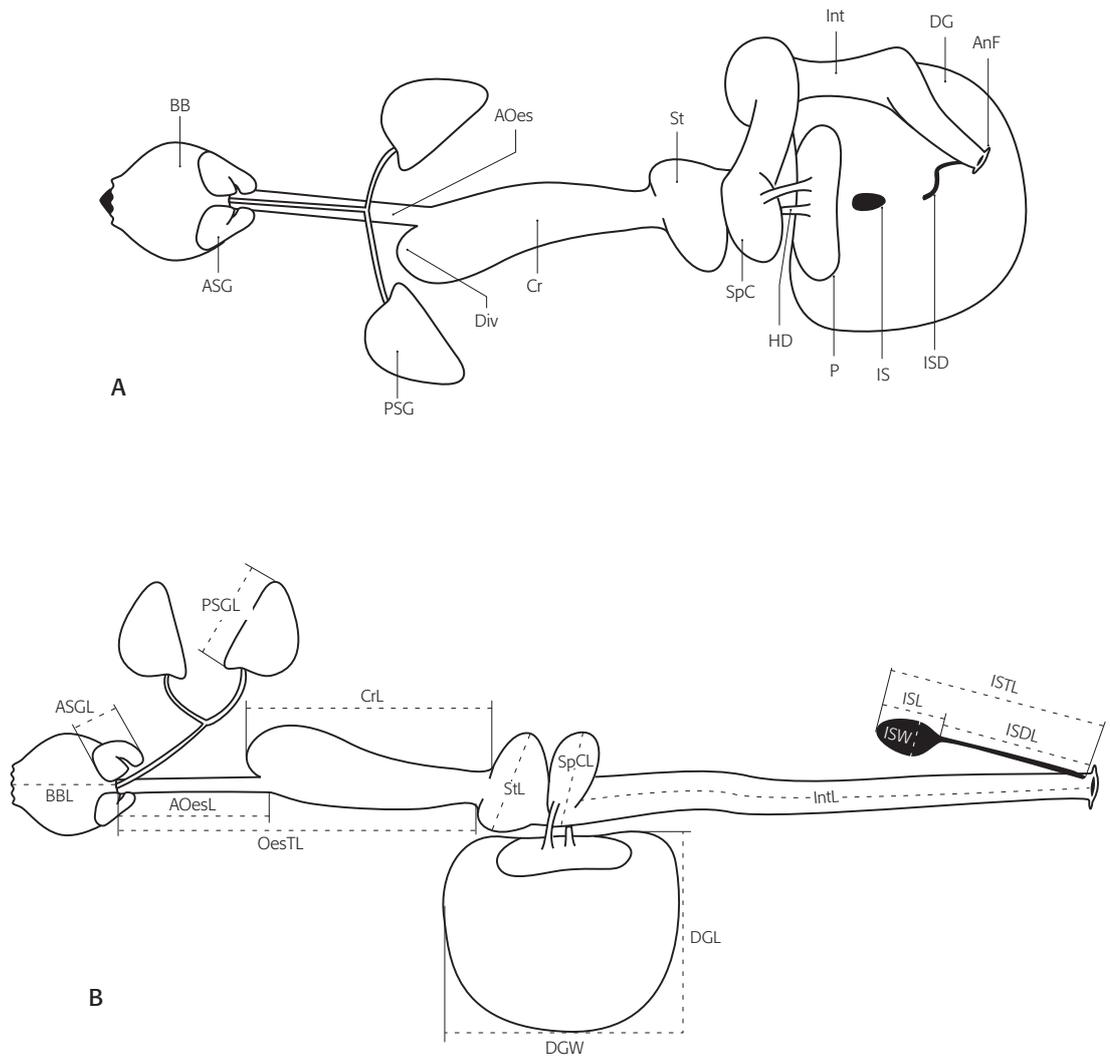


FIGURE 5. ALIMENTARY CANAL. A) TERMINOLOGY. AnF. Anal Flaps; AOes. Anterior Oesophagus; ASG. Anterior Salivary Gland; BB. Buccal Bulb; Cr. Crop; Div. Diverticulum; DG. Digestive Gland; HD. Hepatic Duct; Int. Intestine; IS. Ink Sac; ISD. Ink Sac Duct; OesTL. Oesophagus Total Length; P. Pancreas; PSG. Posterior Salivary Gland; SpC. Spiral Caecum; St. Stomach. **B) MEASURES.** L. Length; TL. Total Length; W. Width.

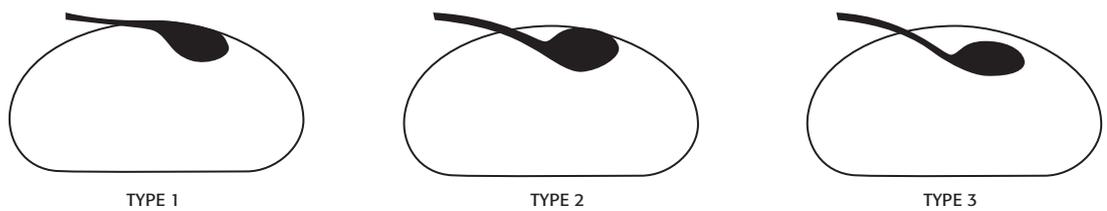


FIGURE 6. INK SAC POSITION. TYPE 1. Ink sac and duct exposed entirely. TYPE 2. Ink sac or part of it exposed; duct not exposed entirely. TYPE 3. Ink sac and duct not exposed.

TABLE 5. DEFINITION OF INTERNAL CHARACTER MEASURES AND COUNTS (Figs 5, 6).

AOESL–ANTERIOR OESOPHAGUS LENGTH. Length of the oesophagus from the buccal bulb to the base of the crop, or stomach when crop is absent. **AOESLI**–ANTERIOR OESOPHAGUS LENGTH. AOesL as a percentage of ML.

ASGL–ANTERIOR SALIVARY GLAND LENGTH. Greatest straight–line length of anterior salivary gland.

BBL–BUCCAL BULB LENGTH. Straight line measured from the oral to aboral points of the buccal bulb, the latter being where the anterior oesophagus enters the buccal bulb. **BBI**–BUCCAL BULB INDEX. BBL as a percentage of ML.

DG (GD)–DIGESTIVE GLAND (GREATEST DIMENSION). Greatest length or width measure.

GILC¹–GILL LMAMELLAE COUNT. Number of lamellae on inner and outer demibranch, excluding terminal lamella.

INTL–INTESTINE LENGTH. Length of intestine measured from the spiral caecum to anus. **INTLI**–INTESTINE LENGTH INDEX. IntL as a percentage of ML.

ISEL–INK SAC EXPOSURE LENGTH. Length of sac and duct exposed on surface of digestive gland.

ISEW–INK SAC EXPOSURE WIDTH. Width of sac exposed on surface of digestive gland.

ISL–INK SAC LENGTH. Length of ink reservoir, measured from ink sac duct to tip. **ISLI**–INK SAC LENGTH INDEX. ISL as a percentage of DGL.

ISW–INK SAC WIDTH. Width of ink sac, measured at its widest point.

ISTL–INK SAC TOTAL LENGTH. Measured from ink sac tip to the end of ink duct. **ISTLI**–INK SAC TOTAL LENGTH INDEX. ISTL as a percentage of ML.

OESTL–OESOPHAGUS TOTAL LENGTH. Measured from the rear (aboral) end of the buccal bulb to the base of stomach. **OESTLI**–OESOPHAGUS TOTAL LENGTH INDEX. OesTL as a percentage of ML.

PSGL–POSTERIOR SALIVARY GLAND LENGTH. Greatest length of posterior salivary glands measured in a straight line. **PSGLI**–POSTERIOR SALIVARY GLANDS LENGTH INDEX. PSGL as a percentage of ML.

SpCL–SPIRAL CAECUM LENGTH. Greatest straight–line dimension of caecum. SpCL as a percentage of ML.

StL–STOMACH LENGTH. Length measured in a straight line from base to distal tip. **StLI**–STOMACH LENGTH INDEX. StL as a percentage of ML.

1. Differs from Roper and Voss (1983), who included the terminal lamella in the counts.

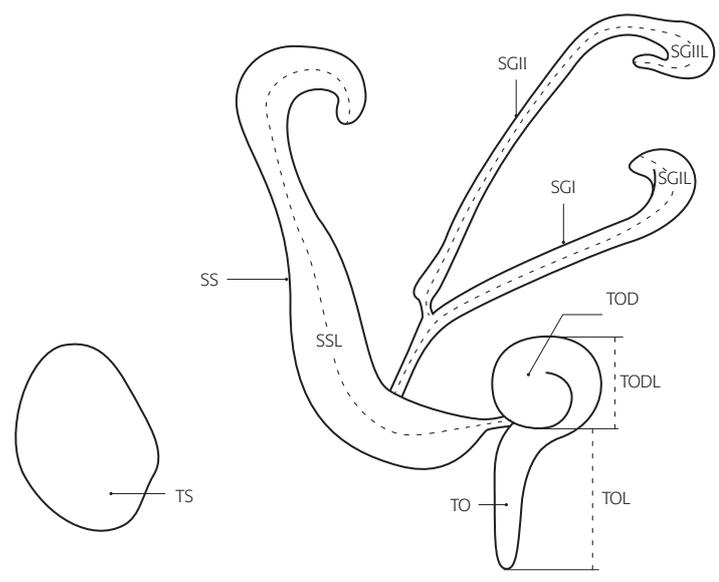


FIGURE 7. MALE REPRODUCTIVE SYSTEM. **A)** TERMINOLOGY. SGI. Spermatophoric Gland I; SGII. Spermatophoric Gland II; SS. Spermatophoric Sac; TS. Testicle Sac; TO. Terminal Organ; TOD. Terminal Organ Diverticulum. **MEASURES.** L. Length.

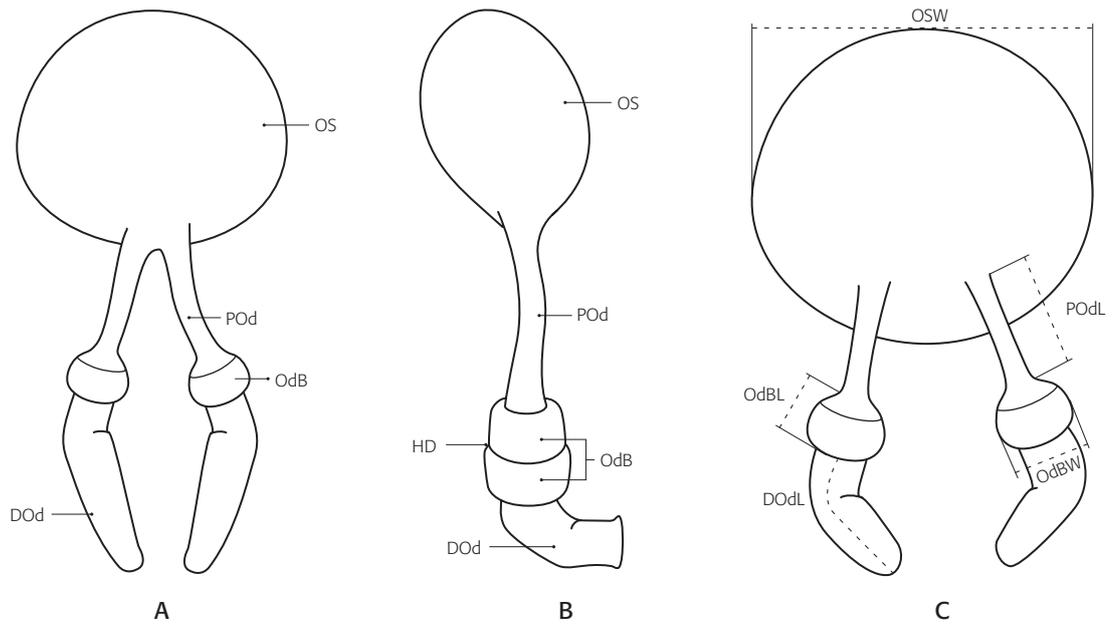


FIGURE 8. FEMALE REPRODUCTIVE SYSTEM. A) INCIRRATE OVARY, B) CIRRATE OVARY. DOd. Distal Oviduct; **HD.** Hemisphere Division; **OdB.** Oviducal Ball; **OS.** Ovary Sac; **POd.** Posterior Oviduct. **C) MEASURES.** L. Length; W. Width.

TABLE 6. DEFINITION OF MALE REPRODUCTIVE SYSTEM MEASURES (Fig. 7).

SGIL-SPERMATOPHORIC GLAND I LENGTH. Length of spermatophoric gland from the attachment to spermatophoric sac to tip.
SGIIL-SPERMATOPHORIC GLAND II LENGTH. Length of spermatophoric gland from the attachment to SGI to tip.
SS-SPERMATOPHORIC SAC LENGTH. Length of spermatophoric sac from terminal organ (TO) to tip.

TOL-TERMINAL ORGAN LENGTH. Length from diverticulum to tip.
TODL-TERMINAL ORGAN DIVERTICULUM LENGTH. Length from diverticulum border to the join with terminal organ (TO).

TABLE 7. DEFINITION OF FEMALE REPRODUCTIVE SYSTEM MEASURES (Fig. 8)

ODL-DISTAL OVIDUCT LENGTH. Length of distal oviduct from oviducal ball to tip.
DODW-DISTAL OVIDUCT WIDTH. Measure of distal oviduct at its widest point.
ODBL-OVIDUCAL BALL LENGTH. Length of oviducal ball from junction with proximal oviduct to distal oviduct.
ODBL-OVIDUCAL BALL WIDTH. Diameter of oviducal ball at its widest point.

OSL-OVARY SAC LENGTH. Ovary sac diameter at its widest point.
PODL-PROXIMAL OVIDUCT LENGTH. Length of proximal oviduct from oviducal ball to junction with ovary sac.
PODL-PROXIMAL OVIDUCT WIDTH. Measure of proximal oviduct at its widest point.

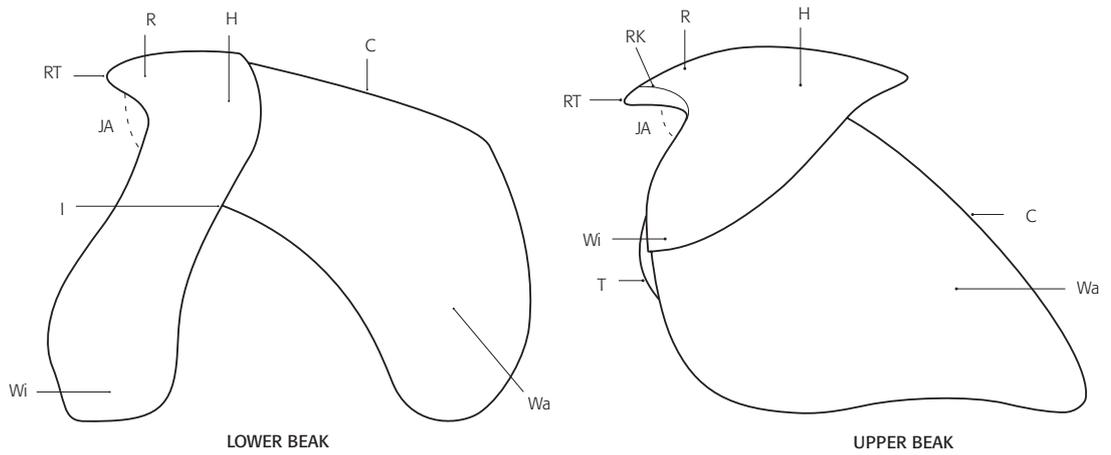


FIGURE 9. BEAK TERMINOLOGY. C. Crest; I. Intersection; H. Hood; JA. Jaw Angle; R. Rostrum; RK. Rostrum Keel; RT. Rostrum Tip; Sh. Shoulder; T. Tooth; Wa. Lateral Wall; Wi. Wing.

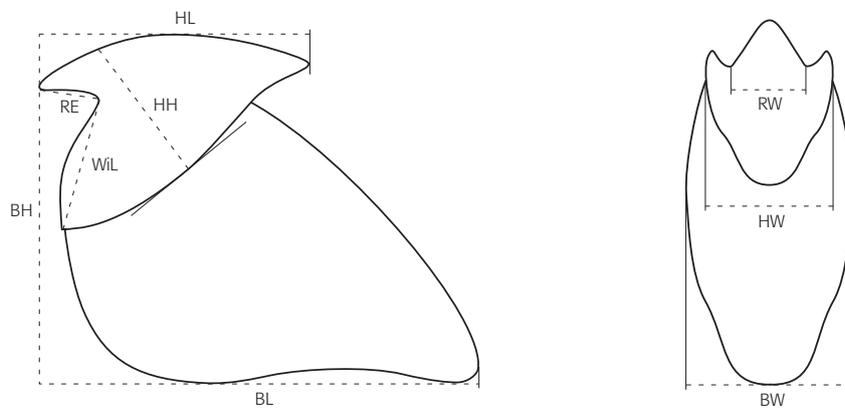


FIGURE 10. UPPER BEAK MEASURES. BL. Beak Length; BH. Beak Height; BW. Beak Width; HL. Hood Length; HH. Hood Height; HW. Hood Width; RE. Rostral Edge; RW. Rostral Width; WiL. Wing Length.

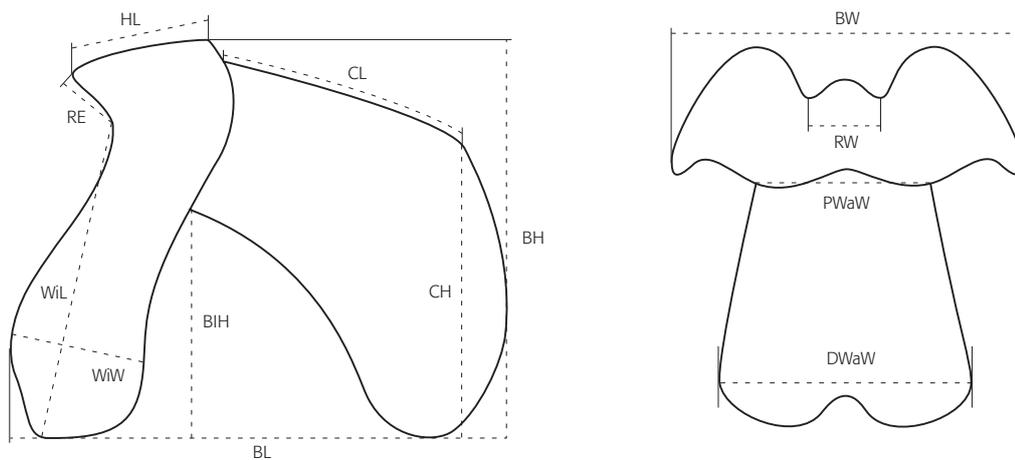


FIGURE 11. LOWER BEAK MEASURES. BL. Beak Length; BH. Beak Height; BIH. Beak Intersection Height; BW. Beak Width; CH. Crest Height; CL. Crest Length; DWaW. Distal Wall Width; HL. Hood Length; PWaW. Proximal Wall Width; RE. Rostral Edge; RW. Rostral Width; WiL. Wing Length; WiW. Wing Width.

TABLE 8. DEFINITION OF UPPER AND LOWER BEAK MEASURES (Figs 9–11).

BL–BEAK LENGTH. Length of beak base along aboral margin, measured from the tip of crest to the wings, or tooth if present in the upper beak. **BBLI–BEAK BASE LENGTH INDEX.** BBL as a percentage of ML.

BH–BEAK HEIGHT. Height of beak measured from aboral margin to the highest point of hood. **BHI–BEAK HEIGHT INDEX.** BH as a percentage of ML.

BIH–BEAK INTERSECTION POINT HEIGHT. For lower beak, the height from base to wall–wing intersection point. **BIHI–BEAK INTERSECTION POINT HEIGHT INDEX.** BIH as a percentage of ML.

BW–BEAK WIDTH. Measured between the widest points of beak. **BWI–BEAK WIDTH INDEX.** BW as a percentage of ML.

CL–CREST LENGTH. Straight-line length of the crest measured from the margin of hood to the margin of wall. **CLI–CREST LENGTH INDEX.** CL as a percentage of ML.

DWAW–PROXIMAL WALL WIDTH. For the lower beak, the width of the wall at its widest point, measured as a straight line. **DWAWI–DISTAL WALL WIDTH INDEX.** DWaW as a percentage of ML.

HL–HOOD LENGTH. Length of hood measured from rostral tip to margin of hood. **HLI–HOOD LENGTH INDEX.** HL as a percentage of ML.

PWAW–PROXIMAL WALL WIDTH. For lower beak, straight-line width of wall at its intersection points with hood. **PWAWI–PROXIMAL WALL WIDTH INDEX.** PWAW as a percentage of ML.

RW–ROSTRUM WIDTH. Widest dimension of rostrum. **RWI–ROSTRUM WIDTH INDEX.** RW as a percentage of ML.

WiL–WING LENGTH. Straight-line measurement from jaw angle to the longest point of wing. **WILI–WING LENGTH INDEX.** WiL as a percentage of ML.

WiW–WING WIDTH. Widest dimension of wing. **WiWI–WING WIDTH INDEX.** WiW as a percentage of ML.

RE–ROSTRAL EDGE. Length of rostrum measured from jaw angle to rostral tip, as a straight line. **REI–ROSTRAL EDGE INDEX.** RE as a percentage of ML.

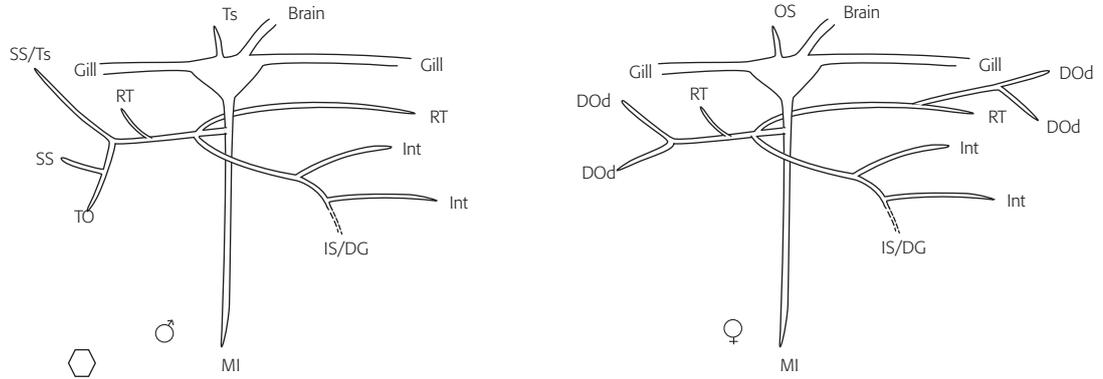


FIGURE 12. ARTERIAL SYSTEM. Male and female diagram of the arterial system main branches. **DG.** Digestive Gland; **DOD.** Distal Oviduct; **Int.** Intestine; **IS.** Ink Sac; **MI.** Mantle Interseptum; **OS.** Ovary Sac; **RT.** Renal Tissue; **SS.** Spermatophoric sac; **TO.** Terminal Organ; **TS.** Testis Sac.

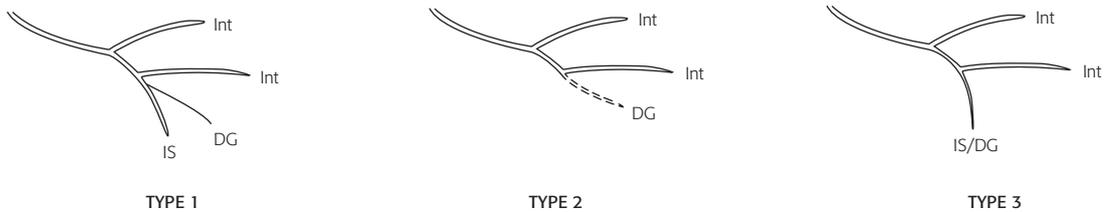


FIGURE 13. INK SAC/DIGESTIVE GLAND ARTERIAL SYSTEM BRANCH. TYPE 1. Ink sac and digestive gland arteries present. TYPE 2. Digestive gland artery away from where ink sac would be or absent. TYPE 3. Digestive gland artery positioned in the same place where ink sac would be.

2.2 MULTIVARIATE ANALYSIS

All measurements, counts, and categorical variables have been analysed using multivariate statistics. In the event that some measurements or counts could not be taken due to damage, the missing values (wherever possible, and when meaningful) were estimated as described in section 2.1. For categorical characters, a number was assigned to each character state, e.g., WAt type 1A = 1, type 1B = 1.5, type 2 = 2; ink sac, ink sac vestige, ink sac artery and duct all absent = 0; only ink sac artery or duct present = 1; ink sac vestigial (formed but not functional), duct and/or artery possibly present = 2; ink sac fully functional, with ink sac artery and duct = 3.

To determine the extent to which external, internal, lower and upper beak characters were correlated, raw measures obtained for each character were plotted against all others using the basic statistics of the software MINITAB® V. 15. As highly correlated values can be redundant, adding no relevant information or statistical support for separating groups, those with correlations greater than 0.900 were removed from analysis; the character removed was the one with highest correlations with other characters, or, should one have the same number of correlations as another, an intuitive value judgment was made as to which was of least taxonomic importance (or was most difficult to measure), and this was removed from subsequent analysis.

Multivariate analyses using PCA (Principal Component Analysis) and MDS (Multidimensional Scaling) were performed once highly correlated characters were removed from data sets; all data were logarithmically transformed to maintain allometric relationships, equalise error over large-size ranges of specimens, and reduce the effects of outlying data points (Bookstein *et al.* 1985, Strauss 1985).

The PCA correlates variables and organises samples in Euclidean space (ordination), reducing the dimensionality of the data cloud and allowing the most noticeable patterns to be observed between samples (in this case individual specimens assigned to species) (Clarke & Warwick 2001). High positive-correlated variables can be identified because of acute angles between their vectors. The further each coefficient is from zero, the greater the contribution of that character to observed groupings of taxa in space (Quinn & Keough 2002), with the length of the vector indicating the influence of the character in relation with the ordination arrangement (Väliiranta & Weckström 2007). The MDS represents the samples as points in a low-dimensional space in a way in which the relative distances apart of all points are in the same rank order as the relative dissimilarities. Therefore, points that are close together

represent species or individuals that are very similar and points that are further apart correspond to very different species or individuals (Anderson *et al.* 2008). The PCA and the MDS were run separately for each set of characters, then for data sets of all characters combined. A cluster was run when combining all sets of characters together.

SYSTEMATICS **3**

3.1 CHARACTER ASSESSMENT

Morphological classification of cephalopods is based primarily on soft-tissue measurements. Although a range of characters have been proposed as basic to descriptions of octopuses (Roper & Voss 1983), the usefulness as well as the variation of characters has not been extensively evaluated. Although indices and counts do vary between species, commonly some of them overlap and they are rarely diagnostic. This section provides information on character variation between genera, and within one genus, *Pareledone*.

EXTERNAL CHARACTERS

All non-sexual characters, with the exception of EOI (known to be significantly affected by preservation when specimens have been frozen (as applies to most specimens reported herein)) (Andrighetto & Haimovici 1988), cited as basic to octopus descriptions by Roper & Voss (1983) (hereafter 'R&V') were included in initial analyses; these comprised ALI I–IV, ASC I–IV, ASIn, AWI, FFI, FuLI, HdLI, HdWI, ML, MWI, PAI, and WDA–E; additional measurements included SR and WAt (for definitions see Table 4). High correlations were found between: the lengths of each arm (AL), ASC along all arms, PA against AW and MW, and MW against FF and ML (Table 9). Consequently, subsequent statistical analyses included the longest arm length (as opposed to all of AL I–IV), sucker count from the longest arm only (as opposed to ASC I–IV), and both MW and PA were eliminated from subsequent analyses.

For all PCAs, PC1 and PC2 explained most of the total morphological variation (Table 10), so graphics were plotted for these two principal components only.

For generic analyses, those characters that contributed most to the grouping of taxa on the basis of their total external morphology using R&V characters (Fig. 14A) were Arm Sucker Count (ASC) and Arm Length Index (ALI) for PC1, and Head Width Index (HdWI) and Free Funnel Index (FFI) for PC2 (Table 13). When Sucker rows (SR) and Web Attachment (WAtt) were

TABLE 9. CORRELATION VALUES FOR EXTERNAL MEASURES. First row shows Pearson correlation and second row P-value

	ALR_1	ALR_2	ALR_3	ALR_4	ALL_1	ALL_2	ALL_3	ALL_4	ASCR_1	ASCR_2	ASCR_3	ASCR_4	ASCL_1
ALR_2	0.996												
	0												
ALR_3	0.949	0.951											
	0	0											
ALR_4	0.971	0.97	0.986										
	0	0	0										
ALL_1	0.992	0.996	0.943	0.958									
	0	0	0	0									
ALL_2	0.996	0.992	0.953	0.979	0.983								
	0	0	0	0	0								
ALL_3	0.951	0.944	0.982	0.982	0.931	0.96							
	0	0	0	0	0	0							
ALL_4	0.978	0.975	0.978	0.992	0.968	0.983	0.974						
	0	0	0	0	0	0	0						
ASCR_1	0.712	0.69	0.658	0.655	0.683	0.692	0.659	0.629					
	0	0	0	0	0	0	0	0					
ASCR_2	0.727	0.707	0.675	0.673	0.699	0.71	0.676	0.647	0.998				
	0	0	0	0	0	0	0	0	0				
ASCR_3	0.453	0.445	0.473	0.414	0.449	0.417	0.425	0.378	0.896	0.89			
	0.006	0.007	0.004	0.012	0.007	0.011	0.01	0.023	0	0			
ASCR_4	0.75	0.723	0.699	0.708	0.708	0.741	0.712	0.681	0.983	0.986	0.831		
	0	0	0	0	0	0	0	0	0	0	0		
ASCL_1	0.695	0.679	0.638	0.633	0.677	0.673	0.631	0.607	0.994	0.994	0.912	0.97	
	0	0	0	0	0	0	0	0	0	0	0	0	
ASCL_2	0.723	0.702	0.671	0.67	0.694	0.707	0.673	0.643	0.997	0.998	0.886	0.988	0.994
	0	0	0	0	0	0	0	0	0	0	0	0	0
ASCL_3	0.625	0.593	0.635	0.623	0.572	0.622	0.664	0.581	0.945	0.945	0.848	0.958	0.925
	0	0	0	0	0	0	0	0	0	0	0	0	0
ASCL_4	0.795	0.771	0.739	0.752	0.76	0.785	0.744	0.738	0.964	0.966	0.781	0.978	0.944
	0	0	0	0	0	0	0	0	0	0	0	0	0
ASIn	0.879	0.877	0.862	0.912	0.857	0.898	0.85	0.916	0.503	0.522	0.206	0.594	0.474
	0	0	0	0	0	0	0	0	0.002	0.001	0.227	0	0.004
AW	0.59	0.621	0.762	0.726	0.621	0.605	0.7	0.705	0.198	0.22	0.134	0.235	0.195
	0	0	0	0	0	0	0	0	0.254	0.205	0.436	0.167	0.263
FF	0.764	0.785	0.86	0.854	0.778	0.775	0.828	0.848	0.312	0.339	0.172	0.368	0.304
	0	0	0	0	0	0	0	0	0.068	0.047	0.314	0.027	0.076
FuL	0.818	0.82	0.807	0.833	0.808	0.818	0.821	0.836	0.514	0.534	0.311	0.556	0.501
	0	0	0	0	0	0	0	0	0.002	0.001	0.065	0	0.002
HdL	0.625	0.642	0.654	0.657	0.641	0.618	0.683	0.664	0.124	0.145	-0.043	0.155	0.121
	0	0	0	0	0	0	0	0	0.478	0.406	0.805	0.367	0.489
HdW	0.671	0.682	0.781	0.76	0.681	0.677	0.787	0.755	0.231	0.251	0.103	0.271	0.213
	0	0	0	0	0	0	0	0	0.181	0.145	0.551	0.11	0.219
ML	0.843	0.85	0.917	0.926	0.83	0.858	0.892	0.915	0.444	0.466	0.262	0.512	0.419
	0	0	0	0	0	0	0	0	0.007	0.005	0.123	0.001	0.012
MW	0.768	0.784	0.87	0.862	0.774	0.78	0.839	0.854	0.324	0.346	0.172	0.375	0.301
	0	0	0	0	0	0	0	0	0.057	0.042	0.316	0.024	0.079
PA	0.603	0.619	0.777	0.738	0.618	0.613	0.728	0.716	0.246	0.26	0.192	0.276	0.225
	0	0	0	0	0	0	0	0	0.155	0.132	0.263	0.104	0.194
SR	0.671	0.646	0.603	0.616	0.638	0.654	0.594	0.605	0.917	0.915	0.759	0.926	0.9
	0	0	0	0	0	0	0	0	0	0	0	0	0
WAt	0.701	0.694	0.719	0.701	0.706	0.683	0.763	0.704	0.313	0.318	0.103	0.319	0.277
	0	0	0	0	0	0	0	0	0.068	0.062	0.55	0.058	0.108

TABLE 9 (CONT). CORRELATION VALUES FOR EXTERNAL MEASURES. First row shows Pearson correlation and second row P-value

	ASCL_2	ASCL_3	ASCL_4	ASIn	AW	FF	FuL	HdL	HdW	ML	MW	PA	SR
ALR_2													
ALR_3													
ALR_4													
ALL_1													
ALL_2													
ALL_3													
ALL_4													
ASCR_1													
ASCR_2													
ASCR_3													
ASCR_4													
ASCL_1													
ASCL_2													
ASCL_3	0.947												
	0												
ASCL_4	0.961	0.919											
	0	0											
ASIn	0.524	0.459	0.65										
	0.001	0.005	0										
AW	0.214	0.227	0.288	0.669									
	0.21	0.183	0.089	0									
FF	0.338	0.31	0.407	0.788	0.873								
	0.044	0.066	0.014	0	0								
FuL	0.53	0.483	0.585	0.708	0.536	0.82							
	0.001	0.003	0	0	0.001	0							
HdL	0.14	0.119	0.189	0.494	0.607	0.76	0.779						
	0.414	0.489	0.27	0.002	0	0	0						
HdW	0.242	0.282	0.319	0.573	0.76	0.853	0.822	0.884					
	0.155	0.095	0.058	0	0	0	0	0					
ML	0.462	0.447	0.558	0.875	0.795	0.931	0.852	0.707	0.821				
	0.005	0.006	0	0	0	0	0	0	0				
MW	0.336	0.324	0.437	0.776	0.863	0.947	0.809	0.787	0.879	0.952			
	0.045	0.054	0.008	0	0	0	0	0	0	0			
PA	0.254	0.285	0.319	0.631	0.92	0.893	0.63	0.671	0.822	0.847	0.925		
	0.135	0.092	0.058	0	0	0	0	0	0	0	0		
SR	0.904	0.867	0.961	0.57	0.193	0.265	0.42	-0.011	0.14	0.418	0.287	0.181	
	0	0	0	0	0.259	0.119	0.011	0.949	0.417	0.011	0.089	0.291	
WAt	0.295	0.322	0.379	0.489	0.596	0.634	0.614	0.747	0.816	0.597	0.69	0.649	0.219
	0.081	0.056	0.023	0.002	0	0	0	0	0	0	0	0	0.199

added to these basic R&V characters (Fig. 14D), the most important characters contributing to taxonomic distribution of taxa were ASC and SR (Table 14). No characters (based on vectors oriented toward a cluster) directly explained grouping of *Pareledone*, *Adelieledone*, *Bentheledone*, or *Thaumeledone* (each of these taxa has a single row of suckers); nor did any single character explain grouping of any other taxon.

Within *Pareledone* (Fig. 15), the characters that best explained observed groupings of taxa in PCA were Web Depth Index (WDI) and Mantle Length (ML) for PC1, and HdWI and FFI for PC2 (Table 12). SR and WAt were not added to these basic R&V characters because their values were the same for all specimens. No characters (based on vectors oriented toward a cluster) directly explained the grouping of species within the genus *Pareledone*, especially the morphologically variable *P. sp. nov. 1*; no single character explained the grouping of any form taxon within this genus.

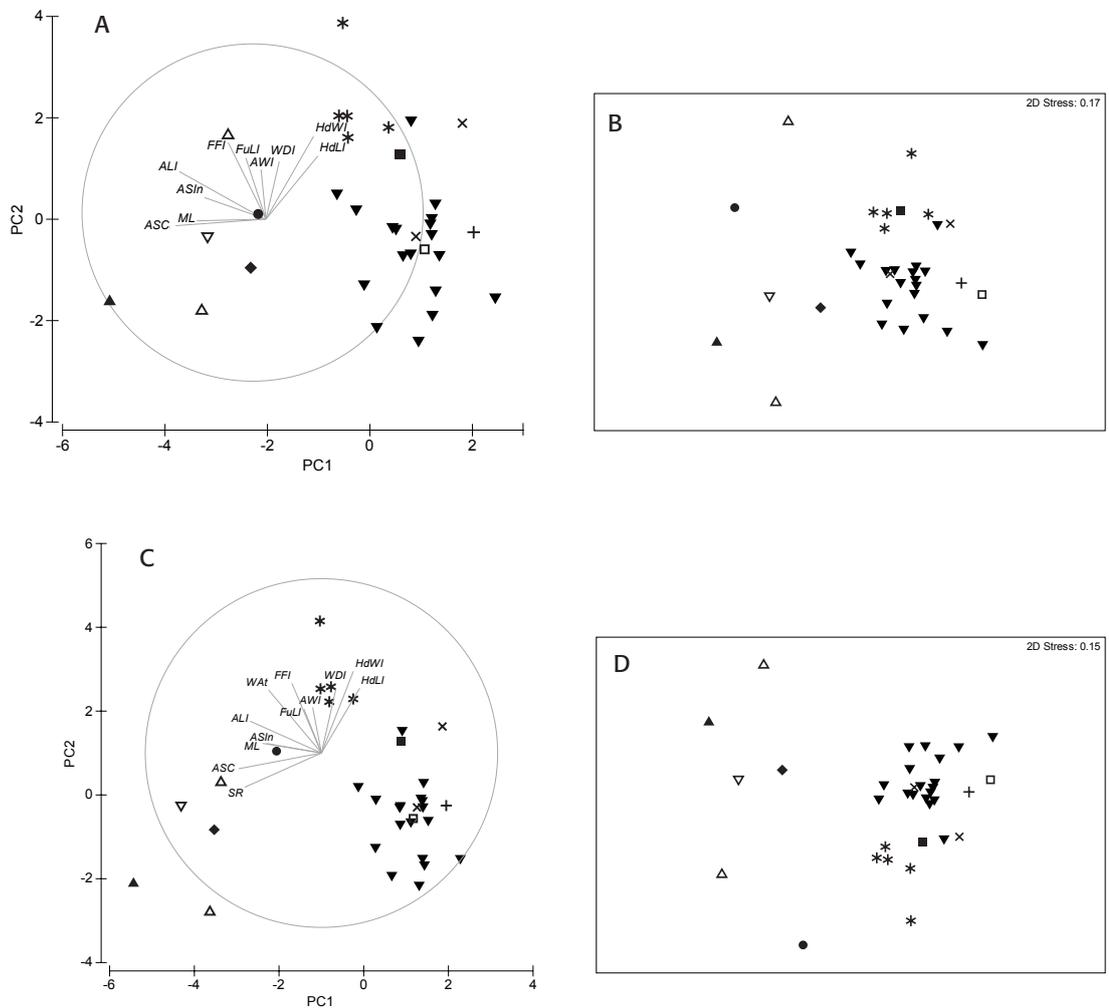


FIGURE 14. RELATIONSHIP BETWEEN GENERA, EXTERNAL CHARACTERS: A) R&V characters PCA. B) R&V characters MDS. C) R&V characters + SR and WAt PCA. D) R&V characters + SR and WAt MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, ● *Megaleledone*, △ *Octopus*, ▾ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

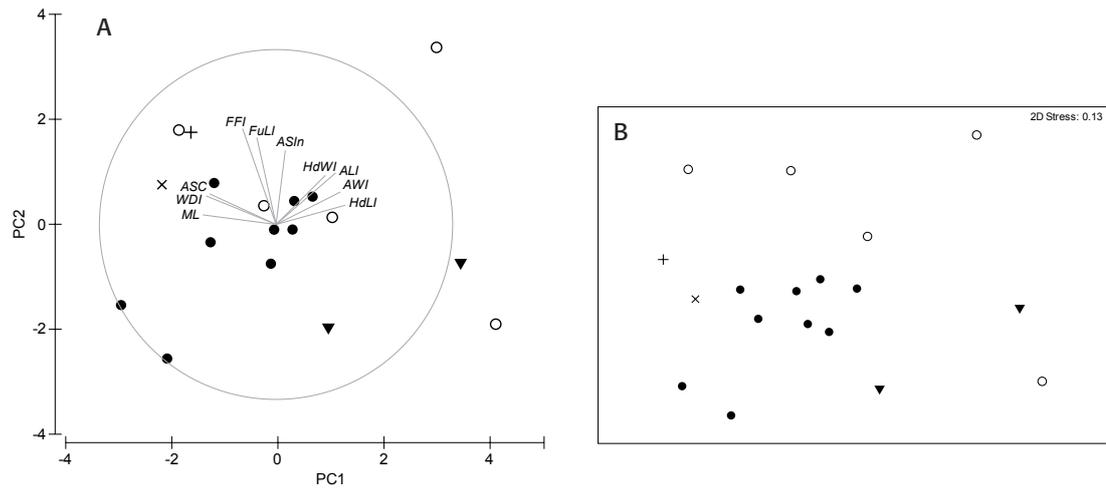


FIGURE 15. RELATIONSHIP BETWEEN SPECIES, EXTERNAL CHARACTERS (R&V ONLY). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 10. EIGENVALUES FOR PCA . External character values.

R&V at generic level

PC	Eigenvalues	%Variation	Cum.%Variation
1	2.9	29	29
2	2.12	21.2	50.2
3	1.57	15.7	65.9
4	1.41	14.1	80
5	0.685	6.9	86.9

R&V +SR, WAt at generic level

PC	Eigenvalues	%Variation	Cum.%Variation
1	3.93	32.7	32.7
2	2.44	20.4	53.1
3	1.62	13.5	66.6
4	1.44	12	78.6
5	0.975	8.1	86.7
1	3.93	32.7	32.7

R&V within genus *Pareledone* (species level)

PC	Eigenvalues	%Variation	Cum.%Variation
1	4.24	35.3	35.3
2	2.56	21.3	56.6
3	2.04	17	73.6
4	0.962	8	81.7
5	0.685	5.7	87.4

TABLE II. EIGENVECTORS (R&V GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using all R&V measures and counts at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
ALI	-0.43	0.243	ASC	HdWI
ASC	-0.53	-0.039	ALI	FFI
ASIn	-0.36	0.128	ML	HdLI
AWI	-0.028	0.294	ASIn	FuLI
FFI	-0.221	0.455	HdLI	WDI
FuLI	-0.118	0.363	HdWI	AWI
HdLI	0.305	0.374	FFI	ALI
HdWI	0.279	0.49	FuLI	ASIn
ML	-0.406	-0.01	WDI	ASC
WDI	0.078	0.342	AWI	ML

TABLE I2. EIGENVECTORS (R&V+SR, WAT, GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using all R&V measures, sucker row arrangement and web-to-arm attachment at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
SR	-0.435	-0.196	ASC	HdWI
WAt	-0.3	0.361	SR	FFI
ALI	-0.406	0.183	ALI	HdLI
ASC	-0.47	-0.09	ML	WDI
ASIn	-0.312	0.055	ASIn	WAt
AWI	-0.05	0.262	WAt	AWI
FFI	-0.168	0.4	HdLI	FuLI
FuLI	-0.099	0.252	HdWI	SR
HdLI	0.217	0.372	FFI	ALI
HdWI	0.181	0.469	FuLI	ASC
ML	-0.333	0.055	WDI	ASIn
WDI	0.082	0.365	AWI	ML

TABLE I3. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using all R&V measures and counts at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
ALI	0.338	0.295	ML	FFI
ASC	-0.376	0.175	WDI	FuLI
ASIn	0.053	0.423	HdLI	ASIn
AWI	0.365	0.186	ASC	ALI
FFI	-0.19	0.548	AWI	HdWI
FuLI	-0.108	0.497	ALI	AWI
HdLI	0.392	0.11	HdWI	ASC
HdWI	0.28	0.281	FFI	WDI
ML	-0.415	0.055	FuLI	HdLI
WDI	-0.396	0.164	ASIn	ML

INTERNAL CHARACTERS

Internal organs are not always considered to be diagnostic for cephalopod taxa, although they are routinely described and illustrated in species descriptions. Certain organ systems have been proposed as valuable for systematics and/or phylogeny (Mangold & Young 1998), but to the best of my knowledge, their utility has not been critically evaluated.

Internal measures analysed include AOesL, ASGL, BBL, DG(GD), GillC, IntL, ISP, OesTL, PSGL, and SpCL (for definitions see Table 5). High correlations were found between BBL, SpCL and StL; DG(GD) against IntL, SpCL and StL; IntL against SpC and StL; and SpCL against StL (Table 14). Consequently DG(GD), SpCL and StL were eliminated from subsequent statistical analyses.

For all the PCAs, PC1 and PC2 explained most of the total morphological variation (Table 15), so graphics were plotted using these two principal components only.

For generic analyses, those characters that contributed most to the grouping of taxa on the basis of internal characters (Fig. 16) were Anterior Salivary Gland Length Index (ASGLI) and Ink Sac presence (ISpres) for PC1, and Intestinal Length Index (IntLI) and Anterior Oesophagus Length Index (AOesLI) for PC2 (Table 16). However, no characters (based on vectors oriented toward any cluster of taxa) directly explained their grouping, with the possible exception of *Pinoctopus*, distinct from all others on grounds of high gill lamellae counts and great oesophagus length; and *Octopus (s.l.)* and *Enteroctopus*, distinct from others because of anterior and posterior salivary gland lengths.

Within the genus *Pareledone*, those characters that contributed most to the grouping of taxa in plots (Fig. 17) were Buccal Bulb Length Index (BBLI) and ASGLI for PC1, and Gill Lamellae Count (GillC) and Posterior Salivary Gland Length Index (PSGLI) for PC2 (Table 17). However, again, no characters (based on vectors oriented toward a cluster) directly explained grouping of any species within this genus.

TABLE 14. CORRELATION VALUES FOR INTERNAL MEASURES. First row shows Pearson correlation and second row P-value.

	AOesL	ASGL	BBL	DG(GD)	GilC	InTL	ISP	OesTL	PSGL	SpCL
ASGL	0.627									
	0									
BBL	0.636	0.779								
	0	0								
DG(GD)	0.783	0.814	0.932							
	0	0	0							
GilC	0.572	0.794	0.546	0.649						
	0	0	0.001	0						
InTL	0.795	0.778	0.897	0.954	0.64					
	0	0	0	0	0					
ISP	0.022	0.434	0.079	0.085	0.385	0.06				
	0.9	0.009	0.652	0.629	0.022	0.731				
OesTL	0.639	0.647	0.438	0.563	0.549	0.52	0.014			
	0	0	0.008	0	0.001	0.001	0.937			
PSGL	0.323	0.667	0.313	0.39	0.643	0.321	0.332	0.805		
	0.058	0	0.067	0.02	0	0.06	0.052	0		
SpCL	0.683	0.857	0.948	0.918	0.686	0.902	0.182	0.53	0.436	
	0	0	0	0	0	0	0.294	0.001	0.009	
StL	0.623	0.808	0.951	0.909	0.641	0.913	0.202	0.352	0.297	0.966
	0	0	0	0	0	0	0.246	0.038	0.083	0

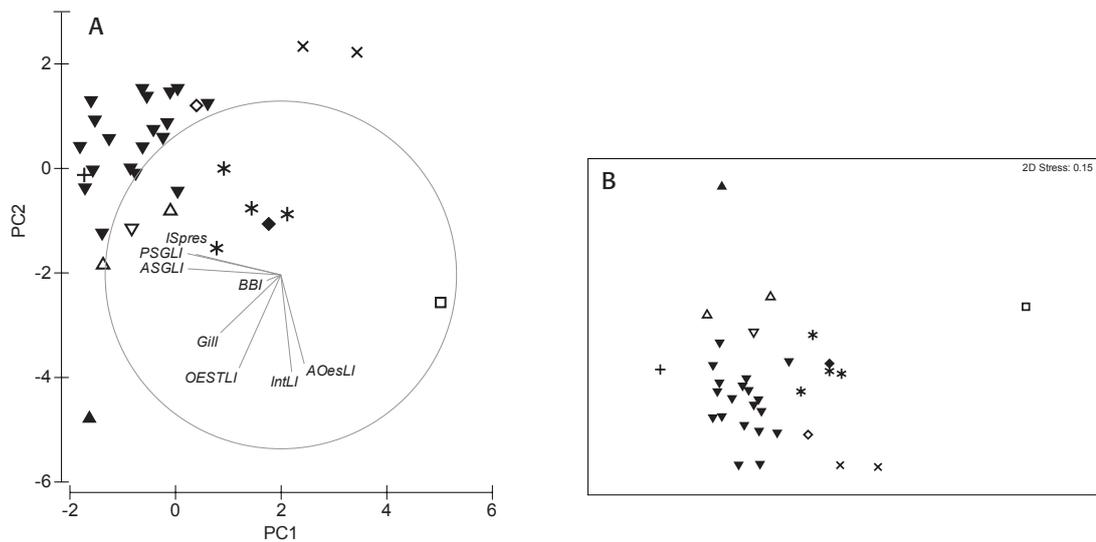


FIGURE 16. RELATIONSHIP BETWEEN TAXA, INTERNAL CHARACTERS AT GENERIC LEVEL. A) PCA. B) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, △ *Octopus*, ▼ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

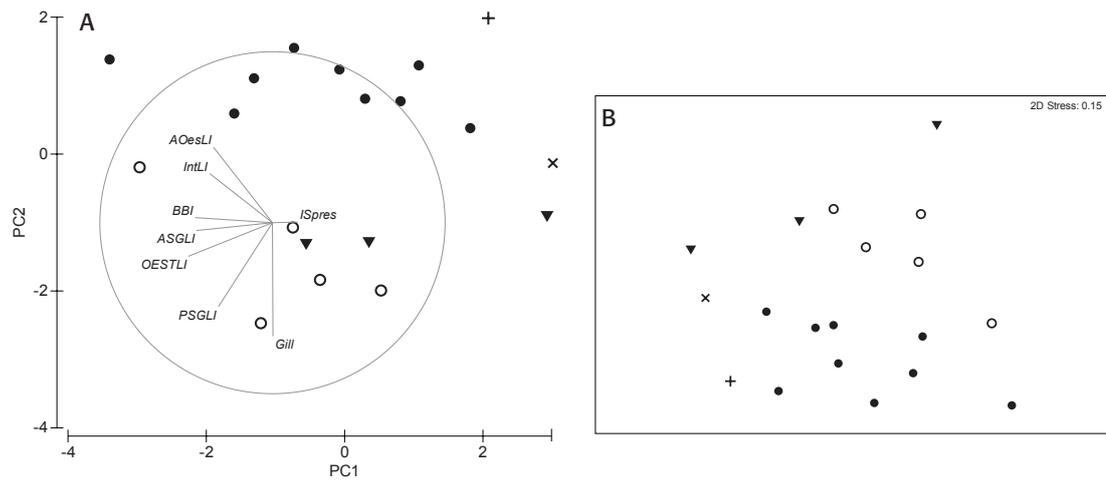


FIGURE 17. RELATIONSHIP BETWEEN TAXA, INTERNAL CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 15. EIGENVALUES FOR PCA

Internal characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	2.73	34.1	34.1
2	2.08	26	60.1
3	1.32	16.5	76.6
4	0.716	9	85.6
5	0.536	6.7	92.3

Internal characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	3.1	38.7	38.7
2	1.95	24.4	63.1
3	1.26	15.7	78.8
4	0.751	9.4	88.2
5	0.377	4.7	92.9
1	3.93	32.7	32.7

TABLE 16. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using internal characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	0.043	-0.538	ASGLI	IntLI
ASGLI	-0.511	0.153	ISpres	AOesLI
BBI	-0.105	0.025	PSGLI	OESTLI
Gill	-0.364	-0.287	Gill	Gill
IntLI	-0.035	-0.561	OESTLI	PSGLI
ISpres	-0.502	0.092	BBI	ASGLI
OESTLI	-0.305	-0.473	AOesLI	ISpres
PSGLI	-0.497	0.239	IntLI	BBI

TABLE 17. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using internal characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	-0.36	-0.375	BBI	Gill
ASGLI	-0.463	0.021	ASGLI	PSGLI
BBI	-0.476	-0.025	OESTLI	AOesLI
Gill	0.044	0.614	AOesLI	ISpres
IntLI	-0.333	-0.145	IntLI	OESTLI
ISpres	-0.197	-0.331	PSGLI	IntLI
OESTLI	-0.444	0.299	ISpres	BBI
PSGLI	-0.284	0.511	Gill	ASGLI

EXTERNAL AND INTERNAL CHARACTERS COMBINED

Intuitively, analysis of data sets combining both internal and external characters should improve resolution (separation) of taxa at both the generic and specific levels. To this end these two data sets were combined, with analyses performed including all internal and external measures with the exception of those already eliminated on grounds of their highly correlated nature (Tables 9, 14). For all the PCAs, PC1 and PC2 explained most of the total morphological variation (Table 18), so graphics were plotted using these two principal components only.

For generic analyses, those characters that contributed most to the grouping of taxa on the basis of combined internal and external anatomy (Fig. 18) were: Arm Sucker Count (ASC), Sucker Rows (SR), Arm Length Index (ALI) and Intestine Length Index (IntLI) for PC1, and Ink Sac presence (ISpres), Posterior Salivary Gland Length Index (PSGLI), Web Depth Index (WDI) and Anterior Salivary Gland Length Index (ASGLI) for PC2 (Fig. 18, Table 19). Unlike previous analyses, some characters (based on vectors oriented toward any cluster of taxa) now directly explain observed groupings of genera, such as HdLI, HdWI, and WDI for *Benthoctopus*, and ASGLI, PSGLI, ISPres and gill lamellae counts for *Octopus*, *Pinnoctopus* and *Enteroctopus*; however, no char-

acters appear to explain the observed grouping of taxa that possess a single row of suckers (i.e., *Pareledone*, *Bentheledone*, *Adelieledone* and *Graneledone*).

Within the genus *Pareledone* alone, those characters that explained the most variability in distribution of taxa within this genus in plots (Fig. 19) were Oesophagus Total Length Index (OesTLI), PSGLI, Head Width Index (HdWI) and Head Length Index (HdLI) for PC1, and IntLI, AOesLI, ISpres and WDI for PC2 (Fig. 19, Table 20). Quite unlike previous analyses, many characters (based on vectors oriented toward any cluster of taxa) could now be used to explain observed grouping of form taxa (= species) within the genus *Pareledone*, although there is considerable individual variation in external and internal morphology within any form taxon, to such a degree that none forms any tight grouping in space.

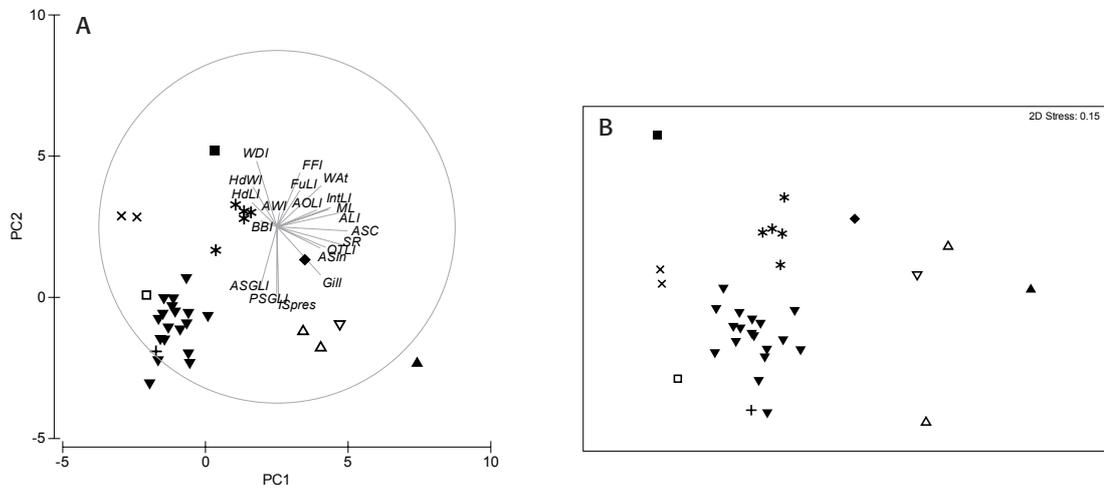


FIGURE 18. EXTERNAL AND INTERNAL CHARACTERS AT GENERIC LEVEL. A) PCA. B) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, △ *Octopus*, ▼ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

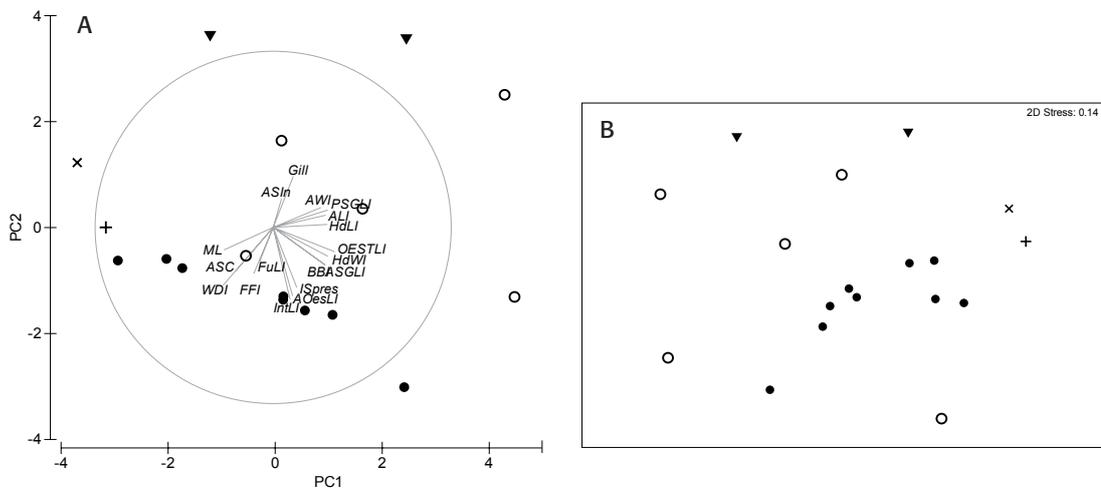


FIGURE 19. EXTERNAL AND INTERNAL CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 18. EIGENVALUES FOR PCA. Internal and external character values.

External and internal characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	5.4	27	27
2	4.14	20.7	47.7
3	3.02	15.1	62.8
4	1.6	8	70.8
5	1.27	6.4	77.2

External and internal characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	5.85	32.5	32.5
2	3.41	18.9	51.4
3	2.36	13.1	64.6
4	1.97	11	75.5
5	1.39	7.7	83.2
1	3.93	32.7	32.7

TABLE 19. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using internal and external characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	0.223	0.096	ASC	ISpres
ASGLI	-0.099	-0.362	SR	PSGLI
BBI	-0.091	0.035	ALI	WDI
Gill	0.245	-0.273	IntLI	ASGLI
IntLI	0.303	0.11	ML	FFI
ISpres	0.009	-0.405	OESTLI	Gill
OESTLI	0.273	-0.116	WAt	WAt
PSGLI	-0.002	-0.38	Gill	HdWI
SR	0.366	-0.102	ASIn	FuLI
WAt	0.249	0.234	AOesLI	HdLI
ALI	0.351	0.079	HdLI	ASIn
ASC	0.397	-0.023	HdWI	OESTLI
ASIn	0.244	-0.121	FFI	IntLI
AWI	0.014	0.08	FuLI	SR
FFI	0.13	0.308	WDI	ML
FuLI	0.129	0.207	ASGLI	AOesLI
HdLI	-0.141	0.138	BBI	AWI
HdWI	-0.135	0.226	AWI	ALI
ML	0.291	0.099	ISpres	BBI
WDI	-0.115	0.373	PSGLI	ASC

TABLE 20. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using internal and external characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	0.109	-0.39	OESTLI	IntLI
ASGLI	0.29	-0.211	PSGLI	AOesLI
BBI	0.293	-0.215	HdWI	ISpres
Gill	0.113	0.289	HdLI	WDI
IntLI	0.095	-0.408	ALI	Gill
ISpres	0.133	-0.341	BBI	FFI
OESTLI	0.346	-0.139	ASGLI	ASC
PSGLI	0.307	0.099	WDI	BBI
ALI	0.295	0.069	ML	ASGLI
ASC	-0.21	-0.246	AWI	FuLI
ASIn	0.046	0.162	ASC	HdWI
AWI	0.268	0.113	ISpres	ASIn
FFI	-0.109	-0.262	Gill	OESTLI
FuLI	-0.076	-0.194	AOesLI	ML
HdLI	0.304	0.017	FFI	AWI
HdWI	0.307	-0.164	IntLI	PSGLI
ML	-0.276	-0.128	FuLI	ALI
WDI	-0.281	-0.328	ASIn	HdLI

BEAKS

Identification of octopod beaks is problematic due to their conservative morphology (Smale *et al.* 1993). Despite this their description is recommended in the guidelines for descriptions of octopuses by Roper & Voss (1983).

Aspects of beak morphology have been long used to estimate body weight and mantle length of prey in predator/prey gut content studies; the most frequently cited measure has been lower beak rostral length. Upper beaks of both octopuses and squids are seldom described, figured or used to reconstruct aspects of species' size or weight (Clarke 1980, Clarke 1986).

Herein the standard measure used to create ratios for statistical analyses is Beak Base Length (BL). The objective was to identify those characters/ratios of importance for differentiating taxa, not for estimating aspects of body size. As an aside, in some cases Hood Length (HL) and Crest Length (CL) have proven to be more accurate for this purpose (Wolff 1984).

LOWER BEAK CHARACTERS

Beak measures analysed include BL, BH, BIH, BW, CH, CL, DWaW, HL, PWaW, RE, RW and WiL (for definitions see Table 8). High correlations were found between many of these measurements, and were eliminated from subsequent analysis; only five characters proved to be

independent of each other (not correlated): BL, CH, RW, WiL and RE (Table 21) with further statistical analyses limited to these measures only.

As with all previous analyses, PC1 and PC2 explained most of the total morphological variation (Table 22), so graphics were plotted using these two principal components only.

For generic analyses, those characters that contributed most to the grouping of taxa on the basis of lower beak morphology (Fig. 20) were RWI and REI for PC1, and CHI and BLI for PC2 (Table 23). Like the previous analysis, some characters (based on vectors oriented toward any cluster of taxa) do directly explain observed grouping of genera (although there is considerable individual variation in beak morphology within the genus *Pareledone* alone); however no genus, with the possible exception of *Graneledone*, forms any tight/coherent grouping in space.

Within the genus *Pareledone*, those characters that contributed the most to the grouping of taxa in plots (Fig. 21) were BLI and REI for PC1, and RWI and CHI for PC2 (Table 24). As for the previous analysis, some characters do directly explain observed grouping of form taxa within the genus *Pareledone*, but the variation in beak morphology within this genus is such that few form taxa (for which there were sufficient numbers of specimens) form any tight/coherent grouping in space.

TABLE 21. CORRELATION VALUES FOR LOWER BEAK MEASURES. First row shows Pearson correlation and second row P-value.

	BL	BH	BIH	BW	CH	CL	DWaW	HL	PWaW	RE	RW	WiL
BH	0.992											
	0											
BIH	0.959	0.967										
	0	0										
BW	0.986	0.975	0.946									
	0	0	0									
CH	0.778	0.79	0.798	0.771								
	0	0	0	0								
CL	0.977	0.977	0.967	0.962	0.756							
	0	0	0	0	0							
DWaW	0.913	0.918	0.91	0.929	0.854	0.874						
	0	0	0	0	0	0						
HL	0.946	0.937	0.888	0.947	0.796	0.899	0.936					
	0	0	0	0	0	0	0					
PWaW	0.944	0.945	0.912	0.961	0.813	0.901	0.975	0.957				
	0	0	0	0	0	0	0	0				
RE	0.891	0.897	0.902	0.906	0.777	0.873	0.914	0.901	0.922			
	0	0	0	0	0	0	0	0	0			
RW	0.894	0.899	0.927	0.906	0.743	0.914	0.84	0.8	0.865	0.828		
	0	0	0	0	0	0	0	0	0	0		
WiL	0.964	0.958	0.948	0.962	0.737	0.95	0.912	0.914	0.93	0.891	0.875	
	0	0	0	0	0	0	0	0	0	0	0	
WiW	0.92	0.911	0.936	0.929	0.716	0.912	0.877	0.836	0.899	0.904	0.906	0.952
	0	0	0	0	0	0	0	0	0	0	0	0

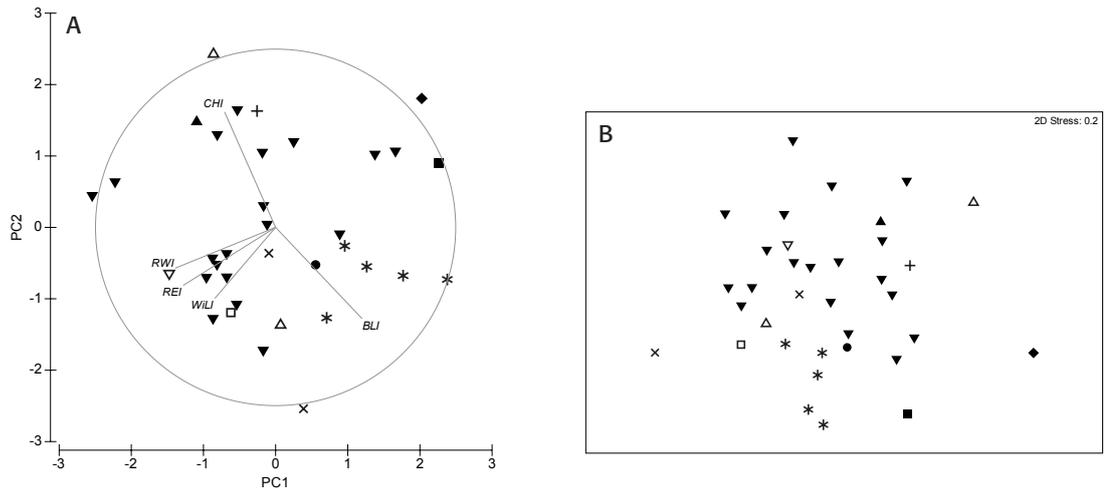


FIGURE 20. LOWER BEAK CHARACTERS AT GENERIC LEVEL. A) PCA. B) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, △ *Octopus*, ▼ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

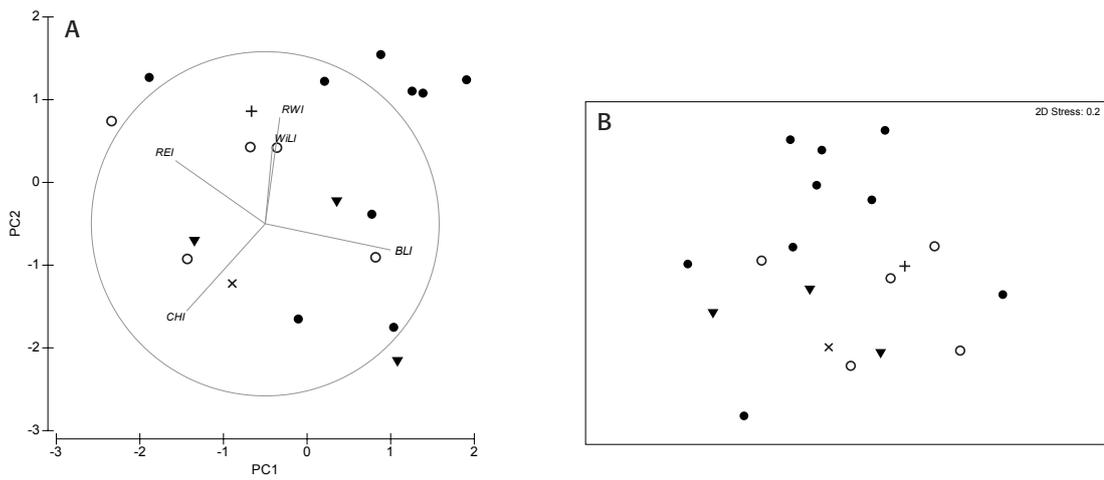


FIGURE 21. LOWER BEAK CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 23. EIGENVALUES FOR PCA. Lower beak character values.

Lower beak characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	1.42	28.4	28.4
2	1.34	26.8	55.2
3	0.872	17.4	72.6
4	0.788	15.8	88.4
5	0.581	11.6	100

Lower beak characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	1.46	29.3	29.3
2	1.41	28.1	57.4
3	0.92	18.4	75.8
4	0.829	16.6	92.4
5	0.38	7.6	100
1	3.93	32.7	32.7

TABLE 22. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using lower beak characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
BLI	0.48	-0.512	RWI	CHI
CHI	-0.283	0.648	REI	BLI
RWI	-0.558	-0.229	BLI	WiLI
WiLI	-0.337	-0.399	WiLI	REI
REI	-0.513	-0.326	CHI	RWI

TABLE 24. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using lower beak characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
BLI	0.721	-0.152	BLI	RWI
CHI	-0.452	-0.507	REI	CHI
RWI	0.084	0.619	CHI	WiLI
WiLI	0.041	0.45	RWI	REI
REI	-0.516	0.367	WiLI	BLI

UPPER BEAK CHARACTERS

Augmenting traditionally measured lower beak characters are the upper beak characters comprising: BL, BH, BW, HH, HL, HW, RE, RW and WiL (for definitions see Table 8); of these BH was correlated with all; BW was correlated with all characters except RW and WiL; HH with all characters except RW; HL with all characters except RW and WiL; HW with all characters except RE; RE with all characters except RE, RW and WiL; RW with all except BL, BH, HH and HW; and WiL with all except BL, BH, HH and HW (Table 25). Therefore, further statistical analyses of these data were limited to the largely (one exception) independent measures of BL, RE, RW and WiL. Although BL was correlated with each character, it was not removed because beak indices were calculated using BL as the standard measurement in all ratios.

As typical of these analyses, PC1 and PC2 explained most of the variability in distribution of taxa between plots (Table 26), so graphics have been plotted using these two principal components only.

For generic analyses, those characters that explained the most variability in distribution of taxa in plots (Fig. 22) were REI and BLI for PC1, and RWI and WiLI for PC2 (Table 27). As for the previous analysis, some of these upper beak characters (based on vectors oriented toward any cluster of taxa) do directly explain the observed grouping of genera, although there is considerable individual variation in beak morphology within the genus *Pareledone* alone that no genus, again with the possible exception of *Graneledone*, forms any tight/coherent grouping in space.

Within the genus *Pareledone*, those characters that explained the most variability in distribution of taxa in the arrangement of the plots for this genus (Fig. 23) remained BLI and REI for PC1, and RWI and CHI for PC2 (Table 28). As for the previous analysis, some characters do directly explain observed grouping of form taxa within the genus *Pareledone*, but the variation in beak morphology within this genus, particularly for *P. spp. nov.* 1 and 3, is such that few form taxa (for which there were sufficient numbers of specimens) form any tight/coherent grouping in space.

TABLE 25. CORRELATION VALUES FOR UPPER BEAK MEASURES. First row shows Pearson correlation and second row P-value

	BL	BH	BW	HH	HL	HW	RE	RW
BH	0.982							
	0							
BW	0.942	0.951						
	0	0						
HH	0.951	0.951	0.946					
	0	0	0					
HL	0.916	0.921	0.92	0.966				
	0	0	0	0				
HW	0.969	0.96	0.931	0.952	0.924			
	0	0	0	0	0			
RE	0.907	0.927	0.901	0.918	0.911	0.886		
	0	0	0	0	0	0		
RW	0.942	0.921	0.888	0.885	0.868	0.928	0.841	
	0	0	0	0	0	0	0	
WLI	0.931	0.947	0.855	0.906	0.877	0.914	0.845	0.878
	0	0	0	0	0	0	0	0

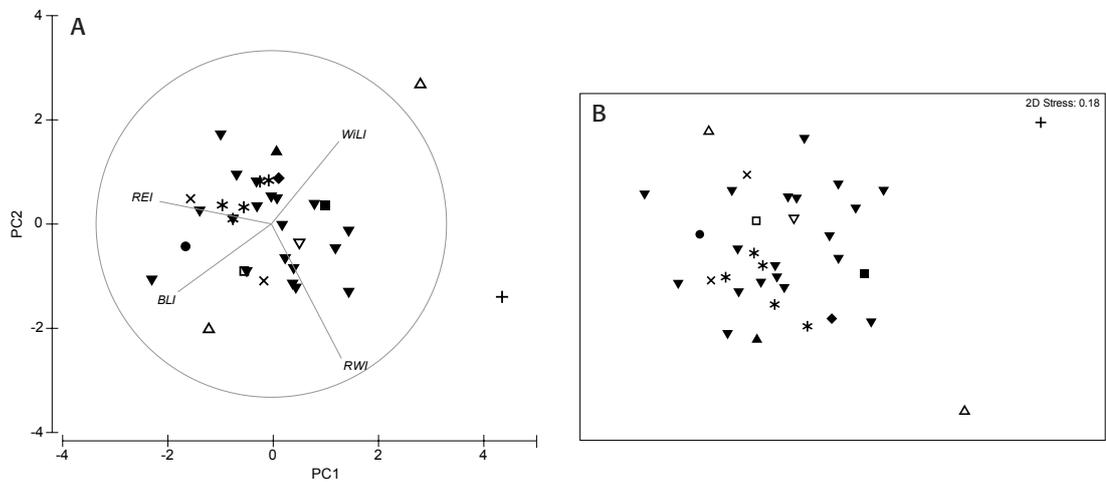


FIGURE 22. UPPER BEAK CHARACTERS AT GENERIC LEVEL. A) PCA. B) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Granelledone*, △ *Octopus*, ▲ *Pinnoctopus*, × *Thaumeledone*.

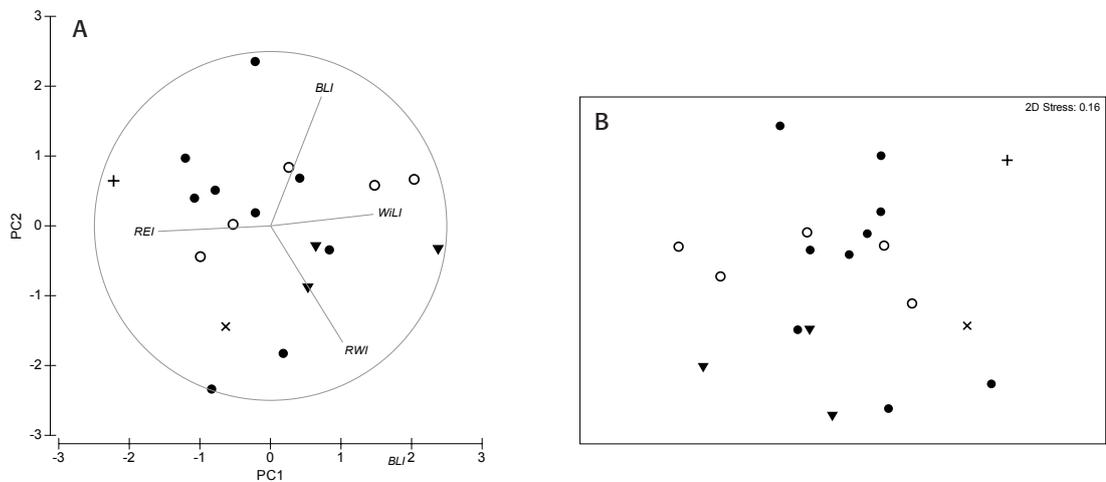


FIGURE 23. UPPER BEAK CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▽ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 26. EIGENVALUES FOR PCA. Upper beak character values.

Upper beak characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	1.57	39.2	39.2
2	0.983	24.6	63.8
3	0.87	21.8	85.6
4	0.578	14.4	100
5	0.581	11.6	100

Upper beak characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	1.35	33.7	33.7
2	1.19	29.7	63.4
3	0.833	20.8	84.2
4	0.631	15.8	100
5	0.38	7.6	100

TABLE 27. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using upper beak characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
BLI	-0.533	-0.392	REI	RWI
REI	-0.637	0.13	BLI	WiLI
RWI	0.4	-0.776	RWI	BLI
WiLI	0.387	0.477	WiLI	REI

TABLE 28. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using upper beak characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
BLI	0.289	0.742	REI	BLI
REI	-0.639	-0.031	WiLI	RWI
RWI	0.409	-0.667	RWI	WiLI
WiLI	0.584	0.067	BLI	REI

UPPER AND LOWER BEAK CHARACTERS

All upper and lower beak measurements (excluding the ones that were highly correlated in Table 21 and Table 25) have been included in the following analysis.

Again, PC1 and PC2 explained most of the variability in distribution of taxa between plots (Table 29); accordingly graphics for these two principal components only have been plotted.

For generic analyses, those characters that explained the most variability in distribution of taxa in plots (Fig. 24) were BLI for both beaks, Upper Beak REI and Lower Beak CHI for PC1, and Upper Beak WiLI, and Lower Beak REI, RWI and WiLI for PC2 (Table 30). As for

the previous analysis, some of these combined beak characteristics (based on vectors oriented toward any cluster of taxa) do directly explain observed grouping of genera, such as upper beak RWI for *Adelieledone*, and upper and lower beak BBLI for *Graneledone*, but again there is such variation in beak morphology within the genus *Pareledone* that few genera form any tight/coherent grouping in space.

Within the genus *Pareledone*, those characters that explained the most variability in distribution of taxa in plots (Fig. 25) were Upper Beak BLI and RWI, and Lower Beak CHI and BLI for PC1, and RWI and WiLI for both beaks for PC2 (Table 31). Similar to the previous analysis for upper beak morphology only, combined upper and lower beak morphologies do directly explain observed grouping of form taxa within the genus *Pareledone*, but the variation in beak morphology within this genus, in particular for *P. spp. nov. 1* and 3, is so great that few form taxa (for which there were sufficient numbers of specimens) form any tight/coherent grouping in space.

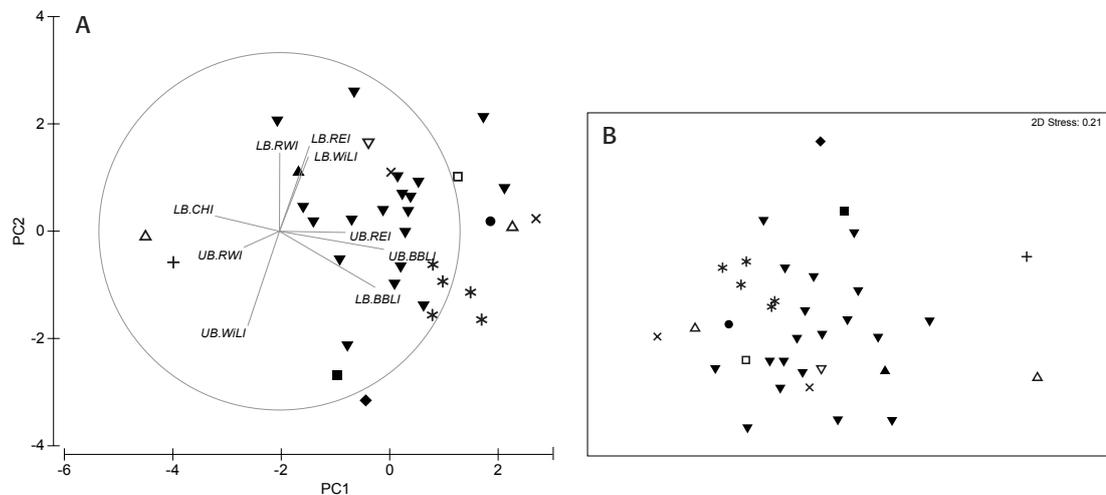


FIGURE 24. UPPER AND LOWER BEAK CHARACTERS AT GENERIC LEVEL. A) PCA. B) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, △ *Octopus*, ▼ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

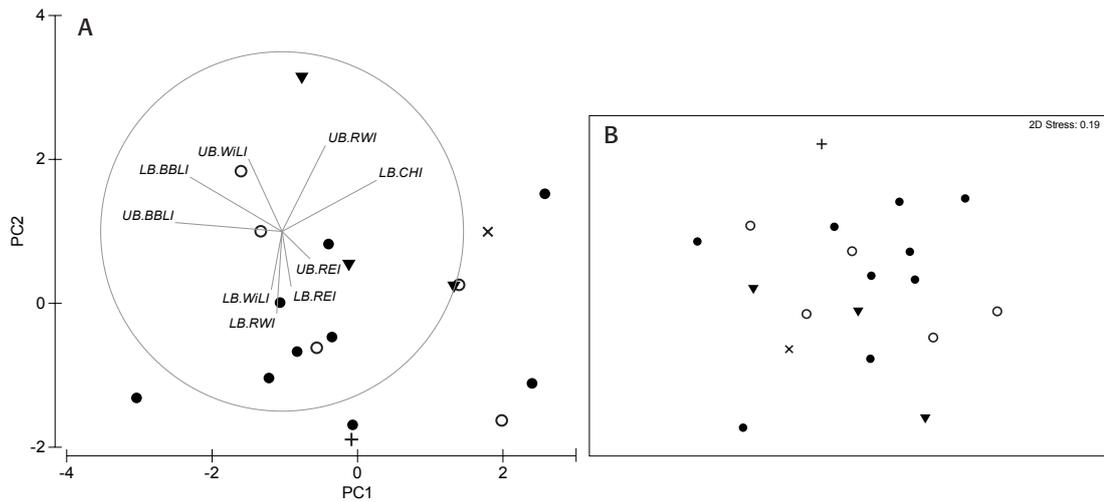


FIGURE 25. UPPER AND LOWER BEAK CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 29. EIGENVALUES FOR PCA. All beak character values.

Upper and lower beak characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	2.49	27.7	27.7
2	1.74	19.4	47.1
3	1.21	13.4	60.5
4	1.05	11.6	72.1
5	0.9	10	82.2

Upper and lower beak characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	2.3	25.5	25.5
2	1.83	20.3	45.8
3	1.25	13.9	59.7
4	1.07	11.9	71.6
5	0.962	10.7	82.3

TABLE 30. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using all beak characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
UB.BLI	0.579	-0.101	UB.BLI	UB.WILI
UB.REI	0.366	-0.006	LB.BLI	LB.REI
UB.RWI	-0.197	-0.09	UB.REI	LB.RWI
UB.WILI	-0.176	-0.529	LB.CHI	LB.WILI
LB.BLI	0.53	-0.314	UB.RWI	LB.BLI
LB.CHI	-0.357	0.086	UB.WILI	UB.BLI
LB.RWI	0.001	0.44	LB.REI	UB.RWI
LB.WILI	0.16	0.417	LB.WILI	LB.CHI
LB.REI	0.166	0.478	LB.RWI	UB.REI

TABLE 31. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using all beak characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
LB.BLI	-0.508	0.303	UB.BLI	UB.RWI
LB.CHI	0.522	0.285	LB.CHI	LB.RWI
LB.RWI	-0.03	-0.457	LB.BLI	UB.WiLI
LB.WiLI	-0.06	-0.324	UB.RWI	LB.WiLI
LB.REI	0.05	-0.307	UB.WiLI	LB.REI
UB.BLI	-0.589	0.049	UB.REI	LB.BLI
UB.REI	0.154	-0.153	LB.WiLI	LB.CHI
UB.RWI	0.239	0.479	LB.REI	UB.REI
UB.WiLI	-0.185	0.404	LB.RWI	UB.BBLI

INTERNAL, EXTERNAL AND BEAK CHARACTERS

Each of the datasets used, in isolation (external, internal and beak characters), has been suggested, to provide some valuable information for differentiating genera and species. This section evaluates whether the combined value of these data sets exceeds their individual value for differentiating taxa at generic and specific levels.

All internal, external and beak measures (excluding the ones that have proven to be highly correlated in previous analyses, Tables 9, 14, 21, 25) have been included in this final analysis.

As usual in these analyses, PC1 and PC2 explained most of the variability in distribution of taxa between plots (Table 32), and graphics have been accordingly limited to these two principal components.

For generic analyses, those characters that explain the most variability in distribution of taxa in plots (Fig. 26) were: Arm Sucker Count (ASC), number of sucker rows (SR), Gill Lamellae Count (GillC) and Mantle Length (ML) for PC1, and Web-arm-attachment (WAt), Ink Sac presence (ISpres), Free Funnel Length Index (FFI) and Arm Length Index (ALI) for PC2 (Table 33). Unlike all previous analyses, almost all genera form relatively tight, coherent groups, with most being characterised (based on vectors oriented toward any cluster of taxa) by a suite of characters; the single-most different taxon is *Octopus*, with two species attributed to this genus not clustering remotely together (in fact these two species appear more different to each other than many other genera are to each other).

Within the genus *Pareledone*, those characters that explain the most variability in distribution of taxa in plots (Fig. 27) differed considerably from those that differentiated genera, being Oesophagus Total Length Index (OesTLLI), Upper Beak Length Index (BLI), Mantle Length (ML) and Head Length Index (HdLI) for PC1, and for PC2 Anterior Oesophagus Length Index (AOesLI),

Intestine Length Index (IntLI), Lower Beak Rostrum Width Index (RWI) and Web Depth Index (WDI) (Table 34). Although form taxa in this genus clearly separate from one another, variation in the external and internal anatomies, and their upper and lower beak morphologies is so great for any single one, particularly those best represented in the data set (*P. spp. nov.* 1 and 3) that relatively tight, coherent groups of form taxa are not apparent.

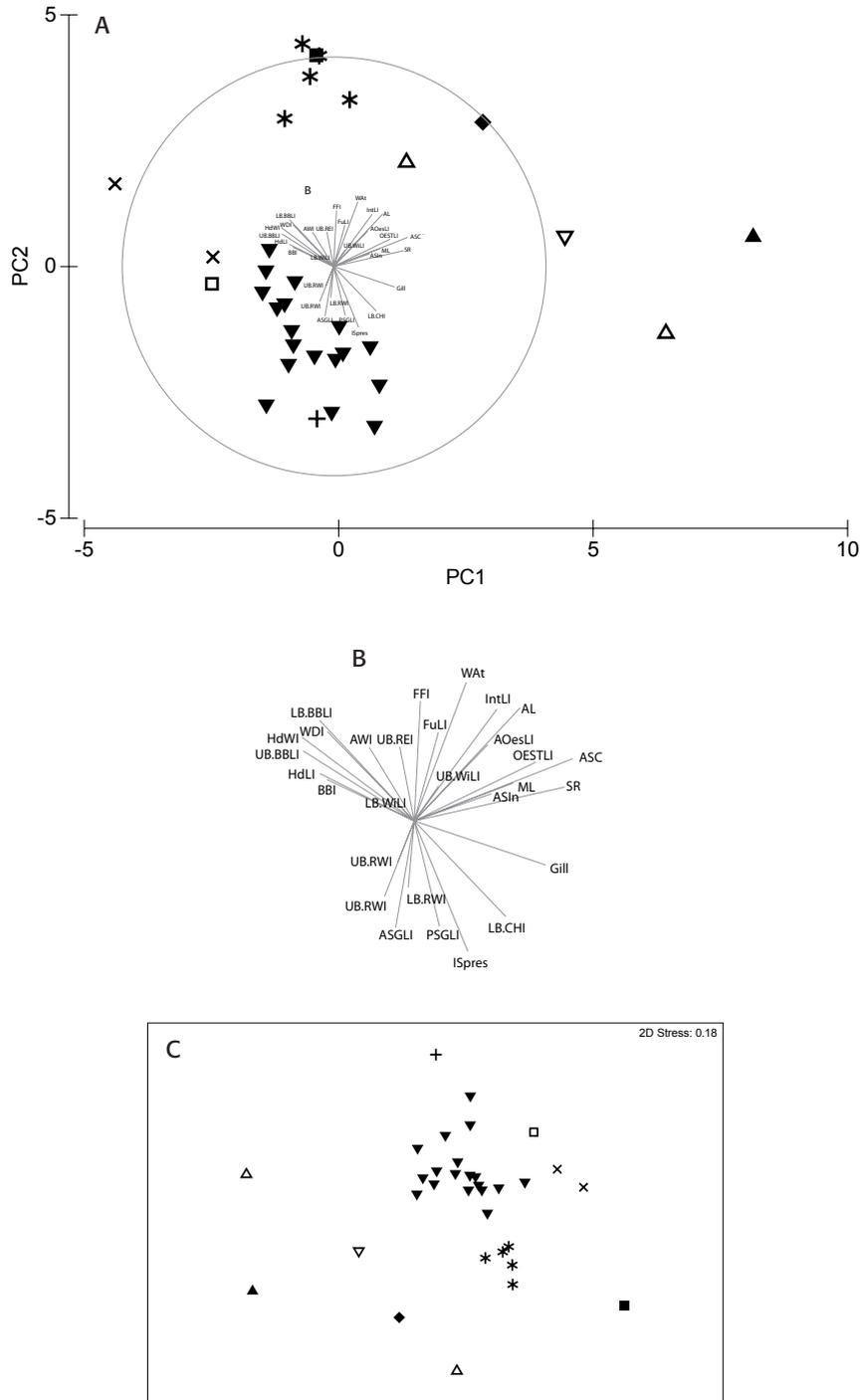


FIGURE 26. ALL CHARACTERS AT GENERIC LEVEL. A) PCA. B) PCA vectors (zoom). C) MDS. + *Adelieledone*, □ *Bentheledone*, ◆ *Muusoctopus*, ■ *Cirroctopus*, ▽ *Enteroctopus*, * *Graneledone*, △ *Octopus*, ▼ *Pareledone*, ▲ *Pinnoctopus*, × *Thaumeledone*.

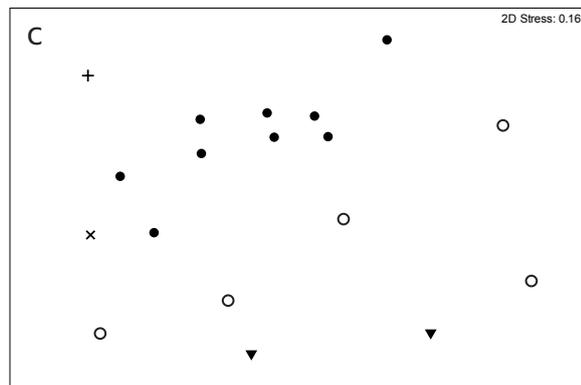
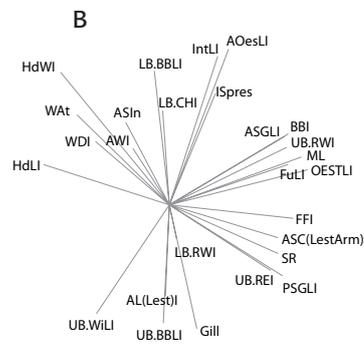
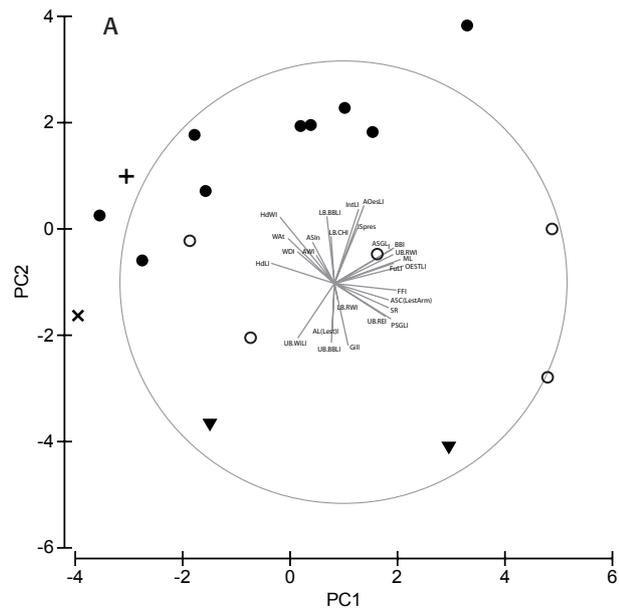


FIGURE 27. ALL CHARACTERS WITHIN GENUS *Pareledone* (SPECIES LEVEL). A) PCA. B) PCA vectors (zoom). C) MDS. ● *Pareledone* sp. nov.1, + *Pareledone* sp. nov.2, ○ *Pareledone* sp. nov.3, ▼ *Pareledone* sp. nov.4, × *Pareledone* sp. nov.5.

TABLE 32. EIGENVALUES FOR PCA. All character values.

All characters at generic level			
PC	Eigenvalues	%Variation	Cum.%Variation
1	5.84	20.2	20.2
2	5.3	18.3	38.4
3	3.92	13.5	51.9
4	2.66	9.2	61.1
5	1.63	5.6	66.7

All characters within genus <i>Pareledone</i> (species level)			
PC	Eigenvalues	%Variation	Cum.%Variation
1	7.6	28.1	28.1
2	4.81	17.8	45.9
3	3.06	11.3	57.3
4	2.59	9.6	66.8
5	1.99	7.4	74.2

TABLE 33. EIGENVECTORS (GENERIC LEVEL). Coefficients in the linear combinations of variables making up PC's using all characters at generic level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	0.166	0.174	ASC	WAt
ASGLI	-0.042	-0.243	SR	ISpres
BBI	-0.197	0.095	Gill	FFI
Gill	0.296	-0.1	ML	ALI
IntLI	0.187	0.255	HdWI	IntLI
ISpres	0.121	-0.298	UB.BLI	ASGLI
OESTLI	0.223	0.087	ALI	PSGLI
PSGLI	0.057	-0.241	OESTLI	LB.BLI
SR	0.339	0.077	HdLI	LB.CHI
WAt	0.117	0.317	LB.BLI	WDI
AL(Lest)I	0.239	0.258	LB.CHI	FuLI
ASC(LestArm)	0.358	0.142	BBI	HdWI
ASIn	0.174	0.062	WDI	AOesLI
AWI	-0.101	0.168	IntLI	LB.REI
FFI	0.014	0.274	ASIn	UB.REI
FuLI	0.054	0.203	AOesLI	AWI
HdLI	-0.213	0.108	ISpres	UB.BLI
HdWI	-0.253	0.191	WAt	LB.RWI
ML	0.274	0.134	AWI	ASC
WDI	-0.196	0.204	LB.REI	ML
UB.BLI	-0.251	0.16	PSGLI	HdLI
UB.REI	-0.033	0.169	UB.WILI	Gill
UB.RWI	-0.037	-0.094	FuLI	BBI
UB.WILI	0.055	0.08	ASGLI	UB.RWI
LB.BLI	-0.213	0.23	UB.RWI	OESTLI
LB.CHI	0.206	-0.218	UB.REI	UB.WILI
LB.RWI	-0.013	-0.152	FFI	SR
LB.WILI	-0.013	0.011	LB.RWI	ASIn
LB.REI	-0.067	-0.172	LB.WILI	LB.WILI

TABLE 34. EIGENVECTORS (SPECIES LEVEL). Coefficients in the linear combinations of variables making up PC's using all characters at species level. Most significant characters for each PCA are presented in descending order according to their values.

Character	PC1	PC2	Desc. order PC1	Desc. order PC2
AOesLI	0.128	0.341	OesTLI	AOesLI
ASGLI	0.249	0.15	UB.BLI	IntLI
BBI	0.257	0.156	ML	LB.RWI
Gill	0.059	-0.271	HdLI	WDI
IntLI	0.105	0.325	BBI	Gill
ISpres	0.1	0.244	HdWI	UB.RWI
OESTLI	0.299	0.077	LB.BLI	ISpres
PSGLI	0.245	-0.155	ASGLI	LB.CHI
ALI	0.235	-0.106	PSGLI	LB.WiLI
ASC	-0.2	0.197	WDI	ASIn
ASIn	-0.009	-0.2	ALI	ASC
AWI	0.235	-0.072	AWI	FFI
FFI	-0.095	0.18	UB.WiLI	BBI
FuLI	-0.079	0.123	ASC	PSGLI
HdLI	0.268	-0.029	UB.REI	ASGLI
HdWI	0.257	0.089	LB.CHI	UB.WiLI
ML	-0.273	0.088	AOesLI	UB.REI
WDI	-0.236	0.29	IntLI	LB.BLI
UB.BLI	0.286	0.105	ISpres	FuLI
UB.REI	-0.16	0.139	FFI	ALI
UB.RWI	-0.013	-0.258	FuLI	UB.BLI
UB.WiLI	0.219	-0.143	Gill	HdWI
LB.BLI	0.254	0.126	LB.RWI	ML
LB.CHI	-0.158	-0.238	LB.WiLI	OesTLI
LB.RWI	-0.033	0.293	LB.REI	LB.REI
LB.WiLI	-0.015	0.206	UB.RWI	AWI
LB.REI	0.015	-0.074	ASIn	HdLI

3.2 DESCRIPTIONS

CIRRATA

Cirroctopus Naef, 1923

The classification of cirrate octopuses requires significant revision (O'Shea 1999, Piertney *et al.* 2003), as no classification of them is presently universally accepted. The phylogenetic placement of the genus *Cirroctopus* is not without exception, and only recently was this genus removed from synonymy of *Opisthoteuthis* and recognised as a discrete taxon (O'Shea 1999); O'Shea (*ibid.*) attributed this genus to the Opisthoteuthidae, although more recent molecular evidence (Piertney *et al.* (2003)) suggests that this taxon might more appropriately be accommodated within a separate family. O'Shea (1999) examined type materials of the four species attributed to this genus, *C. antarctica* (Kubodera & Okutani, 1986) *C. glacialis* (Robson, 1930), *C. hochbergi* (O'Shea, 1999), *C. mawsoni* (Berry, 1917), and concluded that the Southern Ocean taxa *C. antarctica*, *C. mawsoni* and *C. glacialis* were likely synonyms (with *C. mawsoni* being the oldest available name for this complex) thus recognising two species only, *C. mawsoni* (Berry) and *C. hochbergi* O'Shea.

DIAGNOSIS (amended from O'Shea 1999). Large robust-bodied cirrates. Fins terminal, massive, paddle-like. Four or six areolar spots present, one supra- 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 along all arms; cirrus length equivalent to greatest sucker diameter. Mantle not tightly enveloping funnel. Interpallial septum membranous, oriented along antero-posterior axis of mantle cavity, extending entire mantle cavity length without perforation. Shell robust, vacuolated; surface texture irregular, saddle short, thick; wings spike-like; muscle insertion points poorly developed. Digestive gland entire (not bilobed); intestine long, 2–2.5 times oesophagus length. 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).

TYPE SPECIES. *Stauroteuthis mawsoni* Berry, 1917 (by designation Naef 1923).

Cirroctopus hochbergi O'Shea, 1999

DIAGNOSIS. As for genus; body mauve to purple, with four areolar spots; arm sucker count to 88, sucker diameter 3.5–6.3 mm; gills with 7 or 8 lamellae per demibranch. (Description [pending])

of recently collected specimens of *C. mawsoni* from the Ross Sea will serve to further differentiate these two taxa).

RECOGNISED DISTRIBUTION. 35°57–40°09'S, 176°30–179°2'E, 700–1350 m, excluding the most shallow record (non-closing trawl net) of NZOI Stn Z8322 (500–1000 m) and NZOI Stn Z8320 (600–950 m), in which specimens were most likely captured toward the deeper end of the trawl range (O'Shea 1999). Locally extinct throughout much of this range (see Remarks).

SYNONYMY. *Cirroctopus hochbergi* O'Shea, 1999: 35–45, Figs 23–25.

MATERIAL EXAMINED. 1 specimen (♀): NMNZ M.100327, ML 107 mm, ♀, 38°37.2'S, 178°44.2'E, 929–1067 m, 25/09/1989, FRV *James Cook* Stn J9/41/89.

DESCRIPTION. Adults of moderate size, ML to 160 mm, TL to 493 mm (Fig. 29; Tables 35, 39). Cephalopedal mass extensively gelatinous, bell-shaped. Head narrower than mantle (HdLI 21, HdWI 31), delimited from mantle by poor pre-ocular constriction. Post-orbital constriction marked. Fins massive, muscular, paddle-like and long, deflected downwards, meeting across anterior-most 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. Arm length about 46–78% TL; arm formula variable, frequently I.II.III.IV or II.I.III.IV, with arms IV usually shortest, arms I and II longest. Suckers uniserial; arm sucker counts to 49–88, increasing with mantle length; no suckers abruptly enlarged, ASIn 3.5–6.3; suckers attain their greatest diameter at a level of the third or fourth sucker from beaks. Cirri commence between suckers 1 and 2 on all arms, gradually increasing in length to suckers 9 or 10, thereafter gradually decreasing in length to arm tip; cirri present to arm tip. Arm-to-web attachment type 2; depth about 45–66% longest arm length; web formula variable, generally A.B.C.D.E, with A and B deepest and E most shallow. Mantle with 4 areolar spots, one at the base of either fin, one below each eye. Dorsal surface of mantle, head, and arms dark purple; margin of orbits pale pink; ventral surfaces of mantle and fins slightly paler than dorsal surfaces; oral surfaces of web sectors A, B, and C (to 16–18th sucker) and D and E (to 12 or 13th sucker) deep mauve to purple; aboral web surfaces of sectors A–E to margin of web and oral surfaces of arms I–IV and suckers, pale mauve.

Shell (Fig. 28D) V-shaped, 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,

TABLE 35. EXTERNAL CHARACTER INDICES.
C. hochbergi.

	NMNZ M.100327 ML 120 mm
Sex	F
ALI1R	163.6
ALI2R	186.9
ALI3R	172.9
ALI4R	172.9
ALI1L	177.6
ALI2L	168.2
ALI3L	177.6
ALI4L	149.5
MAI	53.5
MWI	102.8
ASIn	2.3
AWI	18.7
EOI	11.2
FFI	28.0
FuLI	37.4
HdLI	32.7
HdWI	60.7
MWI	102.8
OAI	97.4
PAI	40.2
WDI	55.0

TABLE 36. INTENRAL CHARACTER INDICES.
C. hochbergi.

	NMNZ M.100327 ML 120 mm
AOesLI	65.4
ASGLI	5.1
BBI	22.4
DG(GD)	42.1
DGI	37.4
IntLI	107.5
OESTLI	56.1
PSGLI	0.0
SpCI	15.9
StI	18.7

TABLE 37. LOWER BEAK INDICES.
C. hochbergi.

	NMNZ M.100327 ML 120 mm
BLI	17.8
BHI	60.5
BIHI	15.8
BWI	89.5
CLI	36.8
DWaWI	39.5
HLI	31.6
PWaWI	42.1
REI	5.3
RWI	13.2
WiLI	57.9
WiWI	31.6

TABLE 38. UPPER BEAK INDICES.
C. hochbergi.

	NMNZ M.100327 ML 120 mm
BLI	14.0
BHI	103.3
BWI	60.0
CHI	16.7
HHI	50.0
HLI	100.0
REI	13.3
RPI	13.3
RWI	33.3
WiLI	60.0

TABLE 39. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *C. hochbergi*.

	NMNZ M.100327 ML 120 mm
Gender	F
ML	120
AL1R	335
AL2R	320
AL3R	310
AL4R	308
AL1L	330
AL2L	325
AL3L	302
AL4L	296
ASC1R	181
ASC2R	171
ASC3R	162
ASC4R	160
ASC1L	161
ASC2L	160
ASC3L	164
ASC4L	184
SD	6
AW	20
EO	12
FFL	30
FuL	40
GilC I	70
GilC O	70
HdL	35
HdW	65
MW	110
PA	43
TL	260
WAt	type 2
WDA	100
WDBR	90
WDBL	80
WDCR	110
WDCL	100
WDDR	90
WDDL	105
WDE	52
FINL	60
FINW	30

TABLE 40. INTERNAL CHARACTER RAW MEASURES. *C. hochbergi*.

	NMNZ M.100327 ML 120 mm
AOesL	70
ASGL	6
BBL	24
DGL	40
DGW	45
DG(GD)	45
InTL	115
ISpres	no
OesTL	60
PSGL	0
SpCL	17
StL	20

TABLE 41. REPRODUCTIVE SYSTEM RAW MEASURES. *C. hochbergi*.

	NMNZ M.100327 ML 120 mm
DOdL	13
DOdW	6
OSL	20
OSW	15
OdTL	69
OdBL	11
OdBW	11
POdL	33
POdW	4

TABLE 42. UPPER BEAK RAW MEASURES. *C. hochbergi*.

	NMNZ M.100327 ML 120 mm
BL	15
BH	16
BW	9
CH	3
HH	8
HL	15
HW	9
RE	2
RP	2
RW	5
WiL	9

TABLE 43. LOWER BEAK RAW MEASURES. *C. hochbergi*.

	NMNZ M.100327 ML 120 mm
BL	19
BH	12
BIH	3
BW	17
CH	3
CL	7
DWaW	8
HL	6
PWaW	8
RE	1
RW	3
WiL	11
WiW	6

spike-like, tapering to acute points at about 20° angle from saddle; muscle insertion points poorly developed.

Mantle cavity with non-perforated interpallial septum, extending as a thin membrane the anterior-posterior length of the mantle cavity, completely compartmentalising left and right sides of the cavity. Gills of 'half-orange' type, with 7 or 8 lamellae per demibranch. Female reproductive system (Fig. 28C, Table 41) with proximal oviduct almost three to five times length of distal oviduct; distal oviduct narrower than oviducal ball; oviducal ball striated with 2 chambers, distal chamber slightly wider than proximal chamber.

Alimentary canal (Fig. 28A; Tables 36, 40) with buccal bulb length about 22% ML. Anterior salivary glands of length about 23% BBL. Posterior salivary glands absent. Oesophagus without crop. Spiral caecum greatest dimension about 85% that of stomach, lacking volutions. Intestine considerably longer than oesophagus, about 192% its length (OesTL). Digestive gland circular, without hepatic peaks or lobes; greatest dimension 42% ML; pancreas well developed. Radula and ink sac absent.

Lower beak (Fig. 28B left; Tables 37, 43) with black hood and brown border; oral margins of wings black, extending past middle of wing, forming clearly marked diagonal line; brown colour to aboral margin; lateral walls black, slightly lightening to brown toward margin; margins translucent. Beak base length 18% ML, height 61% BBL. Hood with rounded crest, elevated from wings. Rostrum tip triangular, blunt, slightly protruded, 3% BBL. Jaw angle 104°. Wing length 58% BBL. Lateral wall crest rounded, with weak basal notch. Proximal and distal walls of comparable width.

Upper beak (Fig. 28B right, Table 38, 42) with black hood wall black, gradually transitioning to brown toward the margin; all margins translucent. Beak base length 14% ML, of comparable height to length, BH 103% BBL. Hood very deep, with squared crest. Rostrum triangular, with blunt tip, slightly orally deflected; length protrusion 13% BBL; wing length protrusion of comparable length to rostrum. Jaw angle 105°. Lateral wall crest rounded, without basal notch, parallel-sided.

REMARKS. This species was included in these analyses as an outlier, and is the only cirrate taxon described herein (all other taxa examined for this research belong to the family Octopodidae).

The taxonomic status of the three described Antarctic species of *Cirroctopus* requires re-evaluation, now that additional, relatively comprehensive collections of species referable to this genus exist for this region. The genus *Cirroctopus* presently is recognised from the Southern Ocean and central and northeastern New Zealand waters. Sadly, the sole New Zealand species is considered endangered ('Nationally Critical' status, Hitchmough (2002), if not already locally extinct throughout most of its recognised range as a consequence of deep-sea fishing activities). Today specimens of this species are very rarely caught and retained in commercial fisheries by-catch — the sole source of all specimens thus-far known, with the exception of one specimen recovered from the stomach contents of a sperm whale 'harvested' in New Zealand waters during the last commercial whaling season in this country (O'Shea 1999).

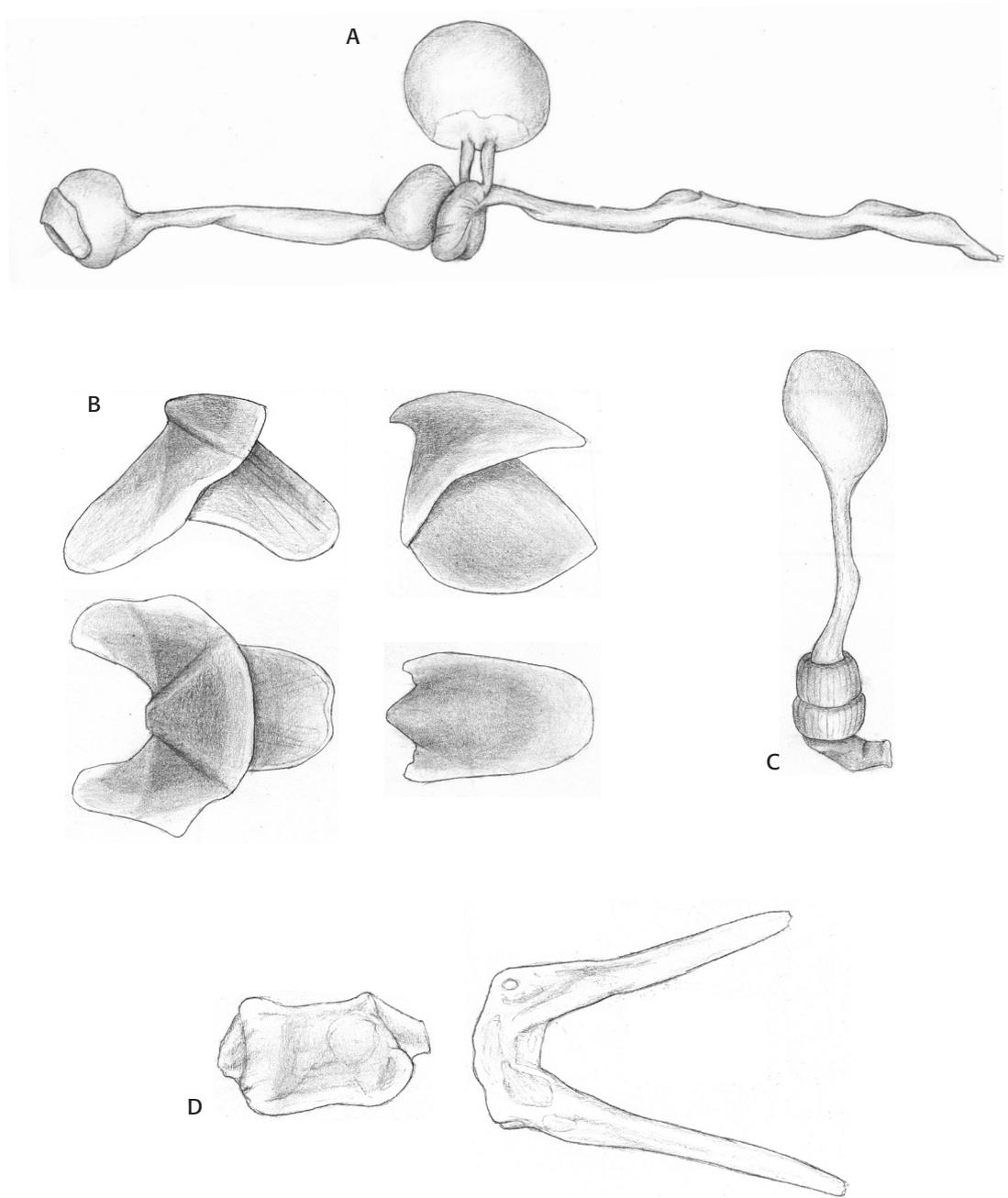


FIGURE 28. *Cirroctopus hochbergi* (NMNZ M.100327, ML 120 mm). A) Alimentary canal. B) Upper and lower beaks. C) Female reproductive system. D) Shell.



FIGURE 29. *Cirroctopus hochbergi* (NMNZ M.100327, ML 120 mm). Dorsal and ventral view of preserved specimen.

INCIRRATA

Adelieledone Allcock, Hochberg, Rodhouse & Thorpe, 2003

The genus *Adelieledone* was erected to accommodate what Lu & Stranks (1994) considered to be two problematic taxa attributed to the genus *Pareledone*: *P. polymorpha* (Robson, 1930) and *P. adeliæana* (Berry, 1917). These species differed from all other taxa attributed to *Pareledone* in their relative mantle size, head width, beak shape and size, and arm and hectocotylus details. *A. polymorpha* is thought to be restricted to western Antarctica while *A. adeliæana* to eastern Antarctica (Allcock *et al.* 1997, Allcock *et al.* 2003b).

DIAGNOSIS. Benthic octopodids, ML to 90 mm. Mantle saccular; arms with small (ASI 4–10) uniserial suckers; third right arm of males hectocotylised, with end clearly differentiated into ligula and calamus; ligula large (LLI 10–16), ligula groove long, well marked and deep with transverse ridges; arm tips not otherwise modified. Web moderately deep (WDI 20–40); funnel organ W-shaped; gills well developed, with 6–8 lamellae; ink sac present, variably reduced; crop well developed, posterior salivary glands large (length of posterior salivary glands up to twice that of buccal mass); rostral tip of lower beak sharp; radula with nine elements, rachidian with large central cusp and sometimes minor lateral cusps. Chromatophores present within connective tissue covering dorsal surface of digestive gland; stylets absent; two short, longitudinal integumentary ridges on mid-dorsal posterior mantle. Diverticulum of penis not coiled; spermatophores moderately long (SpLI 60–80) and slender (Allcock *et al.* 2003).

TYPE SPECIES. *Moschites adeliæana* Berry, 1917; designation Allcock *et al.* 2003.

Adelieledone adeliæana (Berry, 1917)

DIAGNOSIS. Rostral tip of lower beak sharp, deflected upwards. Ligula long (LLI 10–15) with well-marked groove crossed by approximately eight transverse ridges. Arms short (mean ALI LI 155, LII 162, LIII 165, LIV 168). Hectocotylised arm with 22–28 suckers. Gills with 6 or 7 lamellae per demibranch. Mantle with widely scattered papillae on dorsal surface; ventral surface smooth (modified from Allcock *et al.* 2003b).

RECOGNISED DISTRIBUTION. Eastern Antarctica, from off Dronning Maud Land (67°52'S, 33°14'E,) (Taki 1961); off Enderby Land (65°50–56'S, 50°34–52'E,); off MacRobertson Land (66°53–67°15'S,

68°56–70°44'E.); off Amery Ice Shelf, Prydz Bay (66°48–67°56'S, 71°56–76°24'E.); off Mertz Glacier (66°55'S, 145°21'E.) (Berry 1917), and the Ross Sea (74°43.57–42.63'S, 167°0.79–1.50'E.), from 139–930 m, bottom temperatures of –2.2––1.7°C, and substrata ranging from mud to sand with pebbles, rocks, sponges, bryozoans and gorgoneans.

SYNONYMY.

Moschites adolieana Berry, 1917: 17, figs 10–13; pl. XI, fig. 5; pl. XII, figs 6–8.

Pareledone adolieana (Berry, 1917) — Robson 1932: 278; Lu & Stranks 1994: 222, figs 1, 9a–d.

Pareledone umitakae Taki, 1961: 308, figs 9–16, pl. 3.

MATERIAL EXAMINED. 1 specimen (♂): NIWA 44133, ML 45 mm ♂, 74°43.57–42.63'S, 167°0.79–1.50'E, 916–930 m, 12/02/2008, RV *Tangaroa* Stn TAN0802/41.

DESCRIPTION. Modified from Lu & Stranks (1994). Adults medium-sized (ML to 55 mm, TL to 160 mm) (Fig. 32, Table 44, 48). Mantle elongate-ovoid (MWI 63–91). Head wide, usually slightly wider than mantle (HWI 67.8–91.6), delimited from it by moderate pre-ocular constriction; orbits large, bulbous, with narrow interspace between both eyes mid-dorsally. Funnel large, stout, bluntly tapered (FuLl 29–41.3). Web-to-arm attachment type 2; depth about 21–32% longest arm length; web formula usually B=C=D.A.E. Arms short, stout, tapering to narrow tips. Arm length formula IV.III.II.I (ALI 221–144). Suckers uniserial; non-hectocotylised arm sucker counts 34–39; ASI 4.3–10.1, no suckers abruptly enlarged; suckers attain their greatest diameter at fourth sucker from beaks. Third right arm of males hectocotylised, shorter than its opposite arm (OAI 81–98), with 24 suckers; hectocotylised portion with ligula 10–15% hectocotylised arm length; ligula groove long, well marked and deep, with approximately 8 transverse ridges; calamus long, pointed, 45–47% ligula length (Fig. 31E).

Large unbranched primary papillae present in ocular region, with one especially enlarged as a super-ocular papilla. Two short, longitudinal integumentary ridges present on mid-dorsal-posterior surface of mantle; ventro-lateral integumentary ridge around mantle present.

Gills with 6 lamellae per inner and outer demibranch. Terminal organ wide and shorter than diverticulum. Male spermatophoric gland I longer than II; spermatophoric sac shorter than both spermatophoric glands (Fig. 31D, Table 50).

Alimentary canal (Fig. 31A; Tables 45, 49) with buccal bulb length 24% ML. Anterior salivary glands of length 16% buccal bulb length (BBL). Posterior salivary glands broadly triangular to ovoid, their greatest dimension slightly longer than buccal bulb length (113% BBL, 28% ML).

TABLE 44. EXTERNAL CHARACTER INDICES.
A. adeliaeana.

	NIWA 44133 ML 45 mm
Sex	M
ALI1R	144.4
ALI2R	157.8
ALI3R	166.7
ALI4R	180.0
ALI1L	148.9
ALI2L	160.0
ALI3L	175.6
ALI4L	182.2
MAI	54.9
MWI	106.7
ASIn	5.6
AWI	20.0
EOI	17.8
FFI	13.3
FuLI	28.9
HdLI	35.6
HdWI	71.1
MWI	106.7
OAI	94.9
PAI	55.6
WDI	25.6

TABLE 45. INTERNAL CHARACTER INDICES.
A. adeliaeana.

	NIWA 44133 ML 45 mm
AOesLI	33.3
ASGLI	15.6
BBI	24.4
DG(GD)	48.9
DGI	44.4
ISTLI	*
ISL	35.6
ISA	11.1
OESTLI	80.0
PSGLI	27.8
SpCI	20.0
StI	22.2

TABLE 46. LOWER BEAK INDICES.
A. adeliaeana.

	NIWA 44133 ML 45 mm
BLI	13.3
BHI	66.7
BIHI	25.0
BWI	91.7
CLI	50.0
DWaWI	75.0
HLI	33.3
PWaWI	50.0
REI	8.3
RWI	16.7
WiLI	58.3
WiWI	25.0

TABLE 47. UPPER BEAK INDICES.
A. adeliaeana.

	NIWA 44133 ML 45 mm
BLI	12.2
BHI	109.1
BWI	100.0
CHI	27.3
HHI	36.4
HLI	36.4
REI	3.6
RPI	1.8
RWI	45.5
WiLI	54.5

TABLE 48. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *A. adeliaana*.

	NIWA 44133 ML 45 mm
Gender	M
ML	45
AL1R	65
AL2R	71
AL3R	75
AL4R	81
AL1L	67
AL2L	72
AL3L	79
AL4L	82
ASC1R	34
ASC2R	35
ASC3R	24
ASC4R	38
ASC1L	34
ASC2L	35
ASC3L	36
ASC4L	39
SD	3
AW	9
EO	8
FFL	6
FuL	13
GilC I	60
GilC O	60
HdL	16
HdW	32
MW	48
PA	25
TL	116
WAt	type 1A
WDA	14
WDBR	17
WDBL	18
WDCR	18
WDCL	21
WDDR	18
WDDL	18
WDE	18

TABLE 49. INTERNAL CHARACTER RAW MEASURES. *A. adeliaana*.

	NIWA 44133 ML 45 mm
AOesL	15
ASGL	7
BBL	11
DGL	19
DGW	22
DG(GD)	22
InTL	20
ISA	yes
ISDL	8
ISEL	2
ISEW	2
ISL	5
ISpres	type 2
ISTL	16
ISW	9*
OesTL	36
PSGL	13
SpCL	9
StL	10

TABLE 50. REPRODUCTIVE SYSTEM RAW MEASURES. *A. adeliaana*.

	NIWA 44133 ML 45 mm
CaL	4.5
LL	85
SGI	32
SGII	37
SS	2.5
TOTL	11

TABLE 51. UPPER BEAK RAW MEASURES.
A. adeliciana.

	NIWA 44133 ML 45 mm
BL	6
BH	6
BW	6
CH	2
HH	2
HL	2
HW	4
RE	0
RP	0
RW	3
WiL	3

TABLE 52. LOWER BEAK RAW MEASURES.
A. adeliciana.

	NIWA 44133 ML 45 mm
BL	6
BH	4
BIH	2
BW	6
CH	2
CL	3
DWaW	5
HL	2
PWaW	3
RE	1
RW	1
WiL	4
WiW	2

Anterior oesophagus narrow, length 42% of oesophagus (OesTL). Crop well developed, with diverticulum. Spiral caecum smaller than stomach, about 90% its diameter, lacking volutions. Intestine markedly shorter than oesophagus, about 56% OesTL. Digestive gland circular, without hepatic peaks; greatest dimension 45% ML; pancreas not well developed. Ink sac present, exposed 40% of sac length (ISL) and 12.5% of its total length (ISTL), type 2 (Fig. 6).

Lower beak (Fig. 31C right, Table 46, 52) with black hood, gradually transitioning to brown toward hood margin; oral side of wings black extending to the middle of wing, forming clearly marked diagonal line with a brown border; remainder of the wing translucent; lateral walls dark, gradually darkening toward hood; margins translucent. Beak base length 13% ML; height 67% BBL. Hood with rounded crest; rostrum tip triangular, sharp, deflected upwards. Rostrum slightly protruded, almost at the same level as the jaw angle. Jaw angle around 140°; wing length 8% BBL. Lateral wall crest rounded. Proximal wall about 33% narrower than distal wall (Distal wall width).

Upper beak (Fig. 31C left, Tables 47, 51) with black hood; lateral walls brown, gradually darkening toward the hood and lightening toward the margin; margins translucent. Beak base length 12% ML, of comparable height and length. Hood with rounded crest; rostrum tip sharp, with no visible protrusion. Jaw angle obtuse, about 180°. Lateral wall crest rounded, without notch; not parallel-sided.

Circulatory system of type 1, with well-developed ink sac artery (Fig. 13).

Radula well developed (Figs 30, 31F). Rachidian teeth unicusped, with rectangular bases and sharply tapering points. First laterals small, triangular. Second laterals well developed, with

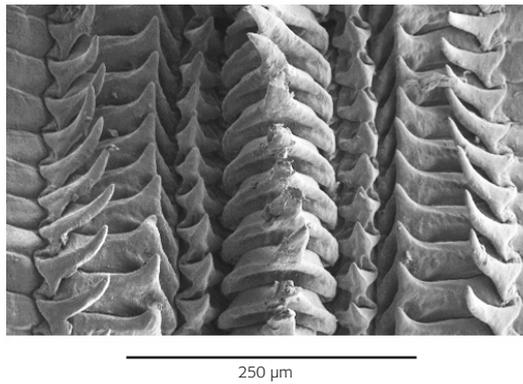


FIGURE 30. *Adelleledone adeliaeana* (NIWA 44133, ML 45mm). ESEM radula.

base slightly longer than rachidian; marginal teeth with single, more delicate cusp. Marginal blocks rectangular, well developed.

REMARKS. The original description of *A. adeliaeana* was based on one female and two juvenile specimens. Lu & Stranks (1994) redescribed this species based on an additional 10 immature and five mature males and 10 submature, one mature and one spent female in accordance with standardised characters and states cited by Roper & Voss (1983).

The type locality of *A. adeliaeana* is 66°55'S, 145°21'E; those specimens described by Lu & Stranks (1994) were from 65–67°S, 50–76°E, and this present material (herein) from proximal to the type locality (74°43'E, 167°0'S). Compared with specimens attributed to this taxon by Lu & Stranks, these current specimens are similar in external morphology (color, MAI, OAI, ASC, WDI), but Lu & Stranks' specimens have a long penis with partially coiled diverticulum; these differences could be attributable to differing states of reproductive maturity of material examined in these two accounts. The holotype of *A. adeliaeana* described by Berry is comparable in its morphology, with similar eyes, head, and MAI. The two syntypes of *Pareledone umitakae* Taki described from 67°51'S, 33°13.5'E, are similar in external morphology, skin color (reddish-brown, with reddish patches), indices and counts. To determine whether all specimens presently attributed to this taxon by Taki, and Lu & Stranks, and herein are conspecific would require detailed re-examination of all specimens; unfortunately this falls beyond the scope of this present research. If all are truly conspecific then this species has an extraordinary latitudinal range for an Antarctic 'pareledonid,' and an extensive depth range (material herein attributed to this taxon the deepest thus-far known).

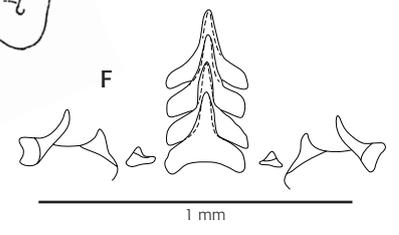
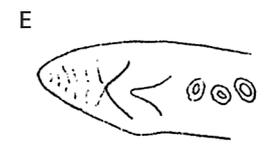
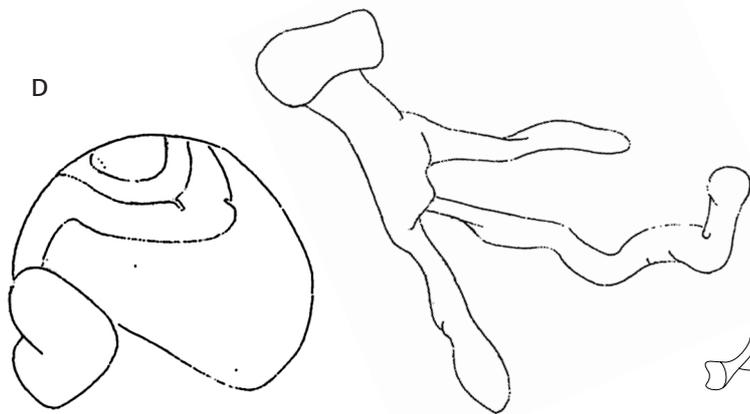
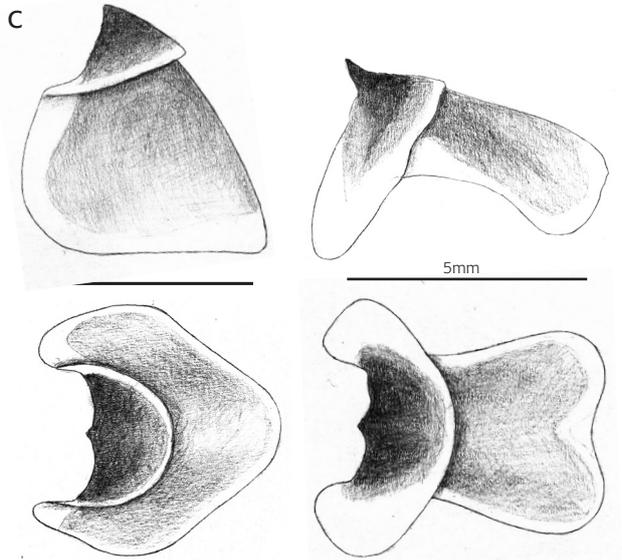
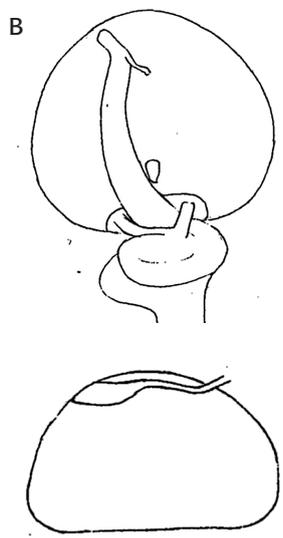
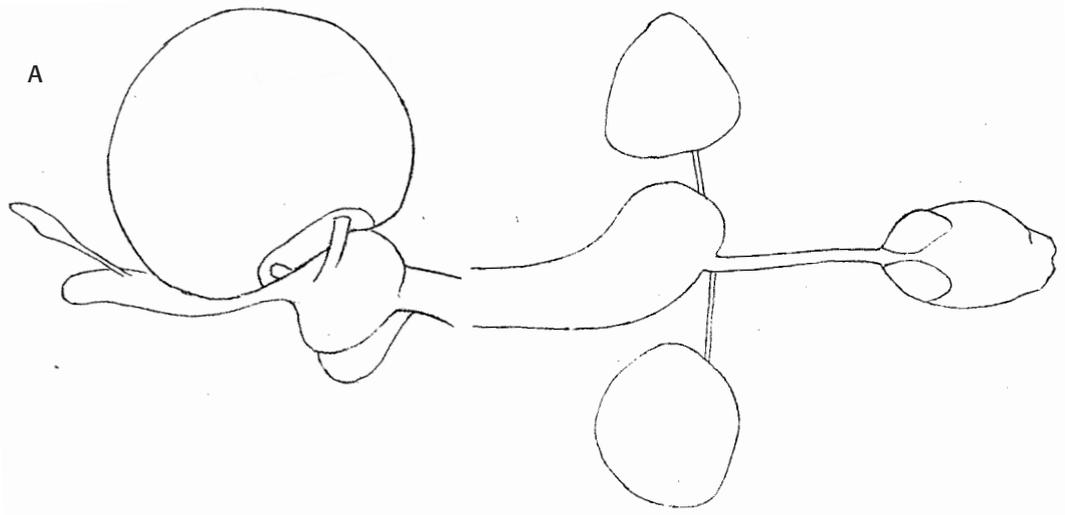


FIGURE 31. *Adelleledone adelleana* (NIWA 44133, ML 45mm) **A)** Alimentary canal. **B)** Ink sac duct and digestive gland in two perspectives (dorsal and lateral view). **C)** Upper and lower beaks. **D)** Male reproductive system. **E)** Hectocotylus. **F)** Radula.



FIGURE 32. *Adelieledone adeliaeana* (NIWA 44133, ML 45mm). Dorsal and ventral view of preserved specimen.

Bentheledone Robson, 1932

Robson (1932) erected this genus to differentiate two deep-sea forms from others he attributed to another concurrently described new genus, *Pareledone*. Subsequent to Robson's description of *Bentheledone*, no further specimens referable to it have been adequately described or recognised, and the genus has received little attention in recent years. The type species of this genus, *B. rotunda* (Hoyle, 1885) was recently transferred to the genus *Thaumeledone* by Allcock *et al.* (2004), rendering *Bentheledone* a junior synonym of *Thaumeledone*, but this synonymy is critically appraised below, and rejected.

DIAGNOSIS (modified from Voss 1988b, Robson 1932). Radula slightly degenerate: with 7 transverse rows of teeth and marginal blocks; rachidian lacks lateral cusps, lateral teeth and marginals reduced. Posterior salivary glands small. Crop absent. Gill with 5 or 6 lamellae.

TYPE SPECIES. *Eledone rotunda* Hoyle, 1885 (by designation Robson (1932)).

Bentheledone albida (Berry, 1917)

RECOGNISED DISTRIBUTION. Southern Ocean, 64°34'S, 127°17'E, (type location) to Ross Sea, 68°33.87–33.36'S, 178°19.75–20.92'E, ~3100–3210 m.

SYNONYMY.

Moschites albida Berry, 1917: 15, pl. X, figs 2 and 3, pl. XI, fig. 4.

Bentheledone albida (Berry) — Robson 1932: 320–321; O'Shea 1999: fig. 150C.

MATERIALEXAMINED. 1 specimen (♂). ML 43 mm♂, NIWA 44160, 68°33.87–33.36'S, 178°19.75–20.92'E, 3203–3210 m, 01/03/2008, RV *Tangaroa* Stn TAN0802/189.

DESCRIPTION. Adults medium-sized (ML 43 mm, TL to 155 mm) (Fig. 34, Tables 53, 57). Mantle ovoid. Head narrower than mantle (HdLI 23, HdWI 65) delimited from it by moderately developed pre-ocular constriction. Orbits bulbous, with marked interspace between both eyes across dorsal midline of head. Postorbital constriction moderately developed. Arms 59–65% TL (excluding hectocotyliised arm); Arm-to-web attachment type 2; depth 34% longest arm length.

Arm sucker count 53–62 (excluding hectocotylised arm); ASIn 3; no suckers abruptly enlarged; suckers attain their greatest diameter at sucker 3 or 4 from beaks. Third right arm of male hectocotylised, shorter than opposite member (OAI 85), with 40 suckers. Hectocotylised portion with ligula 8% hectocotylised arm length; ligula without transverse rugae; calamus 38% ligula length (Fig. 33E; Tables 53, 57). Spermatophoral groove not well developed, narrow.

Gills with 5 lamellae per inner and outer demibranch. Male with spiral terminal organ diverticulum oriented to the left of terminal organ. Spermatophoric gland I longer than II; spermatophoric sac extremely short, 25% of SGII (Fig. 33C, Table 59).

Alimentary canal (Fig. 33A, Tables 54, 58) with buccal bulb length 28% ML. Anterior salivary glands of length about 42% BBL. Posterior salivary gland elliptical or triangular (shape differs between right and left sides), their greatest dimension more than 3/4 that of buccal bulb length (83% BBL, 23% ML). Anterior oesophagus narrow; length 35% of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension 50% that of stomach, lacking volutions. Intestine slightly shorter than oesophagus, 87% OesTL. Digestive gland wider than long, with well-developed peaks either side of hepatic ducts; greatest dimension 51% ML; pancreas well developed. Functional ink sac absent; neither vestige of ink sac, duct nor ink sac artery apparent.

Lower beak (Fig. 33B left, Tables 55, 61) with black hood; oral margin of wings black extending to below middle of the wing forming clearly marked diagonal; brown colour from below mid-wing to aboral margin; lateral walls dark brown, slightly darkening to black toward hood; margins translucent. Beak base length 21% ML, 72% height. Hood with rounded crest, elevated from wings. Rostrum tip chisel-like, slightly protruded, 4% BBL. Jaw angle 120°. Wing protrusion length 33% BBL; wing length 83% BBL. Lateral wall crest rounded, with strong basal notch. Proximal and distal wall of comparable width.

Upper beak (Fig. 33B right, Table 56, 60) with black hood and brown border; lateral walls brown, slightly darkening to black toward the hood; all margins translucent. Beak base length 19% ML, as high as wide. Hood with rounded crest; rostrum triangular, rostral tip pointed, with apparent lateral keel; length protrusion 12% BBL; wing length protrusion of comparable length to rostral protrusion. Jaw angle 110°. Lateral wall crest rounded, without basal notch; parallel-sided.

Circulatory system damaged; presence or absence and ink sac artery could not be determined.

Radula (Fig. 33D) with robust, well-developed rachidian tooth, wider than long, lacking lateral cusps. First laterals small, with single outer cusp. Second laterals well developed, with large cusp. Marginal teeth smaller than second laterals. Marginal blocks present, small.

TABLE 53. EXTERNAL CHARACTER INDICES.
B. albida.

	NIWA 44160 ML 43 mm
Sex	M
ALI1R	227.9
ALI2R	232.6
ALI3R	183.7
ALI4R	220.9
ALI1L	237.2
ALI2L	237.2
ALI3L	216.3
ALI4L	214.0
MAI	42.2
MWI	95.3
ASIn	3.5
AWI	27.9
EOI	7.0
FFI	14.0
FuLI	25.6
HdLI	23.3
HdWI	65.1
MWI	95.3
OAI	84.9
PAI	55.8
WDI	34.3

TABLE 54. INTERNAL CHARACTER INDICES.
B. albida.

	NIWA 44160 ML 43 mm
AOesLI	20.9
ASGLI	11.6
BBI	27.9
DG(GD)	51.2
IntLI	52.3
ISA	*
OESTLI	60.5
PSGLI	23.3
SpCI	10.5
StI	20.9

TABLE 55. LOWER BEAK INDICES.
B. albida.

	NIWA 44160 ML 43 mm
BLI	20.9
BHI	72.2
BIHI	22.2
BWI	105.6
CLI	38.9
DWaWI	55.6
HLI	38.9
PWaWI	55.6
REI	11.1
RWI	16.7
WiLI	83.3
WiWI	44.4

TABLE 56. UPPER BEAK INDICES.
B. albida.

	NIWA 44160 ML 43 mm
BLI	18.6
BHI	100.0
BWI	75.0
CHI	25.0
HHI	37.5
HLI	62.5
REI	12.5
RPI	12.5
RWI	31.3
WiLI	43.8

TABLE 57. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *B. albida*.

	NIWA 44160 ML 43 mm
Gender	M
ML	43
AL1R	98
AL2R	100
AL3R	79
AL4R	95
AL1L	102
AL2L	102
AL3L	93
AL4L	92
ASC1R	60
ASC2R	62
ASC3R	40
ASC4R	54
ASC1L	62
ASC2L	60
ASC3L	57
ASC4L	53
SD	2
AW	12
EO	3
FFL	6
FuL	11
GilC I	50
GilC O	50
HdL	10
HdW	28
MW	41
PA	24
TL	155
WAt	type 2
WDA	21
WDBR	32
WDBL	27
WDCR	35
WDCL	27
WDDR	*
WDDL	28
WDE	*

TABLE 58. INTERNAL CHARACTER RAW MEASURES. *B. albida*.

	NIWA 44160 ML 43 mm
AOesL	9
ASGL	5
BBL	12
DGL	15
DGW	22
DG(GD)	22
InTL	23
ISpres	no
OesTL	26
PSGL	10
SpCL	05
StL	09

TABLE 59. REPRODUCTIVE SYSTEM RAW MEASURES. *B. albida*.

	NIWA 44160 ML 43 mm
CaL	3.5
LL	6
SGL	37.5
SGII	34
SS	16.5
TODL	
TOL	4.5
TOTL	1

TABLE 60. UPPER BEAK RAW MEASURES.
B. albida.

	NIWA 44160 ML 43 mm
BL	0.8
BH	0.8
BW	0.6
CH	0.2
HH	0.3
HL	0.5
HW	0.5
RE	0.1
RP	0.1
RW	0.3
WiL	0.4

TABLE 61. LOWER BEAK RAW MEASURES.
B. albida.

	NIWA 44160 ML 43 mm
BL	0.9
BH	0.7
BIH	0.2
BW	1.0
CH	0.2
CL	0.4
DWaW	0.5
HL	0.4
PWaW	0.5
RE	0.1
RW	0.2
WiL	0.8
WiW	0.4

REMARKS. Five genera occurring in Antarctic waters share a number of characters and their states with the genus *Bentheledone* Robson, 1932, as originally diagnosed by Robson (1932): *Bathypurpurata* Vecchione *et al.*, 2005; *Praealtus* Allcock *et al.*, 2004; *Graneledone* Joubin, 1918; *Thaumeledone* Robson, 1930; and *Pareledone* Robson, 1932. Given initial somewhat inadequate descriptions, at least by modern standards (*sensu* Roper & Voss 1983), the status of these genera and most species attributed to them, particularly those in the genera *Thaumeledone* and *Bentheledone*, is uncertain.

One problematic taxon that proves central to any debate on the nomenclatural and systematic status of these Southern Ocean genera is *Bentheledone rotunda* (Hoyle, 1885). The type species of the genus, *B. rotunda*, and the type specimen of a second species referred to this genus, *B. albida* are in poor condition, but sufficient characters were described for them to enable their re-identification in the event that new collections were made from respective type localities. Herein a unique specimen that agrees in every pertinent character described and illustrated by Berry (1917) for the type species of *B. albida* (Berry) is identified, and as such I attribute this specimen to this taxon. Particulars of this specimen also agree far more closely with unique characters originally described and illustrated for the type specimen of *B. rotunda* (Hoyle) by Hoyle (1885) and Robson (1932), the type species of the genus, although not as redescribed by Allcock *et al.* (2004).

Allcock *et al.* (2004) had at their disposal specimens of a deep-sea gelatinous octopod that agreed in many morphological and anatomical respects to others concurrently attributed to *Thaumeledone* but differed in several respects from descriptions available for the poorly known

Bentheledone rotunda; these differences were attributed to antiquity of the type specimen of this species, loss of key parts of its anatomy, and inaccuracies in the original and subsequent descriptions of this species by Hoyle (1885) and Robson (1932). They attributed their specimens to *T. rotunda* (Hoyle). Given that *Bentheledone rotunda* was the type species of the genus *Bentheledone*, this genus was thus rendered a junior synonym of *Thaumeledone*. Moreover, the status of a second described species in this genus, *B. albida* became unresolved. The situation was complicated further by their description of a second new taxon, *Praealtus*, and proposition of a close relationship between its sole species, *P. paralbida*, and the problematic *B. albida*.

The type locality of *B. rotunda*, 55°55'S, 108°35'E, is on the opposite side of Antarctica to those specimens subsequently referred to this species by Allcock *et al.* (2004) collected at 60°37'S, 54°56'W and 60°39'S, 53°58'W, although the depth of capture of the type and subsequently referred specimens are broadly comparable, ~3500 m and 2896–3222 m respectively (Allcock *et al.* 2004). The single greatest differences in descriptions of the type specimens and those later referred to this species are in details of the radula; the type species is described and illustrated with 7 well-developed transverse rows of teeth, in addition to a row of acutely pointed marginal blocks either side of these teeth (Robson 1932: fig. 74), whereas subsequently referred specimens possess 5 rows only and lack marginal blocks (Allcock *et al.* 2004: fig. 8A); the shape of individual teeth also differs considerably. As the radula is lost from type material of this species (in addition to other parts of the anatomy), Allcock *et al.* (2004) could not confirm the accuracy of Robson's illustrations of same, and disregarded these differences in their redescription of this taxon.

The type locality of *B. albida*, 64°34'S, 127°17'E, also is on the opposite side of Antarctica to that material referred to as *T. rotunda* (Allcock *et al.* 2004, not Hoyle, 1885); moreover, the type locality of *B. albida* is close to the type locality of the type species of this genus (*B. rotunda*); the depths of capture of these two species are also similar, ~3100 m depth. The holotype of *B. albida* is now in deplorable condition, figured by O'Shea (1999: fig. 150C), and few characters or states of systematic value can be discerned from it, but from the original description of this species (Berry 1917) it is apparent that it shared with *B. rotunda* similar radular dentition, in having 7 well-developed rows of teeth, a series of marginal plates either side of these rows, and very similar individual teeth. Additional characters of relevance that assist in differentiating this taxon from that of externally, superficially similar species of *Thaumeledone* include the relatively high arm sucker count (57 in the type), smooth skin, and colourless and loosely adherent skin, and from *B. rotunda*, by its longer arms and pale colouration (Berry 1917: 15–17).

Both the type species of *B. rotunda* and *B. albida* have high arm-sucker counts relative to other species of *Thaumeledone*, and both also possess a more conventional octopodid radula

comprising 7 teeth in a transverse row, with marginal blocks (although the rachidian of neither possesses lateral cusps). These two characters alone differ markedly from those described for specimens referred to *T. rotunda* (not Hoyle, 1885) by Allcock *et al.* (2004), or any species presently accommodated in the genus *Thaumeledone*, and in radular detail, from the sole taxon referred to *Praealtus*.

Although not from the exact same locality as the type species, the unique specimen herein attributed to *B. albida* differs in no consequential manner from any prior description available for this species, or from what limited characters can be discerned from the poorly conserved type material. Moreover, the characters described for this specimen agree in almost every respect with those described for the type species of the genus, *B. rotunda* (*sensu* Hoyle, 1885; Robson, 1932; not Allcock *et al.* 2004).

Several courses of action could be followed here: 1) accept the redescription of *T. profunda* (Hoyle) of Allcock *et al.* (2004), thereby accepting *Bentheledone* as a junior synonym of *Thaumeledone*, necessarily creating a new genus to accommodate the unique specimen herein referred to *B. albida*; 2) redescribe this unique specimen herein attributed to *B. albida* (Berry) in the genus *Praealtus*, as *P. albida* (Berry), rediagnosing this genus to accommodate this taxon; or 3) reject the identification of Allcock *et al.* (2004), remove the genus *Bentheledone* from synonymy of *Thaumeledone*, redescribe this unique specimen as *B. albida*, but as a consequence of this course of action, attribute those specimens referred to *T. rotunda* (Allcock *et al.* 2004, not Hoyle, 1885) to a new, undescribed species, *Thaumeledone* sp. nov.

Given the obvious anatomical differences between the specimen herein referred to *B. albida* and those referred to both *Thaumeledone* and *Praealtus*, most obviously (but not limited to) their radular detail, attribution of this unique specimen to either genus is unacceptable. Creation of a new genus is unnecessary, because the redescription of *B. rotunda* by Allcock *et al.* (2004) is inconsistent with the descriptions of the type material made by Hoyle (1885) and Robson (1932), and the latter two are entirely consistent with that proffered herein for the unique specimen referred to *B. albida*. Moreover, the proximity of capture (depth, latitude and longitude) of the unique specimen reported herein as *B. albida* is far closer to the type localities of both *Bentheledone* species thus far described.

As a consequence of this review, the genera *Praealtus*, *Thaumeledone* and *Bentheledone* are all retained as valid Southern Ocean genera, this specimen is redescribed as *B. albida* (Berry), and at least one new species of *Thaumeledone* awaits description, that formerly referred to as *T. rotunda* (Allcock *et al.* 2004, not Hoyle, 1885).

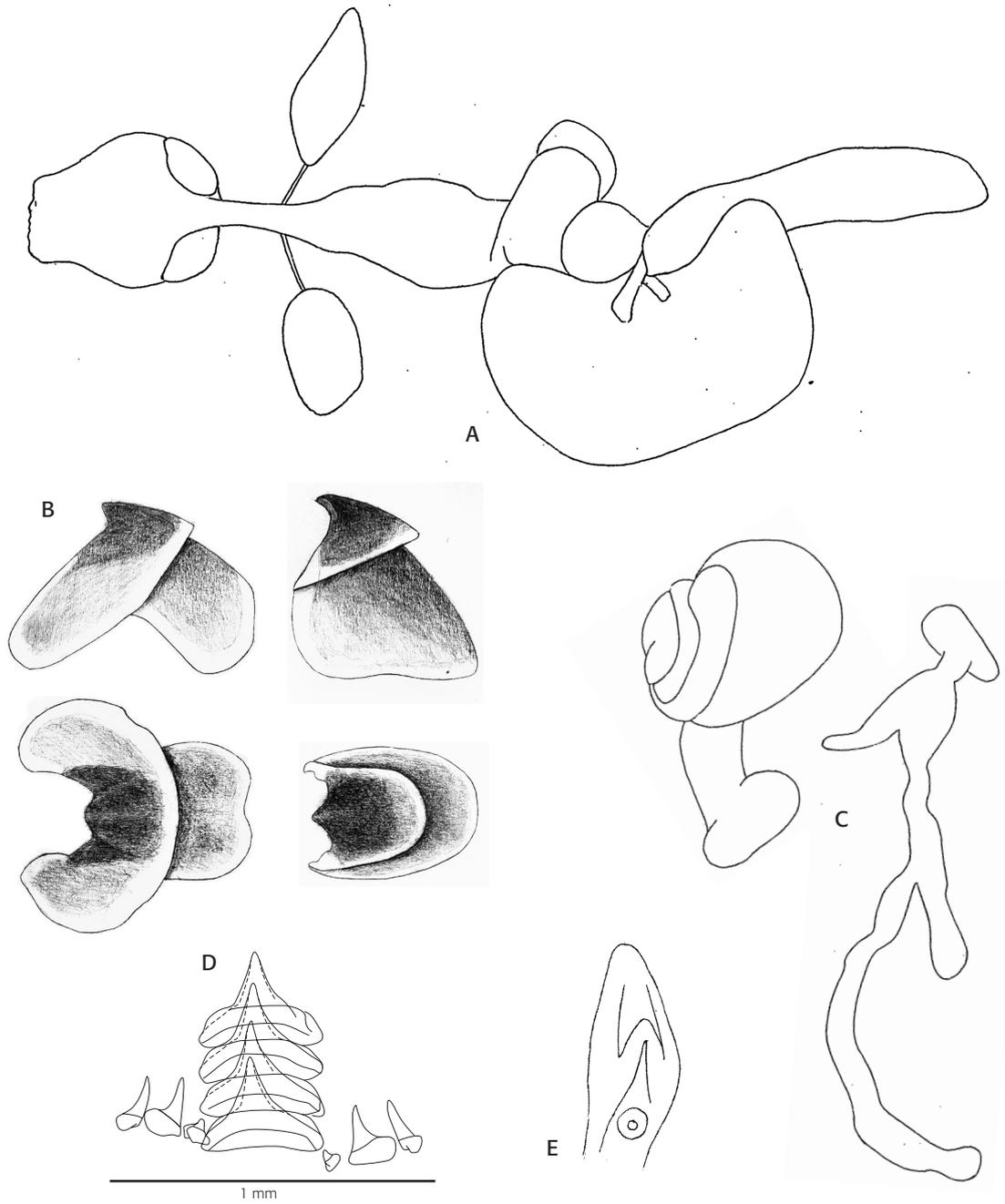


FIGURE 33. *Bentheledone albida* (NIWA 44160, ML 43 mm). **A)** Alimentary canal. **B)** Upper and lower beaks. **C)** Male reproductive system **D)** Radula. **E)** Hectocotylus.



FIGURE 34. *Bentheledone albida* (NIWA 44160, ML 43 mm). ABOVE: Dorsal and ventral view of preserved specimen. BELOW: Dorsal and ventral view of fresh specimen.

Enteroctopus Rochebrune and Mabile, 1889

This genus was erected to accommodate *E. membranaceus*, the description of which was very brief, based on one specimen of unknown location collection details (Ré 1980). Robson (1929) considered it a probable young specimen and junior synonym of *E. megalocyathus*; others have treated this taxon as a *nomen dubium* due to its poor description, immaturity, and lack of a holotype (Hochberg 1998). By virtue of generic monotypy, Hochberg (1998) treated *E. megalocyathus* Gould, 1852, the second described specimen in this genus, as the type species of the genus — a course of action followed herein.

DIAGNOSIS (amended from O’Shea 1999): Species attain massive proportions; arms of subequal length; all arm pairs with comparably sized enlarged suckers; posterior salivary glands large; diverticulum of crop reduced or absent; penis and penis diverticulum of exaggerated length, penis diverticulum oriented along anterior–posterior axis of mantle, extending over renal and reproductive tissues to anterior–most point of visceral mass; membranes between renal tissue and ventral inner surface of mantle absent, interpallial septum extends to anterior–most point along ventral inner surface of mantle.

TYPE SPECIES. *Enteroctopus membranaceus* Rochebrune & Mabile, 1889 by subsequent designation of Hoyle, 1929: 175 = *Octopus megalocyathus* Gould, 1852 following Hochberg, 1998(p. 203).

Enteroctopus zealandicus (Benham, 1944)

DIAGNOSIS. Massive, smooth-bodied octopus with short to long subequal arms, 48–81% TL (excluding hectocotylied arm); non-hectocotylied arm sucker counts 135–252, hectocotylied arm sucker counts 80–91; moderate to large suckers on all 4 arm pairs (AS1e 10–18% ML); 12 or 13 outer gill lamellae per demibranch; hectocotylied third right arm with ligula of exaggerated length, in mature specimens to about 20% arm length; penis and diverticulum of exaggerated length.

RECOGNISED DISTRIBUTION: New Zealand, 41°43–52°34'S, 166°37'E,–178°37'W, east coast of South Island, Chatham Rise, Campbell Plateau; Stewart, Auckland and Antipodes Islands.

Southernmost specimens frequently littoral, extending to ~530 m, more northern specimens deeper-dwelling, ~300–522 m.

SYNONYMY.

Pinnoctopus cordiformis (not Quoy & Gaimard) — Filhol 1885: 521.

Octopus maorum (not Hutton) — Filhol 1885: 520–521; Dell 1952 (*vide* Filhol): 15; Batham 1957 (*partim*, type *Parooctopus zealandicus* Benham): 636–637.

Parooctopus zealandicus Benham, 1944: 256–259, pl 40, figs 1–4; Powell 1946: 100.

Octopus zealandicus (Benham) — Dell 1951: 97, fig. 19; 1952: 28–29, pl. 6, figs 2–4; Powell 1957: 125; Powell 1962: 125; Powell 1976: 133; Powell 1979: 444.

Octopus dofleini (not Wülker, 1910) — Imber 1992: 248; Spencer & Willan 1995: 53.

Enterooctopus zealandicus (Benham) — O’Shea 1999: 183–191, figs 110–114; O’Shea & Jackson 2010: 555.

MATERIAL EXAMINED. 1 specimen (♂): NIWA (not registered), collection coordinates not presently available, New Zealand (RV *Tangaroa* Stn TAN0317/63).

DESCRIPTION (modified from O’Shea 1999). Adult animal attains massive size (ML to 272 mm, TL to ~1.4 m) (Fig. 37; Tables 62, 63). Mantle ovoid, broad, dorso-ventral compression, lateral keel or fold of skin, and ventral longitudinal groove or depression absent. Head well developed, narrower than mantle (HdLI 17–37, HdWI 28–74), separated from it by weak pre-ocular constriction. Orbits large, dorso-laterally oriented, situated above base of arm pairs I and II. Funnel well developed, base entirely free of brachial crown, not attached to arm bases III or IV. Post-orbital constriction poorly developed. Brachial crown robust, wider than head. Arm-to-web attachment type 1B, depth 10–30% longest arm length. Arms thick; arm length 62–76% TL (excluding hectocotylied arm), gradually tapering to tips; no consistent disparity in relative arm lengths apparent. Suckers biserial, with 10–13 suckers between beaks and web margin along arm pair I. Non-hectocotylied arm sucker counts variable, ASC 135–252 (excluding hectocotylied arm); suckers extend to arm tips. Sucker size similar in male and female (ASIn about 10–18); no suckers abruptly enlarged in either sex; suckers attain greatest diameter along any arm at level where web attaches to dorso-lateral surface of each arm. Male with third right arm hectocotylied, shorter than opposite arm (OAI 73–82); with 80–91 suckers; terminal hectocotylied portion (Fig. 36D) very long (LLI 5.8–19.8), ligula with thick margins enclosing shallow groove, with inner surface (proximal to calamus) bearing three longitudinal rows of large, block-like papillae marked by

three longitudinal central ridges; transverse rugae indistinct; calamus short (CaLI 7.7–13.2), with groove extending entire structure length. Spermatophoral groove narrow, with thickened, crenulate web margin, spermatophoral groove not markedly differentiated from web sector D. Web formula variable, sectors A and E usually shallowest, sectors C and B deepest, with no consistent disparity in relative sector depths. 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.

Gills large, with 12 or 13 lamellae per outer demibranch. Male with terminal organ diverticulum oriented to left of terminal organ; terminal organ very long. Spermatophoric gland I longer than II; spermatophore sac slightly shorter than SGII (Fig. 36E, Table 68).

Alimentary canal (Fig. 36A; Tables 63, 67) with buccal bulb length (BBL) 22–29% ML. Anterior salivary glands 35–53% BBL. Posterior salivary glands heart-shaped to broadly triangular, their greatest dimension slightly shorter BBL (90–97% BBL, 20% ML). Anterior oesophagus narrow, length 30% that of oesophagus (OesTL). Crop well developed, with scarcely discernable or absent diverticulum. Spiral caecum greatest dimension 74% that of stomach, with 1.5 volutions. Intestine approximately 1.5 times oesophagus length (144% OesTL). Digestive gland elongated, heart-shaped, slightly longer than wide, with broad peak on either side of hepatic ducts; greatest dimension 40% ML; pancreas well developed. Ink sac present, type 1 (Fig. 6).

Lower beak (Fig. 36B left; Tables 64, 70) with black hood, with brown border; wings black from oral margin to 2/3 of the wing, thereafter slightly lightening to dark brown, forming clearly marked diagonal through anterior half of the wing; lateral walls black, slightly lightening toward margin; margins translucent. Beak base length 17% ML, height 75% BBL. Hood with rounded crest, elevated from wings. Rostrum chisel-like, with small protrusion, 3% BBL. Jaw angle 120°. Wing protrusion length 41% BBL, wing length 71% BBL. Lateral wall crest rounded, with strong basal notch. Proximal and distal wall of comparable width.

Upper beak (Fig. 36B right; Tables 65, 69) with black hood with brown border; lateral walls black, slightly lightening to brown toward the margin; all margins translucent. Beak base length 15% ML, slightly shorter than wide. Hood with rounded crest; rostral tip blunt, triangular, length protrusion 7.5% BBL; wing as protruded as rostrum. Jaw angle 100°. Lateral wall crest squared, without basal notch, parallel-sided.

Circulatory system of type 1 (Fig. 13), with well-developed ink sac artery.

Radula (Figs 35, 36F) with robust, broadly triangular rachidian, taller than wide, with two small, asymmetrically disposed lateral cusps either side of large central cusp. First laterals small, with single outer cusp. Second laterals well developed, wider than rachidian, with large cusp.

TABLE 62. EXTERNAL CHARACTER INDICES.
E. zealandicus.

	ML 205 mm
Sex	M
ALI1R	287.8
ALI2R	258.5
ALI3R	229.3
ALI4R	273.2
ALI1L	234.1
ALI2L	317.1
ALI3L	278.0
ALI4L	248.8
MAI	31.5
MWI	85.4
ASIn	11.2
AWI	11.7
EOI	6.8
FFI	22.0
FuLI	30.2
HdLI	17.1
HdWI	39.0
MWI	85.4
OAI	82.5
PAI	35.6
WDI	21.5

TABLE 63. INTERNAL CHARACTER INDICES.
E. zealandicus.

	ML 205 mm
AOesLI	20.0
ASGLI	7.8
BBI	22.4
DG(GD)	39.0
IntLI	97.6
ISTLI	41.0
ISLI	20.0
OESTLI	67.3
PSGLI	20.2
SpCI	17.1
StI	22.9

TABLE 64. LOWER BEAK INDICES.
E. zealandicus.

	ML 205 mm
BLI	16.6
BHI	75.0
BIHI	39.7
BWI	86.8
CLI	50.0
DWaWI	44.1
HLI	26.5
PWaWI	44.1
REI	11.8
RWI	22.1
WiLI	70.6
WiWI	55.9

TABLE 65. UPPER BEAK INDICES.
E. zealandicus.

	ML 205 mm
BLI	14.6
BHI	91.7
BWI	51.7
CHI	21.7
HHI	33.3
HLI	43.3
REI	10.0
RPI	13.3
RWI	30.0
WiLI	43.3

TABLE 66. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *E. zealandicus*.

ML 205 mm	
Gender	*
ML	205
AL1R	590
AL2R	530
AL3R	470
AL4R	560
AL1L	480
AL2L	650
AL3L	570
AL4L	510
ASC1R	*
ASC2R	214
ASC3R	89
ASC4R	260
ASC1L	181
ASC2L	221
ASC3L	255
ASC4L	*
SD	23
AW	24
EO	14
FFL	45
FuL	62
GilC I	120
GilC O	120
HdL	35
HdW	80
MW	175
PA	73
TL	860
WAt	*
WDA	100
WDBR	100
WDBL	140
WDCR	130
WDCL	103
WDDR	140
WDDL	130
WDE	100

TABLE 67. INTERNAL CHARACTER RAW MEASURES. *E. zealandicus*.

ML 205 mm	
AOesL	41
ASGL	16
BBL	46
DGL	80
DGW	72
DG(GD)	80
InTL	200
ISA	yes
ISpres	type 1
ISDL	42
ISEL	38
ISEW	24
ISL	42
ISTL	84
ISW	26
OesTL	138
PSGL	42
SpCL	35
StL	47

TABLE 68. REPRODUCTIVE SYSTEM RAW MEASURES. *E. zealandicus*.

ML 205 mm	
CaL	9
LL	101
SGI	652
SGII	440
SS	450
TODL	–
TOL	–
TOTL	138

TABLE 69. UPPER BEAK RAW MEASURES.
E. zealandicus.

	ML 205 mm
BL	30
BH	28
BW	16
CH	7
HH	10
HL	13
HW	15
RE	3
RP	4
RW	9
WiL	13

TABLE 70. LOWER BEAK RAW MEASURES.
E. zealandicus.

	ML 205 mm
BL	34
BH	26
BIH	14
BW	30
CH	07
CL	17
DWaW	15
HL	9
PWaW	15
RE	4
RW	8
WiL	24
WiW	19

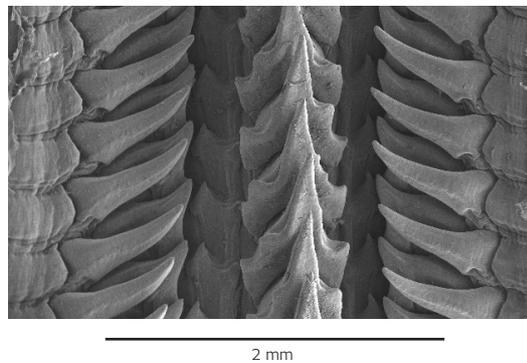


FIGURE 35. *Enteroctopus zealandicus*. ESEM radula.

Third laterals robust, cusp more delicate than that of either rachidian or second lateral; marginal blocks well developed, rectangular.

REMARKS. Recently it was proposed that this species was a synonym of *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832) (Norman & Hochberg 2005). Both species are large bodied and share a number of external features, counts and measures. However, the largest suckers of *Enteroctopus* are comparably sized on each arm, whereas those of *Pinnoctopus* reduce in size from the dorsal to the ventral arms. Arm lengths are variable in both species, with any of the arms of *Enteroctopus* potentially the longest, while in *P. cordiformis* arms I and/or II are almost always the longest, and III and IV the shortest. The ovary of *Pinnoctopus* has distal oviducts about two times longer than the greatest diameter of the ovary sac, they are narrower, and they extend along the lateral face of the interpallial septum musculature, with the genital apertures opening proximal to the

anus, whereas those of *Enteroctopus* (*vide* O’Shea 1999) are only slightly longer than the ovary sac greatest dimension, are as wide as the oviducal ball, and the genital apertures open proximal to the bases of the gills (not extending along the interpallial musculature). The male reproductive system of these two species also differs greatly, with the terminal organ of *Pinnoctopus* being relatively shorter than that of *Enteroctopus*; the first one is around 2 times the size of the diverticulum (which has two volutions) while the latter is more than 6 times the size of the diverticulum (without volutions). Moreover, the hectocotylus of *Enteroctopus* has longitudinal rows of papillae, whereas that of *Pinnoctopus* does not. The alimentary canal of these two genera differs also, with that of *Enteroctopus* having a shorter digestive gland and a spiral caecum that does not form a complete second volution, whereas that of *Pinnoctopus* has three complete volutions.

The bathymetric distributions of *Enteroctopus zealandicus* and *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832) do not overlap when their geographic ranges do; *Enteroctopus* occurs at considerably greater depth than *Pinnoctopus* at more northern latitudes. Moreover, *P. cordiformis* is the only large-bodied species of octopus occurring in the Nelson region, its type locality. There seems little doubt that the taxon herein referred to *E. zealandicus* is conspecific with that described by Benham from deep water off the Otago Peninsula; it agrees with it in all sundry characters and character states as described by Benham, and subsequently O’Shea (1999), and differs demonstrably from that herein attributed to *P. cordiformis*.

Enteroctopus zealandicus shares a number of characters and states with deeper-dwelling taxa conventionally referred to the genus *Muusoctopus* (*Benthooctopus*), most notably: reduction in the number of lateral cusps on the rachidian tooth of the radula; reduction (to absence) of a diverticulum of the crop; lack of connective tissue membranes between renal and reproductive tissues and the inner ventral surface of the mantle cavity; and opening of the female genital apertures proximal to the base of the gills. However, *Enteroctopus zealandicus* differs from these typical deeper-dwelling forms in having a well-developed ink sac, large size, very small eggs and planktonic young for all but the type species of this genus, and its greatly elongated ligula — all characters departing from those of deeper-sea forms, but more typical of littoral octopuses. The phylogenetic position of *Enteroctopus* is presently unclear, but taxa presently attributed to it could prove somewhat basal, transitional between littoral and deep-sea octopuses, as suggested for several taxa (Robson 1932: 51, 244), developed further by O’Shea (1999: 191, 268), and corroborated with genetic data (Strugnell *et al.* 2010). Conversely, on grounds of counts, measures and indices, *E. zealandicus* does not differ greatly from other, more common, littoral octopodid genera (Fig. 14).

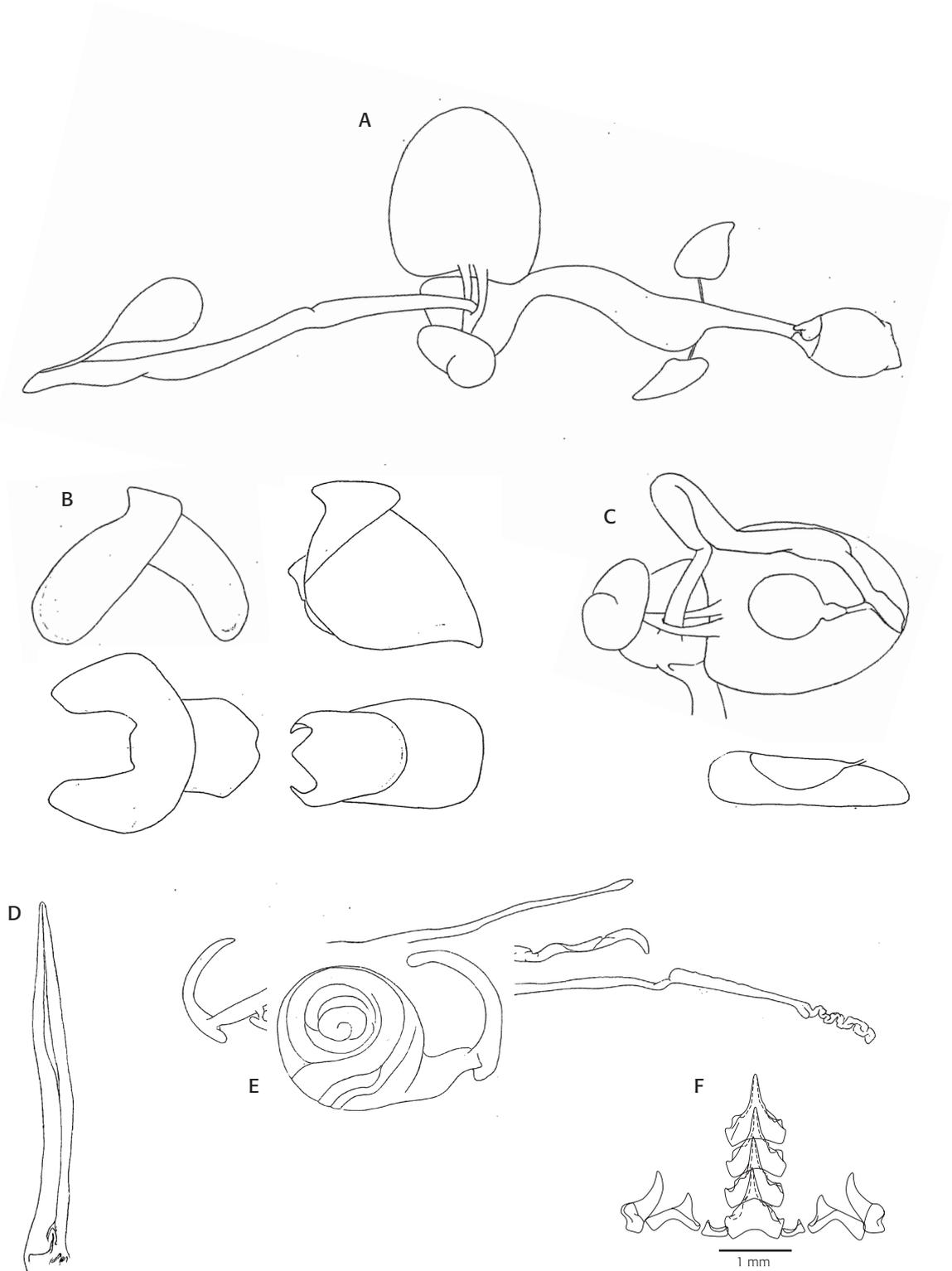


FIGURE 36. *Enteroctopus zealandicus*. A) Alimentary canal. B) Upper and lower beaks. C) Ink sac duct and digestive gland in two perspectives (dorsal and lateral view). D) Hectocotylus. E) Male reproductive system. F) Radula.



FIGURE 37. *Enteroctopus zealandicus*. ABOVE: Dorsal and ventral view of fresh specimen. BELOW: Ventral view of preserved specimen.

Graneledone Joubin, 1918

Species attributed to this genus generally live at great depths, and are distributed throughout the Atlantic, Pacific and Southern Oceans. Presently seven species and are assigned to this genus, although several still await description (O'Shea 1999, Guerra *et al.* 2000).

DIAGNOSIS. Sucker arrangement uniserial. Funnel organ VV-shaped. Radula variable (homodont or heterodont), teeth narrow to broad. Hectocotylus clearly differentiated into calamus and ligula; ligula without well-developed transverse rugae. Gill lamellae number 6–9 per outer demibranch; inner demibranch not markedly reduced. Crop diverticulum absent; posterior salivary glands small; functional ink sac absent. Dorsal and ventral surfaces of mantle, head, arms and web variably covered with clusters of cartilage-like tubercles, each cluster comprising numerous smaller elements (modified from O'Shea 1999, Allcock *et al.* 2003a).

TYPE SPECIES. *Eledone verrucosa* (Verrill, 1881).

***Graneledone* sp. 1**

SYNONYMY. *Graneledone* n. sp. O'Shea (pers comm.) in Roeleveld 1998: 10.

MATERIAL EXAMINED. 1 specimen (♂): SAM 2735, South African Museum (Cape Town), ML 68 mm, (collection details unknown; ex display specimen).

DESCRIPTION. Specimen 68 mm ML, 410 mm TL (Fig. 40; Tables 71, 75). Mantle ovoid, wide. Head slightly narrower than mantle (HdLI 43, HdWI 83), delimited from it by poorly developed pre-ocular constriction. Orbits large, bulbous; midline of head with a narrow interspace between eyes; post-orbital constriction poorly developed. Arm-to-web attachment type 1A; depth 29% longest arm length. Left web formula B=C=D.A=E. Arms 70–79% TL (excluding hectocotylised arm); arm pairs I and II longest, arm IV shortest. Arm sucker counts 66–75 (excluding hectocotylised arm); suckers extend to arm tips. ASIn 5, none abruptly enlarged; suckers attain their greatest diameter beyond first two or three suckers from beaks. Third right arm of male hectocotylised, shorter than opposite member (OAI 79), with 51 suckers. Hectocotylised portion (Fig. 38D) with ligula around 5% hectocotylised arm length, without transverse rugae; calamus about 47% lig-

ula length. Spermatophoral groove well developed, narrow. Skin over dorsal surfaces of mantle, head, arms I and II, dorso-lateral surfaces of arms III, basal part of web sectors A and B, beset with irregular-sized clusters of cartilage-like processes; processes not extending along arms and absent from arms IV; those around eye larger than the others, two or three especially enlarged over each eye. Colour (preserved, alcohol) pale brown dorsally and ventrally.

Gills with 7 lamellae per demibranch. Male with well-developed spiral terminal organ diverticulum oriented to left of terminal organ; spermatophoric gland I longer than II; spermatophoric sac shorter than both spermatophoric glands (Fig. 39C; Table 77).

Alimentary canal (Fig. 39A; Tables 72, 76) with buccal bulb length 25% ML. Anterior salivary glands 35% BBL. Posterior salivary glands elliptical-rectangular, narrow, about 75% the length of BBL (88% BBL, 22% ML). Anterior oesophagus narrow, length 47% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum 91% the diameter of stomach, without volutions. Intestine longer than oesophagus, 157% OesTL. Digestive gland circular, without hepatic peaks, its greatest dimension 46% ML; pancreas well developed. Functional ink sac absent, but type-3 vestige of ink sac duct embedded in digestive gland, extending to lower intestine proximal to the anus.

Circulatory system damaged; presence/absence of ink sac artery could not be determined.

Lower beak (Fig. 39B left; Table 73, 79) with black hood and brown border; wings black from oral margin to middle of wing forming a clearly marked diagonal line that lightens to brown toward aboral margin; lateral walls black, slightly lightening toward distal wall peaks; margins translucent. Beak base length 25% ML, height 71% BBL. Hood almost flat-topped, elevated from wings. Rostrum tip triangular, blunt, with clear protrusion, 6.5% BBL. Jaw angle 96°. Wing protrusion length 9% BBL, wing length 16% BBL. Lateral wall crest rounded, with basal notch. Proximal wall about 7% narrower than distal wall (distal wall width).

Upper beak (Fig. 39B right; Tables 74, 78) with black hood, with brown border; lateral walls black, abruptly lightening toward margin; all margins translucent. Beak base length 19% ML, 85% height. Hood with rounded crest; rostrum triangular, rostral tip slightly blunt, deflected down; length protrusion 12% BBL; wings slightly more protruded than rostrum. Jaw angle 88°. Lateral wall crest rounded, without basal notch; parallel-sided.

Radula (Figs 38, 39) with robust, broadly triangular rachidian, taller than wide, without lateral cusps. First lateral cusp longer than that of rachidian, with smaller admedial cusp. Second laterals well developed, with large cusp. Third laterals robust, cusp slightly narrower than that of either rachidian or second lateral; marginal blocks short, rectangular.

TABLE 71. EXTERNAL CHARACTER INDICES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
Sex	M
ALI1R	308.8
ALI2R	311.8
ALI3R	220.6
ALI4R	279.4
ALI1L	305.9
ALI2L	313.2
ALI3L	279.4
ALI4L	222.1
MAI	31.9
MWI	100.0
ASIn	5.1
AWI	14.7
EOI	8.8
FFI	19.1
FuLI	44.1
HdLI	42.6
HdWI	83.1
MWI	100.0
OAI	78.9
PAI	50.0
WDI	28.6

TABLE 72. EXTERNAL CHARACTER INDICES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
AOesLI	25.7
ASGLI	8.8
BBI	25.0
DG(GD)	45.6
IntLI	85.3
ISA	*
OESTLI	54.4
PSGLI	22.1
SpCI	25.0
StI	30.9

TABLE 73. LOWER BEAK INDICES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
BLI	25.0
BHI	70.6
BIHI	29.4
BWI	88.2
CLI	52.9
DWaWI	41.2
HLI	32.4
PWaWI	38.2
REI	5.9
RWI	14.7
WiLI	64.7
WiWI	35.3

TABLE 74. UPPER BEAK INDICES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
BLI	19.1
BHI	84.6
BWI	61.5
CHI	15.4
HHI	46.2
HLI	69.2
REI	11.5
RPI	11.5
RWI	23.1
WiLI	46.2

TABLE 75. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Graneledone* sp. 1.

	SAM 2735 ML 68 mm
Gender	M
ML	68
AL1R	210
AL2R	212
AL3R	150
AL4R	190
AL1L	208
AL2L	213*
AL3L	190
AL4L	151
ASC1R	77
ASC2R	75
ASC3R	42
ASC4R	74
ASC1L	75
ASC2L	73*
ASC3L	76
ASC4L	66
SD	4
AW	10
EO	6
FFL	13
FuL	30
GilC I	70
GilC O	70
HdL	29
HdW	57
MW	68
PA	34
TL	297
WAt	type 1B
WDA	40
WDBR	53
WDBL	58
WDCR	61
WDCL	58
WDDR	*
WDDL	55
WDE	40

TABLE 76. INTERNAL CHARACTER RAW MEASURES. *Graneledone* sp. 1.

	SAM 2735 ML 68 mm
AOesL	18
ASGL	6
BBL	17
DGL	21
DGW	31
DG(GD)	31
InTL	58
ISpres	duct
OesTL	37
PSGL	15
SpCL	17
StL	21

TABLE 77. REPRODUCTIVE SYSTEM RAW MEASURES. *Graneledone* sp. 1.

	SAM 2735 ML 68 mm
CaL	35
LL	75
SGL	6
SGII	38
SS	43
TODL	075
TOL	115
TOTL	19

TABLE 78. UPPER BEAK RAW MEASURES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
BL	13
BH	11
BW	8
CH	02
HH	06
HL	9
HW	8
RE	2
RP	2
RW	3
WiL	6

TABLE 79. LOWER BEAK RAW MEASURES.
Graneledone sp. 1.

	SAM 2735 ML 68 mm
BL	17
BH	12
BIH	5
BW	15
CH	2
CL	9
DWaW	7
HL	6
PWaW	7
RE	1
RW	3
WiL	11
WiW	6

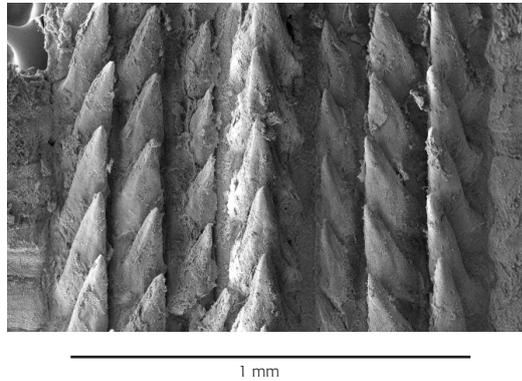


FIGURE 38. *Graneledone* sp. 1 (SAM 2735, ML 68 mm)
ESEM radula.

REMARKS. The presence of a vestige of an ink sac in this taxon, with a duct embedded in the digestive gland and attaching to the lower intestine proximal to the anus, clearly indicates that species within this genus are derived from ancestors with a functional ink sac. Therefore, this diagnosis has been amended to include “lack of a functional ink sac” as opposed to absence of this structure. This genus, and *Benthooctopus* Robson, 1929 (*fide* O’Shea 1999: 269), = *Muusooctopus* Gleadall, 2004 (Gleadall *et al.* 2010: 547), now include two taxa with species reported to have vestiges of an ink sac in genera historically reported to lack this structure altogether.

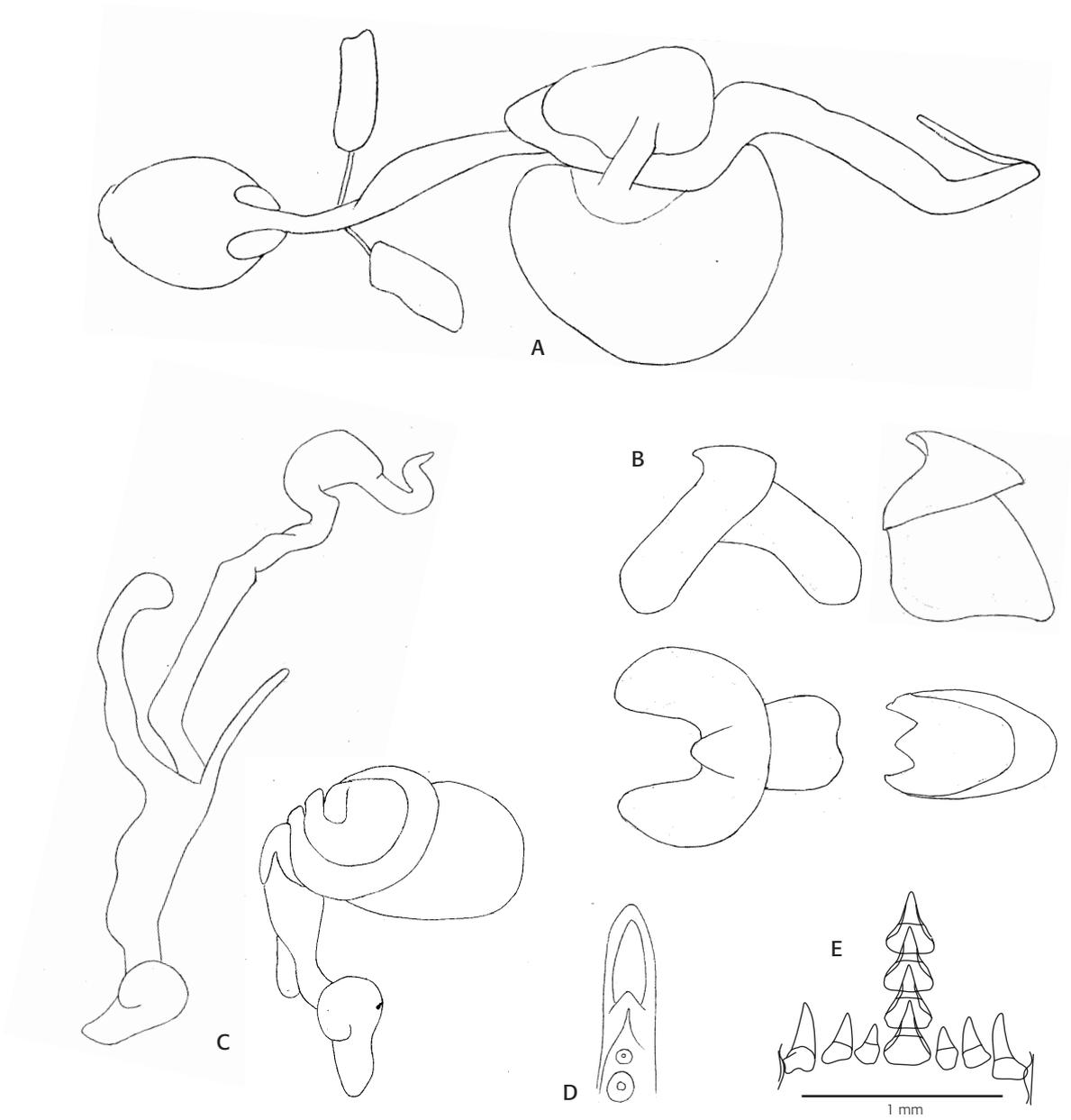


FIGURE 39. *Graneledone* sp. 1 (SAM 2735, ML 68 mm) A) Alimentary canal. B) Upper and lower beaks. C) Male reproductive system. D) Hectocotylus. E) Radula.



FIGURE 40. *Graneledone* sp. 1 (SAM 2735, ML 68 mm). Dorsal and ventral view of preserved specimen.

***Graneledone* sp. 2**

RECOGNISED DISTRIBUTION. Specimens unlocalised; presumed South African waters

MATERIAL EXAMINED. 2 specimens (♂). ML 83, 75 mm, SAM-S3569 (collection details unknown).

DESCRIPTION. Adults medium-sized (ML to 83 mm, TL to 410 mm) (Fig. 42; Tables 80, 84). Head narrower than mantle (HdLI 48–51; HdWI 84–87), delimited from it by moderate pre-ocular constriction. Orbits large, bulbous, midline of head with a narrow interspace between eyes; post-orbital constriction moderate. Arm-to-web attachment type 1A; web formula C=B.A.E.D. Arms 61–73% TL (excluding hectocotylished arm); arm pairs I and II longest, arms III and IV shortest, with no consistent disparity in relative arm lengths. Arm sucker counts 75–80 (excluding hectocotylished arm); suckers extend to arm tips, ASIn 5–6, no suckers abruptly enlarged, attain in greatest diameter beyond first two or three suckers from beaks. Third right arm of male hectocotylished, shorter than opposite member (OAI 82–83), with 57 suckers. Hectocotylished portion (Fig. 41D) with ligula 2.9–4.7% hectocotylished arm length; ligula without transverse rugae; calamus about 45–57% ligula length. Spermatophoral groove well-developed, narrow. Dorsal surfaces of mantle and head, and dorso- and ventro-lateral surfaces of basal portion of arms I and II covered by regularly distributed, close-set warts, with those surrounding eye variable in size, forming distinct circlet; arms III, IV and web sectors A–E without warts; lateral margin of mantle without distinct line of warts. Colour (in alcohol) pale purple brown on dorsal, ventral and oral surfaces.

Gills with 7 lamellae per inner and outer demibranch. Male with well-developed spiral terminal organ diverticulum oriented to left of terminal organ; spermatophoric gland I longer than SG II; spermatophoric sac longer than SGII length, shorter than SGI length (Fig. 41D, Table 86).

Alimentary canal (Fig. 41A; Table 81, 85) with buccal bulb length (BBL) 30% ML. Anterior salivary glands 28% BBL. Posterior salivary glands elliptical or triangular (right side differs from left side), narrow, their greatest dimension about half the length of BBL (48% BBL, 14% ML). Anterior oesophagus narrow, its length 35% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension 90% that of stomach, lacking volutions. Intestine longer than oesophagus, 129% OesTL. Digestive gland circular, without hepatic peaks; greatest dimension 69% ML; pancreas well developed. Functional ink sac absent; vestige of ink sac duct present, embedded in digestive gland, attaching to the lower intestine proximal to anus.

Circulatory system of type 2 (Fig. 13), without apparent ink sac artery.

Lower beak (Fig. 41B left; Tables 82, 88) with black hood and brown border; oral margins of wings black, extending to the middle of wing, forming clearly marked diagonal line with brown border; colour brown from mid-wing to aboral margin; lateral walls black, slightly lightening to brown toward margin; margins translucent. Beak base length 25% ML, height 71% BBL. Hood with rounded crest, elevated from wings. Rostrum tip chisel-like, slightly protruded, 2% BBL. Jaw angle 115°. Wing protrusion length 39% BBL; wing length 68% BBL. Lateral wall crest rounded, with basal notch. Proximal and distal wall of comparable width.

Upper beak (Fig. 41B right; Tables 83, 87) with black hood, with brown border; lateral walls black, gradually transitioning to brown toward aboral margin; all margins translucent. Beak base length 19% ML, higher than wide, BH 119% BBL; hood with rounded crest; rostral tip blunt, triangular; length protrusion 10% BBL; wing markedly more protruded than rostrum. Jaw angle 91°. Lateral wall crest rounded, without notch; walls parallel-sided.

Radula (Fig. 4F) asymmetrical, with 8 teeth in each transverse row, and two marginal blocks; rachidian robust, of comparable width and height, with one or two small, asymmetrically disposed cusps either side of large central cusp. One first lateral tooth on right side of rachidian; two teeth on left side of rachidian, both smaller than that on right side; left first lateral with a small medial cusp, left second lateral smaller, with feeble central cusp; single right lateral with single, well-developed medial cusp. Both second laterals well developed, with large, massive-based cusp. Marginal teeth robust, cusp triangular; marginal blocks present.

REMARKS. The larger specimen was damaged, lacking skin on the ventral surfaces of the mantle and arms (except basal part of the dorsal and lateral arms); no web was present. The smaller specimen was not damaged but was not dissected. The presence of a vestigial ink sac in the larger specimen, with a duct embedded in the digestive gland and attaching to the lower intestine proximal to the anus, clearly provides further evidence that species within this genus are derived from ancestors with a functional ink sac.

TABLE 80. EXTERNAL CHARACTER INDICES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm	SAM S3569 ML 75 mm
Sex	M	M
ALI1R	349.4	*
ALI2R	349.4	*
ALI3R	283.1	240.0
ALI4R	301.2	266.7
ALI1L	361.4	*
ALI2L	349.4	306.7
ALI3L	341.0	293.3
ALI4L	301.2	266.7
MAI	27.7	*
MWI	126.5	126.7
ASIn	6.0	5.3
AWI	22.9	22.7
EOI	20.5	13.3
FFI	36.1	26.7
FuLI	44.6	53.3
HdLI	48.2	50.7
HdWI	84.3	86.7
MWI	126.5	126.7
OAI	83.0	81.8
PAI	60.2	61.3
WDI	*	*

TABLE 81. INTERNAL CHARACTER INDICES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm
AOesLI	26.5
ASGLI	8.4
BBI	30.1
DG(GD)	68.7
IntLI	96.4
OESTLI	74.7
PSGLI	14.5
SpCI	18.1
StI	19.9

TABLE 82. LOWER BEAK INDICES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm
BLI	24.7
BHI	70.7
BIHI	26.8
BWI	85.4
CLI	43.9
DWaWI	46.3
HLI	31.7
PWaWI	43.9
REI	9.8
RWI	17.1
WiLI	68.3
WiWI	36.6

TABLE 83. UPPER BEAK INDICES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm
BLI	18.7
BHI	119.4
BWI	71.0
CHI	19.4
HHI	48.4
HLI	71.0
REI	12.9
RPI	9.7
RWI	25.8
WiLI	61.3

TABLE 84. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Graneledone* sp. 2.

	SAM S3569 ML 83 mm	SAM S3569 ML 75 mm
Gender	M	M
ML	83	75
AL1R	290	*
AL2R	290	*
AL3R	235	180
AL4R	250	200
AL1L	30	*
AL2L	290	230
AL3L	*	220
AL4L	250	200
ASC1R	*	*
ASC2R	*	*
ASC3R	44	43
ASC4R	*	73
ASC1L	*	*
ASC2L	82	80
ASC3L	*	79
ASC4L	76	75
SD	5	4
AW	19	17
EO	17	10
FFL	30	20
FuL	37	40
GilC I	70	*
GilC O	70	*
HdL	40	38
HdW	70	65
MW	105	95
PA	50	46
TL	410	320
WAt	type 1B	type 1B
WDA	*	50
WDBR	*	63
WDBL	*	70
WDCR	*	60
WDCL	*	62
WDDR	*	*
WDDL	*	35
WDE	*	43

TABLE 85. INTERNAL CHARACTER RAW MEASURES. *Graneledone* sp. 2.

	SAM S3569 ML 83 mm
AOesL	22
ASGL	7
BBL	25
DGL	35
DGW	57
DG(GD)	57
InTL	80
ISA	no
ISpres	duct
OesTL	62
PSGL	12
SpCL	15
StL	17

TABLE 86. REPRODUCTIVE SYSTEM RAW MEASURES. *Graneledone* sp. 2.

	SAM S3569 ML 83 mm
CaL	5
LL	11
SGI	10
SGII	78
SS	88
TODL	23
TOL	13
TOTL	37

TABLE 87. UPPER BEAK RAW MEASURES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm
BL	16
BH	19
BW	11
CH	3
HH	8
HL	11
HW	11
RE	02
RP	02
RW	04
WiL	10

TABLE 88. LOWER BEAK RAW MEASURES.
Graneledone sp. 2.

	SAM S3569 ML 83 mm
BL	21
BH	15
BIH	6
BW	18
CH	3
CL	9
DWaW	10
HL	7
PWaW	9
RE	2
RW	4
WiL	14
WiW	8



FIGURE 41. *Graneledone* sp. 2 (SAM S3569, ML 83 mm). A) Alimentary canal. B) Upper and lower beaks. C) Ink sac duct. D) Hectocotylus. E) Male reproductive system. F) Radula.



FIGURE 42. *Graneledone* sp 2. (SAM S3569, ML 83 mm). Dorsal and ventral view (preserved specimen).

Graneledone taniwha taniwha O'Shea, 1999

DIAGNOSIS (modified from O'Shea 1999). Moderate to large-sized animals; arms with 58–97 suckers; hectocotylied arm sucker count 39–45; hectocotylied portion of arm 3–7.6% arm length; ASIn 3.8–8.6; mantle with 24–29 cartilage-like 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 in each (most frequently 12–17); well-developed, triangular supra-ocular cirrus almost invariably present.

RECOGNISED DISTRIBUTION. New Zealand, off the Wairarapa coast, Chatham Rise to Auckland and Campbell Islands, 42°43'–49°25.55'S, 168°28.82'–175°44'E, 477–1157 m, bottom temperature range (recorded) 4.1–7.8°C (O'Shea 1999).

SYNONYMY.

Graneledone sp. O'Shea & Kubodera, 1996: 153–163, figs 1–4.

Graneledone taniwha taniwha O'Shea, 1999: 222–233, figs 136, 137.

MATERIAL EXAMINED. 1 specimen (♂): ML 117 mm, NIWA (not registered), collection coordinates not presently available, New Zealand (RV *Tangaroa* Stn TAN0317/30).

DESCRIPTION (modified from O'Shea 1999). Adults of moderate to large size (ML to 170 mm, TL to 660.0 mm) (Fig. 45, Tables 89, 93). Male and female similar in gross morphology. Mantle ovoid, dorso-ventral compression. Head narrower than mantle (HdLI 30–43, HdWI 63–102), delimited from it by slightly developed pre-ocular constriction. Orbits large, bulbous. Post-orbital constriction poorly developed. Brachial crown and arms robust. Web-to-arm attachment type 1A; depth 15–35% longest arm length. Web formula variable; sector A usually shallowest, C and D deepest, with no consistent disparity in relative sector depths. Arms 50–73% TL; arm pairs I and II usually longest, arms III and IV shortest, with no consistent disparity in relative arm lengths. Suckers uniserial. Arm sucker counts greater in mature females than males, female ASC 71–97, male 58–88; suckers extend to arm tips. Sucker size different in males and females, ASIn 3.8–7.4 (male), 5.3–8.6 (female); no suckers abruptly enlarged; suckers attain their greatest diameter just before web margin attachment to the arms. Third right arm of male hectocotylied, shorter than opposite member (OAI about 75–90), with 44 suckers. Hectocotylied portion (Fig. 44D) with ligula 3.0–7.6% hectocotylied arm length, increasing with maturity; calamus 32–68%

ligula length. Spermatophoral groove well developed, wide; web margin thickened. Dorsal surfaces of mantle, head, arms I and II, web sectors A–C, and dorso-lateral surfaces of arms III covered with irregular-sized clusters of cartilage-like processes; processes not extending along arms and absent on arms IV; ventral side of mantle without processes, with clear edge formed by warts extending laterally around mantle margin. Supraocular cirrus large, single, triangular.

Gills compact, with 7 or 8 lamellae per inner and outer demibranch. Male with well-developed spiral terminal organ diverticulum oriented to left of terminal organ. Spermatophoric gland I longer than II; spermatophoric sac shorter than both spermatophoric glands (Fig. 44C, Table 95).

Alimentary canal (Fig. 44A; Tables 90, 94) with buccal bulb length (BBL) 25% ML. Anterior salivary glands of length 16% BBL. Posterior salivary glands elliptical, narrow, their greatest dimension slightly more than half that of BBL (60% BBL, 13% ML). Anterior oesophagus narrow, its length 25% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension 90% that of stomach, lacking volutions. Intestine more than twice the length of oesophagus (~205% OesTL). Digestive gland circular, with or without weak hepatic peaks; greatest dimension 36% ML; pancreas well developed. Functional ink sac absent; no apparent ink sac artery or vestige of ink sac duct leading to anus.

Circulatory system of type 3 (Fig. 13), with apparent, thin ink sac artery where ink sac duct would be.

Lower beak (Fig. 44B left; Tables 91, 97) with black hood, abruptly lightening toward margins; oral margin of wings black, extending to middle of wing, forming clearly marked diagonal line that lightens to brown toward aboral margin; lateral walls black, slightly lightening toward margin; margins translucent. Beak base length 20% ML, height 70–76.2% BBL. Hood almost flat-topped, elevated from wings. Rostrum tip chisel-like, with clear protrusion, 4% BBL. Jaw angle 105°. Wing protrusion length 9% BBL; wing length 15% BBL. Lateral wall crest rounded, with basal notch. Proximal wall width 9% narrower than distal wall width.

Upper beak (Fig. 44B right; Tables 92, 96) with black hood abruptly lightening toward the margins; lateral walls black, abruptly transitioning to brown toward aboral margin; all margins translucent. Beak base length 20% ML, its height and length comparable; hood with rounded crest; rostral tip blunt, orally deflected, triangular; length protrusion 13% BBL; wing markedly more protuded than rostrum. Jaw angle 90°. Lateral wall crest rounded, without basal notch; walls parallel-sided.

Radula (Fig. 43) with robust, broadly triangular, rachidian tooth, taller than wide, with one or two small, symmetrically disposed cusps either side of large central cusp. First laterals small, with single outer cusp. Second laterals well developed, with large, massive-based cusp.

TABLE 89. EXTERNAL CHARACTER INDICES.
G. taniwha taniwha.

	ML 117 mm
Sex	M
ALI1R	241.0
ALI2R	242.7
ALI3R	198.3
ALI4R	222.2
ALI1L	235.0
ALI2L	241.0
ALI3L	230.8
ALI4L	205.1
MAI	41.2
MWI	119.7
ASIn	4.3
AWI	14.5
EOI	16.2
FFI	30.8
FuLI	47.0
HdLI	41.0
HdWI	65.0
MWI	119.7
OAI	85.9
PAI	54.7
WDI	37.0

TABLE 90. INTERNAL CHARACTER INDICES.
G. taniwha taniwha.

	ML 117 mm
AOesLI	16.2
ASGLI	7.3
BBI	21.4
DG(GD)	35.9
IntLI	131.6
OESTLI	64.1
PSGLI	12.8
SpCI	17.1
StI	23.1

TABLE 91. LOWER BEAK INDICES.
G. taniwha taniwha.

	ML 117 mm
BLI	19.7
BHI	69.6
BIHI	34.8
BWI	87.0
CLI	47.8
DWaWI	47.8
HLI	34.8
PWaWI	43.5
REI	6.5
RWI	15.2
WiLI	73.9
WiWI	39.1

TABLE 92. UPPER BEAK INDICES.
G. taniwha taniwha.

	ML 117 mm
BLI	17.1
BHI	105.0
BWI	60.0
CHI	20.0
HHI	40.0
HLI	60.0
REI	15.0
RPI	12.5
RWI	27.5
WiLI	47.5

TABLE 93. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *G. taniwha taniwha*.

ML 117 mm	
Gender	M
ML	117
AL1R	282
AL2R	284
AL3R	232
AL4R	260
AL1L	275
AL2L	282
AL3L	270
AL4L	240
ASC1R	81
ASC2R	80
ASC3R	44
ASC4R	73
ASC1L	76
ASC2L	78
ASC3L	75
ASC4L	73*
SD	5
AW	17
EO	19
FFL	36
FuL	55
GilC I	70
GilC O	70
HdL	48
HdW	76
MW	140
PA	64
TL	440
WAt	type 1A
WDA	98
WDBR	98
WDBL	94
WDCR	105
WDCL	102
WDDR	104
WDDL	104
WDE	83

TABLE 94. INTERNAL CHARACTER RAW MEASURES. *G. taniwha taniwha*.

ML 117 mm	
AOesL	19
ASGL	9
BBL	25
DGL	42
DGW	42
DG(GD)	42
InTL	154
ISA	yes
ISpres	no
OesTL	75
PSGL	15
SpCL	20
StL	27

TABLE 95. REPRODUCTIVE SYSTEM RAW MEASURES. *G. taniwha taniwha*.

ML 117 mm	
CaL	6
LL	11.5
SGI	13
SGII	77
SS	86
TODL	12.5
TOL	24
TOTL	36.5

TABLE 96. UPPER BEAK RAW MEASURES.
G. taniwha taniwha.

	ML 117 mm
BL	2.0
BH	2.1
BW	1.2
CH	0.4
HH	0.8
HL	1.2
HW	1.0
RE	0.3
RP	0.3
RW	0.6
WiL	1.0

TABLE 97. LOWER BEAK RAW MEASURES.
G. taniwha taniwha.

	ML 117 mm
BL	2.3
BH	1.6
BIH	0.8
BW	2.0
CH	0.4
CL	1.1
DWaW	1.1
HL	0.8
PWaW	1.0
RE	0.2
RW	0.4
WiL	1.7
WiW	0.9

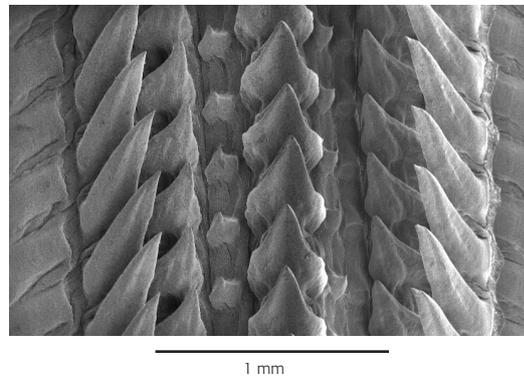


FIGURE 43. *Graneledone taniwha taniwha*. ESEM radula.

Marginals robust, cusp more delicate than that of either rachidian or second lateral; marginal blocks short, rectangular.

REMARKS. Whereas the preceding two (presently undescribed) species each possess a vestige of the ink sac, in that the duct remains but a functional ink sac is absent, no such duct was apparent in this species, *G. taniwha taniwha*. However, it does possess an arterial branch positionally homologous to that which leads to the ink sac in those taxa that have this structure (e.g., *Octopus* [s.l.]). Unfortunately, the arterial system in both preceding species of *Graneledone* was damaged, so it could not be determined whether either taxon possessed an ink sac artery (or positional homologue). Despite this, the presence of this ink sac artery (or positional homologue) in this current taxon provides additional support for the notion that species within this genus are derived from species with a functional ink sac.

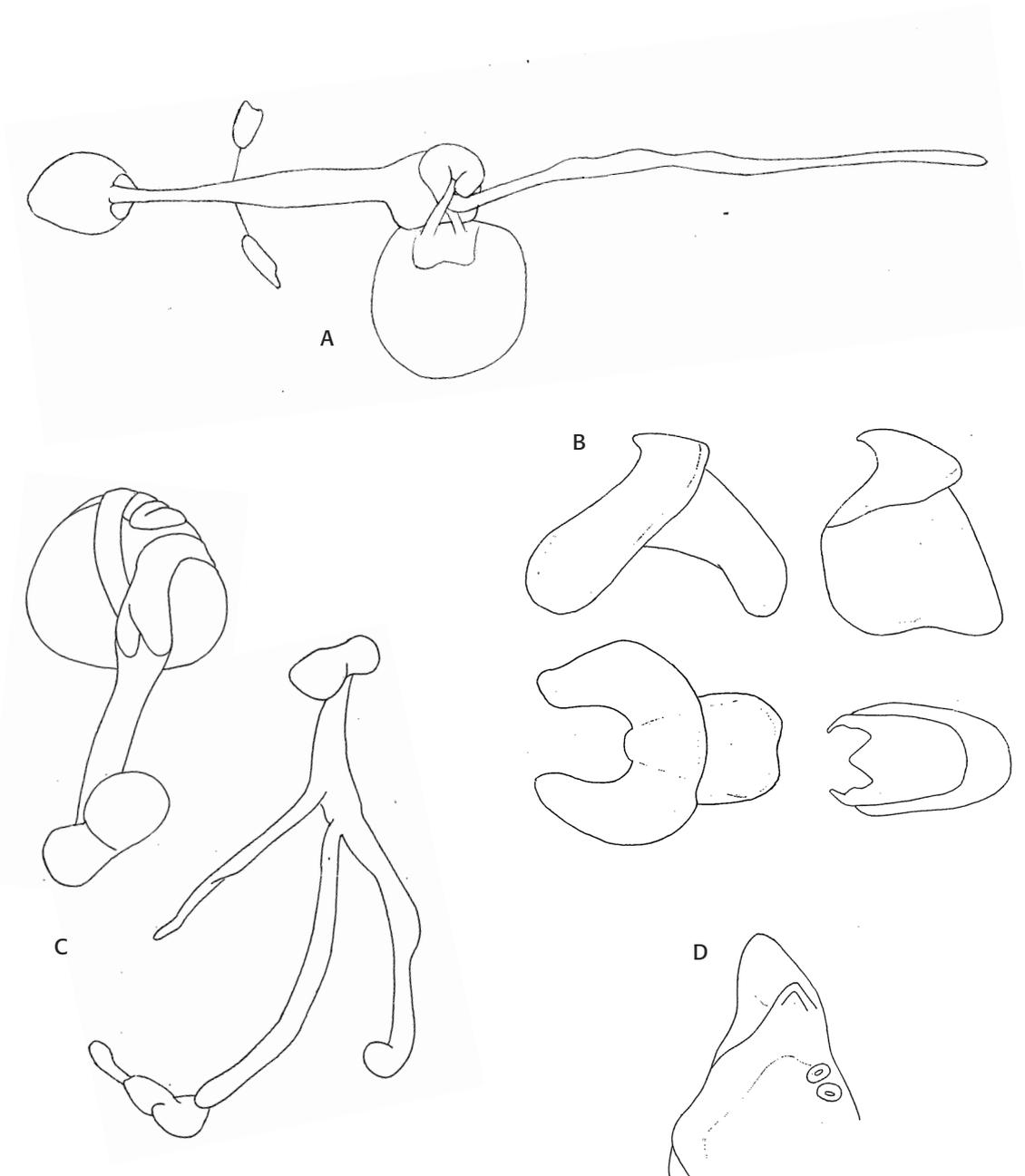


FIGURE 44. *Graneledone taniwha taniwha*. A) Alimentary canal. B) Upper and lower beaks. C) Male reproductive system. D) Hectocotylus.



FIGURE 45. *Graneledone taniwha taniwha*. Dorsal and ventral view of preserved specimen.

Graneledone antarctica Voss, 1976

RECOGNISED DISTRIBUTION. Abyssal species inhabiting waters to 2341 m, presently known from the Ross Sea (Voss 1976, herein) and, if correctly identified, from the South Shetland Islands (Vecchione *et al.* 2005), rendering the species unusually circum-Antarctic.

SYNONYMY.

Graneledone antarctica Voss, 1976: 447–454, Figs 1, 2 — O’Shea 1999: 240–245, Fig. 142A–C; Vecchione *et al.* 2005: 112, 113, Fig. 3.

MATERIAL EXAMINED. 2 specimens (♂,♀). NIWA 44052, ML 90 mm, ♂, 71°51.6’S, 174°01.8’E, 1954–1990 m, 25/02/2008, RV *Tangaroa* Stn TAN802/167; NIWA 44051, ML 85 mm, ♀, 71°51.6’S, 174°01.8’E, 1954–1990 m, 25/02/2008, RV *Tangaroa* Stn TAN802/167.

DESCRIPTION (modified from Voss 1976). Adults large-bodied, mantle to 90 mm length, total length to 360 mm (Fig. 47; Tables 98, 102). Mantle broadly rounded posteriorly; wide. Head slightly narrower than mantle (HdLI 35–37, HdWI 65–100), delimited from it by moderate pre-ocular constriction. Orbits large, bulbous, with marked interspace between both eyes across dorsal midline of head. Post-orbital constriction marked. Arm-to-web attachment type 1A; depth 27–36% longest arm length; web formula variable, usually A and E shallowest and C and B deepest. Arms long and stout, 58–79% TL; arm pairs I and II longest, arm IV shortest; arm formula I.II.III.IV. Suckers uniserial; arm sucker counts 63–69; ASIn 6–8, with none abruptly enlarged; suckers attain greatest diameter at about sixth sucker from beaks. Third right arm of male hectocotylised (Fig. 46D), shorter than opposite member (OAI 86), with 39 suckers. Ligula with thickened margins, its oral face crossed by low fleshy folds. Spermatophoral groove well developed. Dorsal surfaces of mantle and head covered by regularly spaced, close-set warts, each comprising one to more than 12 small cone-shaped papillae; warts extend along dorso- and ventro-lateral surfaces of Arms I, and dorso-lateral surfaces of Arms II and III to about 2/3 of each arm length, but neither dorso- nor ventro-laterally along arms IV; warts extend in web sectors A through C; lateral surface of mantle with distinct line of fine warts, arranged like a keel running from the corners of the mantle aperture and extending posteriorly; ventral surface of mantle and head lacking warts, except for several bordering lower eyelid; dorsal surfaces of eyes with distinct circlet of warts, two or three enlarged over each eye.

Colour (preserved) pale yellowish–brown dorsally becoming purplish at base of brachial crown and between the arm bases. Mantle, head, funnel and arm bases reddish–brown suffused with purple.

Gills with 6 lamellae per demibranch. Male with well–developed spiral terminal organ diverticulum oriented to the left of terminal organ. Spermatophoric gland I longer than II; spermatophoric sac longer, of comparable length to SGII (Fig. 46C, Table 104). Female reproductive system (Fig. 46E) with proximal oviduct 25% the length of distal oviduct, narrower; distal oviduct longer than ovary sac, of comparable diameter to the oviducal ball.

Alimentary canal (Fig. 46A; Tables 99, 103) with buccal bulb length 24% ML. Anterior salivary gland length 32% buccal bulb length. Posterior salivary glands elliptical, narrow, small, their greatest dimension about 25% that of BBL (25% BBL, 6% ML). Anterior oesophagus narrow, its length 32% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension about 75% that of stomach, lacking volutions. Intestine almost twice as long as oesophagus, ~196% OesTL. Digestive gland circular, with poorly developed peaks on either side of hepatic ducts; greatest dimension 47% ML; pancreas well developed. Functional ink sac absent; without apparent ink sac artery or vestige of ink sac duct leading to anus.

Circulatory system damaged; presence/absence of ink sac artery could not be determined.

Lower beak (Fig. 46B left, Tables 100, 105) with black hood, abruptly lightening to brown toward margins; oral margin of wings black extending to middle of wing, forming clearly marked diagonal line that lightens to brown toward aboral margin; lateral walls black, slightly lightening toward margin; margins translucent. Beak base length 21% ML, height 79% BBL. Hood with rounded crest, elevated from wings. Rostrum tip triangular, blunt, with clear protrusion, 5.8% BBL. Jaw angle 95°. Wing protrusion length 26% BBL; wing length 37% BBL. Lateral wall crest rounded, without basal notch; proximal and distal wall of similar width.

Upper beak (Fig. 46B right, Tables 101, 104) with black hood, abruptly lightening to brown close to margin; lateral walls black, gradually transitioning to brown toward aboral margin; all margins translucent. Beak base length 17% ML, of comparable height and width. Hood with rounded crest; rostrum triangular, tip slightly blunt, orally deflected, with lateral keel; length protrusion 13% BBL; wing length protrusion of comparable length to that of rostrum. Jaw angle 90°. Lateral wall crest rounded, without basal notch; parallel–sided.

REMARKS. Both specimens appear mature, with spermatophores present in the diverticulum of male’s terminal organ, and eggs recovered from the oviducts of the female. The female was in good condition externally, but the buccal bulb had been previously cut in half and a portion of

TABLE 98. EXTERNAL CHARACTER INDICES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
Sex	F	M
ALI1R	335.3	331.1
ALI2R	337.6	288.9
ALI3R	308.2	240.0
ALI4R	278.8	255.6
ALI1L	357.6	316.7
ALI2L	343.5	303.3
ALI3L	343.5	277.8
ALI4L	303.5	273.3
MAI	28.0	29.7
MWI	111.8	111.1
ASIn	5.9	5.6
AWI	20.0	16.7
EOI	15.3	20.0
FFI	29.4	27.8
FuLI	35.3	33.3
HdLI	35.3	37.2
HdWI	75.3	66.7
MWI	111.8	111.1
OAI	89.7	86.4
PAI	61.2	59.4
WDI	28.9	35.6

TABLE 99. INTERNAL CHARACTER INDICES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
AOesLI	0.0	20.0
ASGLI	8.2	7.8
BBI	24.7	24.4
DG(GD)	45.9	46.7
IntLI	103.5	124.4
OESTLI	72.9	63.3
PSGLI	6.5	6.1
SpCI	19.4	16.7
StI	24.7	22.2

TABLE 100. LOWER BEAK INDICES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
BLI	21.2	21.1
BHI	72.2	78.9
BIHI	25.0	28.9
BWI	91.7	89.5
CLI	38.9	47.4
DWaWI	44.4	47.4
HLI	33.3	36.8
PWaWI	44.4	47.4
REI	5.6	7.9
RWI	16.7	15.8
WiLI	66.7	63.2
WiWI	38.9	21.1

TABLE 101. UPPER BEAK INDICES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
BLI	17.6	17.2
BHI	100.0	100.0
BWI	60.0	54.8
CHI	13.3	16.1
HHI	46.7	45.2
HLI	53.3	58.1
REI	10.0	12.9
RPI	13.3	12.9
RWI	23.3	25.8
WiLI	53.3	48.4

TABLE 102. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Graneledone antarctica*.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
Gender	F	M
ML	85	90
AL1R	285	298
AL2R	287	260
AL3R	262	216
AL4R	237	230
AL1L	304	285
AL2L	292	273
AL3L	292	250
AL4L	258	246
ASC1R	65	65
ASC2R	69	66
ASC3R	66	39
ASC4R	64	62
ASC1L	67	64
ASC2L	69	65
ASC3L	66	64
ASC4L	63	64
SD	5	5
AW	17	15
EO	13	18
FFL	25	25
FuL	30	30
GilC I	60	60
GilC O	60	60
HdL	30	34
HdW	64	60
MW	95	100
PA	52	54
TL	395	396
WAt	type 1A	type 1A
WDA	60	63
WDBR	87	74
WDBL	82	73
WDCR	82	88
WDCL	85	78
WDDR	66	108
WDDL	88	*
WDE	64	*

TABLE 103. INTERNAL CHARACTER RAW MEASURES. *Graneledone antarctica*.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
AOesL	*	18
ASGL	7	7
BBL	21	22
DG(GD)	39	42
InTL	39	42
ISA	88	112
ISpres	no	duct
OesTL	62	57
PSGL	6	6
SpCL	17	15
StL	21	20

TABLE 104. MALE REPRODUCTIVE SYSTEM RAW MEASURES. *Graneledone antarctica*

	NIWA 44051 ML 85 mm
CaL	7
LL	12
SGI	150
SGII	95
SS	118
TODL	28.5
TOL	18.5
TOTL	32

TABLE 105. FEMALE REPRODUCTIVE SYSTEM RAW MEASURES. *Graneledone antarctica*.

	NIWA 44051 ML 85 mm
DOdL	27
DOdW	27
OSL	20
OSW	19
OdTL	37
OdBL	5
OdBW	9
POdL	6
POdW	3

TABLE 106. UPPER BEAK RAW MEASURES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
BL	15	16
BH	15	16
BW	9	9
CH	2	3
HH	7	7
HL	8	9
HW	10	9
RE	2	2
RP	2	2
RW	4	4
WiL	8	8

TABLE 107. LOWER BEAK RAW MEASURES.
Graneledone antarctica.

	NIWA 44051 ML 85 mm	NIWA 44052 ML 90 mm
BL	18	19
BH	13	15
BIH	5	6
BW	17	17
CH	2	3
CL	7	9
DWaW	8	9
HL	6	7
PWaW	8	9
RE	1	2
RW	3	3
WiL	12	12
WiW	7	4

the anterior oesophagus and posterior salivary glands were missing. The male was well preserved internally and externally, with only portions of the web being damaged.

This current species is remarkable, compared to the preceding three species (two of which possess an ink sac vestige (an ink sac duct), and one of which does not, although it retains an arterial branch positionally homologous with an ink sac artery) because it has no ink sac vestige, duct, or even apparent ink sac artery. It would appear that some taxa referable to *Graneledone* have lost the ink sac and associated arterial system faster than others. Moreover, it could be interpreted that the more northern taxa, with apparent vestiges of the ink sac or associated arterial system (the ancestral state), are phylogenetically older than those that have completely lost it (the derived condition). Accordingly, it is possible that Antarctic species of *Graneledone* are younger than more northern (latitude) congeners, and that the origin of this taxon is more northern than southern (or, alternatively, that rates of speciation in Antarctic waters are occurring at a greater speed than more northern latitudes).

Specimens attributed to *G. antarctica* herein have been collected from very close to the type locality of this species. Sufficient characters are not described for those specimens referred to *G. antarctica* by Vecchione *et al.* (2005) to critically appraise their taxonomic status, but the latter specimens were collected from the opposite side of Antarctica to those herein, which, if correctly identified, would render this species very widely distributed for a Southern Ocean octopodid.

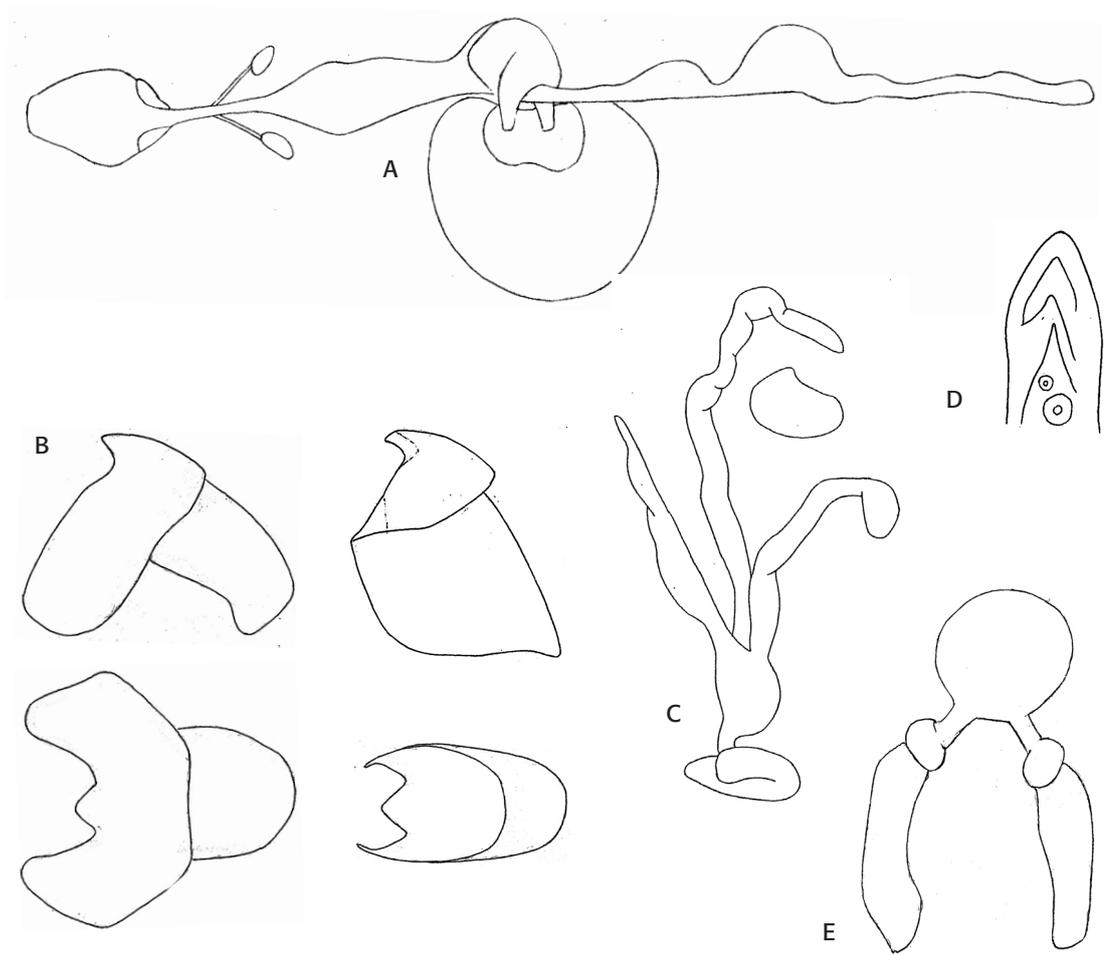


FIGURE 46. *Graneledone antarctica* (NIWA 44052, ML 90 mm). **A)** Alimentary canal. **B)** Upper and lower beaks. **C)** Male reproductive system. **D)** Hectocotylus. **E)** Female reproductive system (NIWA 44051, ML 85 mm).



FIGURE 47. *Graneledone antarctica*. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44051, ML 85 mm, ♂. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44052, ML 90 mm, ♀.

Megaleledone Taki, 1961

The subfamily Megaleledoninae and genus *Megaleledone* were proposed by Taki (1961) to accommodate a single large-bodied species *Megaleledone senoi*. Both subfamily, genus and species have been the subject of debate since, with the subfamily and genus being considered invalid by Voss (1988a), the genus and species considered valid but subfamily invalid by Kubodera & Okutani (1994, 1986) and Lu & Stranks (1994), or the genus valid but species invalid, the species being considered synonymous with '*Graneledone*' *setebos* Robson, 1932 (Allcock *et al.* 2003). Specimens referred to this genus have been reported from depths of 32–803 m (Allcock 1997); it is presently known only from the Southern Ocean.

DIAGNOSIS. An eledonid of great size (ML to 900 mm); mantle wider than long, ink sac small, crop absent; rachidian tooth of radula symmetrical, unicuspid. Ovarian eggs large (Taki 1961).

TYPE SPECIES. (By original designation): *Megaleledone senoi* (Taki, 1961). By monotypy.

Megaleledone cf. setebos (Robson, 1932)

DIAGNOSIS (modified from Allcock *et al.* 2003c). Large benthic octopus, TL to 900 mm, maturing at over 200 mm ML. Mantle saccular and broad. Stylets present. Arms with uniserial row of suckers. Arms 2–3 times length of body. Right third arm of males hectocotyliised; copulatory organ with clearly differentiated ligula and calamus; ligula simple, without transverse ridges, calamus of moderate length. Arm tips not otherwise modified. Suckers moderately large; distinct enlarged suckers absent. Web deep, well developed. Funnel organ VV-shaped. Gills with 10–13 lamellae per outer demibranch. Ink sac present; anal flaps absent. Radula composed of seven teeth per transverse row; marginal plates vestigial. Capsule length of spawned eggs over 40 mm.

RECOGNISED DISTRIBUTION. Circum-Antarctic, not extending to sub-Antarctic islands. Depth range intertidal (species type, albeit dead, collected from rock pool), live from 32 m (Nesis & Propp 1968) to 850 m.

SYNONYMY.

Moschites sp. Massy, 1916: 159–161, fig. 33.

Graneledone setebos Robson, 1932: 313–314, fig. 72 — Grimpe 1933: 497; Castellanos & Menni 1969: 78; Dell 1972: 86; Voss 1976: 457 [designation as *nomen dubium*].

Megaleledone senoi Taki, 1961: 297–304, figs 1–8, 16, pl 1, 2 — Nesis & Propp 1968: 66–68, fig. 1; Dell 1972: 86–87; Lipinski & Woyciechowski 1981: 163–166, fig. 1a, b; Kubodera & Okutani 1986: 133–134, fig. 2A, B, pl 2 (figs A–D); Kubodera & Okutani 1994: 210–212; Lu & Stranks 1994: 233, fig. 8, 9u–x; Piatkowski *et al.* 1998: 44; Ogden *et al.* 1998: 29–34.

Pareledone senoi (Taki) — Voss 1988a: 302, fig. 6 [map].

MATERIAL EXAMINED. 1 specimen (♀): NIWA 44147, ML ~202 mm, 76°49.98–49.14'S, 179°57.0–58.2'E, 663–664 m, 16/02/2008, RV *Tangaroa* Stn TAN0802/77.

DESCRIPTION (modified from Taki 1961, Allcock *et al.* 2003c). Animal large (ML to 280 mm, TL to 900 mm) (Fig. 50; Table 108, 112). Mantle shape variable, slightly broader than long to slightly longer than broad. Head narrower than mantle (HdLI 20, HdWI 46); post-ocular constriction poorly developed. Brachial crown and arms robust. Arm-to-web attachment type 1A; web deep, with points of web attachment extending nearly half way along arms. Web depth 45–53% longest arm length; web formula usually C=D.B.A=E. Arms long, 2–3 times mantle length (ALI 188–222), of similar length. Suckers uniserial; arm sucker counts 60–67; ASI 8.5, none abruptly enlarged; suckers attain greatest diameter at the 5th or 6th sucker from beaks. Enlarged super-ocular papillae absent; mantle with well developed ventro-lateral integumentary ridge; ventral and oral surfaces of mantle, head and arms smooth, slightly paler in coloration than similarly smooth dorsal surfaces of same.

Gill on sole Ross Sea specimen examined with 11 lamellae per outer demibranch.

Female reproductive system (Fig. 49C, Table 114) with length of proximal oviduct 1/9 distal oviduct length; distal oviduct approximately 1.5 longer than ovary sac length, of comparable diameter to oviducal ball.

Alimentary canal (Fig. 49A, B; Tables 109, 113) with buccal bulb length (BBL) 25% ML. Anterior salivary glands of length 27% BBL. Crop present, without diverticulum. Spiral caecum of diameter 78% that of stomach, lacking volutions. Intestine very long, about 3 times length of digestive gland length. Digestive gland circular, with poorly developed peaks on either side of hepatic ducts; greatest dimension 52.5% ML; pancreas not well developed. Ink sac present, type 2 (Fig. 6), just covered by digestive gland membranes; anal flaps absent.

Circulatory system of type 1 (Fig. 13), with thick ink sac artery.

Lower beak (Fig. 49 left; Tables 110, 116) with black hood and thin brown border; oral margin of wings black, extending to middle of wing, forming soft diagonal line that marks colour transition from black to brown. Lateral walls black, abruptly lightening to brown toward margin; margins translucent. Beak base length 24% ML, height 74% BBL. Hood with rounded crest, elevated from wings. Rostrum tip blunt-rectangular, slightly chiseled, with clear protrusion, 6.5% BBL. Jaw angle 105°. Wing protrusion length 20% BBL; wing length 62.5% BBL. Lateral wall crest rounded, with weak basal notch. Proximal and distal wall of comparable width.

Upper beak (Fig. 49 right; Tables 111, 115) with black hood and thin brown border; lateral walls black, abruptly transitioning to brown toward margin; all margins translucent. Beak base length 19% ML, of comparable height and length. Hood with rounded crest; rostral tip slightly blunt, triangular, with lateral keel; length protrusion 8% BBL; wing length protrusion markedly longer than that of rostrum. Jaw angle 115°. Lateral wall crest rounded, without basal notch; parallel-sided.

Radula (Fig. 48) with robust, broadly triangular rachidian, as tall as wide, without lateral cusps. First laterals unicuspid, broad based. Second laterals with broad cusp, of similar length to rachidian. Marginal teeth unicuspid, gently curved. Marginal plates vestigial.

REMARKS. The holotype of this species is a specimen in very poor condition, collected from a rock pool at McMurdo Sound, Ross Sea. All other specimens attributed to this species, with the exception of those reported by Nesis & Propp (1968), have been collected from considerably greater depth. The beaks of the holotype of this species (Fig. 49F herein) bear little resemblance to those illustrated for it by Allcock *et al.* (2003: figs A–C). Moreover, beak morphology of the single specimen available for study described herein differs in several details from that of the holotype. Given the pronounced differences in depth of collection and capture of the holotype and only other described specimen of this species from the Ross Sea, and that subtle differences in octopodid beak morphology generally indicate the existence of different species, attribution of this present specimen to Robson's '*Graneledone*' *setebos* is made with some reservation; similarly, attribution of other deeper-dwelling specimens referred to this species by all other authors (see synonymy) is also made with some reservation. Until more comprehensive collections of littoral octopodids from the Ross Sea region are available for study (no recent collections include littoral specimens), especially those from the McMurdo Sound region, attribution of littoral (especially intertidal, albeit dead) and deep-sea specimens to a common taxon should be treated with caution. It is possible that two large-bodied species occur in the Ross Sea. This specimen is attributed to *Megaleledone* cf. *setebos* (Robson, 1932) largely on grounds of Nesis & Propp's (1968) record of this species from

TABLE 108. EXTERNAL CHARACTER INDICES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
Sex	F
ALI1R	188.1
ALI2R	198.0
ALI3R	212.9
ALI4R	222.8
ALI1L	198.0
ALI2L	198.0
ALI3L	198.0
ALI4L	198.0
MAI	44.9
MWI	113.9
ASIn	8.7
AWI	29.7
EOI	8.4
FFI	33.7
FuLI	20.8
HdLI	19.8
HdWI	46.0
MWI	113.9
OAI	107.5
PAI	69.3
WDI	53.3

TABLE 109. INTERNAL CHARACTER INDICES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
AOesLI	–
ASGLI	7.4
BBI	29.7
DG(GD)	56.9
DGI	56.9
IntLI	173.3
ISTLI	50.0
ISLI	21.3
OESTLI	–
PSGLI	–
SpCI	–
StI	37.1

TABLE 110. LOWER BEAK INDICES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
BLI	23.8
BHI	74.0
BIHI	33.3
BWI	86.5
CLI	41.7
DWaWI	53.1
HLI	43.8
PWaWI	53.1
REI	12.5
RWI	14.6
WiLI	62.5
WiWI	38.5

TABLE 111. UPPER BEAK INDICES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
BLI	18.8
BHI	106.6
BWI	84.2
CHI	26.3
HHI	50.0
HLI	69.7
REI	15.8
RPI	7.9
RWI	26.3
WiLI	39.5

TABLE II2. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *M. cf. setebos*.

	NIWA 44147 ML 202 mm
Gender	F
ML	202*
AL1R	380
AL2R	400
AL3R	430
AL4R	450
AL1L	400
AL2L	400
AL3L	400
AL4L	400
ASC1R	60
ASC2R	65
ASC3R	65
ASC4R	65
ASC1L	62
ASC2L	66
ASC3L	67
ASC4L	67
SD	18
AW	60
EO	17
FFL	68
FuL	42
GiLC I	11
GiLC O	11
HdL	40*
HdW	93
MW	230
PA	14*
TL	690*
WAt	type 1B
WDA	140
WDBR	180
WDBL	180
WDCR	200
WDCL	200
WDDR	240
WDDL	220
WDE	*

TABLE II3. INTERNAL CHARACTER RAW MEASURES. *M. cf. setebos*.

	NIWA 44147 ML 202 mm
AOesL	–
ASGL	15
BBL	60
DGL	115
DGW	105
DG(GD)	115
InTL	350
ISA	yes
ISpres	type 2
ISDL	38
ISEL	14
ISEW	7
ISL	43
ISTL	101
ISW	9
OesTL	–
PSGL	–
SpCL	*
StL	75

TABLE II4. REPRODUCTIVE SYSTEM RAW MEASURES. *M. cf. setebos*.

	NIWA 44147 ML 202 mm
DOdL	58
DOdW	14
OSL	30
OSW	45
OdTL	80
OdBL	10
OdBW	15
POdL	12
PODW	07

TABLE 115. UPPER BEAK RAW MEASURES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
BL	38
BH	41
BW	32
CH	10
HH	19
HL	27
HW	21
RE	06
RP	3
RW	10
WiL	15

TABLE 116. LOWER BEAK RAW MEASURES.
M. cf. setebos.

	NIWA 44147 ML 202 mm
BL	48
BH	36
BIH	16
BW	42
CH	10
CL	20
DWaW	26
HL	21
PWaW	26
RE	6
RW	7
WiL	30
WiW	19

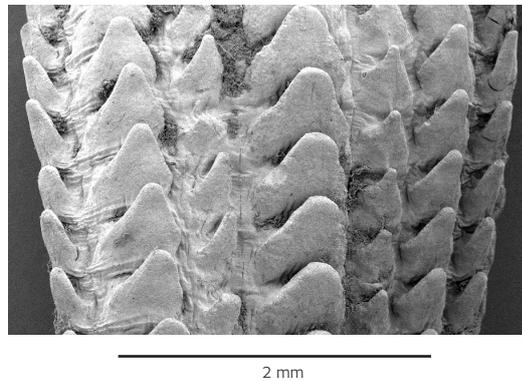


FIGURE 48. *Megaleledone cf. setebos* (NIWA 44147, ML 202 mm). ESEM radula.

depths as shallow as 32 metres. This specimen does not differ in any remarkable manner from that reported by Taki (1961), referred to *M. senoi*, but without additional material from around Antarctica, the presence of more than one species cannot be critically evaluated.

Given that few eledonid octopods have circum-Antarctic distributions, it is surprising that this taxon is purportedly so widely distributed. Additional analysis might show there to be more than one species tied up in this complex, particularly given that gill lamellae counts show regional variation (mode Weddell Sea 11, Antarctic Peninsula 12, eastern Antarctica 11 (Allcock 2003).

An analysis of partial 16s rDNA sequence data showed that *Megaleledone* grouped within a clade containing *Graneledone* and *Pareledone* spp. (Allcock & Piertney 2002), supporting abandonment of the subfamily Megaleledoninae.

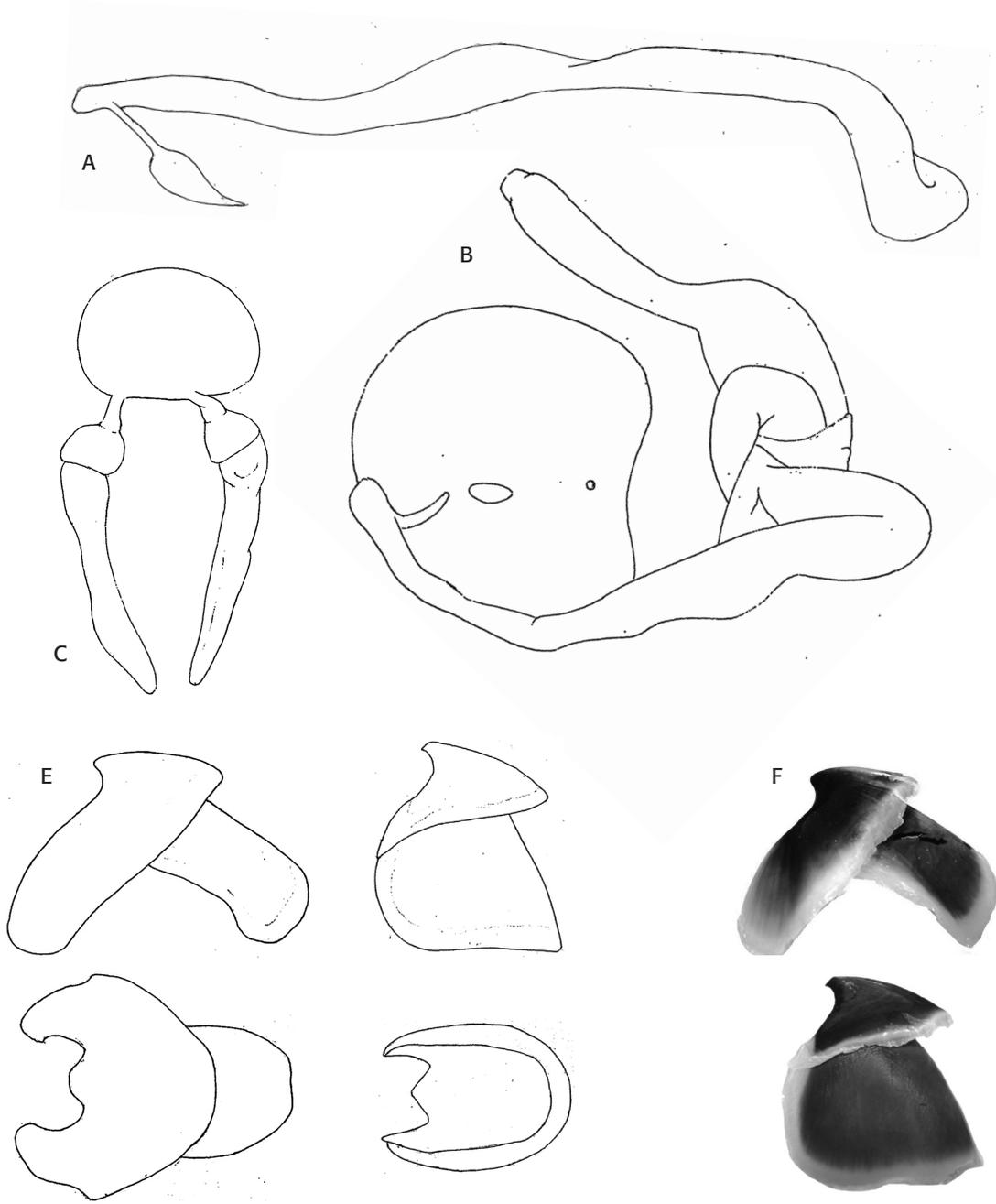


FIGURE 49. *Megaleledone cf. setebos*. **A)** intestine and ink sac (NIWA 44147, ML 202 mm). **B)** Alimentary canal (minus buccal bulb) (NIWA 44147, ML 202 mm). **C)** Female reproductive system (NIWA 44147, ML 202 mm). **E)** Upper and lower beaks (NIWA 44147, ML 202 mm). **F)** Upper and lower beaks (holotype of *G. setebos* (Robson 1932)).



FIGURE 50. *Megaleledone* cf. *setebos* (NIWA 44147, ML 202 mm). Dorsal view of preserved specimen.

Muusoctopus Gleadall, 2004

The systematics of species within the genera *Benthoctopus*, *Bathypolypus* and *Muusoctopus* are fraught with confusion; the relationship between two of them, *Benthoctopus* and *Bathypolypus*, has been deliberated for nearly a century, and particularly over the last decade (e.g., Robson 1929, 1932; Voss 1988; O’Shea 1999; Gleadall 2004; Strugnell *et al.* 2009; Gleadall *et al.* 2010). O’Shea (1999: 269) wrote that ‘the generic diagnoses of *Benthoctopus* and *Bathypolypus* are clearly inadequate to accommodate all species, but synonymy of them is probably premature given that *Bathypolypus articus* (Prosch) (the type species of *Bathypolypus*) is so different from the greatest majority of species historically attributed to *Benthoctopus* that additional genera would be required to accommodate many of these species should synonymy be effected. Rather than the simple act of synonymy, what was required was detailed examination of many species in each genus, including the type species, and detailed anatomical and biogeographic analysis to evaluate and redefine genera.’ To this, of course, should be added a genetic evaluation of relationships between taxa, such as that recently conducted by Strugnell *et al.* (2009).

The nomenclatural status of species attributed to one of these genera, *Benthoctopus*, was further confused when Muus (2002) considered the type specimen of *Benthoctopus piscatorum* (Verrill, 1879) (the type species of the genus *Benthoctopus*) to be an aberrant specimen of *Bathypolypus bairdii* (Verrill, 1873), effectively relegating *Benthoctopus* to synonymy of *Bathypolypus*. Resulting nomenclatural problems were partially resolved by Gleadall (2004), who described a new genus, *Muusoctopus*, to accommodate many of those taxa historically attributed to *Benthoctopus*. However, the status of this new genus hinges entirely on the species type of *B. piscatorum* truly being an aberrant specimen, and should another taxon be recognised from or proximal to the type locality of *B. piscatorum* that is consistent in features described for the type of this species (and genus), and inconsistent with the type of *B. bairdii*, then the validity of *Benthoctopus* and *Muusoctopus* will again be the subject of considerable debate.

Herein I uncritically accept the synonymy proposed by Muus (2002), and new genus proposed by Gleadall (2004), *Muusoctopus*, and attribute a single specimen herein reported to this genus, given that it differs in no significant detail from those historically attributed to the genus *Benthoctopus*. This latter genus contains at least 20 nominal species, with representatives from nearly every ocean basin (Strugnell *et al.* 2009b). Given the presumed invalidity of the genus *Benthoctopus*, Gleadall (2004) assigned *Muusoctopus januarii* (Hoyle, 1885) as the type species of *Muusoctopus*.

DIAGNOSIS (AMENDED). Animal moderate in size; skin smooth, lacking papillae or ocular cirri; arm lengths 1.5–4 times ML; suckers biserial; ligula slightly to moderately excavated with indistinct midrib, smooth or bearing low, often indistinct rugae, never laminate; crop present, usually with diverticulum; posterior salivary glands vestigial to large (relative to mantle length); functional ink sac absent; anal flaps absent; radula with uni- to multicuspid rachidian (O’Shea 1999, Strugnell *et al.* 2009b, Voss & Pearcy 1990, Gleadall 2004).

TYPE SPECIES. *Octopus januarii* Hoyle, 1885, by original designation.

***Muusoctopus* sp.**

RECOGNISED DISTRIBUTION. Ross Sea, represented in collections by single specimen, 72°20.37–21.05’S, 175°31.93–34.58’E, 945–950 m.

MATERIAL EXAMINED. 1 specimen (♀): NIWA 44151, ML 120 mm, 72°20.37–21.05’S, 175°31.93–34.58’E, 945–950 m, 21/02/2008, RV *Tangaroa* Stn TAN0802/121.

DESCRIPTION. Large benthic octopus, TL to 460 mm, ML 120 mm (Fig. 53; Tables 117, 121). Mantle broadly rounded, wide; head narrower than mantle (HdLI 18, HdWI 57), delimited from it by moderate pre-ocular constriction; post-orbital constriction well developed. Arms long, 73% TL; arm formula I.II.III.IV. Suckers biserial, arm sucker counts 160–184, none abruptly enlarged (ASIn 5); suckers attain greatest diameter at 10th sucker from the beaks. Arm-to-web attachment type 1B; depth 23% longest arm length; web formula A=B=C=D.E. Skin smooth, without papillae. Colour (preserved) pink-purplish, without apparent difference between ventral and dorsal surfaces; oral surface close to brachial crown slightly paler.

Gills with 7 lamellae per demibranch. Female reproductive system (Fig. 52C, Table 123) with proximal oviduct almost twice as long as oviducal ball diameter, considerably narrower than same; oviducal ball large, wide; distal oviduct as long as proximal oviduct, narrower than oviducal ball.

Alimentary canal (Fig. 52A; Tables 118, 122) with buccal bulb length (BBL) 25% ML. Anterior salivary glands 27% BBL. Posterior salivary glands elliptical or triangular (left side differs from right side), small (43% BBL, 11% ML). Anterior oesophagus narrow, length 34% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum 77% the diameter of stomach, without volutions. Intestine almost twice as long as oesophagus, 191% OesTL. Diges-

TABLE 117. EXTERNAL CHARACTER INDICES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
Sex	F
ALI1R	279.2
ALI2R	266.7
ALI3R	258.3
ALI4R	256.7
ALI1L	275.0
ALI2L	270.8
ALI3L	251.7
ALI4L	246.7
MAI	35.8
MWI	116.7
ASIn	5.0
AWI	18.3
EOI	10.8
FFI	20.8
FuLI	31.7
HdLI	18.3
HdWI	56.7
MWI	116.7
OAI	102.6
PAI	58.3
WDI	22.7

TABLE 118. INTERNAL CHARACTER INDICES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
AOesLI	21.7
ASGLI	6.7
BBI	25.0
DG(GD)	52.5
DGI	39.2
IntLI	120.8
OESTLI	63.3
PSGLI	10.8
SpCI	14.2
StI	18.3

TABLE 119. LOWER BEAK INDICES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
BLI	23.8
BHI	77.2
BIHI	31.6
BWI	77.2
CLI	47.4
DWaWI	35.1
HLI	31.6
PWaWI	36.8
REI	7.0
RWI	17.5
WiLI	42.1
WiWI	24.6

TABLE 120. UPPER BEAK INDICES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
BLI	15.8
BHI	110.5
BWI	63.2
CHI	36.8
HHI	50.0
HLI	63.2
REI	15.8
RPI	10.5
RWI	28.9
WiLI	63.2

TABLE 121. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Muusoctopus* sp.

	NIWA 44151 ML 120 mm
Gender	F
ML	120
AL1R	335
AL2R	320
AL3R	310
AL4R	308
AL1L	330
AL2L	325
AL3L	302
AL4L	296
ASC1R	181
ASC2R	171
ASC3R	162
ASC4R	160
ASC1L	161
ASC2L	160
ASC3L	164
ASC4L	184
SD	6
AW	22
EO	13
FFL	25
FuL	38
GiLC I	7
GiLC O	7
HdL	22
HdW	68
MW	140
PA	70
SR	20
TL	460
WAt	type 1A
WDA	67
WDBR	72
WDBL	72
WDCR	76
WDCL	73
WDDR	75
WDDL	75
WDE	47

TABLE 122. INTERNAL CHARACTER RAW MEASURES. *Muusoctopus* sp.

	NIWA 44151 ML 120 mm
AOesL	26
ASGL	8
BBL	30
Div	no
DGL	47
DGW	63
DG(GD)	63
InTL	145
ISpres	no
OesTL	76
PSGL	13
SpCL	17
StL	22

TABLE 123. REPRODUCTIVE SYSTEM RAW MEASURES. *Muusoctopus* sp.

	NIWA 44151 ML 120 mm
DOdL	50
DOdW	8
OSL	50
OSW	73
OdTL	112
OdBL	15
OdBW	25
POdL	47
POdW	06

TABLE 124. UPPER BEAK RAW MEASURES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
BL	19
BH	21
BW	12
CH	07
HH	10
HL	12
HW	10
RE	3
RP	2
RW	6
WiL	12

TABLE 125. LOWER BEAK RAW MEASURES.
Muusoctopus sp.

	NIWA 44151 ML 120 mm
BL	29
BH	22
BIH	9
BW	22
CH	7
CL	14
DWaW	10
HL	9
PWaW	11
RE	2
RW	5
WiL	12
WiW	7

tive gland almost circular, wider than long, without pronounced hepatic peaks; greatest dimension 52% ML; pancreas well developed. Functional ink sac absent.

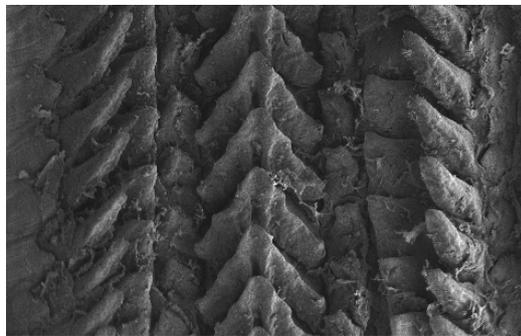
Lower beak (Fig. 52 left; Tables 119, 125) with black hood, with thin brown border; wings black from the oral margin to mid-portion of wing, lightening to brown toward aboral margin; lateral walls black, lightening slightly to brown toward aboral margin; margins translucent. Beak base length 24% ML, 77% height. Hood with rounded crest, markedly elevated from wings. Rostral tip chisel-like, with small protrusion ~2% BBL. Jaw angle 138°. Wing protrusion length 17.5% BBL; wing length 42% BBL. Lateral wall crest rounded, with basal notch. Proximal wall of comparable width to distal wall.

Circulatory system damaged during dissection; presence or absence of ink sac artery could not be determined.

Upper beak (Fig. 52 right; Tables 120, 124) with black hood and thin brown border; lateral walls black, with brown border; all margins translucent. Beak base length 16% ML, slightly shorter than wide. Hood with rounded crest; rostrum triangular, tip blunt, deflected slightly down; length protrusion 10% BBL; wing as protuded as rostrum. Jaw angle 118°. Lateral wall crest rounded, parallel-sided, with basal notch.

Radula (Fig. 51) with robust, broadly triangular, unicuspid rachidian tooth, taller than wide, with groove extending to accommodate subsequent rachidian cusp. First laterals small, with single outer cusp. Second laterals well developed, with broad cusp. Marginal teeth robust, with cusp more delicate than that of either rachidian or second lateral; marginal blocks rectangular.

REMARKS. Given earlier reported problems with this genus, and the fact that only single specimen of this species was available for examination, I refer to it simply as *Muusoctopus* sp. Identification of this specimen would benefit from critical comparison with other Southern Ocean specimens referable to this genus. The fact that rachidian tooth of this species lacked lateral cusps necessitated amendment of the generic diagnosis as formulated by Gleadall (2004), originally diagnosed as pentacuspoid. Variation in the number of lateral cusps on either side of the rachidian has been well documented for species historically attributed to the genus *Benthooctopus* (now *Muusoctopus*) (see O’Shea 1999), so the initial diagnosis proposed for this genus was in error (in the event that many of those species historically attributed to *Benthooctopus* are truly referable to *Muusoctopus*).



2 mm

FIGURE 51. *Muusoctopus* sp. (NIWA 44151, ML 120 mm). ESEM radula.

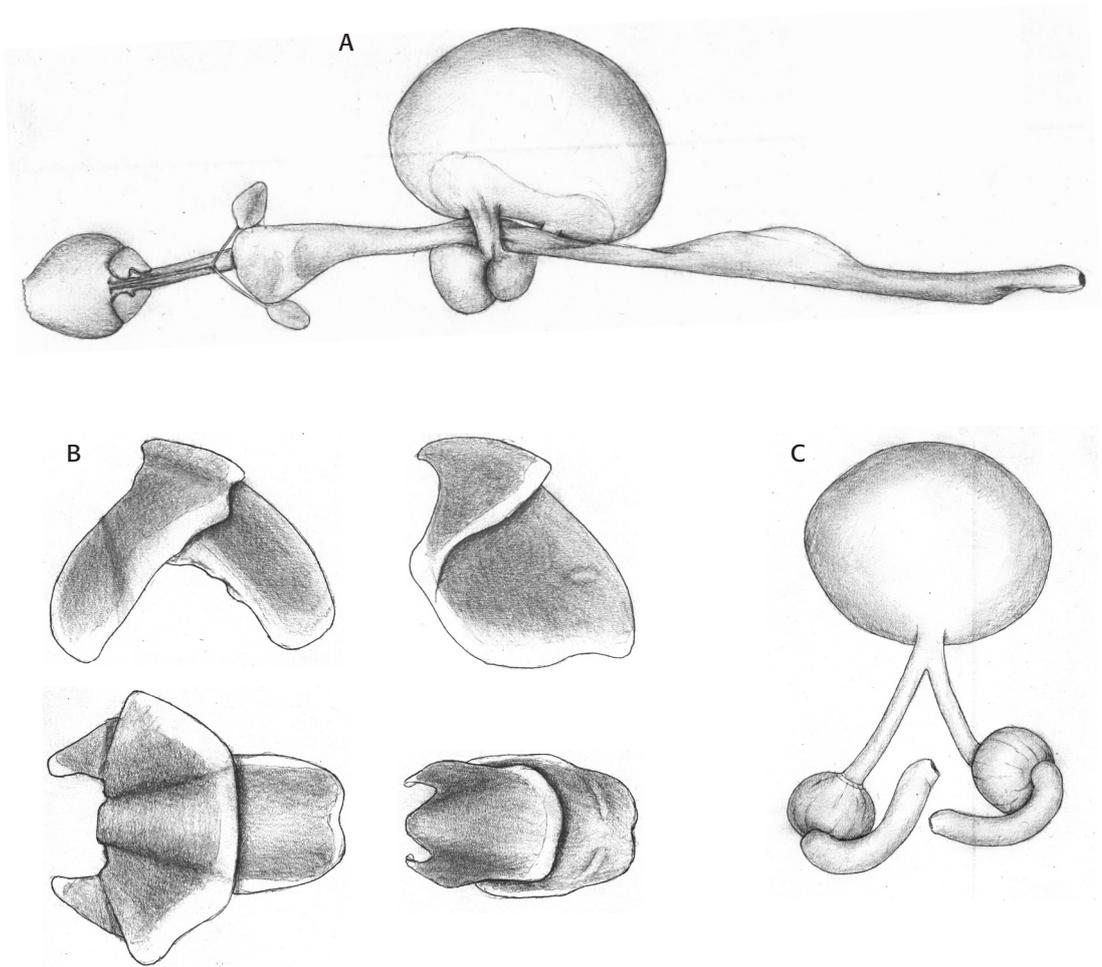


FIGURE 52. *Muusoctopus* sp. (NIWA 44151, ML 120 mm). A) Alimentary canal. B) Upper and lower beaks. C) Female reproductive system.



FIGURE 53. *Muusoctopus* sp. (NIWA 44151, ML 120 mm). Dorsal and ventral view of preserved specimens.

Octopus Cuvier, 1797

The genus *Octopus* is the most speciose and widely distributed of all octopuses, and its monophyly is in question. Few characters presently serve to group closely related species (Guzik *et al.* 2005, Norman & Hochberg 2005), and the genus is in urgent need of review (Norman *et al.* 2009). Too few species referable to this genus (*sensu lato*) were available for study when conducting this current research, precluding any critique of relationships between taxa.

DIAGNOSIS. With normal ink sac and moderately deep web. Web sector C or D usually deepest. The penial diverticulum is single. Hecotcotylus dextral, usually short; eggs (so far as known) small (under 5 mm long). No velar pouches or “fins”. Mantle aperture wide (Robson 1929). No diagnosis of this genus is proffered. Species attributed to this genus herein are as uncritically referred to it in accordance with most recent generic allocation of any given species.

TYPE SPECIES. *Octopus vulgaris* Cuvier, 1797.

Octopus kaurna (Stranks, 1990)

DIAGNOSIS. Species with elongate ovoid mantle; skin with characteristic dorsal pattern of rounded tubercles, without large papillae over the eyes; small, not prominent eyes; very long, unequal arms (3.1–6.2 times ML in mature animals); small suckers, none enlarged; small ligula (4–8% of third right arm in mature animals); large eggs (9–11 mm long), and 9–11 gill lamellae.

RECOGNISED DISTRIBUTION. Temperate waters of south-eastern Australia, from the Great Australian Bight to eastern Victoria, including Bass Strait and northern Tasmania. An inshore species, living on sand bottom, and among sea grass, 0–49 m (Stranks 1988).

SYNONYMY.

Octopus Species B Stranks, 1988: 61, figs 26–30

Octopus kaurna Stranks, 1990: 460–462, figs 2A–F.

Octopus flindersi (not Cotton, 1932) — Macpherson 1966 (*partim*): 241, text-fig. 1, pl. 2, figs 1–3 (*fide* Stranks 1990).

MATERIAL EXAMINED. 1 specimen (♀): SAuM D17989, ML 76 mm, 35.06.66'S, 137°45.42'E, 0–5 m, 17/02/08.

DESCRIPTION. Medium-sized animal (ML to 85 mm, TL to 420 mm) (Fig. 56; Tables 126, 130). Mantle elongate-ovoid (MWI 40–107). Head narrower than mantle (HWI 37–89), delimited from it by poorly developed pre-ocular constriction. Orbits small, barely projecting above surface of head. Funnel large, slender, bluntly tapered (FuLl 44–89). Arm-to-web attachment type 2; web depth 10–19% longest arm length; web formula variable. Arms very long (310–620% ML in mature animals), slender, tapering to narrow tips. Arm lengths unequal; arm formula I.II.III.IV. Suckers biserial, deeply set in arms, small to moderately sized (ASIn 3–9), none abruptly enlarged; arm sucker counts 291–325; suckers attain greatest diameter around sixth to eighth sucker. Integumental sculpture comprises fine, rounded and widely set epidermal tubercles, largest dorsally; those on ventral surfaces smaller and less prominent; some tubercles on ventro-lateral surface more elongate, but no more prominent than those on dorsal and ventral surfaces; no larger papillae in ocular region; no lateral integumentary ridge or fold around mantle. Preserved animals (ethanol) uniformly light brown to dark purple dorsally, creamy red to light brown ventrally.

Gill lamellae 8–11. Female reproductive system (Fig. 55D, Table 132) with proximal oviduct slightly shorter than half the length of distal oviduct; distal oviduct of comparable length to ovary sac length, narrower than oviducal ball diameter.

Alimentary canal (Fig. 55A, B; Tables 127, 131) with buccal bulb length (BBL) 16% ML. Anterior salivary glands 50% BBL. Posterior salivary glands elliptical, wide, their greatest dimension longer than buccal bulb length (125% BBL, 20% ML). Anterior oesophagus narrow, its length 38% that of oesophagus (OesTL). Crop well developed, with diverticulum. Spiral caecum greatest dimension 86% that of stomach, lacking volutions. Intestine shorter than oesophagus, 75% OesTL. Digestive gland elongate, with marked peaks on either side of hepatic ducts; greatest dimension 53% ML; pancreas well developed. Ink sac present, type 1 (Fig. 6).

Circulatory system of type 1 (Fig. 13), with thick, well-developed ink sac artery.

Lower beak (Fig. 55C left; Tables 128, 134) with black hood, abruptly lightening to brown toward margins; wings brown; lateral walls brown, slightly lightening toward distal wall peaks; margins translucent. Beak base length 10.5% ML, 62.5% height. Hood with rounded crest. Tip of rostrum chisel-like, with protrusion 2% BBL. Jaw angle 125°. Wing protrusion length 2.6% BBL; wing length 6.6% BBL. Proximal wall markedly narrower than distant wall; width 22% distal wall width.

TABLE 126. EXTERNAL CHARACTER INDICES.
O. kaurna.

	SAuM D17989 ML 76 mm
Sex	F
ALI1R	421.1
ALI2R	401.3
ALI3R	355.3
ALI4R	342.1
ALI1L	401.3
ALI2L	394.7
ALI3L	361.8
ALI4L	285.5
MAI	23.8
MWI	72.4
ASIn	3.3
AWI	10.5
EOI	6.6
FFI	21.1
FuLI	46.1
HdLI	19.7
HdWI	42.1
MWI	72.4
OAI	98.2
PAI	52.6
WDI	12.5

TABLE 127. INTERNAL CHARACTER INDICES.
O. kaurna.

	SAuM D17989 ML 76 mm
AOesLI	32.9
ASGLI	7.9
BBI	15.8
DG(GD)	52.6
IntLI	64.5
ISTLI	61.8
ISLI	7.2
OESTLI	72.4
PSGLI	19.7
SpCI	15.8
StI	18.4

TABLE 128. LOWER BEAK INDICES.
O. kaurna.

	SAuM D17989 ML 76 mm
BLI	18.3
BHI	72.7
BIHI	27.3
BWI	90.9
CLI	45.5
DWaWI	54.5
HLI	36.4
PWaWI	45.5
REI	13.6
RWI	18.2
WiLI	68.2
WiWI	40.9

TABLE 129. UPPER BEAK INDICES.
O. kaurna.

	SAuM D17989 ML 76 mm
BLI	8.6
BHI	107.7
BWI	76.9
CHI	30.8
HHI	38.5
HLI	46.2
REI	7.7
RPI	7.7
RWI	23.1
WiLI	61.5

TABLE 130. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *O. kaurna*.

	SAuM D17989 ML 76 mm
Gender	F
ML	76
AL1R	320
AL2R	305
AL3R	270
AL4R	260
AL1L	305
AL2L	300
AL3L	275
AL4L	217
ASC1R	325
ASC2R	315
ASC3R	314
ASC4R	291
ASC1L	321
ASC2L	323
ASC3L	290
ASC4L	291
SD	3
AW	8
EO	5
FFL	16
FuL	35
GilC I	8
GilC O	9
HdL	15
HdW	32
MW	55
PA	40
SR	20
TL	412
Wat	type 2
WDA	32
WDBR	37
WDBL	33
WDCR	40
WDCL	37
WDDR	35
WDDL	32
WDE	32

TABLE 131. INTERNAL CHARACTER RAW MEASURES. *O. kaurna*.

	SAuM D17989 ML 76 mm
AOesL	25
ASGL	06
BBL	12
DGL	40
DGW	19
DG(GD)	40
InTL	49
ISA	yes
ISpres	type 1
ISDL	39
ISEL	33
ISEW	03
ISL	6
ISTL	47
ISW	3
OesTL	55
PSGL	15
SpCL	12
StL	14

TABLE 132. REPRODUCTIVE SYSTEM RAW MEASURES. *O. kaurna*.

	SAuM D17989 ML 76 mm
DOdL	20
DOdW	3
OSL	24
OSW	18
OdTL	28
OdBL	3
OdBW	4
POdL	5

TABLE 133. UPPER BEAK RAW MEASURES.
O. kaurna.

	SAuM D17989 ML 76 mm
BL	7
BH	7
BW	5
CH	2
HH	3
HL	3
HW	4
RE	1
RP	1
RW	2
WiL	4

TABLE 134. LOWER BEAK RAW MEASURES.
O. kaurna.

	SAuM D17989 ML 76 mm
BL	8
BH	5
BIH	3
BW	7
CH	2
CL	4
DWaW	5
HL	2
PWaW	4
RE	1
RW	2
WiL	5
WiW	3

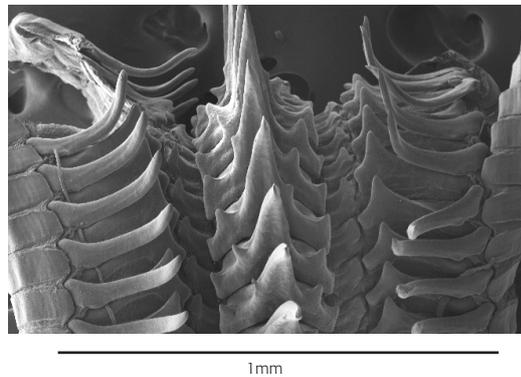


FIGURE 54. *Octopus kaurna* (SAuM D17989, ML 76 mm). ESEM radula.

Upper beak (Fig. 55C right; Tables 129, 133) with black hood, slightly lightening toward margin; lateral walls brown, slightly lightening toward margin; all margins translucent. Beak base length 8.5% ML, of comparable height and length (108% height). Hood with rounded crest; rostrum triangular, tip pointed, deflected upwards; length protrusion 7.7% BBL; wing length protrusion markedly longer than that of rostrum. Jaw angle 110°. Lateral wall crest rounded, parallel-sided.

Radula (Fig. 54) with well-developed, broad-based rachidian, taller than wide, with one or two asymmetrically disposed lateral cusps. First laterals small, with single admedial cusp. Second laterals well developed, of similar height to rachidian, with single large broad-based cusp and inner. Third laterals of similar height as second laterals, with a more delicate cusp; marginal blocks well developed, rectangular.

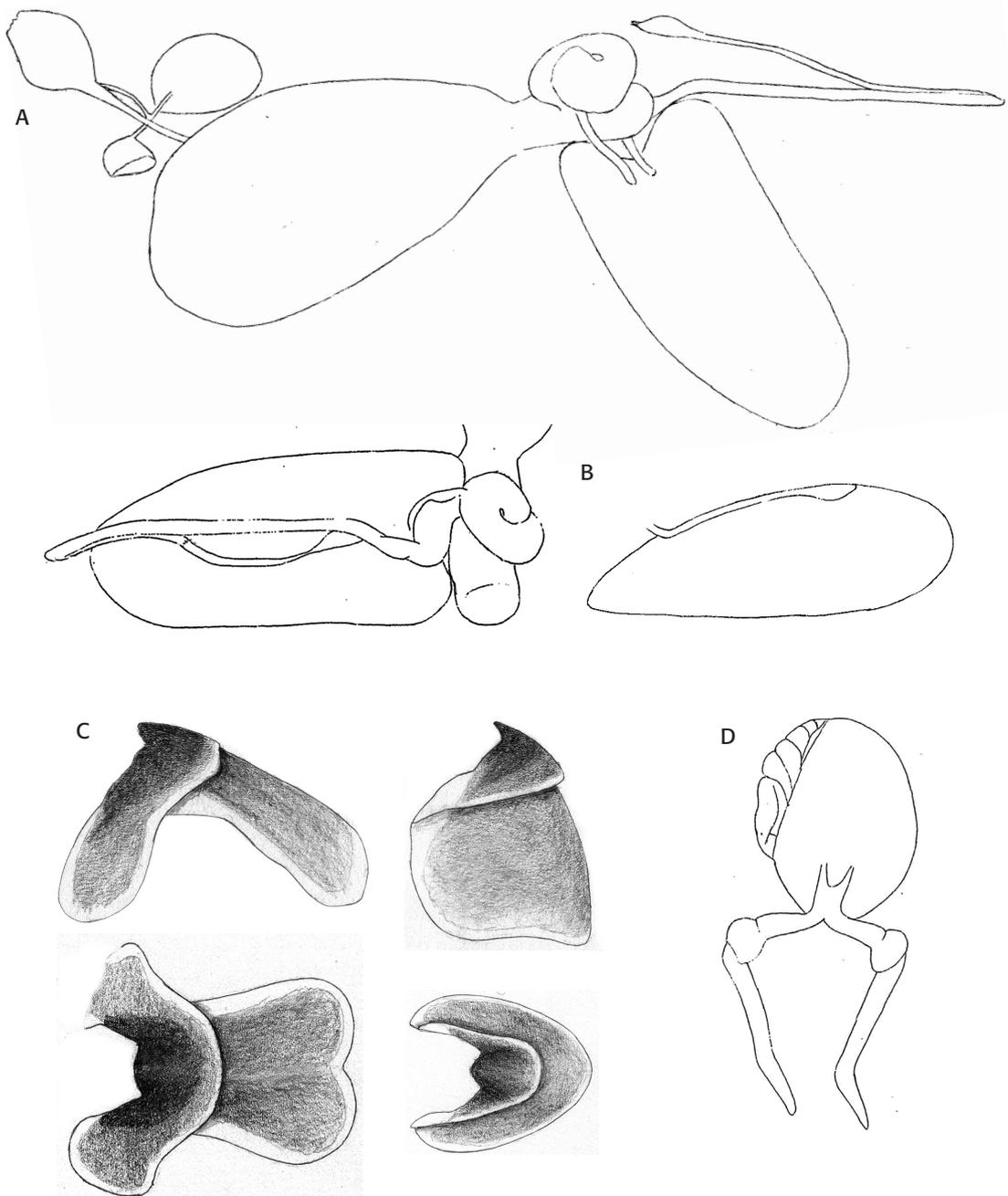


FIGURE 55. *Octopus kurna* (SAuM D17989, ML 76 mm). **A)** Alimentary canal. **B)** Ink sac duct and digestive gland in two perspectives (dorsal and lateral view). **C)** Upper and lower beaks. **D)** Female reproductive system.



FIGURE 56. *Octopus kaurna* (SAuM D17989, ML 76 mm). Dorsal view of preserved specimen.

Octopus oliveri (Berry, 1914)

RECOGNISED DISTRIBUTION. *Sargassum* belt (intertidal to shallow sublittoral). With certainty, Kermadec Islands, New Zealand.

SYNONYMY.

Polypus oliveri Berry, 1914: 136 — Berry 1916: 49 pl. VI, Fig. 2.

Octopus oliveri (Berry) — O'Shea 1999: 114–120, Figs 74, 75.

MATERIAL EXAMINED. 1 specimen (♀): OMNZ A 454.82, ML 40 mm, 29°16.20'S, 177°56.57'W, 0 m.

DESCRIPTION (modified from O'Shea 1999). Adults to 69 mm ML, 262 mm TL (Fig. 58; Tables 135, 139). Head narrower than mantle (HdLI 30–43, HdWI 63–102), delimited from mantle by poorly developed pre-ocular constriction. Orbits small; postorbital constriction slight. Arms about four times as long as mantle, 365% ML, 73% TL (excluding hectocotyliised arm), of subequal length, with arm pairs II and III usually longest, and arm pairs I and IV shortest, with no consistent disparity in relative arm lengths. Arm-to-web attachment type 2; web extending to less than a quarter the length of the arms; depth to 28% longest arm length. Web formula B=C=D.A.E. Arm sucker counts 95–180 (excluding hectocotyliised arm); sucker size variable on each arm (arm sucker diameter formula 2.3.1=4; suckers attain greatest diameter near where web and arm fuse. Third right arm of male hectocotyliised, shorter than opposite member (OAI about 65–99), with 76–110 suckers. Ventral surface of mantle smooth; dorsal surfaces of mantle and head ornamented by numerous low, rough, conical tubercles, with smaller papillae extending over the entire outer and lateral arm surfaces, and inner surface of web; conspicuous supra-ocular cirri absent, but eye aperture is surrounded by a cirlet of 5 or 6 low and indistinct papillae. Hectocotyliised portion of arm IIIIR (Fig. 57F) small, with ligula 1.6–2.2% hectocotyliised arm length, with about 5 transverse rugae; calamus about 33% ligula length. Spermatophoral groove well developed, wide. Preserved colouration dark slate, slightly lighter on the ventral surface of the mantle; suckers light brown to cream.

Gills with 7 lamellae per demibranch. Male with terminal organ curving under itself; spermatophoric gland I longer and thinner than II; spermatophoric sac shorter than both spermatophoric glands (Fig. 57D, Table 141).

Alimentary canal (Fig. 57A, B; 136, 140) with buccal bulb length (BBL) 31% ML. Anterior salivary glands 44% BBL. Posterior salivary glands roughly triangular, their greatest dimension slightly shorter than BBL (88% BBL, 27% ML). Anterior oesophagus narrow, its length 48% that of oesophagus (OesTL). Crop well developed, with diverticulum. Spiral caecum greatest dimension 70% that of stomach, with two complete volutions. Intestine markedly longer than oesophagus, about 196% OesTL. Digestive gland longer than wide, with poorly developed peaks on either side of hepatic ducts; greatest dimension 61% ML; pancreas well developed. Ink sac present, type 1 (Fig. 6).

Circulatory system of type 1 (Fig. 13), with well-developed ink sac artery.

Lower beak (Fig. 57C left; Tables 137, 143) with black hood and wings; the latter lightening to brown near margin. Lateral walls black with brown border; margins translucent. Beak base length 25% ML, 70% height. Hood with rounded crest, weakly elevated from wings. Rostrum tip chisel-like, barely protruded, 0.5% BBL. Jaw angle 120°. Wing protrusion length around 7.5% BBL; wing length 17.5% BBL. Lateral wall crest rounded. Proximal wall 13% narrower than distal wall.

Upper beak (Fig. 57C right; Tables 138, 142) with black hood; lateral walls black and brown bordered; all margins translucent. Beak base length 22.5% ML, 89% height. Hood with rounded crest; rostrum triangular, tip blunt; length protrusion 6% BBL; wing length protrusion slightly longer than that of rostrum. Jaw angle acute (87°). Lateral wall crest rounded, without basal notch; walls parallel-sided.

Radula (Fig. 57E) with robust, broadly triangular rachidian, taller than wide, with one or two symmetrically disposed small lateral cusps either side of large central cusp. First laterals small, with single admedial cusp. Second laterals well developed, with large, massive-based cusp, longer than rachidian. Third laterals thinner, curved, cusp more delicate than that of either rachidian or second lateral; marginal blocks short, rectangular.

REMARKS. This species is found in the *Sargassum* algal belt and presently is known only from littoral depths. Berry (1914) said that is similar to *Octopus vitiensis* species-group, which have broad heads, arms 4–5 times ML, with arm pairs II, III and IV of similar length and I shorter except *O. oliveri*, where arm pairs I are longer), and species are typically maroon to purple-black (Ward 2002). *Abdopus aculeatus*, which is a common intertidal octopus from the Philippines and common throughout Indonesia, Northern Australia (Huffard 2007) has been confused with *O. oliveri* (Kaneko & Kubodera 2007), and it is possible that *O. oliveri* should be transferred to this genus.

TABLE 135. EXTERNAL CHARACTER INDICES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
Sex	M
ALI1R	362.5
ALI2R	350.0
ALI3R	310.0
ALI4R	350.0
ALI1L	365.0
ALI2L	350.0
ALI3L	350.0
ALI4L	350.0
MAI	27.4
MWI	86.3
ASIn	22.5
AWI	35.0
EOI	7.5
FFI	25.0
FuLI	37.5
HdLI	25.0
HdWI	56.3
MWI	86.3
OAI	88.6
PAI	58.8
WDI	28.1

TABLE 136. INTERNAL CHARACTER INDICES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
AOesLI	33.8
ASGLI	13.8
BBI	31.3
DG(GD)	61.3
IntLI	137.5
ISTLI	31.3
ISLI	16.3
OESTLI	70.0
PSGLI	27.5
SpCI	26.3
StI	37.5

TABLE 137. LOWER BEAK INDICES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
BLI	24.9
BHI	70.4
BIHI	40.2
BWI	85.4
CLI	45.2
DWaWI	40.2
HLI	30.2
PWaWI	35.2
REI	10.1
RWI	20.1
WiLI	70.4
WiWI	35.2

TABLE 138. UPPER BEAK INDICES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
BLI	22.5
BHI	88.9
BWI	55.6
CHI	22.2
HHI	38.9
HLI	55.6
REI	16.7
RPI	27.8
RWI	38.9
WiLI	44.4

TABLE 139. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *O. oliveri*.

	OMNZ A 54.82 ML 40 mm
Gender	M
ML	40
AL1R	145
AL2R	140
AL3R	124
AL4R	140
AL1L	146
AL2L	140
AL3L	140
AL4L	140
ASC1R	152
ASC2R	149*
ASC3R	103
ASC4R	157
ASC1L	152
ASC2L	149
ASC3L	160
ASC4L	151
SD1R	7
SD2R	9
SD3R	9
SD4R	7
SD1L	7
SD2L	0.9
SD3L	0.9
SD4L	7
AW	14
EO	3
FFL	10
FuL	15
GiLC I	70
GiLC O	70
HdL	10
HdW	23
MW	35
PA	24
TL	190
WAt	type 2
WDA	35
WDBR	40
WDBL	38
WDCR	40
WDCL	40
WDDR	37
WDDL	41
WDE	30

TABLE 140. INTERNAL CHARACTER RAW MEASURES. *O. oliveri*.

	OMNZ A 54.82 ML 40 mm
AOesL	14
ASGL	6
BBL	13
DGL	25
DGW	22
DG(GD)	25
InTL	55
ISA	yes
ISpres	type 1
ISDL	6
ISEL	8
ISEW	2
ISL	7
ISTL	13
ISW	03
OesTL	28
PSGL	11
SpCL	11
StL	15

TABLE 141. REPRODUCTIVE SYSTEM RAW MEASURES. *O. oliveri*.

	OMNZ A 54.82 ML 40 mm
CaL	1
LL	3
SGL	35
SGLI	53
SS	30.5
TODL	6
TOL	7
TOTL	9.5

TABLE 142. UPPER BEAK RAW MEASURES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
BL	9
BH	8
BW	5
CH	2
HH	4
HL	5
HW	5
RE	2
RP	3
RW	4
WiL	4

TABLE 143. LOWER BEAK RAW MEASURES.
O. oliveri.

	OMNZ A 54.82 ML 40 mm
BL	10
BH	7
BIH	4
BW	9
CH	2
CL	5
DWaW	4
HL	3
PWaW	4
RE	1
RW	2
WiL	7
WiW	4

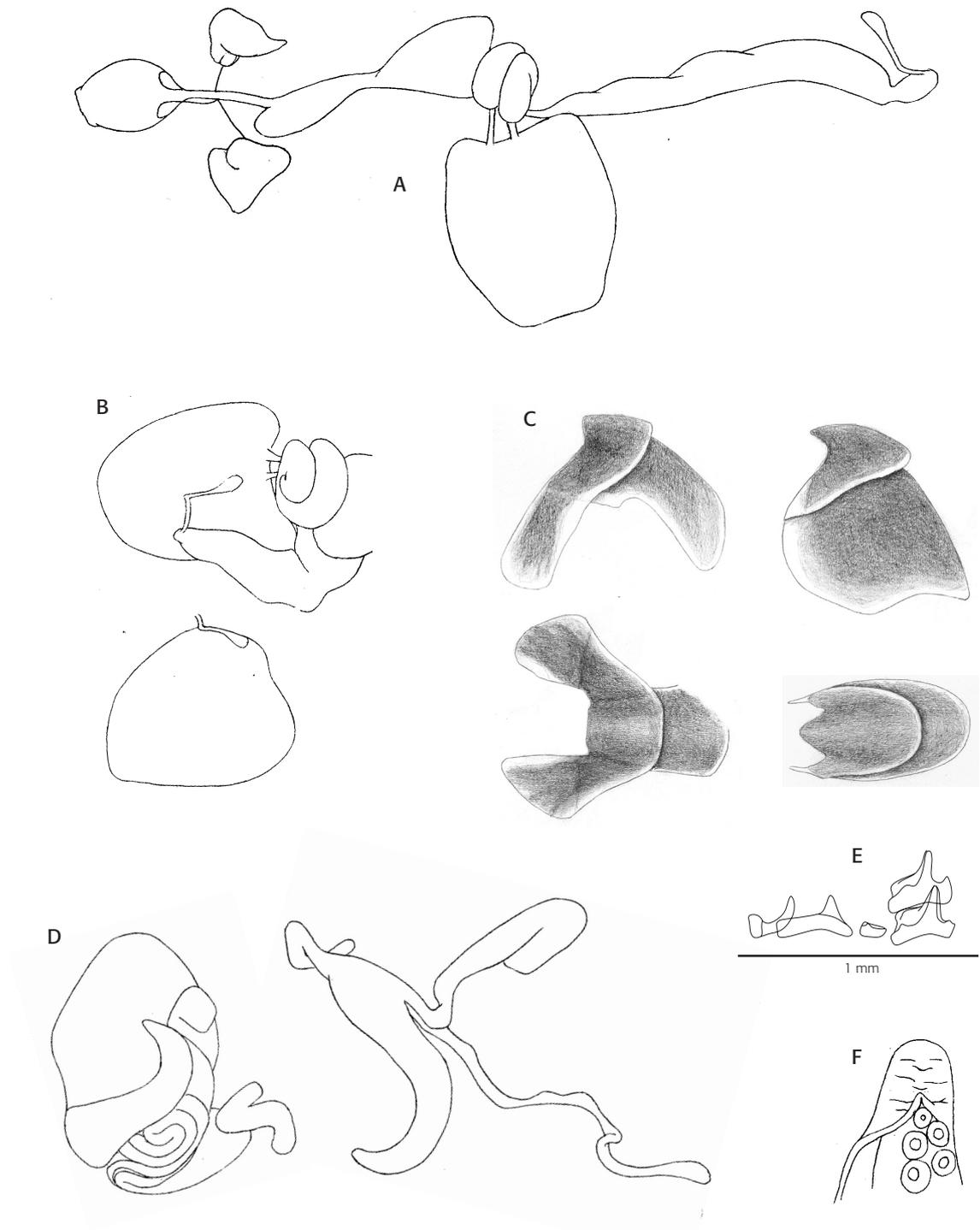


FIGURE 57. *Octopus oliveri* (OMNZ A54.82, ML 40 mm). A) Alimentary canal. B) Ink sac duct and digestive gland in two perspectives (dorsal and lateral view). C) Upper and lower beaks. D) Male reproductive system. E) Radula. F) Hectocotylus.



FIGURE 58. *Octopus oliveri* (OMNZ A54.82, ML 40 mm), Dorsal and ventral view of preserved specimen.

Pareledone Robson, 1932

TYPE SPECIES. *Eledone charcoti* Joubin, 1905, by original designation.

DIAGNOSIS (modified from Allcock & Piertney 2002). Benthic octopodids; arms with small, uniserial suckers. Third right, and rarely (possibly aberrant specimen) left arm of male hectocotylied, with tip clearly differentiated into ligula and calamus; ligula groove long, well marked, shallow, without transverse ridges; arm tips not otherwise modified. Web well developed. Funnel organ VV shaped; gills well developed, with 6–11 lamellae. Ink sac fully functional, vestigial or absent; crop well developed; cartilaginous stylets absent; spermatophores long and slender; rostral tip of lower beak rounded.

***Pareledone* sp. nov. 1**

RECOGNISED DISTRIBUTION: Ross Sea, 74°34.83–76°35.94'S, 167°18.70–176°49.68'E, 283–522 m.

MATERIAL EXAMINED. 9 specimens (5♂, 4♀): NIWA 44059, ML 58 mm, ♂, 74°34.90–34.83'S, 170°14.99–17.58'E, 285 m, 11/02/2008, RV *Tangaroa* Stn TAN0802/26; NIWA 44060, ML 46 mm, ♀, 74°35.43–35.32'S, 170°16.54–16.15'E, 283 m, 11/02/2008, RV *Tangaroa* Stn TAN0802/31; NIWA 44069, ML 60 mm, ♂, 75°37.30–37.23'S, 169°48.27–48.68'E, 520–522 m, 14/02/2008, RV *Tangaroa* Stn TAN0802/61; NIWA 44070, ML 73 mm, ♀, 75°37.45–36.51'S, 167°19.27–18.70'E, 480–474 m, 14/02/2008, RV *Tangaroa* Stn TAN0802/66; NIWA 44067, ML 73 mm, ♂, 76°11.58–12.30'S, 176°17.77–14.63'E, 447 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/94; NIWA 44091, ML 90 mm, ♀, 76°12.12–12.24'S, 176°14.88–14.46'E, 451–447 m, 18/02/2008, RV *Tangaroa* Stn TAN0802/100; NIWA 44066, ML 68 mm, ♂, 76°35.64–35.94'S, 176°49.68–45.30'E, 369–365 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/81; NIWA 44054, ML 70 mm, ♀, 76°35.64–35.94'S, 176°49.68–45.30'E, 369–365 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/81.

DESCRIPTION. Mature animal of moderate size (ML to 90 mm, TL to 243 mm) (Figs 65–68; Tables 144, 148). Mantle ovoid (MWI 94–113). Head narrower than mantle (HdLI 23–38, HdWI 44–70), delimited from it by slightly developed pre-ocular constriction. Orbits large, bulbous, with marked interspace between both eyes across dorsal midline of head. Post-orbital constriction weak developed. Funnel free for over half its length. Arm-to-web attachment type 2 (Fig.

4); depth 24–32% longest arm length. Web formula variable; sectors A and E usually shallowest. Arms 49–62% TL (excluding hectocotylied arm); arm formula variable; ventral arms usually slightly longer than dorsal. Suckers uniserial; arm sucker counts 44–58 (excluding hectocotylied arm); suckers extend to arm tips; no suckers abruptly enlarged, ASIn 3.4–4.6; suckers attain greatest diameter at fourth sucker from beaks. Third right (and in one case left) arm of male hectocotylied, shorter than opposite member (OAI 74–86), with 31–37 suckers. Hectocotylied portion with (Fig. 64C) ligula 5–10% hectocotylied arm length, without transverse rugae; calamus 32–57% ligula length. Spermatophoral groove well developed, narrow; web margin thickened. Papillae simple, regularly shaped, flat topped, covering dorsal surfaces of mantle and head, dorso and ventro-lateral surfaces of arms I, and dorso-lateral surfaces of arms II and III to arm tips, and web sectors A, B and C; papillae stop abruptly fold running laterally and extending the entire periphery of the mantle, marked by line of crowded chromatophores that continue beyond lateral fold, albeit more sparsely distributed; central, ventral portion of mantle without apparent chromatophores; orbits with enlarged supra-ocular papilla.

Gills with 7 lamellae per inner and outer demibranch. Male with well-developed spiral terminal organ diverticulum oriented to left of terminal organ; spermatophoric gland I longer than II; spermatophoric sac coiled, longer than SGII, and either slightly shorter or longer than SGI (Fig. 64B, Table 150). Female reproductive system (Fig. 64A, Table 149) with proximal oviduct about 25% the length of distal oviduct, narrower than oviducal ball width; distal oviducts of comparable length or slightly longer than ovary sac, of comparable diameter to oviducal ball width.

Alimentary canal (Figs 60, 61; Table 145, 151) with buccal bulb length (BBL) 25–28% ML. Anterior salivary glands of length 20–28% BBL. Posterior salivary glands elliptical to triangular, of variable size relative to BBL (56–89% BBL, 14–22% ML). Anterior oesophagus narrow, its length 29–44% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum slightly smaller than stomach, 70–87% its diameter, lacking volutions. Intestine length variable, slightly to considerably longer than oesophagus, 116–172% OesTL. Digestive gland circular, with poorly developed hepatic peaks; greatest dimension 37–49% ML; pancreas well developed. Ink sac present, exposed to variable extent, of type 2 (Fig. 4).

Circulatory system of type 1 (Fig. 13), with ink sac artery.

Lower beak (Figs 62, 63 left; Table 146, 153) with black hood, abruptly lightening to brown toward margins; oral margin of wings black extending to the middle of wing, forming clearly marked diagonal line that lightens to brown abruptly near aboral margin; lateral walls dark brown or black, slightly lightening toward margin; margins translucent. Beak base length 14–23% ML, height 55–76% BBL. Hood with rounded crest, elevated from wings. Rostrum tip variable, blunt

triangular with clear protrusion or chisel-like with small protrusion, RPI 1–2% BBL. Jaw angle obtuse (97–132°). Wing protrusion length around 24–33% BBL; wing length 52–83% BBL. Lateral wall crest rounded, with weak basal notch. Proximal wall narrower than or as wide as distal wall.

Upper beak (Figs 62, 63 right; Table 147, 152) with black hood and brown border; lateral walls black or dark brown, gradually lightening toward the margin; all margins translucent. Beak base length 13–21% ML, of comparable height as length (BBL 95–110% BH). Hood with rounded crest; rostrum triangular, tip blunt, with lateral keel; length protrusion 9.1–20% BBL; wing protrusion variable, more or less protruded than rostrum. Jaw angle generally obtuse (85–102°). Lateral wall crest rounded, without basal notch, walls generally parallel-sided.

Radula (Fig. 59) with robust, broadly triangular rachidian, taller than wide, with or without one or two asymmetrically disposed lateral cusps either side of large central cusp. First laterals small, unicuspid; second laterals well developed, with large-based cusp. Marginal teeth with cusp more delicate than that of either rachidian or second lateral; marginal blocks rectangular.

REMARKS. Of the four females available, two were immature, but two had eggs within the ovary sac, their maximum dimensions 8 and 17 mm. NIWA specimen 44069 was remarkable in that the third left arm was hectocotylised, but in other characters and states it did not differ discernably, although the spermatophoric sac was comparable in length to SGII and not coiled, while in the other males it was longer than SGII and coiled.

The extent to which the ink sac is exposed on the face of the digestive gland is variable in this species, with the sac barely to completely exposed on the surface of the digestive gland. The internal organs' counts and measures are very similar between specimens, with none differing in any remarkable manner. The extent of papillation over the dorsal and lateral surfaces of the mantle was the single-most important character enabling differentiation of this taxon from other *Pareledone* species recognised amongst available Ross Sea collections.

This species resembles *P. aequipapillae* most closely in external morphology, particularly in the presence of a lateral fold extending around the entire periphery of the mantle, with simple, similar-sized papillae not extending below this fold onto the ventral surfaces of the mantle. Some other measures overlap, like total arm sucker counts (ASC) and hectocotylised arm sucker counts, but they differ markedly in mantle aperture index (MAI), MAI 54.1–69.5 for *P. sp. nov.* 1 and 51.1 ± 4.2 for *P. aequipapillae*.

TABLE 144. EXTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
Sex	F	M	M	F	M	M	F	M	F
ALI1R	169.6	143.1	141.7	153.8	147.1	165.7	128.8	143.8	144.4
ALI2R	173.9	155.2	145.0	149.2	139.7	132.9	132.9	150.7	152.2
ALI3R	184.8	144.8	166.7	146.2	127.9	135.7	134.2	130.1	150.0
ALI4R	184.8	155.2	150.0	146.2	169.1	180.0	143.8	157.5	152.2
ALI1L	173.9	139.7	150.0	146.2	147.1	160.0	128.8	143.8	133.3
ALI2L	173.9	172.4	155.0	146.2	139.7	157.1	137.0	150.7	127.8
ALI3L	173.9	165.5	136.7	146.2	172.1	157.1	137.0	150.7	155.6
ALI4L	180.4	167.2	150.0	146.2	170.6	171.4	138.4	157.5	155.6
MAI	54.1	58.0	60.0	65.0	58.1	55.6	69.5	63.5	64.3
MWI	113.0	112.1	108.3	113.8	110.3	100.0	95.9	100.0	94.4
ASIn	4.3	3.4	4.2	4.6	4.4	5.0	3.4	4.1	4.4
AWI	15.2	13.8	13.3	16.9	14.7	11.4	11.0	13.7	10.0
EOI	13.0	19.0	11.7	12.3	14.7	15.7	11.0	13.7	11.1
FFI	21.7	25.9	19.2	18.5	22.1	21.4	16.4	20.5	21.1
FuLI	32.6	34.5	28.3	33.8	32.4	40.0	28.8	34.2	27.8
HdLI	28.3	34.5	33.3	38.5	41.2	30.0	26.0	28.8	23.3
HdWI	69.6	56.9	58.3	50.8	60.3	55.7	45.2	53.4	44.4
MWI	113.0	112.1	108.3	113.8	110.3	100.0	95.9	100.0	94.4
OAI	106.3	87.5	122.0	100.0	74.4	86.4	98.0	86.4	96.4
PAI	76.1	63.8	55.0	61.5	58.8	57.1	54.8	54.8	46.7
WDI	27.1	24.0	30.0	32.0	30.8	31.7	25.7	31.3	28.6

TABLE 145. INTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 1

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
AOesLI	23.9	20.7	26.7	18.5	19.1	15.7	17.8	19.2	17.8
ASGLI	15.2	11.2	13.3	12.3	10.3	10.0	11.0	13.7	10.0
BBI	28.3	27.6	23.3	27.7	27.9	20.0	24.7	23.3	22.2
DG(GD)	47.8	43.1	45.0	43.1	36.8	40.0	49.3	38.4	44.4
IntLI	119.6	100.0	78.3	76.9	91.2	71.4	79.5	60.3	83.3
ISA	yes								
ISTLI	45.7	46.6	36.7	32.3	34.6	34.3	41.1	26.0	33.3
ISLI	21.7	22.4	11.7	12.3	13.2	15.7	12.3	13.7	11.1
OESTLI	71.7	60.3	60.0	64.6	52.9	51.4	56.2	52.1	53.3
PSGLI	18.5	22.4	20.0	15.4	17.6	17.9	17.1	13.7	18.3
SpCI	23.9	22.4	20.0	23.1	14.7	15.7	17.8	17.8	16.7
StI	28.3	25.9	25.0	29.2	22.1	22.9	25.3	20.5	20.0

TABLE 146. LOWER BEAK INDICES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
BLI	22.8	20.7	19.2	20.0	19.1	20.0	19.9	16.4	14.4
BHI	76.2	75.0	69.6	69.2	73.1	67.9	62.1	70.8	73.1
BIHI	33.3	33.3	30.4	34.6	34.6	28.6	27.6	29.2	34.6
BWI	85.7	95.8	87.0	88.5	96.2	92.9	86.2	100.0	115.4
CLI	57.1	50.0	43.5	46.2	42.3	39.3	34.5	50.0	53.8
DWaWI	47.6	41.7	52.2	53.8	65.4	50.0	48.3	62.5	61.5
HLI	38.1	25.0	39.1	42.3	30.8	39.3	27.6	33.3	30.8
PWaWI	42.9	41.7	52.2	38.5	65.4	53.6	44.8	58.3	53.8
REI	9.5	8.3	8.7	7.7	7.7	7.1	6.9	8.3	11.5
RWI	23.8	25.0	21.7	23.1	30.8	21.4	17.2	25.0	30.8
WiLI	68.6	70.8	82.6	61.5	61.5	64.3	51.7	66.7	61.5
WiWI	33.3	45.8	43.5	30.8	42.3	32.1	41.4	41.7	38.5

TABLE 147. UPPER BEAK INDICES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
BLI	20.7	17.2	16.7	15.4	16.2	12.9	16.4	15.1	12.2
BHI	94.7	100.0	100.0	110.0	104.5	122.2	108.3	95.5	109.1
BWI	63.2	60.0	65.0	65.0	68.2	83.3	50.0	54.5	72.7
CHI	15.8	20.0	20.0	30.0	18.2	66.7	25.0	18.2	31.8
HHI	36.8	30.0	40.0	50.0	36.4	44.4	41.7	45.5	40.9
HLI	52.6	50.0	60.0	80.0	54.5	72.2	70.8	54.5	54.5
REI	10.5	10.0	10.0	15.0	13.6	16.7	12.5	13.6	9.1
RPI	10.5	10.0	20.0	10.0	13.6	16.7	12.5	9.1	13.6
RWI	21.1	35.0	25.0	20.0	27.3	38.9	25.0	22.7	31.8
WiLI	42.1	45.0	50.0	50.0	50.0	44.4	41.7	45.5	45.5

TABLE 148. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Pareledone* sp. nov. 1. Numbers in bold refer to male hectocotylistised arm.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
Gender	F	M	M	F	M	M	F	M	F
ML	46	58	60	65	68	70	73	73	90
AL1R	78	83	85	100	100	116	94	105	130
AL2R	80	90	87	97	95	93	97	110	137
AL3R	85	84	100	95	87	95	98	95	135
AL4R	85	90	90	95	115	126	105	115	137
AL1L	80*	81	90	95	100	112	94	105	120
AL2L	80	100	93	95	95	110	100	110	115
AL3L	80	96	82	95	117	110	100	110	140
AL4L	83	97	90	95	116	120	101	115	140*
ASC1R	51*	39*	48*	51	52	54	51*	50	52
ASC2R	51	47*	54	50	53	43	49	51	50
ASC3R	44	31	50*	50	37	34	53	37	52
ASC4R	51	46	52	51	54	51	52	51	44
ASC1L	51	42	48*	50	53	52	51	50	51
ASC2L	51	46	52	51	50	53	50	51	44
ASC3L	52	46	35*	50	50	49	54	51	53
ASC4L	52	44	53	51	55	53	47	51	50*
SD	2	2	3	3	3	4	3	3	4
AW	7	8	8	11	10	8	8	10	9
EO	6	11	7	8	10	11	8	10	10
FFL	10	15	12	12	15	15	12	15	19
FuL	15	20	17	22	22	28	21	25	25
GilC I	7	7	7	6	7	7	7	7	7
GilC O	7	7	7	6	7	7	7	7	7
HdL	13	20	20	25	28	21	19	21	21
HdW	32	33	35	33	41	39	33	39	40
MW	52	65	65	74	75	70	70	73	85
PA	35	37	33	40	40	40	40	40	42
TL	150	160	170	178	190	205	190	185	243
WAt	type 2								
WDA	20	23	*	25	22	*	22	20	23
WDBR	20	23	23	30	30	*	25	30	35
WDBL	22	23	28	30	35	*	25	30	32
WDCR	22	23	*	32	33	*	26	36	40
WDCL	23	24	30	32	33	40	27	36	37
WDDR	22	23	*	30	36	*	25	36	40
WDDL	23	*	*	30	30	*	27	30	40
WDE	18	20	20	20	21	*	23	30	29

TABLE 149. FEMALE REPRODUCTIVE SYSTEM RAW MEASURES.
Pareledone sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44067 ML 65 mm	NIWA 44070 ML 73 mm	NIWA 44091 ML 90 mm
DOdL	12	12	20	26
DOdW	3	4	7	10
OSL	7	10	0	*
OSW	7	12	*	*
OdTL	28	18	26	*
OdBL	2	4	3	5
OdBW	3	4	7	9
POdL	3	2	3	*
POdW	0	0	4	*

TABLE 150. MALE REPRODUCTIVE SYSTEM RAW MEASURES. *Pareledone* sp. nov. 1.

	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44067 ML 73 mm
CaL	4	3	2.5	3	10
LL	7	8.5	5.5	9.5	9
SGL	103	85	82	93	77
SGII	67	45	62	58	54
SS	92	66	98	100	90
TODL	18	17	18	25	17
TOL	13	9	*	27	15
TOTL	29	26	32	40	32

TABLE 151. INTERNAL CHARACTER RAW MEASURES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
AOesL	11	12	16	12	13	11	13	14	16
ASGL	7	7	8	8	7	7	8	10	9
BBL	13	16	14	18	19	14	18	17	20
DGL	20	25	24	25	25	26	34	27	36
DGW	22	24	27	28	25	28	36	28	40
DG(GD)	22	25	27	28	25	28	36	28	40
InTL	55	58	47	50	62	50	58	44	75
ISpres	Type 2								
ISDL	11	14	15	13	18	14	21	9	20
ISEL	9	13	7	7	7	10	7	7	6
ISEW	6	6	3	3	4	7	2	6	2
ISL	10	13	7	8	9	11	9	10	10
ISTL	21	27	22	21	24	24	30	19	30
ISW	6	7	4	4	4	8	4	6	4
OesTL	33	35	36	42	36	36	41	38	48
PSGL	9	13	12	10	12	13	13	10	17
SpCL	11	13	12	15	10	11	13	13	15
StL	13	15	15	19	15	16	19	15	18

TABLE 152. UPPER BEAK RAW MEASURES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
BL	10	10	10	10	11	9	12	11	11
BH	9	10	10	11	12	11	13	11	12
BW	6	6	7	7	8	8	6	6	8
CH	2	2	2	3	2	6	3	2	4
HH	4	3	4	5	4	4	5	5	5
HL	5	5	6	8	6	7	9	6	6
HW	5	7	3	6	6	6	7	6	7
RE	1	1	1	2	2	2	2	2	1
RP	1	1	2	1	2	2	2	1	2
RW	2	4	3	2	3	4	3	3	4
WiL	4	5	5	5	6	4	5	5	5

TABLE 153. LOWER BEAK RAW MEASURES. *Pareledone* sp. nov. 1.

	NIWA 44060 ML 46 mm	NIWA 44059 ML 58 mm	NIWA 44069 ML 60 mm	NIWA 44067 ML 65 mm	NIWA 44066 ML 68 mm	NIWA 44066 ML 36 mm	NIWA 44070 ML 73 mm	NIWA 44067 ML 73 mm	NIWA 44091 ML 90 mm
BL	11	12	12	13	13	14	15	12	13
BH	8	9	8	9	10	10	9	9	10
BIH	4	4	4	5	5	4	4	4	5
BW	9	12	10	12	13	13	13	12	15
CH	2	2	2	3	2	6	3	2	4
CL	6	6	5	6	6	6	5	6	7
DWaW	5	5	6	7	9	7	7	8	8
HL	4	3	5	6	4	6	4	4	4
PWaW	5	5	6	5	9	8	7	7	7
RE	1	1	1	1	1	1	1	1	2
RW	3	3	3	3	4	3	3	3	4
WiL	7	9	10	8	8	9	8	8	8
WiW	4	6	5	4	6	5	6	5	5

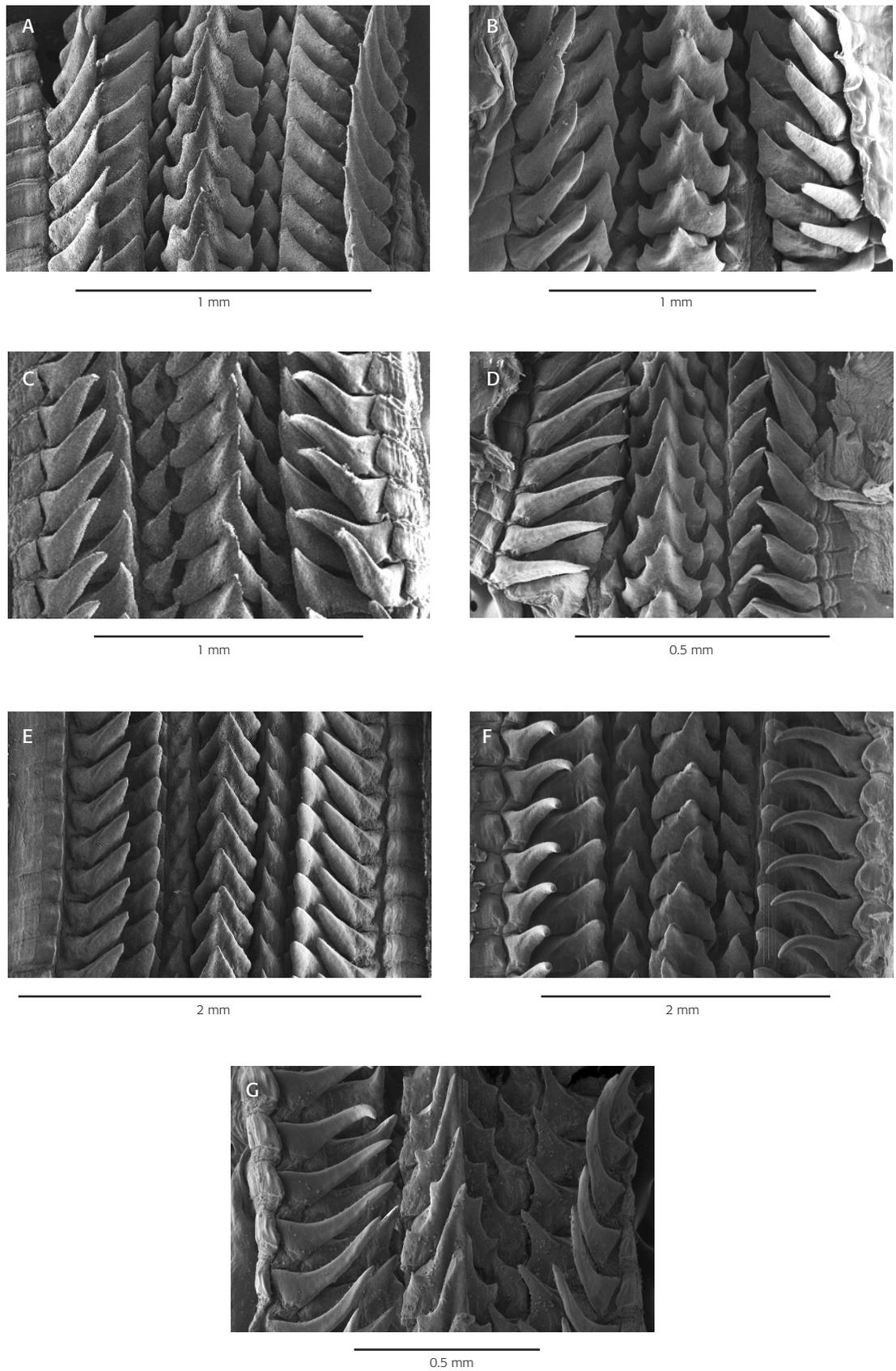


FIGURE 59. RADULA VARIATION WITHIN *Pareledone* sp. nov. 1. A) NIWA 44059, ML 58 mm. B) NIWA 44066, ML 70 mm. C) NIWA 44069, ML 60 mm. D) NIWA 44066, ML 68 mm. E) NIWA 44091, ML 90 mm. F) NIWA 44060, ML 46 mm. G) NIWA 44070, ML 73 mm.

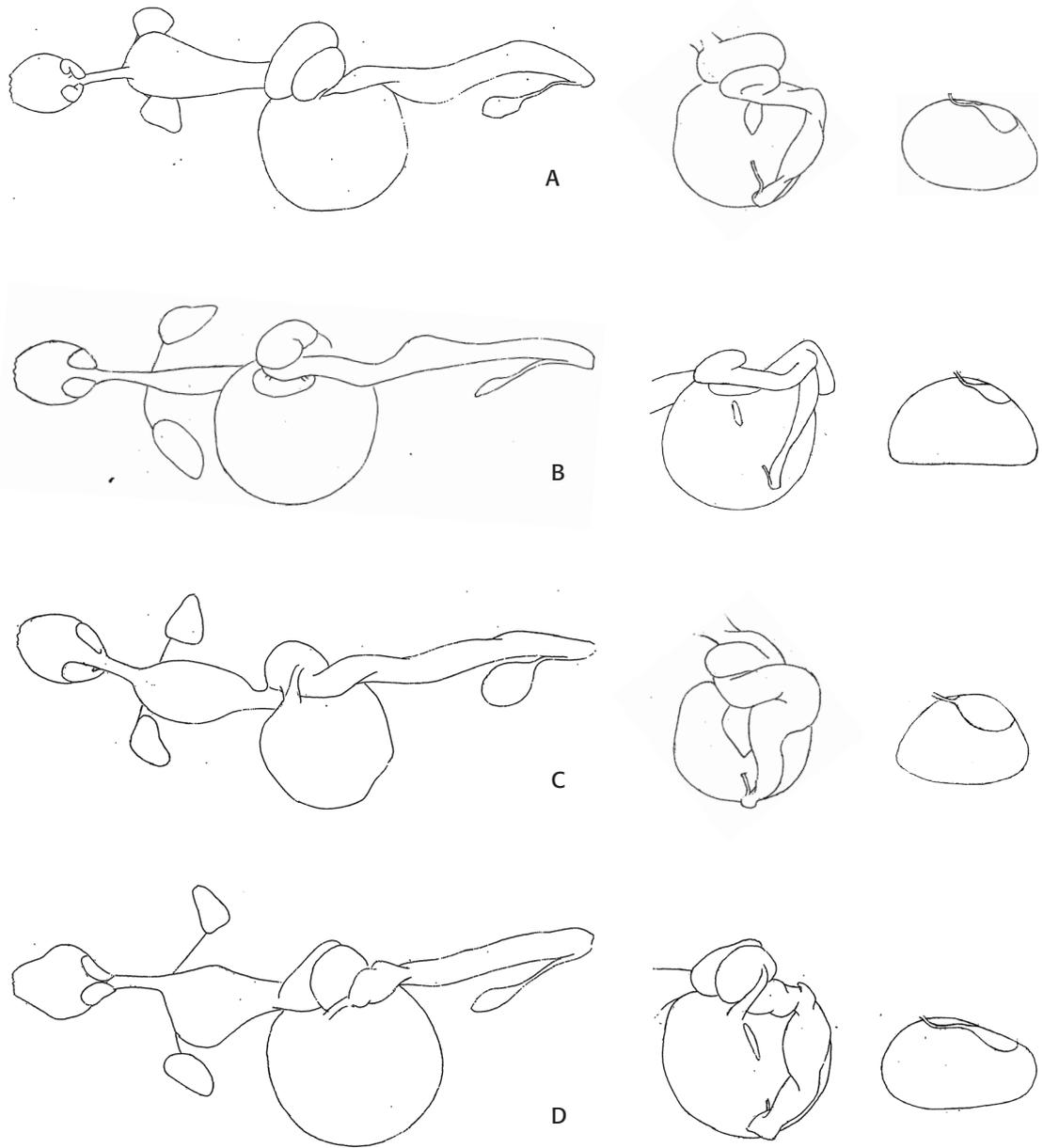


FIGURE 60. ALIMENTARY CANAL VARIATION WITHIN *Pareledone* sp. nov. 1. Female Specimens. A) NIWA 44067, ML 65 mm. B) NIWA 44091, ML 90 mm. C) NIWA 44060, ML 46 mm. D) NIWA 44070, ML 73 mm.

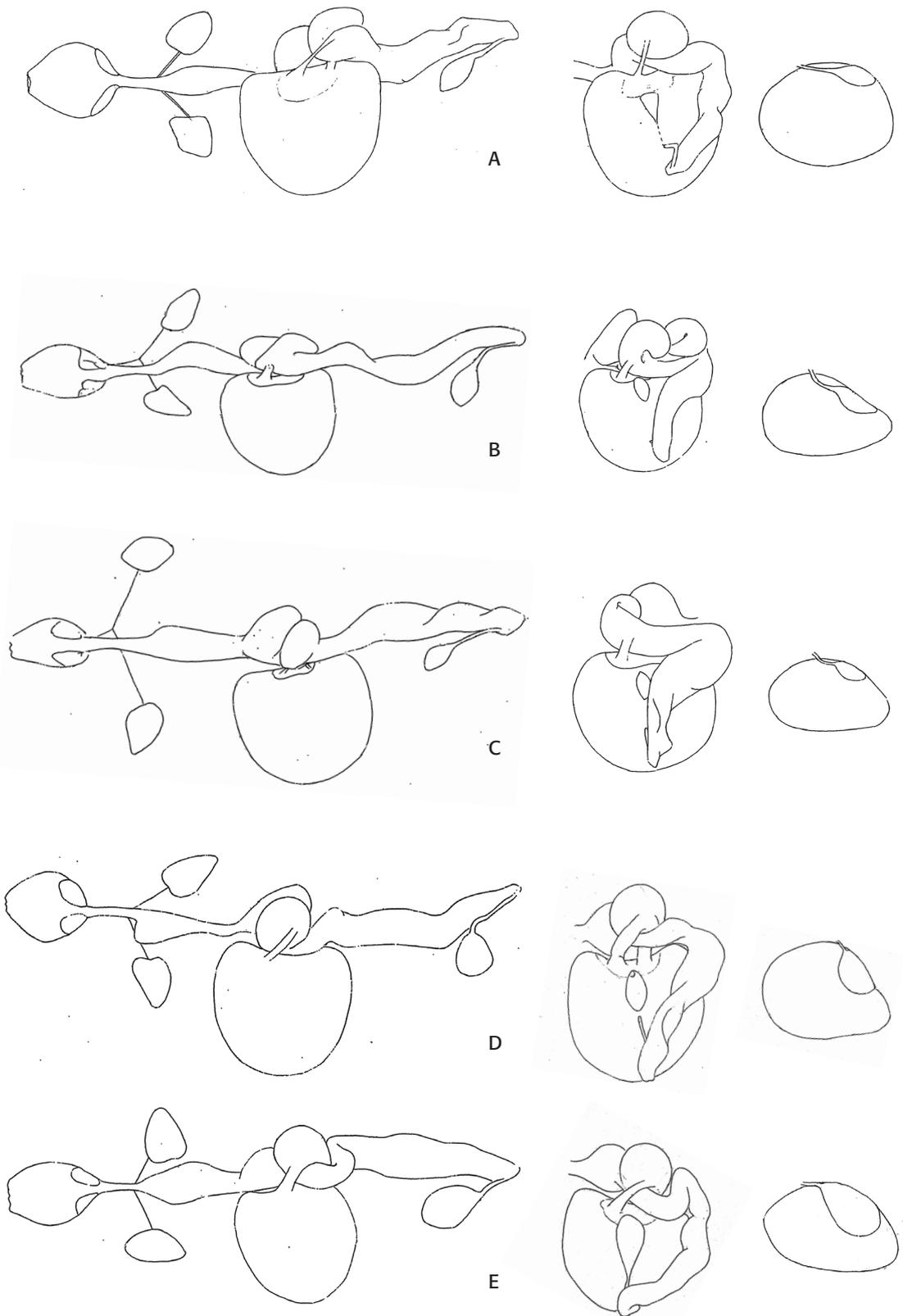


FIGURE 61. ALIMENTARY CANAL VARIATION WITHIN *Pareledone* sp. nov. 1. Male specimens. A) NIWA 44067, ML 73 mm. B) NIWA 44066, ML 68 mm. C) NIWA 44069, ML 60 mm. D) NIWA 44066, ML 70 mm. E) NIWA 44059, ML 58 mm.

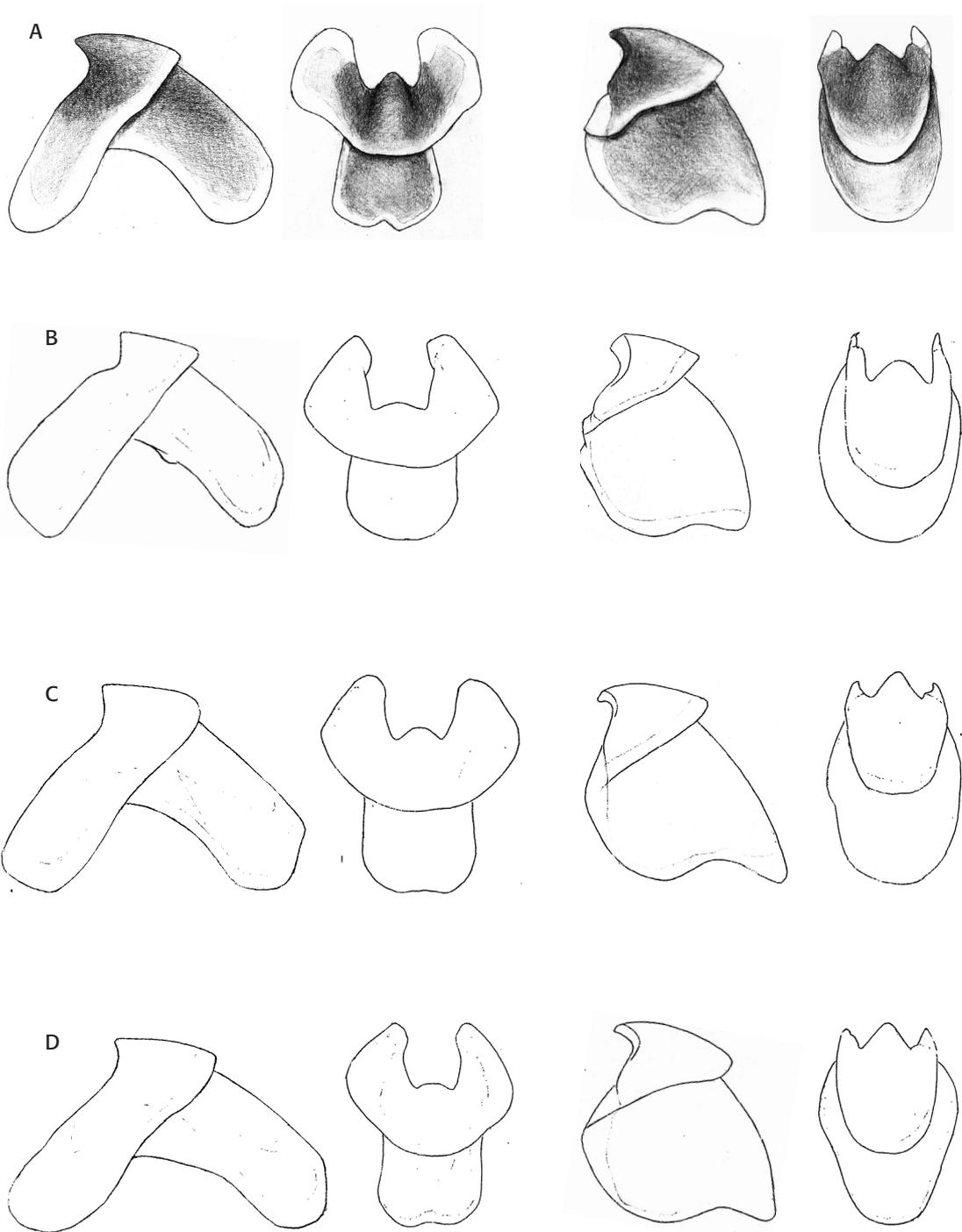


FIGURE 62. UPPER AND LOWER BEAK VARIATION WITHIN *Pareledone* sp. nov. Females specimens A) NIWA 44067, ML 65 mm. B) NIWA 44091, ML 90 mm. C) NIWA 44060, ML 46 mm. D) NIWA 44070, ML 73 mm.

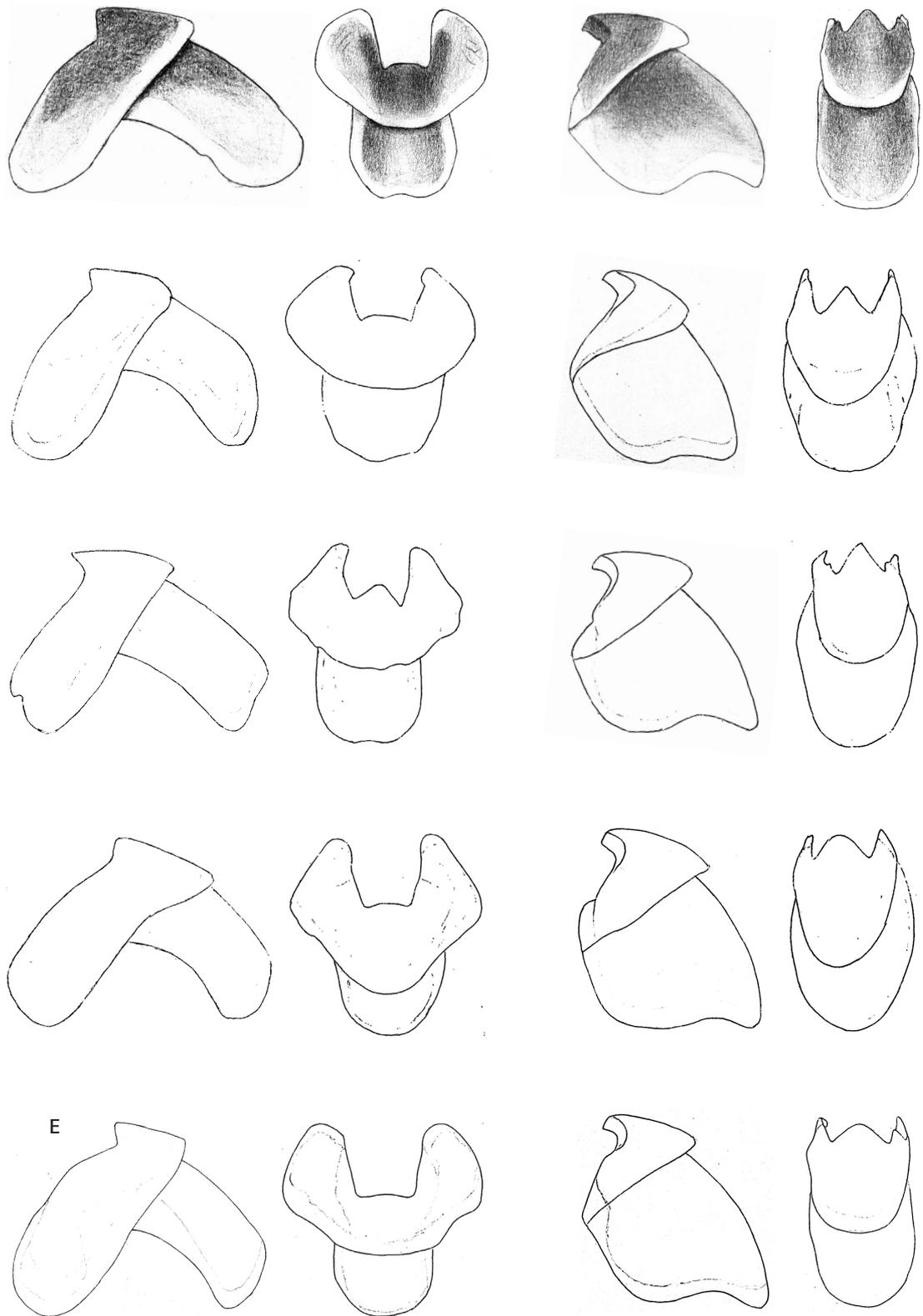


FIGURE 63. UPPER AND LOWER BEAK VARIATION WITHIN *Pareledone* sp. nov. 1. Male Specimens. A) NIWA 44067, ML 73 mm. B) NIWA 44066, ML 68 mm. C) NIWA 44069, ML 60 mm. D) NIWA 44066, ML 70 mm. E) NIWA 44059, ML 58 mm.

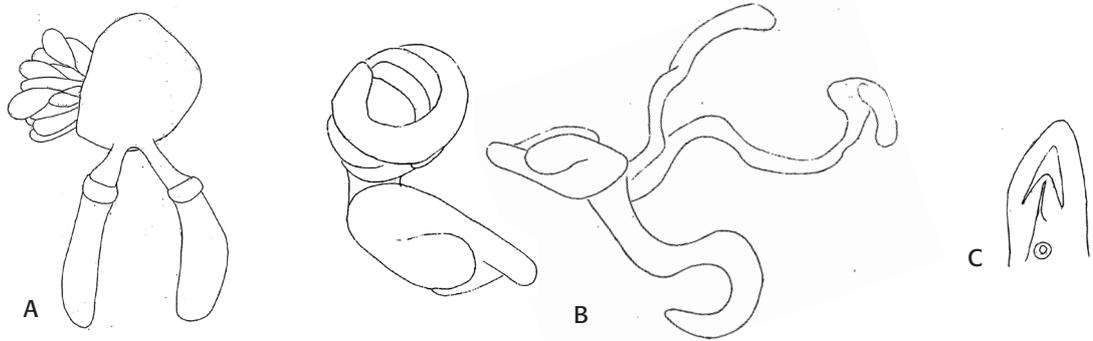


FIGURE 64. REPRODUCTIVE SYSTEM OF *Pareledone* sp. nov. 1. A) Female. NIWA 44070, ML 73 mm. B) Male. NIWA 4066, ML 70 mm. C) Hectocotylus. NIWA 44067, ML 73 mm.



FIGURE 65. *Pareledone* sp. nov. 1. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44091, ML 90 mm, ♀. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44067, ML 65 mm, ♀.



FIGURE 66. *Pareledone* sp. nov. 1. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44070, ML 73 mm, ♀. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44069, ML 60 mm, ♂.



FIGURE 67. *Pareledone* sp. nov. 1. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44066, ML 68 mm, ♂.
BELOW: Dorsal and ventral view of preserved specimen, NIWA 44067, ML 73 mm, ♂.



FIGURE 68. *Pareledone* sp. nov. 1. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44059, ML 58 mm, ♂. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44066, ML 70 mm, ♂.



FIGURE 69. *Pareledone* sp. nov. 1. Dorsal and ventral view of preserved specimen, NIWA 44060, ML 46 mm, ♀.

***Pareledone* sp. nov. 2**

RECOGNISED DISTRIBUTION. Only known from one location (below).

MATERIAL EXAMINED. 1 specimen (♂): NIWA 44097, ML 60 mm, 72°19.73–18.97'S, 175°28.25–26.06'E, 915–936 m, 21/02/2008, RV *Tangaroa* Stn, TAN0802/123.

DESCRIPTION. Adults of moderate size (ML to 60 mm, TL to 170 mm) (Fig. 72, Tables 154, 158). Mantle ovoid (MWI 125); head narrower than mantle (HdLI 25, HdWI 45), delimited from it by weak developed pre-ocular constriction. Orbits large, bulbous, with narrow mid-dorsal interspace between orbits. Postorbital constriction slight developed. Funnel free for more than half its length. Arm-to-web attachment type 2 (Fig. 4); depth 29% longest arm length. Web formula A=B=C=D.E. Arms about 140–150% TL; arm pairs I and IV slightly longer than II and III, formula 3=2.1.4. Suckers uniserial; arm sucker count 44–51; suckers extend to arm tips, none abruptly enlarged (ASIn 5), attaining greatest diameter at sixth sucker from the beaks. Third right arm of male hectocotylied, shorter than opposite member (OAI 76), with 32 suckers. Hectocotylied portion (Fig. 71D) with ligula, 10% hectocotylied arm length, with shallow groove lacking transverse rugae; calamus 37% ligula length. Spermatophoral groove well developed, narrow, with thickened web margin. Dorsal surfaces of mantle, web sectors A, B and C, dorso-lateral surfaces of arms I–III from their bases to arm tips, and dorso-lateral surface of arms IV covered in papillae from arm-web fusion point to arm tip; individual papillae simple, irregularly shaped, gradually disappearing onto ventral surface of mantle below the lateral fold around mantle; enlarged supra-ocular papilla present.

Gills with 6 lamellae per inner and outer demibranch. Male with well-developed spiral terminal organ diverticulum oriented to right of terminal organ; spermatophoric gland I longer than II; spermatophoric sac coiled, longer than SGII and shorter than SGI (Fig. 71E, Table 160).

Alimentary canal (Fig. 71A, C; Tables 155, 159) with buccal bulb length (BBL) about 20% ML. Anterior salivary glands of length 42% BBL. Posterior salivary glands elliptical to triangular, their greatest dimension 75% that of BBL (15% ML). Anterior oesophagus narrow, its length 38% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension 83% that of stomach, lacking volutions. Intestine longer than oesophagus, 125% OesTL. Digestive gland circular, with poorly developed hepatic peaks; greatest dimension 38% ML; pancreas well developed. Ink sac present, vestigial, type 3 (Fig. 6, Table 155, 159).

Circulatory system of type 1 (Fig. 13), with ink sac artery.

Lower beak (Fig. 71B left, Tables 156, 162) with black hood, abruptly lightening to brown toward margins; oral margin of wings black, to mid-portion of the wing, forming clearly marked diagonal line that lightens to brown abruptly toward aboral margin; lateral walls black, slightly lightening toward margin; margins translucent. Beak base length 18% ML, height 73% BBL. Hood with rounded crest, elevated from wings. Rostrum tip variable, blunt-triangular, with clear protrusion, RPI 10% BBL. Jaw angle acute (88°). Wing protrusion length 27% BBL; wing length 68% BBL. Lateral wall crest rounded, with weak basal notch. Proximal wall slightly narrower than distal wall.

Upper beak (Fig. 71B right, Tables 157, 161) with black hood and brown border; lateral walls black, gradually lightening toward the margin; all margins translucent. Beak base length 18% ML; beak deeper than long (119% BBL). Hood with rounded crest; rostrum triangular, rostral tip pointed, orally deflected, without lateral keel; protrusion length 18% BBL; rostrum length protrusion longer than wings. Jaw angle acute (68°). Lateral wall crest rounded, without basal notch; parallel-sided.

Radula (Fig. 70, 71F) with robust, broadly triangular, unicuspid rachidian, taller than wide. First laterals small, with large cusp; second laterals well developed, with large-based cusp; marginal teeth with cusp more delicate than that of either rachidian or second lateral; marginal blocks rectangular.

REMARKS. Skin papillation differentiates this species from species 1, in that papillae are irregularly shaped and the lateral fold is less-well developed, with papillae extending onto the ventral surfaces of the mantle in sp. nov. 2.

Although an ink sac is present, it is very small, lacks apparent ink, and is completely embedded within the digestive gland tissues. The only other known *Pareledone* species reported to lack an ink sac is *P. panchroma* Allcock, 2005, captured at depths of 427–804 m, marginally shallower than the depth at which this new taxon (915–936 m) was collected. Whether an ink sac artery is present in *P. panchroma* has not been ascertained. From *P. panchroma* differs most notably in shape and distribution of papillae, which stop gradually rather than abruptly after the mantle fold, and in hectocotylised arm sucker count, 32 suckers in this single *P. sp. nov. 2* individual, 23–25 for *P. panchroma*. These two differ in sufficient characters to recognise them as discrete species, and from all others referred to this genus, none of which has been described with an ink sac so reduced in size.

TABLE 154. EXTERNAL CHARACTER INDICES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
Sex	M
ALI1R	158.3
ALI2R	166.7
ALI3R	130.0
ALI4R	150.0
ALI1L	160.0
ALI2L	166.7
ALI3L	170.0
ALI4L	158.3
MAI	58.8
MWI	125.0
ASIn	5.0
AWI	15.0
EOI	10.0
FFI	33.3
FuLI	46.7
HdLI	25.0
HdWI	45.0
MWI	125.0
OAI	76.5
PAI	66.7
WDI	29.4

TABLE 155. INTERNAL CHARACTER INDICES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
AOesLI	20.0
ASGLI	8.3
BBI	20.0
DG(GD)	38.3
IntLI	66.7
ISA	yes
ISTLI	22.5
ISLI	5.8
OESTLI	53.3
PSGLI	15.0
SpCI	16.7
StI	20.0

TABLE 156. LOWER BEAK INDICES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
BLI	18.3
BHI	72.7
BIHI	27.3
BWI	90.9
CLI	45.5
DWaWI	54.5
HLI	36.4
PWaWI	45.5
REI	13.6
RWI	18.2
WiLI	68.2
WiWI	40.9

TABLE 157. UPPER BEAK INDICES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
BLI	18.3
BHI	81.8
BWI	54.5
CHI	22.7
HHI	36.4
HLI	54.5
REI	18.2
RPI	18.2
RWI	27.3
WiLI	31.8

TABLE 158. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Pareledone* sp. nov. 2.

	NIWA 44097 ML 60 mm
Gender	M
ML	60
AL1R	95
AL2R	100
AL3R	78
AL4R	9*
AL1L	96
AL2L	100
AL3L	102
AL4L	95
ASC1R	47
ASC2R	52
ASC3R	32
ASC4R	52*
ASC1L	44
ASC2L	52
ASC3L	51
ASC4L	52
SD	3
AW	9
EO	6
FFL	20
FuL	28
GiLC I	6
GiLC O	6
HdL	15
HdW	27
MW	75
PA	40
TL	170
WAt	type 2
WDA	26
WDBR	26
WDBL	26
WDCR	26
WDCL	26
WDDR	30
WDDL	26
WDE	22

TABLE 159. INTERNAL CHARACTER RAW MEASURES. *Pareledone* sp. nov. 2.

	NIWA 44097 ML 60 mm
AOesL	12
ASGL	5
BBL	12
DGL	16
DGW	23
DG(GD)	23
InTL	40
ISpres	type 3 (v)
ISDL	10
ISEL	0
ISEW	2
ISL	4
ISTL	14
ISW	3
OesTL	32
PSGL	9
SpCL	10
StL	12

(v)= vestigial

TABLE 160. REPRODUCTIVE SYSTEM RAW MEASURES. *Pareledone* sp. nov. 2.

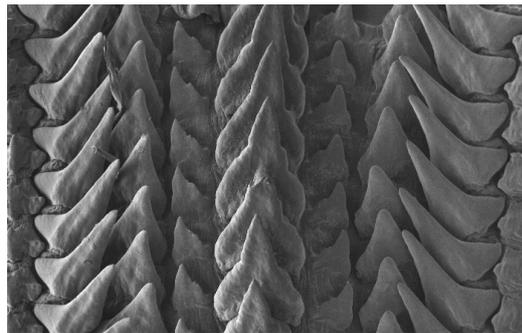
	NIWA 44097 ML 60 mm
CaL	3
LL	8
SGL	84
SGII	60
SS	72
TODL	15
TOL	15
TOTL	30

TABLE 161. UPPER BEAK RAW MEASURES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
BL	11
BH	9
BW	6
CH	3
HH	4
HL	6
HW	6
RE	2
RP	2
RW	3
WiL	4

TABLE 162. LOWER BEAK RAW MEASURES.
Pareledone sp. nov. 2.

	NIWA 44097 ML 60 mm
BL	11
BH	8
BIH	3
BW	10
CH	3
CL	5
DWaW	6
HL	4
PWaW	5
RE	2
RW	2
WiL	8
WiW	5



1 mm

FIGURE 70. *Pareledone* sp. nov. 2 (NIWA 44097, ML 60 mm). ESEM radula.

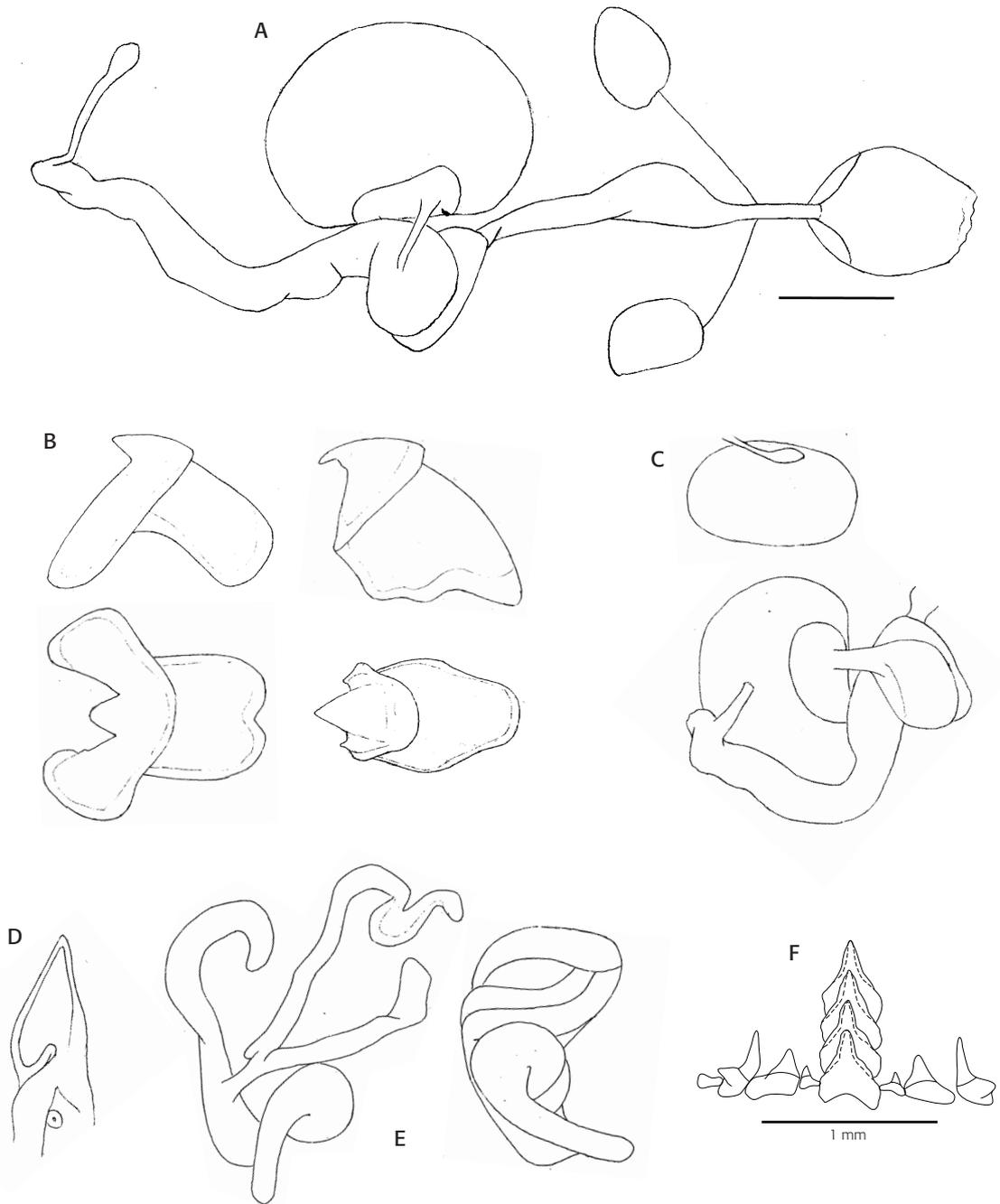


FIGURE 71. *Pareledone* sp. nov. 2 (NIWA 44097, ML 60 mm). A) Alimentary canal. B) Upper and lower beaks. C) Ink sac duct. D) Hectocotylus. E) Male reproductive system. F) Radula.



FIGURE 72. *Pareledone* sp. nov. 2 (NIWA 44097, ML 60 mm) Dorsal and ventral view of preserved specimen.

***Pareledone* sp. nov. 3**

RECOGNISED DISTRIBUTION: 72°35.42–76°36.14'S, 175°20.54–176°48.12'E, 343–479 m.

MATERIAL EXAMINED. 5 specimens (2♂, 3♀). NIWA 44120, ML 35 mm, ♂, 72°35.42–35.58'S, 175°20.54–20.55'E, 479–475 m, 21/02/2008, RV *Tangaroa* Stn TAN0802/117; NMNZ M.160553, ML 110 mm, ♀, 73°07.2'S, 174°36.00'E, 343 m, 15/01/2001, FV *San Aotea II*, MFish SOP Stn 1430/3R; NIWA 44122, ML 46 mm, ♀, 76°36.14–36.13'S, 176°48.12–47.65'E, 360 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/17; NIWA 44113, ML 63 mm, ♂, 76°11.58–12.3'S, 176°17.77–14.63'E, 447 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/94; NIWA 44073, ML 89 mm, ♀, 76°36.14–36.13'S, 176°48.12–47.65'E, 360 m, 17/02/2008, RV *Tangaroa* Stn TAN0802/84.

DESCRIPTION. Adult of moderate size (ML to 89 mm, TL to 260 mm) (Figs 78–80; Table 163, 167). Mantle ovoid (MWI 89–107); head narrower than mantle (HdLI 30–43, HdWI 48–72), delimited from it by moderate pre-ocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head. Postorbital constriction slightly developed. Funnel free for at least half its length. Arm-to-web attachment type 2 (Fig. 4); depth 11–23% longest arm length. Web formula variable. Arms 54–70% TL (excluding hectocotylied arm); arm formula variable, ventral arms frequently slightly shorter than dorsal arms. Suckers uniserial, but tending to alternate, sucker counts 40–59 (excluding hectocotylied arm), none abruptly enlarged (ASIn 4.3–6.7), attaining greatest diameter at third or fourth sucker from beaks. Third right arm of male hectocotylied, shorter than opposite member (OAI 82–102), with 35–39 suckers. Hectocotylied portion (Fig. 77A) with ligula 2.9% hectocotylied arm length, lacking transverse rugae; calamus 57% ligula length. Spermatophoral groove not well developed, narrow. Colour (preserved) pink, pale dorsally, lighter ventrally. Body smooth, with sparse blotches of pigment over mantle, head, dorsal basal part of arms I and II, and web sectors A and B. likely flattened papillae (specimens frozen prior to examination).

Gills with 7–10 lamellae per inner and outer demibranch. Male with well-developed spiral terminal organ diverticulum oriented to left of terminal organ; spermatophoric gland I markedly longer than II; spermatophoric sac not coiled, shorter than both SGI and II (Fig. 77A, B, Table 169). Female reproductive system (Fig. 76 A, B, Table 168) with proximal oviduct about $\frac{1}{4}$ the length of distal oviduct, slightly narrower than oviducal ball diameter; distal oviducts slightly longer than ovary sac length, of comparable diameter to oviducal ball.

Alimentary canal (Fig. 74A–E; Tables 164, 170) with buccal bulb length (BBL) 22–28% ML. Anterior salivary glands 47–60% BBL. Posterior salivary glands elliptical to triangular, length 85–95% BBL (14–22% ML). Anterior oesophagus narrow, its length 22–36% that of oesophagus (OesTL). Crop well developed, lacking diverticulum. Spiral caecum greatest dimension 72–92% that of stomach, lacking volutions. Intestine almost of comparable length to oesophagus, about 98–112% OesTL. Digestive gland circular, with poorly developed hepatic peaks, its greatest dimension 41–49% ML; pancreas well developed. Ink sac present, exposed, generally type 2 (Fig. 6), but variable.

Circulatory system of type 1 (Fig. 13), with well-developed ink sac artery.

Lower beak (Fig. 75A–E left; Tables 165, 172) with black hood, abruptly lightening to brown toward the margins; oral margin of wings black extending to middle of wing, forming clearly marked diagonal line that lightens to brown abruptly toward aboral margin; lateral walls dark brown or black, slightly lightening toward margin; margins translucent. Beak base length 17–22% ML, height 70–74% BBL. Hood with rounded crest, elevated from wings. Rostrum tip triangular, with clear protrusion, RPI 5–13% BBL. Jaw angle acute to slightly obtuse (71–108°). Wing protrusion length 20–29% BBL; wing length 57–67% BBL. Lateral wall crest rounded, with weak basal notch. Proximal wall narrower than distal wall.

Upper beak (Fig. 75A–E right, Tables 166, 171) with black hood and brown border; lateral walls black or dark brown, gradually lightening toward the margin; all margins translucent. Beak base length 15–20% ML, of comparable height to length. Hood with rounded crest; rostrum triangular, tip pointed, without lateral keel, straight or orally deflected; length protrusion 15–19% BBL; wing length protrusion of comparable length to that of rostrum. Jaw angle acute to obtuse (65–100°). Lateral wall crest rounded, without basal notch; generally parallel-sided.

Radula (Fig. 73A–C) with robust, broadly triangular rachidian, taller than wide, with two or three lateral cusps either side of large central cusp. First laterals small, with feeble cusps. Second laterals well developed, with large-based cusp. Marginal teeth with cusp more delicate than that of either rachidian or second lateral; marginal blocks rectangular.

REMARKS. With one exception (a female) all specimens were immature (no eggs or spermatophores present). The ink sac was variable in size and in the extent to which it was exposed on the surface of the digestive gland, with only a portion to the entire sac exposed (type 2), and in one case (Fig. 74C), part of the duct was exposed (but not all as in type 3). It is interesting to note such variation in the development of the ink sac within a species that is not particularly deep-dwelling (with a recognised depth distribution of 343–479 m), compared to other taxa herein reported

that have less-variably developed ink sacs; the variable expression of this structure in this species further supports the contention that its presence, absence, or degree of enclosure within the digestive gland tissues are not the most meaningful characters or states to use for differentiating octopus taxa, or for reconstructing phylogenetic relationships between taxa.

TABLE I63. EXTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
Sex	M	F	M	F	F
ALI1R	157.1	197.8	190.5	170.8	136.4
ALI2R	165.7	208.7	196.8	180.9	136.4
ALI3R	162.9	191.3	190.5	196.6	140.9
ALI4R	174.3	223.9	207.9	197.8	159.1
ALI1L	168.6	204.3	182.5	174.2	140.9
ALI2L	168.6	215.2	198.4	177.5	140.9
ALI3L	174.3	232.6	214.3	193.3	136.4
ALI4L	171.4	230.4	209.5	197.8	172.7
MAI	57.4	43.0	46.7	50.6	57.9
MWI	88.6	91.3	87.3	106.7	82.7
ASIn	4.3	6.5	4.8	6.7	7.3
AWI	17.1	17.4	17.5	16.9	11.8
EOI	17.1	16.3	12.7	12.4	8.2
FFI	11.4	32.6	19.0	16.9	27.3
FuLI	28.6	39.1	27.0	28.1	33.6
HdLI	37.1	43.5	33.3	30.3	25.5
HdWI	68.6	71.7	55.6	48.3	64.5
MWI	88.6	91.3	87.3	106.7	82.7
OAI	93.4	82.2	88.9	101.7	103.3
PAI	54.3	54.3	47.6	47.2	40.9
WDI	11.5	21.5	22.2	22.7	23.7

TABLE I64. INTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 3

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
AOesLI	14.3	21.7	22.2	15.7	14.5
ASGLI	12.9	15.2	14.3	13.5	10.9
BBI	27.1	28.3	22.2	22.5	27.3
DG(GD)	48.6	45.7	41.3	39.3	44.5
IntLI	71.4	80.4	66.7	57.3	73.6
ISTLI	1.35	44.6	28.6	32.6	30.0
ISLI	11.4	13.0	12.7	15.7	10.0
OESTLI	65.7	71.7	61.9	58.4	60.9
PSGLI	25.7	23.9	19.0	19.1	22.7
SpCI	22.9	26.1	20.6	20.2	17.3
StI	28.6	28.3	23.8	28.1	23.6

TABLE 165. LOWER BEAK INDICES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
BLI	20.0	21.7	18.3	16.9	14.5
BHI	71.4	70.0	73.9	73.3	75.0
BIHI	28.6	30.0	30.4	26.7	37.5
BWI	85.7	90.0	95.7	96.7	106.3
CLI	35.7	40.0	47.8	46.7	43.8
DWaWI	64.3	70.0	56.5	66.7	87.5
HLI	35.7	35.0	34.8	43.3	43.8
PWaWI	57.1	50.0	52.2	56.7	71.9
REI	14.3	10.0	13.0	10.0	12.5
RWI	21.4	15.0	17.4	16.7	21.9
WiLI	57.1	60.0	65.2	66.7	68.8
WiWI	35.7	35.0	43.5	40.0	43.8

TABLE 166. UPPER BEAK INDICES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
BLI	18.6	19.6	16.7	15.2	15.5
BHI	92.3	100.0	95.2	100.0	82.4
BWI	61.5	66.7	66.7	74.1	76.5
CHI	30.8	27.8	23.8	48.1	38.2
HHI	46.2	38.9	38.1	40.7	47.1
HLI	61.5	61.1	57.1	66.7	70.6
REI	10.8	11.1	9.5	14.8	11.8
RPI	15.4	16.7	19.0	18.5	17.6
RWI	30.8	33.3	23.8	25.9	29.4
WiLI	69.2	55.6	47.6	51.9	35.3

TABLE 167. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
Gender	M	F	M	F	F
ML	35	46	63	89	110
AL1R	55	91	120	152	150
AL2R	58	96	124	161	150
AL3R	57	88*	120	175	155
AL4R	61	103	131	176	175
AL1L	59	94	115	155	155
AL2L	59	99	125	158	155
AL3L	61	107	135	172	150
AL4L	60	106	132	176	190
ASC1R	40*	42	51	56	47
ASC2R	40	42	51	56	51
ASC3R	35	40*	39	59	54
ASC4R	40*	45	34	59	54
ASC1L	39	46*	51	56	49
ASC2L	40*	45*	53	56	53
ASC3L	39*	44	56	59	56
ASC4L	40	45*	55	58	56
SD	2	3	3	6	6
AW	6	8	11	15	13
EO	6	8	8	11	9
FFL	4	15	12	15	30
FuL	10	18	17	25	37
GilC I	9	7	10	10	9
GilC O	9	7	10	10	9
HdL	13	20	21	27	28
HdW	24	33	35	43	71
MW	31	42	55	95	91
PA	19	25	30	42	45
TL	102	153	197	265	290
WDA	12	20	25	32	37
WDBR	13	22	24	32	45
WDBL	14	20	24	35	40
WDCR	12	20	30	34	40
WDCL	10	20	29	40	*
WDDR	14	23	29	39	40
WDDL	15	18	29	37	*
WDE	13	18	21	40	40

TABLE 168. FEMALE REPRODUCTIVE SYSTEM MEASURES.
Pareledone sp. nov. 3.

	NIWA 44122 ML 46 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
DodL	7	12	19
DodW	2	4	10
OSL	7	13	45
OSW	7	13	54
OdTL	10	16	30
OdBL	1	3	4
OdBW	2	4	7
POdL	2	2	7
POdW	1	3	5

TABLE 169. MALE REPRODUCTIVE SYSTEM MEASURES. *Pareledone* sp. nov. 3.

	NIWA 44113 ML 63 mm
CaL	2
LL	3.5
SGL	35.5
SGII	1.95
SS	27
TODL	5
TOL	25
TOTL	9

TABLE 170. INTERNAL CHARACTER RAW MEASURES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
AOesL	5	10	14	14	16
ASGL	5	7	9	12	12
BBL	10	13	14	20	30
DGL	16	21	25	31	46
DGW	17	21	26	35	49
DG(GD)	17	21	26	35	49
InTL	25	37	42	51	81
ISpres	type 2				
ISA	*	*	yes	yes	not revised
ISDL	10	15	10	15	22
ISEL	3	5	7	19	9
ISEW	1	2	1	5	4
ISL	4	6	8	14	11
ISTL	0	21	18	29	33
ISW	2	3	3	6	2
OesTL	23	33	39	52	67
PSGL	9	11	12	17	25
SpCL	8	12	13	18	19
StL	10	13	15	25	26

TABLE 171. UPPER BEAK RAW MEASURES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
BL	7	9	11	14	17
BH	6	9	10	14	14
BW	4	6	7	10	13
CH	2	3	3	7	7
HH	3	4	4	6	8
HL	4	6	6	9	12
HW	4	6	6	7	11
RE	1	1	1	2	2
RP	1	2	2	3	3
RW	2	3	3	4	5
WiL	5	5	5	7	6

TABLE 172. LOWER BEAK RAW MEASURES. *Pareledone* sp. nov. 3.

	NIWA 44285 ML 36 mm	NIWA 44122 ML 46 mm	NIWA 44113 ML 63 mm	NIWA 44073 ML 89 mm	NMNZ M.160553 ML 110 mm
BL	7	7	10	12	15
BH	6	5	7	9	11
BIH	4	2	3	4	4
BW	2	6	9	11	15
CH	3	2	3	3	7
CL	4	3	4	6	7
DWaW	4	5	7	7	10
HL	1	3	4	4	7
PWaW	1	4	5	6	9
RE	2	1	1	2	2
RW	5	2	2	2	3
WiL	1	4	6	8	10
WiW	4	3	4	5	6

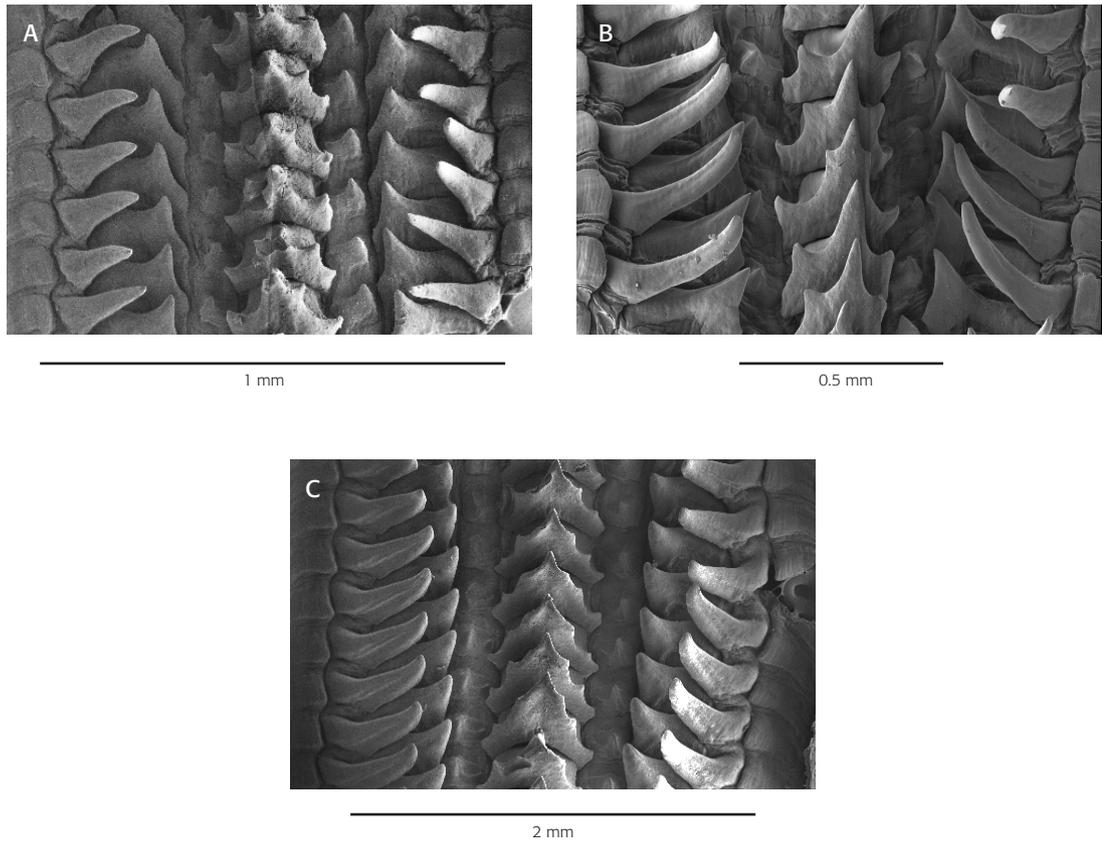


FIGURE 73. RADULA VARIATION WITHIN *Pareledone* sp. nov. 3. A) NIWA 44120, ML 35 mm, ♂. B) NIWA 44122, ML 46 mm, ♀. C) NIWA 44073, ML 89 mm, ♀.

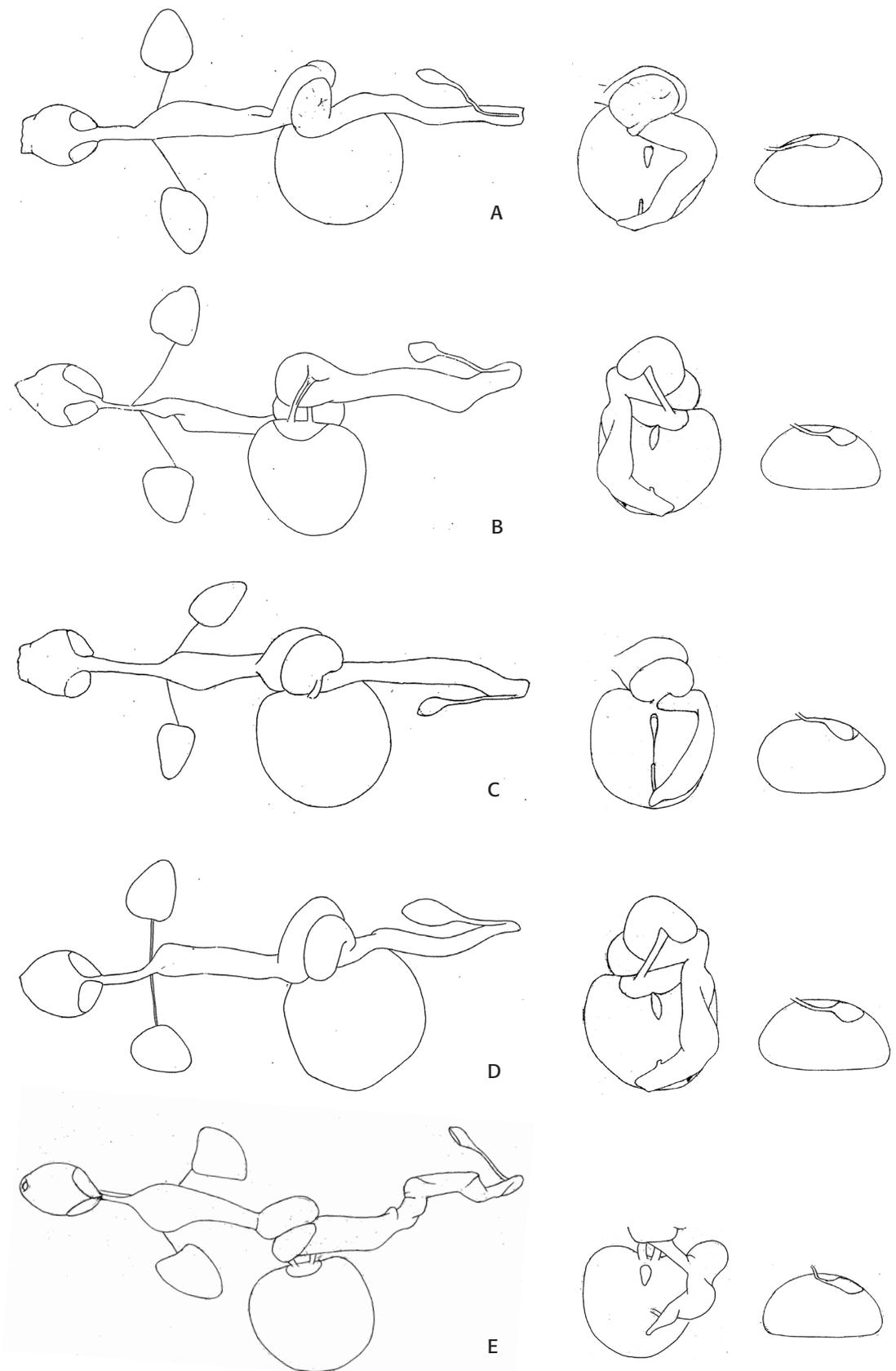


FIGURE 74. ALIMENTARY CANAL VARIATION WITHIN *Paredone* sp. nov. 3. A) NIWA 44120, ML 35 mm, ♂. B) NIWA 44122, ML 46 mm, ♀. C) NIWA 44113, ML 63 mm, ♂. D) NIWA 44073, ML 89 mm, ♀. E) NMNZ M.160553, ML 110 mm, ♀.

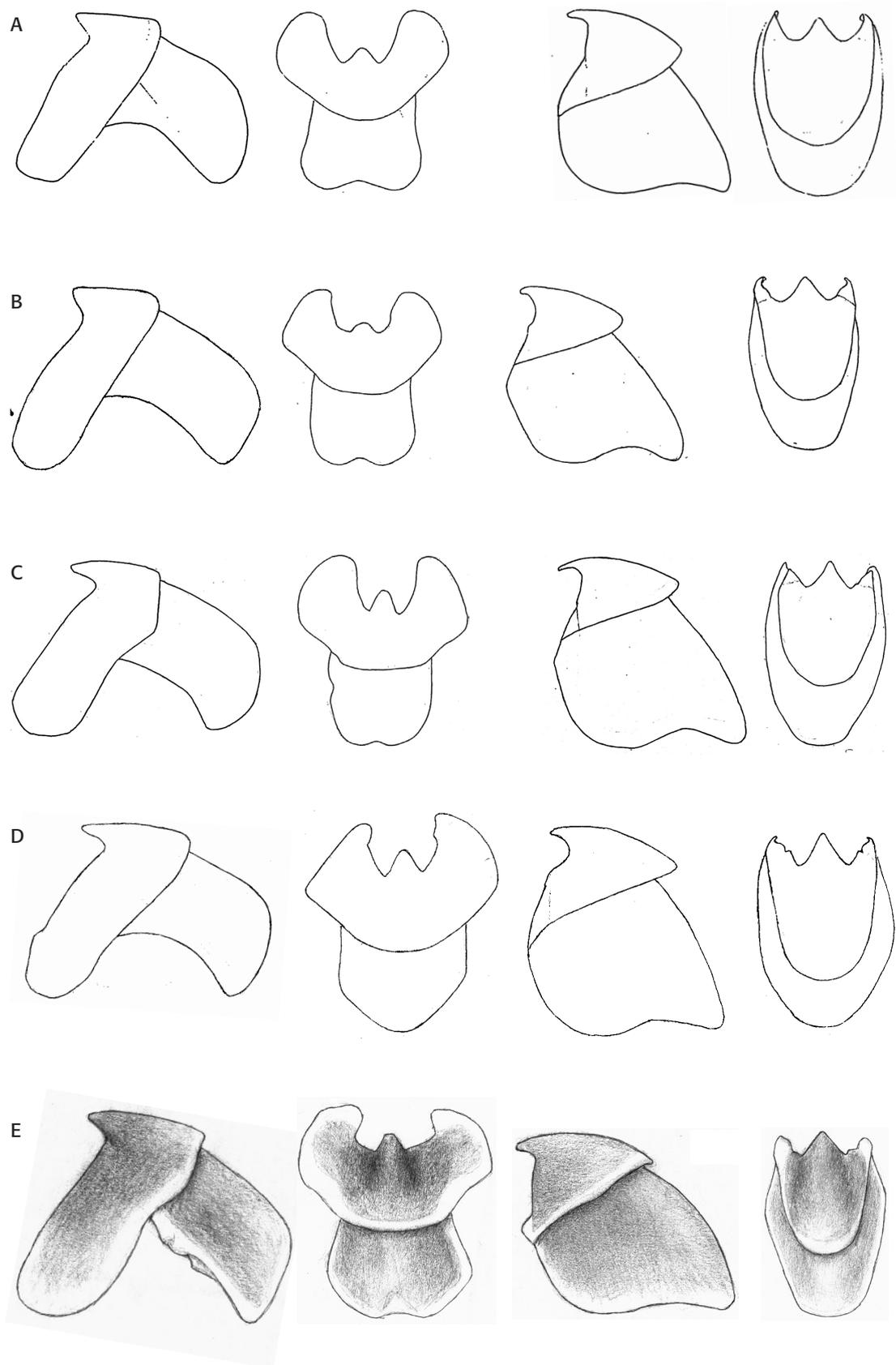


FIGURE 75. BEAK VARIATION WITHIN *Pareledone* sp. nov. 3. A) NIWA 44120, ML 35 mm, ♂. B) NIWA 44122, ML 46 mm, ♀. C) NIWA 44113, ML 63 mm, ♂. D) NIWA 44073, ML 89 mm, ♀. E) NMNZ M.160553, ML 110 mm, ♀.

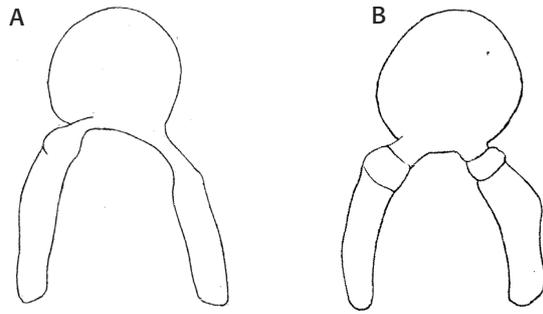


FIGURE 76. FEMALE REPRODUCTIVE SYSTEM OF *Pareledone* sp. nov. 3 A) NIWA 44122, ML 46 mm. B) NIWA 44073, ML 89 mm.

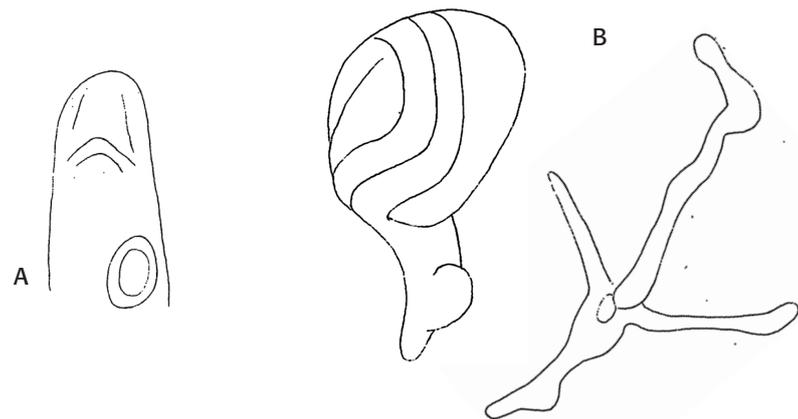


FIGURE 77. MALE REPRODUCTIVE SYSTEM OF *Pareledone* sp. nov. 3 (NIWA 44113, ML 63 mm). A) Hectocotylus. B) Reproductive system.



FIGURE 78. *Pareledone* sp. nov. 3. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44073, ML 89 mm, ♀. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44113, ML 63 mm, ♂.



FIGURE 79. *Pareledone* sp. nov. 3. ABOVE: Dorsal and ventral view of preserved specimen, NMNZ M.160553, ML 110 mm, ♀. BELOW: Dorsal and ventral view of preserved specimen, NIWA 44120, ML 35 mm, ♂.



FIGURE 80. *Pareledone* sp. nov. 3. Dorsal and ventral view of preserved specimen, NIWA 44122, ML 46 mm, ♀.

***Pareledone* sp. nov. 4**

RECOGNISED DISTRIBUTION: Ross Sea, known only from one location (below), 1990–1954 m.

MATERIAL EXAMINED: 3 specimens (♀). NIWA 44258 ML 36, 61, 62 mm, 71°51.34–53.40'S, 174°01.98–06.59'E, 1990–1954 m, 25/02/2008, RV *Tangaroa* Stn TAN0802/167.

DESCRIPTION. Adults of moderate size (ML to 62 mm, TL to 161 mm) (Fig. 83; Tables 173, 177). Mantle ovoid (MWI 72–82); head narrower than mantle (HdLI 26–36, HdWI 49–51), delimited from it by weak developed pre-ocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head. Postorbital constriction slight developed. Funnel free for at least half to slightly more than half its length. Arm-to-web attachment type 2 (Fig. 4); depth 12–23% longest arm length. Web formula variable, with sector A or E usually the shallowest. Arms 59–102% TL, all similar length. Suckers uniserial, sucker counts 36–42, none abruptly enlarged (ASIn 4.9–5.6), attaining greatest diameter at third or fourth sucker from beaks. Skin over all body surfaces entirely smooth. Colour (preserved) over all body surfaces, pale pink, with the web slightly darker.

Gills with 8 or 9 lamellae per inner and outer demibranch. Female reproductive system (Fig. 82E) with proximal oviduct about 25% length of distal oviduct, slightly narrower than oviducal ball diameter; distal oviducts slightly longer than ovary sac length, of comparable diameter to oviducal ball.

Alimentary canal (Fig. 82A, B; Tables 174, 178) with buccal bulb length (BBL) 18–28% ML. Anterior salivary glands 40–48% length of BBL. Posterior salivary gland greatest dimension comparable in length to BBL (80–104% BBL, 14–22% ML). Anterior oesophagus narrow, its length 24–29% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension 92–83% that of stomach, lacking volutions. Intestine 95–133% OesTL. Digestive gland circular, with poorly developed hepatic peaks, its greatest dimension 37–44% ML; pancreas well developed. Ink sac absent, or when present, vestigial and completely buried within digestive gland tissues, lacking ink, being thin and delicate, and seemingly not joined to the intestine.

Circulatory system of type 2 (Fig. 13), without apparent ink sac artery; digestive gland artery present, between hepatic ducts.

Lower beak (Fig. 82 C, D left; Tables 175, 181) with black hood, abruptly lightening to brown toward the margins; oral margins of wings black, extending to middle of wing forming a

clearly marked diagonal line that lightens to brown abruptly toward aboral margin; lateral walls dark brown or black, slightly lightening toward margin; margins translucent. Beak base length 16–21% ML, height 67–95% BBL. Hood with rounded crest, elevated from wings. Rostrum triangular, clearly protruding, RPI 7–8% BBL. Jaw angle acute to slightly obtuse (81–107°). Wing protrusion length 21–27% BBL; wing length 58–60% BBL. Lateral wall crest rounded, with weak basal notch. Proximal wall slightly narrower than distal wall.

Upper beak (Fig. 82C, D right; Tables 176, 180) with black hood and brown border; lateral walls black, gradually lightening toward margin; all margins translucent. Beak base length 14–18% ML; height slightly shorter than length (BH 90–92% BL). Hood with rounded crest; rostrum triangular, tip pointed, without lateral keel, straight or orally deflected; length protrusion 12–19% BBL; wing length protrusion of comparable length to rostrum. Jaw angle acute to obtuse (79–119°). Lateral wall crest rounded, without basal notch; generally parallel-sided.

Radula (Figs 81, 82 F, G) with robust, broadly triangular rachidian, taller than wide, with one or two asymmetric lateral cusps either side of large central cusp. First laterals small, without variably developed cusps from feeble (82G) to large (81); second laterals well developed, with large-based cusp; marginal teeth with cusp more delicate than that of either rachidian or second lateral; marginal blocks rectangular.

REMARKS. None of the specimens appears to be sexually mature (none had eggs in the ovary sac). This is the first octopodid species so far described (to the best of my knowledge) that can possess a vestigial (non-functional) ink sac, or can lack this structure altogether; when present this structure possessed no obvious ink and was barely formed and buried within the digestive gland; the ink duct was not exposed, nor joined to the intestine, and an ink sac artery was also not apparent. This is particularly remarkable, because it indicates that both the ink sac duct and ink sac artery could be lost from a taxon prior to the loss of the ink sac vestige itself. In other taxa that lack a functional ink sac, the ink sac vestige has been lost prior to the loss of an ink sac artery or duct. Were it not for the multicuspid rachidian tooth of the radula, and if not carefully dissected, this species could be mistaken for one of *Bentheledone*, as herein rediagnosed; it differs from the single specimen herein attributed to *B. albida* (Berry) in radular morphology, and bears little resemblance to it in overall body shape; from those attributed to *Thaumeledone* and *Praealtus*, its fresh condition is quite dissimilar in pigmentation, and anatomically, in radular details. Collection of larger/mature specimens, and males is required to more fully evaluate the systematic position of this rather unique species.

TABLE 173. EXTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
Sex	F	F	F
ALI1R	202.8	155.7	193.5
ALI2R	200.0	149.2	206.5
ALI3R	197.2	165.6	200.0
ALI4R	197.2	163.9	200.0
ALI1L	197.2	154.1	196.8
ALI2L	205.6	150.8	201.6
ALI3L	208.3	172.1	206.5
ALI4L	194.4	162.3	196.8
MAI	48.0	58.1	48.4
MWI	72.2	82.0	75.8
ASIn	5.6	4.9	4.8
AWI	15.3	14.8	19.4
EOI	16.7	14.8	14.5
FFI	16.7	16.4	24.2
FuLI	30.6	23.0	32.3
HdLI	36.1	31.1	25.8
HdWI	51.4	49.2	48.4
MWI	72.2	82.0	75.8
OAI	94.7	96.2	96.9
PAI	41.7	49.2	40.3
WDI	12.0	22.9	16.4

TABLE 174. INTERNAL CHARACTER INDICES. *Pareledone* sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
AOesLI	16.7	13.1	16.1
ASGLI	11.1	8.2	9.7
BBI	27.8	18.0	20.2
DG(GD)	40.3	36.9	43.5
IntLI	55.6	65.6	88.7
OESTLI	58.3	55.7	66.9
PSGLI	22.2	18.0	21.0
SpCI	20.8	16.4	17.7
StI	23.6	19.7	19.4

TABLE 175. LOWER BEAK INDICES.
Pareledone sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
BLI	20.8	15.6	19.4
BHI	66.7	94.7	79.2
BIHI	26.7	26.3	25.0
BWI	93.3	94.7	83.3
CLI	40.0	42.1	41.7
DWaWI	66.7	73.7	54.2
HLI	33.3	31.6	33.3
PWaWI	53.3	68.4	50.0
REI	6.7	10.5	8.3
RWI	13.3	15.8	16.7
WiLI	60.0	57.9	75.0
WiWI	33.3	42.1	33.3

TABLE 176. UPPER BEAK INDICES.
Pareledone sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
BLI	18.1	13.9	16.9
BHI	92.3	82.4	90.5
BWI	69.2	70.6	66.7
CHI	30.8	23.5	23.8
HHI	38.5	41.2	38.1
HLI	61.5	58.8	66.7
REI	7.7	7.1	9.5
RPI	15.4	11.8	19.0
RWI	38.5	29.4	33.3
WiLI	53.8	41.2	42.9

TABLE 177. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Pareledone* sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
Gender	F	F	F
ML	35	36	61
AL1R	55	73	95
AL2R	58	72	91
AL3R	57	71	101
AL4R	61	71	100
AL1L	59	71	94
AL2L	59	74	92
AL3L	61	75	105
AL4L	60	70	99
ASC1R	40*	36	39
ASC2R	40	36*	36*
ASC3R	35	36*	40*
ASC4R	40*	37*	39*
ASC1L	39	38*	38
ASC2L	40*	38*	37*
ASC3L	39*	39*	41
ASC4L	40	36	38*
SD	2	2	3
AW	6	6	9
EO	6	6	9
FFL	4	6	10
FuL	10	11	14
GiLC I	9	8	8
GiLC O	9	8	8
HdL	13	13	19
HdW	24	19	30
MW	31	26	50
PA	19	15	30
TL	102	108	161
WAt	type 2	type 2	type 2
WDA	13	13	18
WDBR	14	13	20
WDBL	12	14	21
WDCR	10	13	23
WDCL	14	11	22
WDDR	15	14	24
WDDL	13	15	22
WDE	22	17	18

TABLE 178. INTERNAL CHARACTER RAW MEASURES. *Pareledone* sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
AOesL	6	8	10
ASGL	4	5	6
BBL	10	11	13
DGL	14	23	24
DGW	15	23	27
DG(GD)	15	23	27
InTL	20	40	55
ISpres	type 3 (v)	type 3 (v)	no
ISA	yes	yes	*
OesTL	21	34	42
PSGL	8	11	13
SpCL	8	10	11
StL	9	12	12

v = vestigial

TABLE 179. REPRODUCTIVE SYSTEM RAW MEASURES. *Pareledone* sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
DodL	6	7	10
DodW	1	12	2
OSL	4	6	5
OSW	4	6	9
OdTL	8	9	14
OdBL	1	1	2*
OdBW	1	2	2
POdL	1	2	2
POdW	1	1	1

TABLE 180. UPPER BEAK RAW MEASURES.
Pareledone sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
BL	7	9	11
BH	6	7	10
BW	5	6	7
CH	2	2	3
HH	3	4	4
HL	4	5	7
HW	4	5	5
RE	1	1	1
RP	1	1	2
RW	3	3	4
WiL	4	4	5

TABLE 181. LOWER BEAK RAW MEASURES.
Pareledone sp. nov. 4.

	NIWA 44285 ML 36 mm	NIWA 44285 ML 61 mm	NIWA 44285 ML 62 mm
BL	8	10	12
BH	5	9	10
BIH	2	3	3
BW	7	9	10
CH	2	3	2
CL	3	4	5
DWaW	5	7	7
HL	3	3	4
PWaW	4	7	6
RE	1	1	1
RW	1	2	2
WiL	5	6	9
WiW	3	4	4

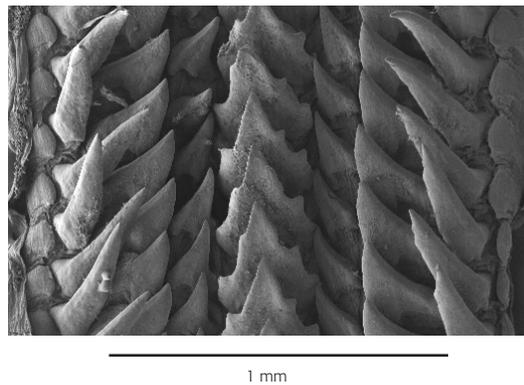


FIGURE 81. *Pareledone* sp. nov. 4. NIWA 44258, ♀, ML 62 mm. ESEM radula.

As for the preceding species, *P.* sp. nov. 3, reduction to complete loss of the ink sac is somewhat remarkable. With the exception of the previous taxon and *P. panchroma* Allcock, 2005 (if correctly attributed to this genus) this is the third-known *Pareledone* to have a markedly reduced ink sac, or to have lost the ink sac entirely. This is consistent with earlier accounts of the presence or absence of this structure being of limited systematic value (Allcock 2005). From *P. panchroma* and the previous species (*P.* sp. nov. 3) it differs most notably in surface sculpture, particularly the complete absence of any discernable papillae or vestige of same on all its body, and its extensively gelatinous nature.

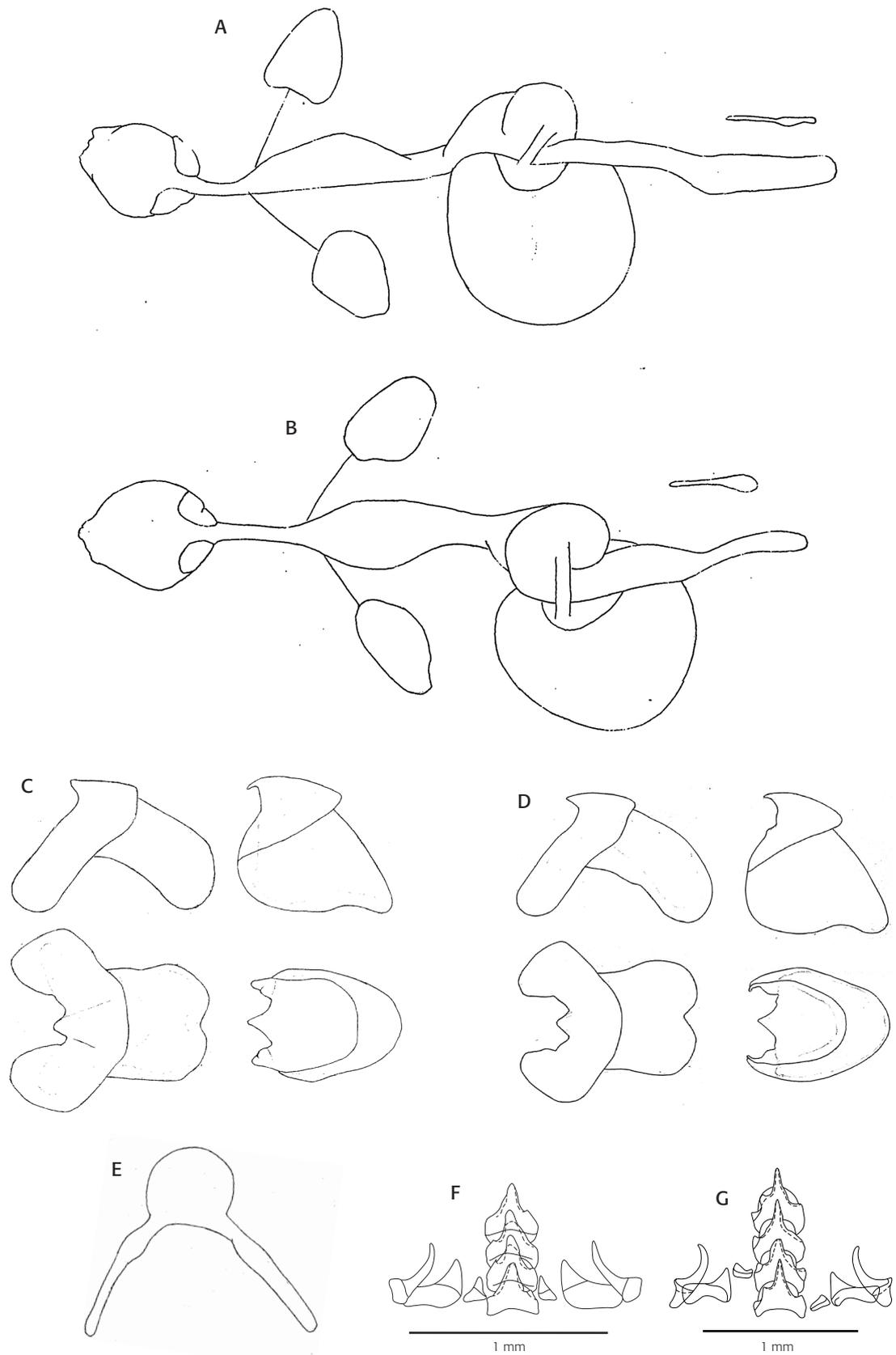


FIGURE 82. *Pareledone* sp. nov. 4. (NIWA 44258, ♀). **A)** Alimentary canal, ML 61 mm. **B)** Alimentary canal, ML 36 mm. **C)** Upper and Lower beaks, ML 61 mm. **D)** Upper and lower beak, ML 36 mm. **E)** Female reproductive system, ML 61 mm. **F)** Radula, ML 36 mm. **G)** Radula, ML 61 mm.



FIGURE 83. *Pareledone sp. nov. 4*. ABOVE: Dorsal and ventral view of preserved specimen, NIWA 44258, ML 61 mm, ♀. BELOW LEFT: Dorsal view of preserved specimen, NIWA 44258, ML 36 mm, ♀. BELOW RIGHT: Dorsal view, NIWA 44258, ML 62 mm, ♀.

***Pareledone* sp. nov. 5**

MATERIAL EXAMINED. 1 specimen (♀). NMNZ M.287686, ML 66 mm, 71°25.80'S, 177°0.00'E, 966 m, 10/01/2007, FV *San Aotea II*, MFish SOP Stn 2332/34.

RECOGNISED DISTRIBUTION. Ross Sea, known only from above station.

DESCRIPTION. Adults of moderate size (ML to 66 mm, TL to 180 mm) (Fig. 86; Tables 182, 186). Mantle ovoid (MWI 121); head narrower than mantle (HdLI 27, HdWI 52), delimited from it by weakly developed pre-ocular constriction. Orbits large, bulbous, not meeting across dorsal midline of head. Post-ocular constriction slightly developed. Funnel free for more than half its length. Arm-to-web attachment type 2 (Fig. 4); web depth about 34% longest arm length; web formula variable; sectors roughly subequal in depth. Arms 45–50% TL, of similar length. Suckers uniserial, sucker counts 47–53, none abruptly enlarged (ASIn 5.3), attaining greatest diameter at third sucker from beaks. Dorsal surfaces of mantle, head, dorso- and ventro-lateral lateral surfaces of arms I, II and III, and web sectors A, B and C, covered in evenly distributed circular-shaped papillae; papillae on dorsal surfaces of mantle extend to ventro-lateral surfaces of mantle, forming no distinct lateral line; ventral surfaces of the mantle, head, both dorso- and ventro-lateral surfaces of arms IV, and web sectors D and E smooth.

Colour (preserved) purple-brownish, darker on ventral and dorsal surfaces of all arms and web sectors.

Gills with 6 lamellae per inner and outer demibranch. Female reproductive system (Fig. 85D, Table 179) with proximal oviduct about 25% the length of distal oviduct, slightly narrower than oviducal ball diameter; distal oviducts less than half the length of ovary sac, of comparable diameter to oviducal ball.

Alimentary canal (Fig. 85A, C; Tables 183, 187) with buccal bulb length (BBL) 17% ML. Anterior salivary glands 55% BBL. Posterior salivary gland greatest dimension almost comparable to that of BBL (95% BBL, 16% ML). Anterior oesophagus narrow, its length 29% that of oesophagus (OesTL). Crop well developed, without diverticulum. Spiral caecum greatest dimension about 69% that of stomach, lacking volutions. Intestine longer than oesophagus, 124% OesTL. Digestive gland circular, with poorly developed hepatic peaks, its greatest dimension 35% that of ML; pancreas well developed. Ink sac present, type 3 (Fig. 6), completely embedded for its length (not exposed along the surface of the digestive gland) within digestive gland tissues.

Circulatory system of type 1 (Fig. 13), with well-developed ink sac artery.

Lower beak (Fig. 85B left; Tables 184, 190) with black hood, abruptly lightening to brown toward the margins; oral margins of wings black extending to mid-portion of wing, forming clearly marked diagonal line that lightens to brown abruptly toward aboral margin; lateral walls black, slightly lightening toward margin; margins translucent. Beak base length 18% ML, height 73% BBL. Hood with rounded crest, elevated from wings. Rostrum triangular, with clear protrusion, RPI 6% BBL. Jaw angle obtuse (98°). Wing protrusion length 36% BBL; wing length 64% BBL. Lateral wall crest rounded, with weak basal notch. Proximal (lateral) wall slightly narrower than distal wall.

Upper beak (Fig. 85B right; Tables 185, 189) with black hood and brown border; lateral walls black, gradually lightening toward margin; all margins translucent. Beak base length 14% ML, height comparable to length. Hood with rounded crest; rostrum triangular, tip pointed, deflected orally, without lateral keel; length protrusion 2.5% BBL; wing length protrusion longer than that of rostrum. Jaw angle obtuse (116°). Lateral wall crest rounded, without basal notch, parallel-sided.

Radula (Fig. 84) with robust, broadly triangular rachidian, taller than wide, with single, asymmetric lateral cusp on either side of large central cusp. First laterals small, with small cusp; second laterals well developed, with large-based cusp; marginal teeth with cusp more delicate than that of either rachidian or second lateral, as long as second lateral; marginal blocks rectangular.

REMARKS. The anatomy of this specimen was damaged slightly prior to dissection, and the posterior salivary gland duct was separated from the buccal bulb. However the ink sac was not damaged, and its position (deeply buried) within the digestive gland was apparent.

This species resembles those of *Thaumeledone* in its general squat-bodied shape and colour, but differs from them (with the exception of the type specimen of *T. zeiss* O'Shea, 1999) in anatomical detail, particularly the conventional octopodid form of the radula (with 7 transverse rows of teeth), large posterior salivary gland size (relative to the greatest buccal bulb dimension), gill lamellae and total arm sucker counts, presence of an ink sac (albeit reduced in size and deeply embedded within the digestive gland), and the form of the papillae distributed over the body surfaces.

Pareledone sp. nov. 5 differs from other papillose species from western Antarctica referred to by Allcock (2005) in having simple, circular-shaped papillae, while those of *P. panchroma* and *P. subtilis* are irregular. It is similar to *P. aequipapillae* in the distribution of papillae, but it lacks leucophores on the mantle fold, and papillae do not stop as abruptly as in *P. aequipapillae*; this species also has considerably longer arms (ALI 73 as opposed to 51.1 ± 4.2 in the latter). Regard-

ing taxa recognised from the Prydz Bay region (Lu & Stranks 1994), this species differs from *P. framensis* in lacking enlarged supra-ocular papillae, having longer arms, deeper web, and lower arm sucker counts (*P. framensis* MAI 29–38, WDI 12–22, and ASC3L 61–80); from *P. harrisoni* it differs in the nature of papillae (scattered in *P. harrisoni*); and from *P. prydzensis* it differs in the presence of a lateral ridge around the mantle, shorter arms, and greater arm sucker counts (*P. prydzensis* MAI 51.7–69.4, ASC3L 29–36). For these reasons this species is also recognised as new to science .

GENERAL REMARKS. Overall, the five species of *Pareledone* herein reported from the Ross Sea region differ from all others described from the Southern Ocean, considerably increasing the recognised diversity of Southern Ocean octopodids. These species, collected from depths of 283 to 1990 metres, possess a variety of characters and states not previously reported for any genus of octopodid to date; the most important of these as far as the systematics of the genus *Pareledone* is concerned is the variable expression of the ink sac, which gradually reduces in size and becomes more deeply embedded within the tissues of the digestive gland with increasing depth, and that this structure can be variably developed within a single taxon, so variable in fact that a vestige can be present or absent. All the specimens of *Pareledone* possess the same basic complement of 7 transverse rows of radular teeth, and lateral marginal blocks; the greatest variation in radular dentition appears to be the number of lateral cusps (if present) on either side of the central rachidian tooth, and the thickness and size of second laterals.

TABLE 182. EXTERNAL CHARACTER INDICES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
Sex	F
ALI1R	122.7
ALI2R	128.8
ALI3R	125.8
ALI4R	136.4
ALI1L	122.7
ALI2L	128.8
ALI3L	128.8
ALI4L	136.4
MAI	73.3
MWI	121.2
ASIn	5.3
AWI	13.6
EOI	15.2
FFI	27.3
FuLI	37.9
HdLI	27.3
HdWI	51.5
MWI	121.2
OAI	97.6
PAI	42.4
WDI	34.4

TABLE 183. INTERNAL CHARACTER INDICES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
AOesLI	15.2
ASGLI	9.1
BBI	16.7
DG(GD)	34.8
IntLI	63.6
ISA	*
ISTLI	21.2
ISLI	
OESTLI	51.5
PSGLI	15.9
SpCI	13.6
StI	19.7

TABLE 184. LOWER BEAK INDICES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
BLI	16.7
BHI	77.3
BIHI	31.8
BWI	86.4
CLI	50.0
DWaWI	54.5
HLI	31.8
PWaWI	54.5
REI	9.1
RWI	13.6
WiLI	63.6
WiWI	36.4

TABLE 185. UPPER BEAK INDICES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
BLI	13.6
BHI	100.0
BWI	77.8
CHI	33.3
HHI	33.3
HLI	55.6
REI	16.7
RPI	16.7
RWI	33.3
WiLI	50.0

TABLE 186. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Pareledone* sp. nov. 5.

	NMNZ M.287686 ML 66 mm
Gender	F
ML	66
AL1R	81
AL2R	85
AL3R	83
AL4R	90
AL1L	81
AL2L	85
AL3L	85
AL4L	90
ASC1R	52
ASC2R	*
ASC3R	55
ASC4R	54
ASC1L	51
ASC2L	53
ASC3L	54
ASC4L	47
SD	4
AW	9
EO	10
FFL	18
FuL	25
GiLC I	8
GiLC O	7
HdL	18
HdW	34
MW	80
PA	28
TL	180
WAt	*
WDA	25
WDBR	27
WDBL	27
WDCR	30
WDCL	31
WDDR	29
WDDL	26
WDE	28

TABLE 187. INTERNAL CHARACTER RAW MEASURES. *Pareledone* sp. nov. 5.

	NMNZ M.287686 ML 66 mm
AOesL	10
ASGL	6
BBL	11
DGL	20
DGW	23*
DG(GD)	23
InTL	42
ISpres	type 3
ISDL	8
ISEL	-
ISEW	-
ISL	6
ISTL	14
ISW	1
OesTL	34
PSGL	11
SpCL	9
StL	13

TABLE 188. REPRODUCTIVE SYSTEM RAW MEASURES. *Pareledone* sp. nov. 5.

	NMNZ M.287686 ML 66 mm
DOdL	10*
DOdW	5
OSL	43
OSW	44
OdTL	14*
OdBL	4*
OdBW	8
POdL	5
POdW	4

TABLE 189. UPPER BEAK RAW MEASURES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
BL	9
BH	9
BW	7
CH	3
HH	3
HL	5
HW	6
RE	2
RP	2
RW	3
WiL	5

TABLE 190. LOWER BEAK RAW MEASURES.
Pareledone sp. nov. 5.

	NMNZ M.287686 ML 66 mm
BL	11
BH	9
BIH	4
BW	10
CH	3
CL	6
DWaW	6
HL	4
PWaW	6
RE	1
RW	2
WiL	7
WiW	4

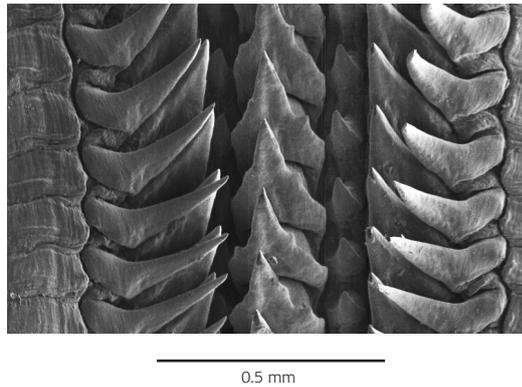


FIGURE 84. *Pareledone* sp. nov. 5. (NMNZ M.287686, ML 66 mm). ESEM radula.

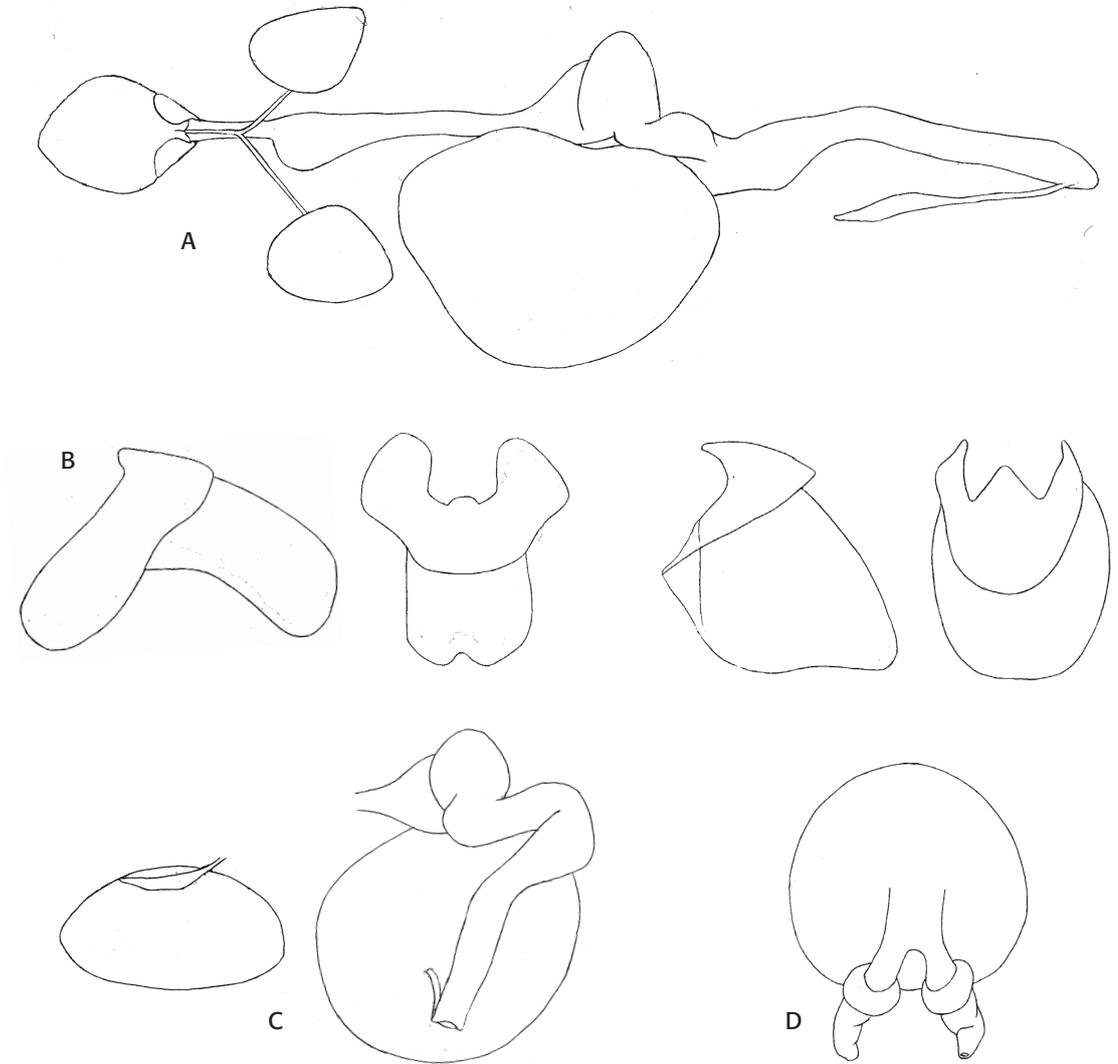


FIGURE 85. *Pareledone* sp. nov. 5. (NMNZ M.287686, ML 66 mm) **A)** Alimentary canal. **B)** Upper and lower beaks. **C)** Ink sac duct and digestive gland in two perspectives (lateral and dorsal view). **D)** Female reproductive system.



FIGURE 86. *Pareledone* sp. nov. 5 (NMNZ M.287686, ML 66 mm). Dorsal and ventral view of preserved specimen.

Pinnoctopus d'Orbigny, 1845

Pinnoctopus is the oldest available generic name serving to characterise a complex of species with arms of unequal length, the dorsal pair usually the longest, with suckers progressively decreasing in diameter from the dorsal to the ventral arm pairs, generally large size, and with a long, tubular hectocotylised portion of the third right arm. This combination of characters also occurs in the genera *Callistoctopus* Taki, 1961 and *Macroctopus* Robson, 1928, and in those species referred to the *macropus* group of octopuses (O'Shea 1999, Anderson 1999, Norman & Hochberg 2005). Such species are distributed throughout the world's oceans, in temperate to sub-Antarctic waters (Anderson 1999).

The systematic status of species referred to these three genera has long been confused. Toll (1991b) considered *Macroctopus* (based on the New Zealand *Octopus maorum* Hutton, 1880) to be a valid genus, and *Pinnoctopus* to be a synonym of *Octopus*. O'Shea (1999) treated *O. maorum* Hutton as a junior synonym of *O. cordiformis*, and as the latter is the type species of *Pinnoctopus* and typical of the *O. macropus* group, *Macroctopus* and *Callistoctopus* became junior synonyms of *Pinnoctopus* (O'Shea 1999). O'Shea (1999) then described a neotype for *P. cordiformis* to standardise this species, as the holotype was no longer extant. I follow the treatment of O'Shea (1999) in recognising *Pinnoctopus* to be discrete from *Octopus* (s.s.), and the most appropriate name to apply to the most common coastal species occurring around New Zealand waters, *P. cordiformis*. Should further evaluation of relationships between species attributed to these genera be required, it would best be achieved by use of independent molecular markers using type species of respective genera.

DIAGNOSIS (modified from O'Shea 1999). Large-bodied octopods; arm formula typically I.II.III.IV; greatest sucker diameter gradually reducing from dorsal to ventral arm pairs; gill lamellae typically exceed 11 per outer demibranch; rachidian tooth of radula multicuspid, with 3 or 4 lateral cusps on either side of central cusp; with extensive connective tissues between renal tissue and ventral, inner surface of mantle; ligula elongate, cylindrical.

TYPE SPECIES. *Octopus cordiformis* Quoy & Gaimard, 1832 (by original designation d'Orbigny 1845).

Pinnoctopus cordiformis (Quoy & Gaimard, 1832)

RECOGNISED DISTRIBUTION. New Zealand, South Australia.

SYNONYMY.

Octopus cordiformis Quoy & 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 (Quoy & Gaimard) — d'Orbigny 1845: 193; Adams & Adams 1858: pl. 1, fig. 3; Chenu 1859: 14, fig. 5; Tryon 1879: 128, pl. 40, fig. 64; Hutton 1880: 2; Hoyle 1886: 14; Hoyle 1888: 222; Hoyle 1909 (*partim*, exclude Campbell Island record): 261; Hoyle 1910: 411 (*pars.*); Suter 1913: 1065; Suter 1915: pl. 70, fig. 3; Robson 1929 (*partim*, exclude Campbell Island record of Filhol 1885): 185; Robson 1929a: 607; Powell 1937: 95; Powell 1946: 100; Dell 1951: 97; Dell 1952 (*partim*, exclude citation Filhol 1885): 31; Powell 1957: 125; Powell 1962: 125; Powell 1976: 133; Powell 1979 (*partim*, *fide* Dell 1952): 44; O'Shea 1999: 135–143, figs 86–89; O'Shea & Jackson 2010: 558.

Octopus maorum Hutton, 1880: 1 (*partim*, exclude paralectotype by designation Suter 1913) — Parker 1885: 586; Hoyle 1886: 13, 220; Hoyle 1888: 221; Dell 1951: 97, fig. 1, 3, 4, 20; Batham 1957 (*partim*, exclude type *Parooctopus zealandicus* Benham): 629–638, figs 1–9; Powell 1957: 125; Powell 1962: 125; Powell 1976: 133; Powell 1979: 444; Kubodera 1990: 349, fig. 277; Hochberg *et al.* 1992: 255–256, figs 265a–c; Spencer & Willan 1995: 53; Anderson 1999: 657–676; Grubert & Wadley 2000: 131–142.

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

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

Macroctopus maorum (Hutton) — 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; Lalas 2009: 635–642.

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

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

Polypus communis (Park) — Powell 1937: 95.

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

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

MATERIAL EXAMINED: 9 specimens, unlocalised, purchased from local fish market (collection New Zealand).

DESCRIPTION. Adult attaining large size (ML to 248 mm, TL to 1.5 m) (Fig. 89; Tables 191, 195). Mantle elongate to ovoid, without dorso-ventral compression. Head narrower than mantle (HdLI 19–33, HdWI 26–56), delimited from it by marked preocular constriction. Orbits large, bulbous, not confluent across dorsal midline of head; postorbital constriction well developed. Funnel base entirely free of brachial crown, not attached to bases of either arms III or IV. Brachial crown robust, of comparable width to head. Arms slender, of very different lengths, 58–83% TL (♀), 32–84% TL (♂); arm pairs I and II usually longest, arms III and IV shortest, with no consistent disparity in relative arm lengths between specimens, and occasionally between right and left sides of the same specimen. Web-to-arm attachment type 1B; depth 7–35%, but usually 8–20% longest arm length. Web formula variable; sector E usually shallowest, A and B deepest, with no consistent disparity in relative sector depths between specimens, and occasionally between left and right sides of the same specimen. Suckers biserial; arm sucker counts greater in mature females than males, ASC to 326(♀) and 278(♂); suckers extend to arm tips. Sucker size variable on each arm, gradually decreasing from dorsal to ventral arm pairs (arm sucker diameter formula 1.2.3.4), ASIn 5.1–16.4, the smallest (arms IV) about 50% the diameter of the largest (arms I); no suckers abruptly enlarged, attaining maximum diameter adjacent to attachment to web to dorso-lateral margin of arm (about the 14th sucker from arm base). Third right arm of male hectocotylised, shorter than opposite member (OAI about 52–96), with 104 suckers; hectocotylised portion (Fig. 88B) ligula 2.7–10.7% hectocotylised arm length, increasing with maturity; ligula with narrow V-shaped groove, with inner surface with about 10 thick, incomplete, opposing fleshy corrugations, alternating with those on opposite side; calamus 16–35% ligula length. Spermatophoral groove well developed, narrow; web margin slightly thickened. 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 I and II with scattered larger conical mounds, each with 5–9 small, lateral, low-profile pimple-like prominences, with two particularly enlarged to form supra-ocular cirri (one dorso-lateral to each eye). Colour (postmortem, post-thaw) over dorsal surfaces of mantle, head, arms I–III and web sectors A–D with light pinks, oranges, reds, and browns; ventral surface of mantle, head, dorso- and ventro-lateral surfaces of arms IV, oral surface of arms I–IV 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 demibranch. Male with well-developed spiral terminal organ diverticulum with two volutions oriented to the left of terminal organ; spermatophoric gland I longer than II; spermatophoric sac shorter than both spermatophoric glands (Fig. 88A, Table 197).

Alimentary canal (Fig. 88D, C; Tables 192, 196) with buccal bulb length (BBL) 20–27% ML. Anterior salivary gland greatest dimension 58–64% BBL. Posterior salivary glands elliptical, narrow, longer than BBL (112–164% BBL, 21% ML). Anterior oesophagus narrow, of length 56% that of oesophagus (OesTL). Crop well developed, with large diverticulum. Spiral caecum greatest dimension 72% that of stomach, with three volutions. Intestine two times as long as oesophagus (OesTL). Digestive gland markedly elongated, twice as long as wide, with prominent peaks either side of each hepatic duct; greatest dimension 58% ML; pancreas well developed. Ink sac present, type 1 (Fig. 6).

Circulatory system of type 1 (Fig. 13), with thick ink sac artery.

Lower beak (Fig. 88E left; Tables 193, 199) with black hood and brown border; wings black from oral margin to mid-portion of wing, forming marked diagonal line that lightens to dark brown toward aboral margin; lateral walls black, slightly lightening to dark brown toward distal margins; margins translucent. Beak base length 14% ML, height 78% BBL. Hood with rounded crest, elevated from wings. Rostrum triangular, tip blunt, with clear protrusion, 6.5% BBL. Jaw angle $\sim 93^\circ$. Wing protrusion length 30% BBL; wing length 70% BBL. Lateral wall crest rounded, with strong basal notch. Proximal wall about 30% narrower than distal wall.

Upper beak (Fig. 88E right; Tables 194, 198) with black hood, with brown border; lateral walls black, abruptly lightening to brown toward margin; all margins translucent. Beak base length 12% ML, 110% height. Hood with rounded crest; rostrum triangular; length protrusion 7.5% BBL; wing more protuded than rostrum. Jaw angle 130° . Lateral wall crest squared.

Radula (Fig. 87) with robust rachidian, taller than wide, with 3 or 4 asymmetric lateral cusps on either side of central cusp. First laterals with two cusps; medial cusp small, admedial higher and larger; second laterals well developed, longer than first laterals, each with single cusp; marginal teeth with single cusp, more delicate than that of second laterals; marginal blocks well-developed, rectangular.

REMARKS. Norman & Hochberg (2005) asserted that *P. cordiformis* should be considered a *nomen dubium*, making *Macroctopus maorum* the available name for the distinctive species found in New Zealand and southern Australian waters. They argued that Quoy & Gaimard's original description of *cordiformis* described a large animal with arms of almost equal length, the lateral pairs being slightly shorter, and that its arm formula differed from specimens typically referred

to *Octopus maorum*: I.II.III.IV (the dorsal arms being obviously longer and more robust than the subsequent arm pairs), proposing that *P. cordiformis* was a name that could be more appropriately applied to *Enteroctopus zealandicus*. However, the bathymetric distributions of these two taxa differ considerably where the two occur at common latitude, and only one of them occurs in the Nelson region, the type locality of *P. cordiformis* — the species so referred to herein.

The genus *Pinnoctopus* was described by d'Orbigny (1845) with the diagnostic character of a fin-like flap around the margin of the mantle. This treatment-history artefact, regularly observed on specimens fixed post-mortem, on which the skin has slumped around the margin of the mantle, is common to at least two taxa described from New Zealand waters, *P. cordiformis* and *P. kermadecensis* (O'Shea 2006). That this lateral fold of skin is an artefact of treatment history has long been recognised, and is well described and figured (Robson 1929: 185; O'Shea 1999: 135–145), contrary to the assertions of Hochberg *et al.* (2005). Although devoid of direct morphological interest (Robson 1929: 7), the type species of the genus, *P. cordiformis*, is still typical of other taxa referred to the genera *Callistoctopus* and *Macroctopus*, and takes priority of these latter-described names. Accordingly, the genus *Pinnoctopus* remains a valid taxon, regardless of whether those characters diagnosed for it were post-mortem artefacts or not.

TABLE 191. EXTERNAL CHARACTER INDICES.
P. cordiformis.

	FByc ML 165 mm
Sex	M
ALI1R	424
ALI2R	421
ALI3R	250
ALI4R	309
ALI1L	424
ALI2L	424
ALI3L	250
ALI4L	309
MAI	24
MWI	91
ASIn	14
AWI	12
EOI	6
FFI	25
FuLI	36
HdLI	21
HdWI	31
MWI	91
OAI	100
PAI	28
WDI	18

TABLE 192. INTERNAL CHARACTER INDICES.
P. cordiformis.

	FByc ML 165 mm
AOesLI	51
ASGLI	11
BBI	19
DG(GD)	58
DGI	58
IntLI	182
ISTLI	73
ISLI	20
OESTLI	90
PSGLI	21
SpCI	16
StI	23

TABLE 193. UPPER BEAK INDICES.
P. cordiformis.

	FByc ML 165 mm
BLI	13.939
BHI	78.261
BIHI	39.130
BWI	78.261
CLI	43.478
DWaWI	60.870
HLI	30.435
PWaWI	43.478
REI	8.696
RWI	17.391
WiLI	69.565
WiWI	36.957
WiWI	36.957

TABLE 194. LOWER BEAK INDICES.
P. cordiformis.

	FByc ML 165 mm
BLI	12.12
BHI	110.00
BWI	70.00
CHI	40.00
HHI	30.00
HLI	45.00
REI	12.50
RPI	7.50
RWI	22.50
WiPI	25.00
WiLI	45.00

TABLE 195. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *P. cordiformis*.

	FByc ML 165 mm
Gender	M
ML	165
AL1R	700
AL2R	695
AL3R	412
AL4R	510
AL1L	700
AL2L	700
AL3L	41.2
AL4L	51
ASC1R	209
ASC2R	209
ASC3R	104
ASC4R	204
ASC1L	209
ASC2L	209
ASC3L	1040
ASC4L	2040
SD	22.5
AW	20
EO	10
FFL	4.2
FuL	6
GiLC I	140
GiLC O	140
HdL	34
HdW	51
MW	150
PA	47
TL	995
WAt	type 1B
WDA	112
WDBR	113
WDBL	*
WDCR	100
WDCL	120
WDDR	100
WDDL	112
WDE	127

TABLE 196. INTERNAL CHARACTER RAW MEASURES. *P. cordiformis*.

	FByc ML 165 mm
AOesL	84
ASGL	18
BBL	31
DGL	96
DGW	46
DG(GD)	96
InTL	300
ISA	yes
ISDL	86.5
ISEL	56
ISEW	25
ISL	33.5
ISpres	type 1
ISTL	120
ISW	25
OesTL	149
PSGL	35
SpCL	27
StL	37.5

TABLE 197. REPRODUCTIVE SYSTEM RAW MEASURES. *P. cordiformis*.

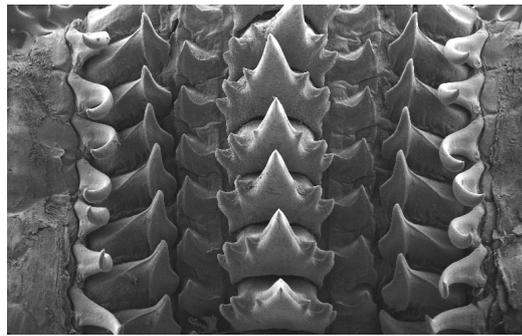
	FByc ML 165 mm
CaL	9
LL	39
SGL	185
SGII	131
SS	143
TODL	13
TOL	22

TABLE 198. UPPER BEAK RAW MEASURES.
P. cordiformis.

	FByc ML 165 mm
BL	2
BH	22
BW	14
CH	8
HH	6
HL	9
HW	10
RE	2.5
RP	1.5
RW	4.5
WiL	9

TABLE 199. LOWER BEAK RAW MEASURES.
P. cordiformis.

	FByc ML 165 mm
BL	23
BH	18
BIH	9
BW	18
CH	08
CL	10
DWaW	14
HL	7
PWaW	10
RE	02
RW	04
WiL	16
WiW	08.5



2 mm

FIGURE 87. *Pinnoctopus cordiformis* (FByc, ML 165 mm).
ESEM radula.

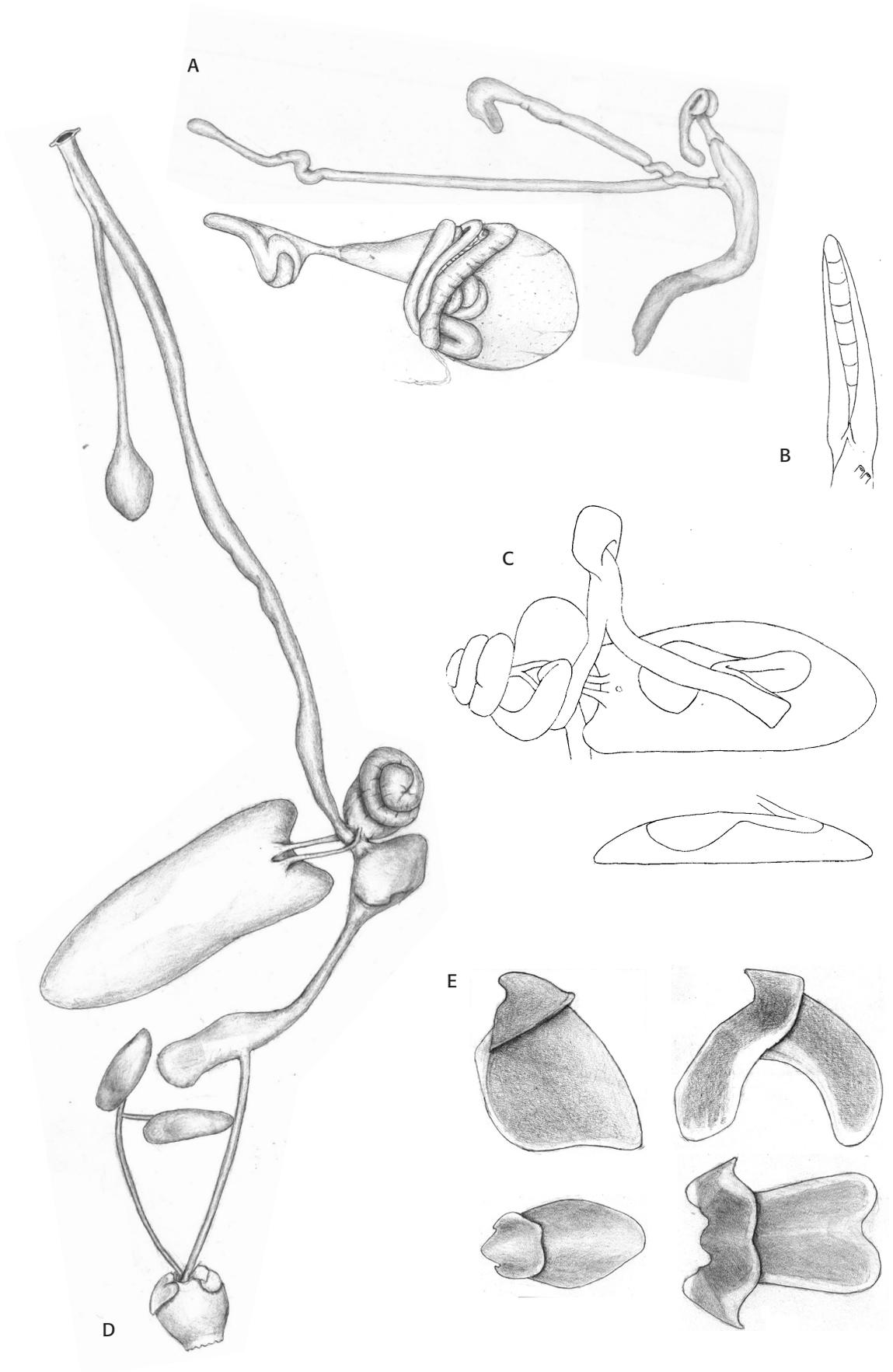


FIGURE 88. *Pinnoctopus cordiformis* (FByc, ML 165 mm). A) Male reproductive system. B) Hectocotylus C) Ink sac and digestive gland in two perspectives (dorsal and lateral view). D) Alimentary canal. E) Upper and lower beaks.



FIGURE 89. *Pinnoctopus cordiformis* (FByc, ML 165 mm). ABOVE: Dorsal and ventral view of preserved specimen of fresh specimens. BELOW: Dorsal view of preserved specimen.

Thaumeledone Robson, 1930

This genus inhabits relatively deep waters in the Southern Hemisphere (Allcock *et al.* 2004). The genus presently contains five described taxa, but at least two more taxa await description — that referred to herein as *Thaumeledone* sp. nov. 1, and *T. robusta* Allcock *et al.* 2004 (not Hoyle, 1885), given my earlier redescription of *Bentheledone albida* (Berry, 1917).

DIAGNOSIS (modified from Robson 1932, O’Shea 1999, Allcock *et al.* 2004). Small-bodied benthic octopodids, ML to 60 mm, TL to 190 mm; arms short (ALI 100–230). Mantle, head, arms and web typically papillose; arms of short to moderate length; arm sucker counts low, less than 40 at maturity; web deep to moderately deep. Posterior salivary glands large to small; radula reduced, rachidian unicuspid, with 1–3 lateral rows of teeth; marginal plates present; gills with 4–6 lamellae per demibranch. Colour distinctively deep purple on oral surfaces of arms and web, and papillae.

TYPE SPECIES. *Eledone brevis* Hoyer, 1885 (by designation Robson 1930).

***Thaumeledone* sp. nov.**

RECOGNISED DISTRIBUTION. Known only from Ross Sea region, Antarctica, 71°51.342–53.40’S, 174°01.98–06.588’E, 1990–1954 m.

MATERIAL EXAMINED. 2 specimens: (♀, ♂): NIWA 44145, ML 64 mm, ♀, 71°51.342–53.40’S, 174°01.98–06.588’E, 1990–1954 m, 25/02/2008, RV *Tangaroa* Stn TAN0802/167; NIWA 44144, ML 56 mm, ♂, 71°51.342–53.40’S, 174°01.98–06.588’E, 1990–1954 m, 25/02/2008, RV *Tangaroa* Stn TAN0802/167.

DESCRIPTION. Adults of medium size (ML 64 mm, TL to 180 mm) (Fig. 92, Tables 200, 204). Head narrower than mantle width (HdLI 30–39%, HdWI 50–71%), delimited from it by moderate pre-ocular constriction. Orbits large, bulbous, with narrow interspace between both orbits mid-dorsally. Post orbital constriction slight. Arm-to-web attachment type 2 (Fig. 4); web depth 45–46% longest arm length; web formula A=B=C=D.E (♀), A.B.C.D.E (♂). Arms 56–66% TL; formula (♂) I.II.III=IV. Suckers uniserial, sucker counts 43–49, none abruptly enlarged (ASIn 4%), attaining greatest diameter from sucker 4 from beaks. Third right arm of male hectocotylied,

shorter than opposite member (OAI 84), with 28 suckers; spermatophoral groove well developed, wide; web margin conspicuously thickened; base of spermatophoral groove where it fuses with web sector D with three or four faint ridges and one large and one small papilla. Hectocotylied portion club-like, proportionally very long, ligula 12% hectocotylied arm length, without apparent transverse rugae; calamus large, 81% ligula length.

External body surfaces appear smooth, but with vestiges of small, simple papillae apparent at least dorsally over mantle and along arms I and II. Colouration off-white to light pink mid-dorsally, along all arms I–IV, ventral surfaces of the orbits, and basal two thirds of funnel; vestiges of papillae on dorsal surfaces of mantle, head, arms I and II from their bases, arms III and IV below the points of web attachment, and web sectors A–C red, darkest along the dorso- and ventro-lateral margins of each arm below the points of web attachment. Ventro-lateral surfaces of mantle and ventral margin of orbits with pronounced concentration of larger, denser wine-red chromatophores; ventral surfaces of mantle and distal third of funnel almost uniformly red; outer surfaces of web sectors A to E almost purple (in translucence). Oral surfaces of arms and web dark purple. Vestige of single supra-ocular papilla on dorsal surface of each orbit, marked by patch of wine-red chromatophores.

Gills with 4 or 5 lamellae per demibranch. Female reproductive system (Fig. 91C, Table 106) with proximal oviduct about half the length of distal oviduct. Distal oviduct of comparable width to oviducal balls; of comparable length to (immature) ovary sac.

Alimentary canal (Fig. 91A; Tables 201, 205) with buccal bulb length (BBL) 23–25% ML. Anterior salivary glands 27–30% BBL. Posterior salivary glands extremely small, narrowly elliptical, their length 23–32% BBL (5–8% ML). Anterior oesophagus narrow, short, its length 40% that of oesophagus (OesTL). Crop present, lacking diverticulum. Spiral caecum of comparable size to stomach, lacking volutions. Intestine slightly longer to twice the length of oesophagus (113–210% OesTL). Digestive gland ovoid, wider than long, with broad hepatic peaks, of greatest dimension 39% ML; pancreas well developed. Functional ink sac absent; vestiges of neither sac nor duct apparent.

Circulatory system of type 3 (Fig. 13), with apparent thin ink sac artery.

Lower beak (Fig. 91B left; Tables 202, 208) with black hood and brown border; oral margin of wings black, extending to mid-portion of wing, forming diagonal line with brown border; brown colour from mid-wing to aboral margin; lateral walls black, slightly lightening to brown toward margin; margins translucent, wide. Beak base length 16% ML, height 76% BBL. Hood with rounded crest, elevated from wings. Rostrum tip chisel-like, slightly protruded, 4%

BBL. Jaw angle 120°. Wing protrusion length 38% BBL; wing length 62% BBL. Lateral wall crest rounded, with strong basal notch. Proximal and distal wall of comparable width.

Upper beak (Fig. 91B right; Tables 203, 207) with black hood and brown border; lateral walls black, gradually transitioning to brown toward aboral margin; all margins translucent. Beak base length 16% ML, as high as wide. Hood triangular, with rounded crest; rostral tip slightly blunt, with lateral keel; length protrusion 10% BBL; wing length protrusion markedly longer than that of rostrum. Jaw angle around 115°. Lateral wall crest rounded, without basal notch; parallel-sided.

Radula (Figs 90, 91D) with broad-based rachidian, without lateral cusps, and two lateral rows of teeth of questionable homology to first and second laterals, marginals or marginal blocks. First lateral row of teeth poorly developed. Positional equivalents of marginal plates long, rectangular.

REMARKS. These specimens are in good condition, with the exception of the web in the sole female, on which some sectors were damaged. Although externally the skin is effectively smooth post preservation (following freezing), vestiges of papillae can be discerned in preserved material, and some papillae were apparent prior to fixation.

Although represented by two specimens reported herein, a fully mature male and an immature female, this species differs from all other described taxa that recognition of it as new is done without reservation. It differs from *T. zeiss* O'Shea, 1999 most notably in hectocotylus detail and hectocotylised arm sucker count (28 in the sole known male herein described, and 19 in the sole known male of *T. zeiss*), and in the shape of the hectocotylus, (club-like in this new species and more conventionally octopodid and slender in *T. zeiss*). From other taxa it differs also in absolute size and, with the exception of *T. rotunda* (*sensu* Allcock *et al.* 2004; not Hoyle, 1885, Robson 1932), in hectocotylised arm sucker count (*T. peninsulae* Allcock *et al.* 2004: 22–25, *T. gunteri* Robson, 1930: 19–22). From *T. rotunda* (*sensu* Allcock *et al.* 2004; not Hoyle, 1885, Robson 1932), a species that is actually new to science (see redescription of *Bentheledone albida* (Berry, 1917) herein), this new taxon differs in anatomical detail, most notably in posterior salivary gland dimension relative to buccal bulb length, and in the extent of apparent (post-mortem) surface papillation and overall pigmentation. The male of *T. brevis* (Hoyle, 1885) has not been described, but given the distances between respective collection localities, and localised speciation of the genus *Thaumeledone* throughout the Southern Ocean, it is extremely unlikely these two forms are conspecific; females of these two species differ in total arm sucker counts; 25–27 (*vide* Allcock *et al.* 2004) for *T. brevis*, and 43–49 in this proposed new species of *Thaumeledone*.

TABLE 200. EXTERNAL CHARACTER INDICES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
Sex	F
ALI1R	143.8
ALI2R	140.6
ALI3R	137.5
ALI4R	143.8
ALI1L	142.2
ALI2L	142.2
ALI3L	153.1
ALI4L	156.3
MAI	64.0
MWI	82.8
ASIn	3.9
AWI	10.9
EOI	13.3
FFI	25.0
FuLI	34.4
HdLI	29.7
HdWI	50.0
MWI	82.8
OAI	89.8
PAI	46.9
WDI	45.0

TABLE 201. INTERNAL CHARACTER INDICES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
AOesLI	18.8
ASGLI	6.3
BBI	23.4
DG(GD)	39.1
IntLI	53.1
OESTLI	46.9
PSGLI	5.5
SpCI	12.5
StI	12.5

TABLE 202. LOWER BEAK INDICES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
BLI	16.4
BHI	76.2
BIHI	28.6
BWI	100.0
CLI	33.3
DWaWI	57.1
HLI	33.3
PWaWI	57.1
REI	9.5
RWI	19.0
WiLI	61.9
WiWI	38.1

TABLE 203. UPPER BEAK INDICES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
BLI	15.6
BHI	100.0
BWI	60.0
CHI	15.0
HHI	40.0
HLI	50.0
REI	10.0
RPI	10.0
RWI	30.0
WiLI	35.0

TABLE 204. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *Thaumeledone* sp. nov.

	NIWA 44145 ML 64 mm
Gender	F
ML	64
AL1R	92
AL2R	90
AL3R	88
AL4R	92
AL1L	91
AL2L	91
AL3L	98
AL4L	100
ASC1R	47
ASC2R	47
ASC3R	47
ASC4R	49
ASC1L	47
ASC2L	48
ASC3L	48
ASC4L	49
SD	3
AW	7
EO	9
FFL	16
FuL	22
GilC I	4
GilC O	4
HdL	19
HdW	32
MW	53
PA	30
TL	160
WAt	type 2
WDA	45
WDBR	42
WDBL	43
WDCR	42
WDCL	45
WDDR	42
WDDL	43
WDE	38

TABLE 205. INTERNAL CHARACTER RAW MEASURES. *Thaumeledone* sp. nov.

	NIWA 44145 ML 64 mm
AOesL	12
ASGL	4
BBL	15
DGL	15
DGW	25
DG(GD)	25
InTL	34
ISA	yes
ISpres	no
OesTL	30
PSGL	4
SpCL	8
StL	8

TABLE 206. REPRODUCTIVE SYSTEM RAW MEASURES. *Thaumeledone* sp. nov.

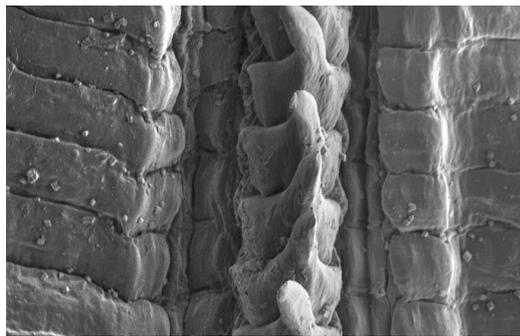
	NIWA 44145 ML 64 mm
DOdL	16
DOdW	6
OSL	15
OSW	17
OdTL	23
OdBL	5
OdBW	8
POdL	2
POdW	4

TABLE 207. UPPER BEAK RAW MEASURES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
BL	10
BH	10
BW	6
CH	2
HH	4
HL	5
HW	6
RE	1
RP	1
RW	3
WiL	4

TABLE 208. LOWER BEAK RAW MEASURES.
Thaumeledone sp. nov.

	NIWA 44145 ML 64 mm
BL	11
BH	8
BIH	3
BW	11
CH	2
CL	4
DWaW	6
HL	4
PWaW	6
RE	1
RW	2
WiL	7
WiW	4



0.3 mm

FIGURE 90. *Thaumeledone* sp. nov. (NIWA 44145, ML 64 mm). ESEM radula

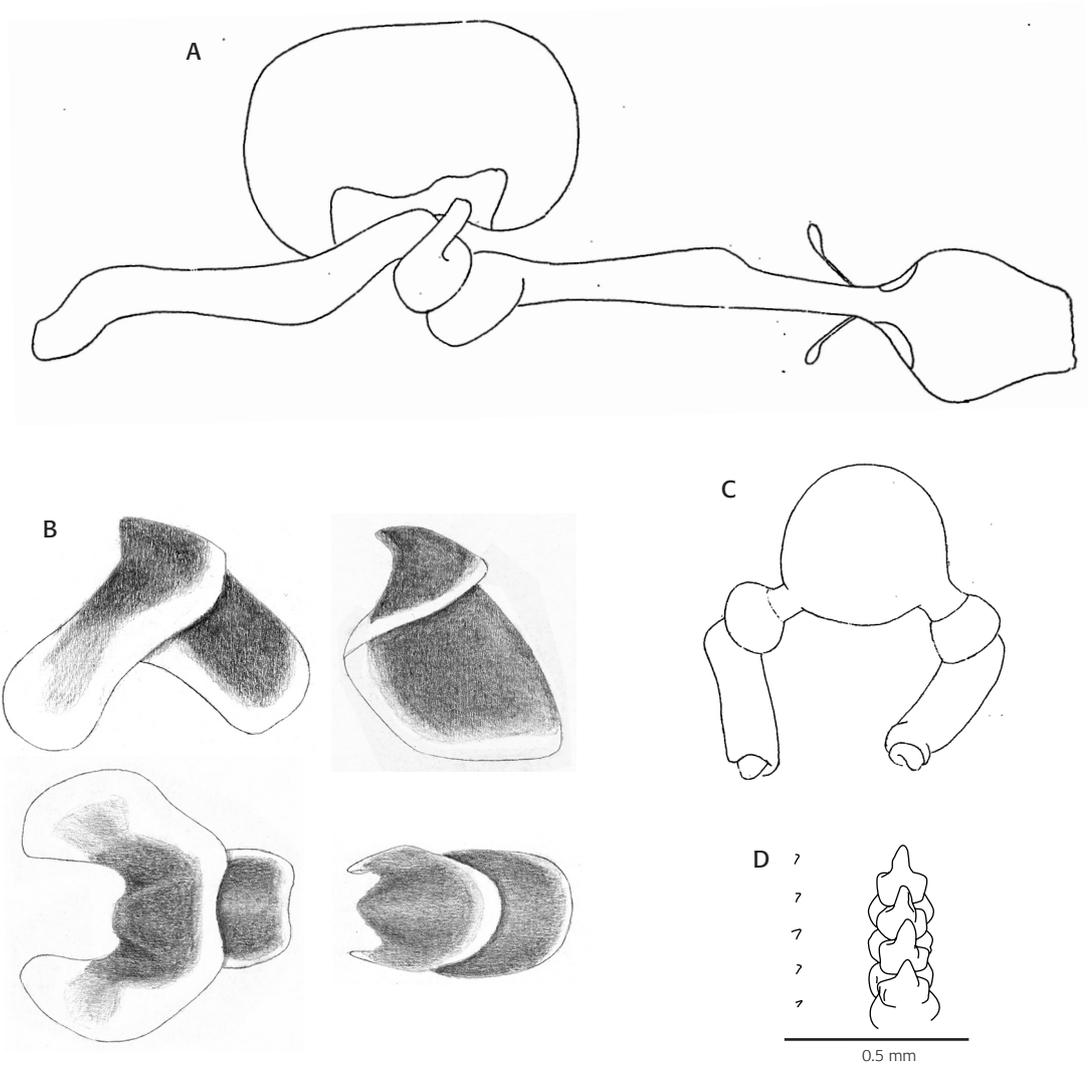


FIGURE 91. *Thaumaledone* sp. nov. (NIWA 44145, ML 64 mm). **A)** Alimentary canal. **B)** Upper and lower beaks. **C)** Female reproductive system. **D)** Radula.



FIGURE 92. *Thaumeledone* sp. nov. ABOVE LEFT: Dorsal view of fresh specimen (NIWA 44145, TAN0802/167). ABOVE RIGHT: Dorsal view of fresh specimen (NIWA 44144). BELOW: Dorsal and ventral view of preserved specimen (NIWA 44145, ML 64 mm).

Thaumeledone zeiss O'Shea, 1999

RECOGNISED DISTRIBUTION: New Zealand, 44°12.86–45°21.1'S, 173°02.81–178°34.20'E, 1004–1386 m (*fide* O'Shea 1999).

SYNONYMY. *Thaumeledone* sp. O'Shea & Kubodera, 1996: 153–164.

Thaumeledone zeiss O'Shea, 1999: 246–249, figs 145, 146.

MATERIAL EXAMINED. 1 specimen (♂): NMNZ M.299399, ML 34 mm, ♂, 48°00.9'S, 164°59.9'E, 1004–1179 m, 30/11/2002, FV *Kap Farvel*, MFish SOP Stn 1693/89.

DESCRIPTION (amended from O'Shea 1999). Adult small (ML to 55 mm, TL 120 mm) (Fig. 95; Tables 209, 213). Mantle ovoid, wide; head narrower than mantle (HdLI 33–41, HdWI 51–76) delimited from mantle by moderate pre-ocular constriction. Orbits large, bulbous, with narrow interspace between orbits across dorsal midline. Post-orbital constriction slight. Arm-to-web attachment type 2 (Fig. 4); depth to 53% longest arm length; web formula variable, without consistent disparity in sector depths. Arms short, 43–66% TL. Arm sucker counts low, 29–33, none abruptly enlarged (ASIn 3.6–6%), attaining greatest diameter from sucker 3. Third right arm of male hectocotylised, shorter than opposite member (OAI 88.9), with 19 suckers; spermatophoral groove well developed, wide; web margin conspicuously thickened; base of spermatophoral groove where it fuses with web sector D without apparent ridges or papillae. Hectocotylised portion proportionally very long, ligula 17% hectocotylised arm length, with 8 faint transverse rugae; calamus large, 63.2% ligula length.

External body surfaces appear smooth, but with vestiges of small, simple papillae apparent at least dorsally over the mantle and along arms I and II. Colouration mid-dorsally, along all arms I to IV, ventral surfaces of orbits, and basal two thirds of funnel off-white to light pink; vestiges of papillae on dorsal surfaces of mantle, head, arms I and II from their bases, arms III and IV below the points of web attachment, and web sectors A–C red. Margins of eye apertures with pronounced concentration of larger, denser wine-red chromatophores; ventral surfaces of mantle and funnel with uniformly distributed red chromatophores; outer surfaces of web sectors A to E almost purple in translucence. Oral surfaces of arms and web dark purple. Vestige of single supraocular papilla on dorsal surface of each orbit, marked by patch of wine-red chromatophores.

Gills with 4 or 5 lamellae per demibranch. Female reproductive system (Fig. 94C) with proximal oviduct about half the length of distal oviduct; distal oviduct of comparable diameter to oviducal ball, and comparable length to ovary sac.

Alimentary canal (Fig. 94A; Tables 210, 214) with buccal bulb length (BBL) 20–23% ML. Anterior salivary glands 27–29% BBL. Posterior salivary glands elliptical to heart-shaped, their greatest dimension 50–72% BBL (12–15% ML). Anterior oesophagus narrow, its length 35% that of oesophagus (OesTL). Crop present, lacking diverticulum. Spiral caecum greatest dimension 80% that of stomach, lacking volutions. Intestine of comparable to slightly greater length than oesophagus (100–133% OesTL). Digestive gland circular, its greatest dimension 31% that of ML; pancreas well developed. Ink sac absent; neither vestigial sac nor duct apparent.

Circulatory system damaged during dissection; presence or absence of an ink sac artery could not be ascertained.

Lower beak (Fig. 94B right; Tables 211, 217) with black hood and brown border; oral margin of wings black, extending to middle of wing, forming clear diagonal line that lightens to brown toward aboral margin; lateral walls black, slightly lightening toward margins; margins translucent. Beak base length 22% ML, 67% height. Hood with rounded crest, elevated from wings. Rostrum tip chisel-like, with clear protrusion, 5% BBL. Jaw angle 127°. Wing protrusion length 33% BBL; wing length 60% BBL. Lateral wall crest rounded, with basal notch. Proximal wall 25% narrower than distal wall.

Upper beak (Fig. 94B left; Table 212, 216) with black hood and brown border; lateral walls black, gradually transitioning to brown toward aboral margin; all margins translucent. Beak base length 19% ML, of comparable height and width. Hood triangular, with rounded crest; rostrum with lateral keel, tip pointed; length protrusion 8% BBL; wing length protrusion markedly longer than that of rostrum. Jaw angle 100°. Lateral wall crest squared; walls parallel-sided.

Radula (Figs 93, 94D) with broad-based rachidian without lateral cusps, and variably developed lateral and marginal teeth; with rows of 7 transverse simple uncuspid lateral and marginal teeth in type specimen, or two lateral rows of teeth of questionable homology to first and second lateral and marginal teeth, with the first lateral row small and poorly developed, and the second (positional) lateral row triangular, with broad bases. Marginal plates, rectangular.

REMARKS. This specimen was in good condition, except for arm pairs I and IIR, which were slightly damaged. It lacked eggs in the ovary. From the type species of *T. zeiss* it differs in no remarkable character or state, with the exception of possessing a slightly more reduced radula

(lacking one row of teeth lateral to the rachidian). This new specimen was collected proximal to the type locality of this species.

TABLE 209. EXTERNAL CHARACTER INDICES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
Sex	F
ALI1R	182.4
ALI2R	176.5
ALI3R	194.1
ALI4R	191.2
ALI1L	182.4
ALI2L	176.5
ALI3L	185.3
ALI4L	191.2
MAI	52.3
MWI	92.6
ASIn	5.9
AWI	14.7
EOI	29.4
FFI	29.4
FuLI	38.2
HdLI	35.3
HdWI	73.5
MWI	92.6
OAI	104.8
PAI	52.9
WDI	46.2

TABLE 210. INTERNAL CHARACTER INDICES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
AOesLI	17.6
ASGLI	7.4
BBI	23.5
DG(GD)	30.9
IntLI	50.0
ISA	*
OESTLI	50.0
PSGLI	11.8
SpCI	11.8
StI	14.7

TABLE 211. LOWER BEAK INDICES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
BLI	22.1
BHI	66.7
BIHI	33.3
BWI	126.7
CLI	40.0
DWaWI	53.3
HLI	26.7
PWaWI	40.0
REI	13.3
RWI	20.0
WiLI	60.0
WiWI	40.0

TABLE 212. UPPER BEAK INDICES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
BLI	19.1
BHI	92.3
BWI	53.8
CHI	7.7
HHI	46.2
HLI	46.2
REI	15.4
RPI	7.7
RWI	23.1
WiLI	46.2

TABLE 213. EXTERNAL CHARACTER RAW MEASURES AND COUNTS. *T. zeiss*.

	NMNZ M.299399 ML 34 mm
Gender	F
ML	34
AL1R	62 *
AL2R	60
AL3R	66
AL4R	65
AL1L	62*
AL2L	60*
AL3L	63
AL4L	65
ASC1R	30
ASC2R	29
ASC3R	30
ASC4R	30
ASC1L	30
ASC2L	30
ASC3L	30
ASC4L	30
SD	2
AW	5
EO	10
FFL	10
FuL	13
GiLC I	4
GiLC O	4
HdL	12
HdW	25
MW	32
PA	18
SR	10
TL	98
WAt	type 2
WDA	29
WDBR	30
WDBL	29
WDCR	29
WDCL	29
WDDR	30
WDDL	30
WDE	25

TABLE 214. INTERNAL CHARACTER RAW MEASURES. *T. zeiss*.

	NMNZ M.299399 ML 34 mm
AOesL	6
ASGL	3
BBL	8
DGL	9
DGW	11
DG(GD)	11
InTL	17
ISpres	no
OesTL	17
PSGL	4
SpCL	4
StL	5

TABLE 215. REPRODUCTIVE SYSTEM RAW MEASURES. *T. zeiss*.

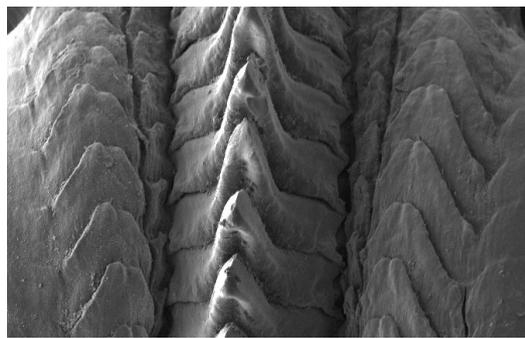
	NMNZ M.299399 ML 34 mm
DOdL	20
DOdW	3
OSL	24
OSW	18
OdTL	28
OdBL	3
OdBW	4
POdL	5

TABLE 216. UPPER BEAK RAW MEASURES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
BL	7
BH	6
BW	4
CH	1
HH	3
HL	3
HW	4
RE	1
RP	1
RW	2
WiL	3

TABLE 217. LOWER BEAK RAW MEASURES.
T. zeiss.

	NMNZ M.299399 ML 34 mm
BL	8
BH	5
BIH	3
BW	10
CH	1
CL	3
DWaW	4
HL	2
PWaW	3
RE	1
RW	2
WiL	5
WiW	3



0.5 mm

FIGURE 93. *Thaumeledone zeiss* (NMNZ M.299399, ML 34 mm). ESEM radula.

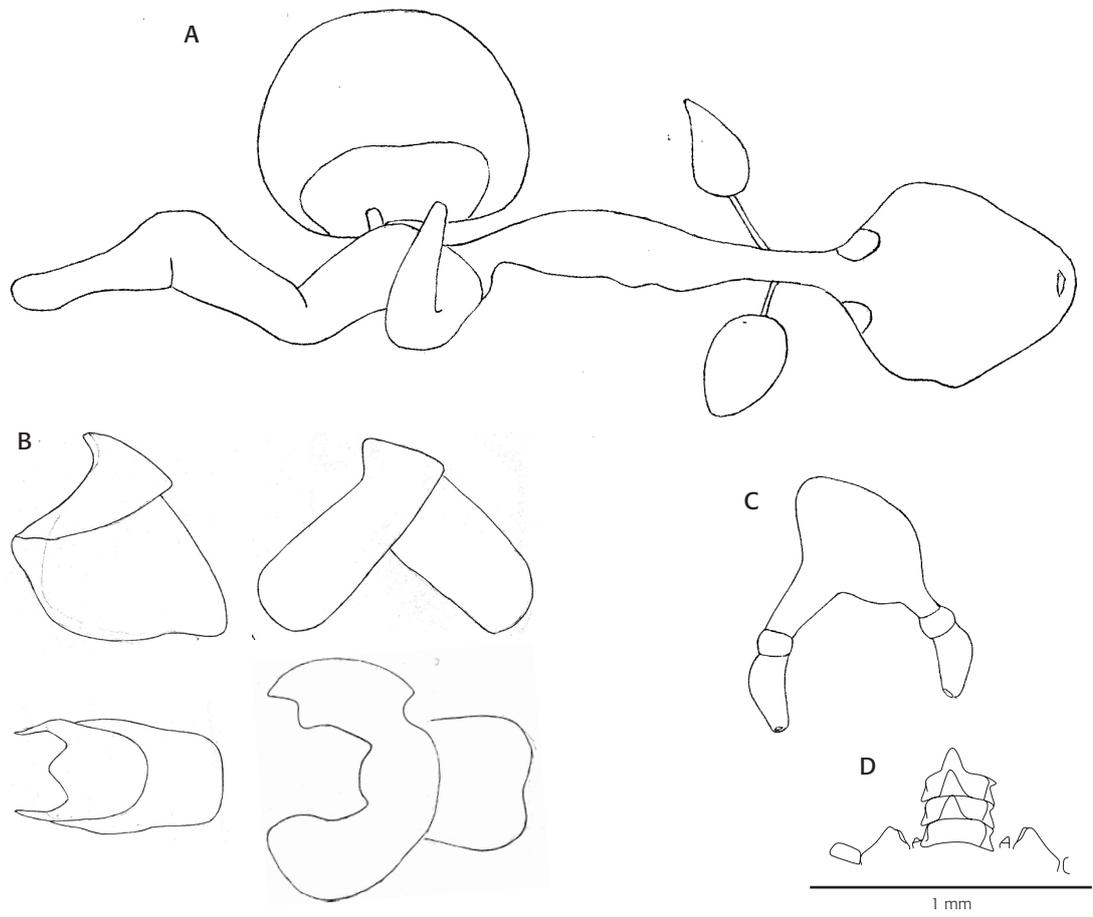


FIGURE 94. *Thaumeledone zeiss* (NMNZ M.299399, ML 34 mm). A) Alimentary canal. B) Upper and lower beaks. C) Female reproductive system. D) Radula.



FIGURE 95. *Thameledone zeiss* (NMNZ M.299399, ML 34 mm). Dorsal and ventral view of preserved specimen.

DISCUSSION⁴

Achieving a stable taxonomic classification requires identification of appropriate taxonomic characters, whether these be of a molecular or morphological nature. Although a combined approach would have been preferable, time and logistical constraints limited the research reported herein to a critical assessment of morphological characters and character states only, and for a more limited amount of taxa, that would have been ideal (molecular analysis was beyond the scope of what could be achieved with available resources and materials (samples), and representatives of all genera could not be procured).

There is a particular need to critically evaluate characters that have previously been deemed valuable for differentiating genera and species of octopodids (those of the family Octopodidae), because this family is the most speciose (number of species) and most diverse (numbers of genera) of the octopuses. As a consequence, this family has been subject to the greatest systematic scrutiny and effort, with numerous new genera and species being routinely described or alluded to (Hochberg *et al.* 2005), yet the characters and their states that are being used to differentiate these taxa, whether genera or species, are largely unproven.

Herein, critical evaluation of taxonomic characters historically used in formulating classifications of the Octopoda is achieved through detailed dissection and description of anatomical characters for a wide variety of octopus taxa, focussing on the family Octopodidae, and collating measures, counts, and characterising categorical states for these characters. Resulting data sets are analysed using multivariate statistics, with analyses presented in series of standardised PCA and MDS plots, each graphically depicting the most appropriate characters and their states to: a) discriminate taxa (at both generic and specific levels), and b) identify those characters and their states that appear to be of greatest value for determining phylogenetic relationships.

Since 1983 almost every new cephalopod taxon has been described in accordance with those guidelines proposed by Roper & Voss (1983) as basic to octopus descriptions. However, despite the significance of Roper & Voss's (1983) contribution, quite remarkably, to the best of my knowledge, only one evaluation of the systematic value of these characters/states has been undertaken (Allcock *et al.* 2008). Subsequent to Roper & Voss's seminal work on the characters

(and their states) of systematic importance in species descriptions, one recent publication cited additional characters, measures and states that would serve to differentiate octopus taxa (Hochberg *et al.* 2005); to the best of my knowledge these have not been critically evaluated, although this is almost certainly due to the recent nature of this publication. The primary objective of this research, therefore, was to re-evaluate the usefulness of those morphological and anatomical characters and their states that have been conventionally used in systematic studies of octopuses (*sensu* Roper & Voss (1983)), as undertaken by Allcock *et al.* (2008), and to compare and contrast the effectiveness of these with a subset of those proposed by Hochberg *et al.* (2005).

Problems with earlier-proposed subfamilial classifications of the Octopodidae stem from their dependence on characters known to vary with depth, potentially obscuring phylogenetic relationships between taxa. Subfamilial classifications have been based on combinations and permutations of external and anatomical characters: primarily, whether the suckers were disposed in one or two rows, and whether the ink sac was present or absent (Robson 1929, 1932; Voss 1988a, b; Allcock 2005). Generic diagnoses, have to a large extent, focussed on characters that also vary with depth, particularly the presence or absence of a diverticulum of the crop, relative size of the posterior salivary glands, and number of teeth per transverse row of the radula, and/or number of lateral cusps on its rachidian tooth (Voss 1988b, O'Shea 1999, Allcock 2005), although the reason for these characters' variation with depth is not well understood. Beak morphology, one of very few characters that have not been reported to vary within any given taxon by depth, has only been used to help diagnose one genus to date (*Adelieledone*).

RADULA

The radula has routinely been used to differentiate octopus taxa, but teeth are reported to differ in number and in features such as size, shape and form (Nixon 1998, Roper & Voss 1983), within species (Samuel & Patterson 2003), individuals, and even on the same individual (Clarke 1998). Amongst species reported herein, the radula of *Pareledone* varies in the expression of lateral cusps on either side of rachidian tooth, and in the robustness and size of the second lateral tooth; otherwise all species of *Pareledone* examined herein possess the same basic complement of 7 vertical rows of teeth, and have rectangular marginal blocks (Figs 59, 70, 73, 81, 84). The radula is extremely reduced in deeper-water taxa such as *Thaumeledone* (Figs 90, 93), and to a lesser extent in the *Bentheledone albida* (Fig. 33), as herein redescribed; it is absent altogether in some cirrates, such as *Cirroctopus hochbergi* and *C. mawsoni*, but is known from a number of others (*Luteuthis*, and some species attributed to *Grimpoteuthis*).

Even though radular morphology can be a useful taxonomic character, great variations within species (e.g. number of cusps on rachidian), and even in number of teeth across a transverse row have been described, and therefore characters associated with radular morphology must be used with some caution in taxonomy (to differentiate species) and in phylogeny (to place taxa into meaningful systematic categories).

BEAKS

Remarkably, descriptions of beak morphology, although recommended in descriptions of cephalopod taxa (Roper & Voss 1983), have seldom been included in any detail, and even more rarely used to differentiate octopus genera or species. Lower beak morphology in octopuses has been considered unreliable for differentiating taxa (Voss 1977), and recently, morphologically too conservative to differentiate congeneric taxa, so that it was not even described for many new species of *Pareledone* by Allcock (2005). However, its morphology has proven valuable for differentiating genera or distantly related species, such as four South African octopodid groups (Smale 1993), and beaks of *Adelieledone* and *Pareledone* (Daly & Rodhouse (1994), Allcock *et al.* (2003)). Upper beaks of cephalopods have seldom been described, since features of the lower beak were considered to be more obvious (Clarke 1986); upper beaks are of some systematic value (Xavier & Chérel 2009), but few descriptions are provided therein, and identification was made to genus level only.

Ogden *et al.* (1998) critiqued the systematic value of octopodid lower beak morphology by comparing beaks of five congeneric species and four confamilial genera. Phylogenetic trees constructed using beak morphology data differed from those constructed using molecular data, and species discrimination was less clear; they suggested inclusion of as many characters as possible to assist in the discrimination of lower beaks at the level of species. To this end, 12 measures were taken from the lower and eight from the upper beaks of taxa examined herein. High correlations between the majority of these upper and lower beak measures (Table 21 and 25) resulted in all but five and four of them (lower and upper beaks respectively) being retained for multivariate analysis; PCA's were run with ratios of rostrum edge (RE), wing length (WiL), rostrum width (RW), and beak length (BL) for both beaks, and crest height (CH) for the lower beak only. At neither generic nor specific levels do either PCAs or MDS plots show any clear grouping of presumed related taxa using beak characteristics (Figs 24 and 25). Although using lower beak characters, those of *Graneledone* do group closely, but this grouping is less apparent when using upper beak characters only (Fig. 22); within the genus *Pareledone* no grouping of taxa is apparent using either upper or lower beaks. As described for *Pareledone* sp. nov. 1 (Figs 62 and 63), the species for which the most specimens were available for study, the beak can vary considerably; the lower

beak rostrum can be triangular or have a bevelled edge (chisel-like), and its edge (REI) can be protruded to varying extents (or not at all).

Identification of Southern Ocean octopodids on the basis of beak morphology is difficult, with numerous species having similar beaks (Xavier & Cherel 2009). Consequently, categorical characters might prove more informative for differentiating taxa, such as the upper beak 'keel' for example (Fig. 9), shared by all *Pareledone* sp. nov. 1 (62 and 63). Colouration of the beaks is another character that differs between some taxa; within *Pareledone* for example, the translucent margins of the wings of the lower beak of *Pareledone* sp. nov.1 are much less extended than those of *Pareledone* sp. nov. 3 and 4. However, in predator-prey studies it is not known to what extent stomach digestive juices affect the colouration of beaks, or digest the delicate translucent margins, and given the obvious difficulties in quantifying colour (exacerbated by potential colour blindness of an observer) the value of beak pigmentation for differentiating taxa might be somewhat limited.

Beaks are of some systematic value for differentiating genera and some species; however their systematic value appears to be more limited than other characters more routinely reported in systematic descriptions. Many of the measures used in statistical analysis herein proved to be highly correlated, adding little useful information for separating taxa, with data also taking considerable time to collect. Accordingly, measurement of more beak characters, as suggested by Ogden *et al.* (1998), does not necessarily improve the systematic value of these structures. Nevertheless, beak morphology should continue to be reported, given that beaks are routinely recovered from stomach contents of predators, and special attention should be given to reporting any distinct feature, such as the acutely pointed and upturned rostrum of *Adelieledone*, and to beak absolute size. Beak-biomass regression equations could then be calculated for genera, something that might prove to be the most accurate way to reconstruct prey biomass in any trophic study.

EXTERNAL CHARACTERS

External characters have long been employed to differentiate genera (Allcock *et al.* 2008). Limiting analysis to those external characters cited as basic to descriptions of cephalopod taxa (Roper & Voss 1983) does provide useful information for separating some of those genera of octopuses examined herein, although not all taxa are clearly separated. For instance, *Thaumeledone* and *Adelieledone* group amongst *Pareledone*, but the cirrate *Cirroctopus hochbergi* groups with *Graneledone*. Suggesting a closer phylogenetic relationship between *Graneledone* and *Cirroctopus* than between *Graneledone* and *Thaumeledone* would not be wise, although suggesting a closer phylogenetic relationship between *Thaumeledone*, *Pareledone* and *Adelieledone*

than between these genera and, e.g., *Pinnoctopus* or *Octopus*, is certainly consistent with historical subfamilial classifications of the Octopodidae, particularly those of Voss (1988a, b).

Limiting analysis to these same external characters for the purposes of separating species within a genus (*Pareledone*) reveals a similar story, with not all species being clearly separated from each other: *Pareledone* sp. nov. 1 is clearly separated from *P.* spp. nov. 3 and 4, but not from other *Pareledone* species (Fig. 15).

Amongst these external measures, high correlations (Table 9) were found between arm sucker counts (ASC) and arms I–IV, as well as AL I–IV, mantle length (ML) with mantle width (MW), and arm width (AW) with pallial aperture width (PA). Most specimens reported herein had a similar mantle shapes, with only one, *O. kaurna*, with a pronounced difference between ML and MW (Fig. 56). Thus, descriptions of mantle shape are largely redundant and of limited systematic and phylogenetic value. The correlation between AW and PA is not as easily explained; if a functional relationship were to exist, then it might have something to do with an animal's behaviour — perhaps the octopus inserts its arms into the mantle cavity, and for this reason one affects the other; these two measures could, however, be entirely independent of each other, and the data presented herein are not capable of identifying cause and effect.

No single external character explained the grouping of taxa in either MDS or PCA plots; rather, a combination of characters best explained observed grouping of taxa. Of the suite of variables measured, the characters that prove to be of greatest value for differentiating genera appear to be one newly proposed character, the Arm-to-web attachment (WAt), and number of sucker rows (SR) (biserial/uniserial), or, in accordance with those characters cited as basic to cephalopod descriptions (Roper & Voss 1983), arm sucker count (ASC), arm length index (ALI), head width index (HdWI) and free funnel length (FFI) (Fig. 14). Quite unexpectedly, those characters that best differentiate species within a single genus (*Pareledone*) prove to be funnel length indices, FFI and FuLI (Fig. 15).

The total number of suckers along all arms per individual octopus can vary from several hundred to thousands (Toll 1988), with the total sucker counts along any non-hectocotylied arm reported for any taxon described herein ranging from 30 (*Thaumeledone*) to 323 (*O. kaurna*). Although arm sucker count (ASC) was one of the most informative characters for differentiating presently recognised genera, its ontogenetic variation (Toll 1988) renders it of limited value when attempting to differentiate taxa of different maturity stages. Although every attempt was made to examine mature individuals of all species herein reported, this was not always possible, with some being considerably more immature than others. Caution should be used when differentiating taxa solely on the basis of ASC ranges if dealing with specimens of different ontogenetic

stages, and even sexes —in the latter case, because sucker counts vary between male and female *Pinnoctopus*, being greater in females, and are also known to vary in *Graneledone taniwha taniwha* (O’Shea 1999). Hectocotylied arm sucker counts are subject to less ontogenetic variation, with the total number of suckers along the hectocotylied arm being reached earlier in development than total non-hectocotylied arm sucker counts (Toll 1988). However, because males were not available for every species reported herein, sexual characters could not be included in statistical analyses. The high correlation between total arm sucker counts between arms of an individual could mean that species descriptions could be simplified to cite only total arm sucker count for one arm (Table 9); third arm would be the best option because in males, its opposite is the hectocotylied arm (enabling the number of suckers on the third arm to be compared with that of its opposite member, the hectocotylied arm). However, should there be octopodid taxa that were not examined herein that had different sucker counts along different arms, omission of arm sucker counts for all arms would ultimately lead to character loss for taxon differentiation, so all arm sucker counts should be provided in species descriptions until such a time as this character has been more fully examined in a greater range of taxa.

The arrangement of suckers along the arms, whether disposed in a single or in two rows, is a character used by Voss to separate his subfamilies (Fig. 1), but the phylogenetic value of this character was questioned by Robson (1932), and more recently (Voight 1993a) and Allcock *et al.* (2008). This character appears to have systematic value, in that it separates genera (Fig. 14), but its phylogenetic value is likely limited. As too few taxa with biserial suckers were examined for the purposes of this research, the validity of this character as monophyletic cannot be assessed.

Arm length ranges are proposed as valuable for diagnosing and differentiating genera and species (Hochberg *et al.* 2005). *Thaumeledone*, for example, has short arms compared to *Graneledone* (Figs 39, 42, 45, 47) or *Pareledone* (Figs 65–69, 72, 78–80, 83, 86), but the arms of *Thaumeledone* sp. nov. (Fig. 92) are largely comparable in length to those of *Bentheledone* (Fig. 34) (although slightly shorter in the former). Therefore, this character alone cannot be used for differentiating genera. Within species of *Pareledone*, arm-length ranges are shown to overlap, accounting for the low explanatory power of this variable to morphological variation for either PC1 or PC2 (Fig. 15, Table 12). Thus, the value of relative arm length for separating congeneric taxa appears to be limited, and should be used with some caution, and not solely to differentiate genera.

Arm formula (AF) is not a character assessed herein, because its variation would need to be described for many individuals of the same species. Within the genus *Pareledone* arm formula is quite variable. Moreover, in *Pinnoctopus cordiformis* and *Enteroctopus zealandicus*, two taxa considered likely synonyms by Hochberg *et al.* (2005), no consistent disparity in relative arm

lengths was apparent, despite examining many specimens (O'Shea 1999), so this character must be used with some caution for differentiating both genera and species, especially if few specimens are available. Arm formula was a character considered by Hochberg *et al.* (2005) to be of value for differentiating species, but given reported variation within it for any given species, it must be used with some caution for this purpose.

The depth of the web (WDI) is also frequently cited in octopus descriptions, although the length of the eigenvector indicates this character is less important for differentiating genera than some others (e.g., ASC, ALI, HdWI, HdLI, FFI) (Fig. 14). Web formula could be of value for characterising genera; however, within the genus *Pareledone* at least, its value is questionable, with the deepest sector being any of B, C or D in most cases for *P. spp. nov.* 1 and 2, or A,B,C,D or E for *sp. nov.* 3 (Table 148, 158, 167); the web formula is accordingly variable. The type of Arm-to-web attachment (Fig. 14), in contrast, is an informative character for differentiating some genera, and with one exception does not vary among congeneric species. All species of *Graneledone* examined had an Arm-to-web attachment of type 1A, all specimens of *Pinnoctopus* had type 1B, and all *Pareledone* and *Thaumeledone* species had type 2 attachments. The exception proved to be the genus *Octopus* (*s.l.*), but it is likely that this taxon will be divided into many taxa in the future (*vide* Hochberg *et al.* 2005).

Head width in relation to mantle width proves to be a valuable character for differentiating genera (Fig. 14), accounting for most variation for PC2 at the generic level (Table 11, 12), although the same does not hold true at the species level (Table 13).

Funnel morphology traditionally has not been considered of great value in the systematics of octopuses given its variable shape within and between taxa (Allcock *et al.* 2007). At a generic level the explanatory power of funnel-associated variables is low (Fig. 14), in that characters associated with its morphology appear to contribute little to observed grouping of taxa in PCA plots, with the length of the free portion of the funnel (FFI) contributing more to observed groupings than the funnel length itself (FLI). In contrast, within the genus *Pareledone* at least, for which external characters are rather similar (Figs 65–69, 72, 78–80, 83, 86), funnel organ indices (FFI and FuLI) contribute most to observed groupings of species. Hochberg *et al.* (2005) proposed funnel shape to be of value for differentiating genera, and its length relative to other taxa of value for differentiating species; this is partly corroborated by findings herein, although 'shape' has not been critiqued (its absolute and free lengths were measures analysed herein), and its length relative to that of the mantle had very low explanatory power for observed generic groupings.

INTERNAL CHARACTERS

Amongst internal characters, high correlations were found between digestive gland length (DG(GD)) and buccal bulb length (BBL), intestinal total length (IntL), spiral caecum greatest diameter (SpCL) and stomach greatest diameter (StL); between BBL and SpCL and StL; and SpCL with StL. As a consequence of this, of the 10 internal characters and states measured or counted, seven were used in subsequent statistical analyses.

Genera differentiate well using internal characters also, yet the resulting PCA and MDS plots differ from those based entirely on external features. For instance, *Thaumeledone* and *Adelieledone* are differentiated from *Pareledone* when using anatomical characters, but *Benthooctopus* groups with *Graneledone* (Fig. 18), a situation contrasting with that when external characters are used (Fig. 14B, D). Moreover, while taxa with two rows of suckers clearly separate from those with a single row of suckers when using external character states only, this separation is not apparent when limiting analyses to anatomical (internal) characters only (Fig. 18). At the level of species, within the genus *Pareledone*, some taxa can be clearly differentiated on the basis of internal characteristics, where no (or limited) differentiation was apparent using external characters only; notably *P. spp. nov. 1* and *3* are now clearly separated, but *P. sp. nov. 4* is not; while when using external characters *P. spp. nov. 1* and *4* are clearly separated, but *sp. nov. 3* is not. Although these three species are similar in most internal measures, and no single character accounts for their separation, a combination of these anatomical characters serve to separate them (Fig. 19).

The difference in the sizes of the stomach and spiral caecum was reported to be of systematic value by Mangold & Young (1998); however, for most species examined herein the stomach and spiral caecum are of similar size, with the stomach usually slightly larger than the spiral caecum. The sizes of these two structures could be co-dependent. Although the size of the caecum relative to the stomach does not appear to be a particularly informative taxonomic character, the number of coils of the caecum is quite variable and likely to be of some taxonomic value; for instance, two large-bodied species in New Zealand waters, *P. cordiformis* and *E. zealandicus*, have 3 and 1.5 spiral coils respectively. Accordingly, the relative size of the stomach to spiral caecum is of less systematic importance than the number of volutions of the spiral caecum.

The digestive gland is important for nutrient assimilation efficiency and therefore growth of an individual (Swift *et al.* 2005); species with a high metabolic rate are expected to have a larger gland than species with a low metabolic rate (Mangold & Young 1998). Digestive gland length was eliminated from statistical analyses due to its correlation with other internal characters, and because its length is known to vary within a given taxon; in the squid *Onykia ingens*, the size of

this gland varies between populations from different sites, with such differences attributed to regional variation in diet (Phillips *et al.* 2003); additionally, with high food intake the digestive gland is larger (Melzner *et al.* 2005). The length of the digestive gland relative to ML (DG(GD)) is shown to vary in at least one taxon herein described, *Pareledone* sp. nov. 1 (Fig. 60, 61); its shape is, however, less variable (e.g. its length relative to its width, and the relative size of the hepatic peaks). Therefore, the length of the digestive gland relative to some other standard (e.g., ML) is not an informative taxonomic character, although its overall shape might be of some value.

Most characters contribute similarly to the arrangement of taxa within PCA plots; those characters that appear to have the least explanatory power for observed grouping of taxa are buccal bulb index (BBI) at a generic level, and ink sac (IS) presence at a species level (Fig. 16, 17), the latter simply because of its variable expression in some *Pareledone* taxa (from present to absent, albeit in a vestigial form).

Octopuses generally have two pairs of salivary glands — an anterior pair closely adpressed to the back of the buccal bulb, one gland on either side of the oesophagus, and a posterior pair, the duct of which passes directly through the super- and suboesophageal ganglia and associated connectives that constitute the octopus brain. The anterior salivary glands are responsible for most mucus secretion, and assist in spreading toxins from the posterior salivary glands; the posterior salivary glands secrete venom and enzymes to immobilise and digest prey (Hanlon & Messenger 1996, Voss 1988). Salivary gland length has been used to differentiate both species and genera, e.g., the posterior salivary gland size relative to mantle length for *Benthoctopus* and *Bathypolypus* (Voss 1988); for *Praealtus* and *Thaumeledone*, and also for species of *Thaumeledone* (Allcock *et al.* 2004); and for the genus *Bathypurpurata* (Vecchione *et al.* 2005). Variation in the size of these glands, as well as that of the crop, has been related to prey size, which in turn has been related to depth (Voss 1988). Despite the fact that the salivary glands are strongly affected by the mode of life and feeding of a species, they have been considered to be valuable for systematic purposes (Mangold & Young 1998) at both generic and species levels (Fig. 16, 17). They should be used with extreme caution to differentiate genera and species.

A larger crop has more space for food storage, which is needed for shallow-water octopuses that tend to catch larger prey than their deeper-dwelling relatives (Voss 1988); the crop can possess a clearly separated diverticulum, as in *P. cordiformis* or *O. kaurna* (Figs 55, 88), both shallow water octopuses, or reduced, as in *Graneledone* (Figs 38, 41, 44, 46) or *Pareledone* (Figs 60, 61, 71, 74, 82, 85), which inhabit greater depths. Like the salivary glands, variation in the size of this structure, or presence/absence of its diverticulum, could be affected by depth of habitat

or diet more so than by phylogenetic relationship. This structure also has been used extensively in species, generic and even subfamilial classifications of the octopodids, but its phylogenetic value has probably been overstated. The size of the crop (complementarily measured with AOesL) is slightly less informative than posterior salivary gland index (PSGLI), anterior salivary gland index (ASGLI), oesophagus total length index (OesTLI) and intestine length index (IntLI) for differentiating genera, and is probably as informative as gill lamellae counts (GiLC) and PSGLI for differentiating congeneric taxa.

Vector angles between ink sac (IS) presence and PSGL at the generic level are very similar (Fig. 16), indicating a high level of correlation between these two, although the reason for such a correlation is not obvious, and might not be direct (perhaps a concomitant reduction in size of the posterior salivary glands and expression of the ink sac are both associated with depth, the former because of reduced prey size, and the latter because of its redundancy in darkness).

EXTERNAL AND INTERNAL CHARACTERS (EXCLUDING BEAKS)

Previously, the value of external and internal characters and their states for differentiating octopus taxa had been evaluated separately. Here, these two data sets are combined and examined to determine whether they collectively explain grouping of taxa in MDS and PCA plots better than any single data set in isolation. Indeed they do, with genera better grouping and separating more clearly from each other than in any previous analysis, with the exception of the problematic genus *Octopus* (Fig. 18). The two *Octopus* (*s.l.*) taxa available, *O. oliveri* and *O. kaurna*, appear to be more different from each other than from representatives in other genera; there would appear to be considerable scope for recognising additional genera within the *Octopus* (*s.l.*) complex of species. In fact, *O. oliveri* could be referable to the recently described *Abdopus*. Within the genus *Pareledone*, the use of both character sets does not facilitate differentiation of species (Fig. 19); Funnel Length Index (FuLI) and Free Funnel Index (FFI), previously explaining much of the grouping of taxa in PCA plots, are now less informative when additional internal characters are added.

ALL CHARACTERS COMBINED

When combining external and internal data sets and those of beak morphology, taxa separate marginally better at the generic level (Fig. 26), in that *Adelieledone* is more removed from the complex of species referred to *Pareledone* (in earlier analyses this taxon was grouped with *Pareledone*); at the species level (Fig. 27), the resulting PCA is better than that of internal and external characters only in that taxa are more coherently grouped. The level of grouping is comparable to that observed when dealing with internal characters only, although the MDS stress lev-

els are greater in the combined character plot than they are for either of the two preceding plots. Combining all three data sets (internal, external and beak morphology) is debatably an improvement on previous analyses. When combined, those characters that best explain the grouping of taxa are arm sucker count (ASC) and the number of sucker rows (SR), Arm-to-web attachment (WAt) and ink sac presence (ISpres) (Fig. 26, Table 33), all of which are consistent with previous analyses based on internal and external characters. Other characters with relatively high explanatory power, when it comes to grouping of taxa in PCA plots (based on the length of the eigenvectors), are gill lamellae count (GilC), intestinal length index (IntLI), and arm length index (ALI).

NON-NUMERIC CHARACTERS

Sexual characters

The reproductive system of octopuses is regularly illustrated in descriptions of taxa, especially that of the male; the female is considered more conservative in anatomy, and descriptions of its system are less regularly detailed. Both the configuration of the male and female reproductive systems of at least two of these genera, *Pinnoctopus* and *Enteroctopus*, differ in detail, further serving to differentiate them, contrary to the assertion of synonymy proposed by Norman & Hochberg (2005). The ovary of *Pinnoctopus* has distal oviducts around two times longer than the greatest diameter of the ovary sac, they are more narrow than the greatest dimension of the oviducal gland, and extend along the lateral faces of the interpallial septum musculature with their apertures opening proximal to the anus, whereas those of *Enteroctopus* (*vide* O'Shea 1999) are only slightly longer than the ovary sac greatest dimension, are as wide as the oviducal ball, and the genital apertures open proximal to the bases of the gills, not extending along the interpallial musculature. The male reproductive system differs greatly as well; the terminal organ of *Pinnoctopus* is proportionately shorter than that of *Enteroctopus*; the former is around twice the size of the diverticulum (which has two volutions) while the latter is more than six times the size of the diverticulum (without volutions).

The hectocotylus is a character that readily discriminates species, i.e. the number of suckers on the arm, and the shape of its terminal modification. The ligula of *Enteroctopus* has longitudinal lines of papillae, but that of *Pinnoctopus* does not. A similar character was used by Allcock *et al.* (2003), mentioned also by Lu & Stranks (1994), to justify separation of the genus *Pareledone* from *Adelieledone*, the latter possessing a ridged ligula, the former lacking these ridges. Given the rarity of a number of the taxa reported herein, and the fact that males were not available for study of every species, sexual characters could not be evaluated in any multivariate statistics con-

ducted herein. Thus, the value of male reproductive features in the systematics of octopuses is necessarily uncritically accepted.

Categorical characters

Of the categorical characters available, the most frequently used in taxonomic descriptions are those that detail features of the skin, particularly shape and distribution of papillae, warts, ocular cirri, and lateral ridges around the margin of the mantle. Additional categorical states include colouration, presence of ocelli, and presence and distribution of leucophores.

Skin texture has been used to differentiate octopus genera (e.g., *Graneledone*) and species (e.g., those of *Pareledone*), but such characters (colour and texture) are significantly affected by fixation methods and initial treatment history of specimens (O'Shea 1997, 1999; Allcock 2005; Gleadall *et al.* 2010), rendering them of limited value post-mortem. For those species of *Pareledone* described herein, differentiation of taxa using multivariate statistical analysis required time-consuming dissection and detailed measurement of many characters and their states. Such analyses certainly confirmed these species to differ from each other in anatomical detail, but the species were initially separated into taxa on the bases of variable skin papillation, most notably the distribution, shape and density of papillae over the mantle, head, arms and web. These categorical characters were far more obvious than anatomical details, and subtle differences in measurements, ratios and counts. Therefore, the distribution, shape and density of papillae over the mantle, head, arms and web provides very useful information for rapid differentiation of octopus taxa.

Initial treatment history in particular, whether frozen prior to fixation, fixed live, narcotised or not, or post mortem (but not frozen) can produce considerably different morphologies of a single taxon (O'Shea 1997). Specimens that have been frozen, then defrosted and fixed post-thaw generally have reduced surface sculpture, and this was observed in at least one taxon herein reported, *P. sp. nov. 3* — a species with less pronounced papillae post-mortem, post-thaw than other specimens of the same species (Figs 78–80) and *Thaumeledone sp. nov.* (Fig. 92), the skin sculpture of which, when fixed (post-thaw), appears to be smooth, but prior to fixation small and sparsely distributed papillae were apparent over the dorsal surfaces of the mantle and arms. The cartilage-like granular processes on the dorsal surfaces of the mantle, head and arms of species of *Graneledone*, for example, can be considerably less pronounced in fresh compared to preserved specimens of this same species (Voight *pers. comm.* in Guerra *et al.* 2000), with tissue dehydration in high-alcohol-content preserved specimens likely accounting for this difference (Guerra *et al.* 2000). Another example of initial treatment history producing manifestly different morpholo-

gies in octopus taxa contributing significantly to systematic confusion, is in the genus *Pinnoctopus*, initially characterised by d'Orbigny (1845) as having a fin-like flap around the margin of the mantle. This treatment-history artefact (skin slumping around the margin of the mantle in a specimen fixed post mortem), is common to two congeners, *P. cordiformis* and *P. kermadecensis* (Berry 1914, O'Shea 1999), and as an artefact of treatment history has long been recognised, and well described and figured (Robson 1929: 185; O'Shea 1999: 135–145), contrary to assertions of Hochberg *et al.* (2005). Such treatment artefacts are devoid of direct morphological interest (Robson 1929: 7), and should not be used in generic or species diagnoses.

Ink sac

Within the one genus examined herein with a great bathymetric range, *Pareledone* (Tables 3, 4), the ink sac can vary from being fully functional to entirely absent, or in size and the extent to which it is exposed on the surface of the digestive gland or buried within it; in fact, within a single taxon, *Pareledone* sp. nov. 4, a non-functional ink sac vestige can be either present or absent (Fig. 82). This accounts for the low explanatory power of this character in the grouping of taxa within PCA plots at the species level (Fig. 27). Since an ink sac serves little purpose at depth (unless the ink is of a luminous nature) its reduction in size, including loss with increasing depth, is not particularly remarkable.

Other taxa herein described with vestiges of an ink sac (a sac that seemingly has no functional role) include two species of *Graneledone*, one specimen of *Benthooctopus robustus* (O'Shea 1999: 269), and most recently, *Muusoctopus bizikov* Gleadall *et al.* 2010. In addition, an ink sac artery is described for specimens that are widely accepted to lack an ink sac, such as *G. taniwha taniwha* and *Thaumeledone* sp. nov. 1. All this evidence suggests relatively recent evolution of these deeper-water taxa from more littoral forms. The ink sac has likely been lost on multiple occasions in otherwise distantly related taxa, and therefore presence or absence of this character need not indicate phylogenetic relationship at the generic or subfamilial levels. This thesis makes a valuable contribution in recognising a vestige of the ink sac, or its arterial supply in the genus *Thaumeledone*, in addition to describing its variable expression within a single species, herein referred to as *Pareledone* sp. nov. 4. Neither has been described before, and certainly no one taxon is described with an ink sac that varies in expression from present (albeit vestigial) to absent within a single species.

Hochberg *et al.* (2005) proposed that presence/absence of an ink sac was valuable for differentiating genera, and the size of the ink sac reservoir valuable for differentiating species. However, there is no supporting evidence for such an assertion. The presence and absence of an ink

sac, its vestige, or associated ink sac artery, and the degree to which this structure is embedded within the digestive gland, and its reservoir size, are all extremely variable characters of extremely limited phylogenetic value, and limited value even at a taxonomic level.

PROBLEMATIC SPECIES

The taxonomic status of one genus, *Bentheledone*, herein redescribed, has only recently been the subject of another review, and the two proffered accounts differ in conclusion.

A single specimen herein is referred to *B. albida* (Berry), which is similar in a number of characters with taxa recently referred to *Thaumeledone* by Allcock *et al.* (2004). Problems arose when Allcock *et al.* had at their disposal a series of specimens of a deep-sea gelatinous octopod that was similar in morphological and anatomical respects to others they referred to *Thaumeledone*, but differed in sundry characters from a specimen earlier assigned to a poorly known genus and species, *Bentheledone rotunda* (Hoyle). They attributed their specimens to Hoyle's species, '*B. rotunda*', but redescribed them as *T. rotunda* (Hoyle) new combination. Given that *B. rotunda* was the type species of the genus *Bentheledone*, in doing so they rendered *Bentheledone* a junior synonym of *Thaumeledone*, and the generic status of a second described species in this genus, *B. albida* (Berry), unresolved (they did not allocate this species to any genus).

The greatest differences in descriptions of the type of *B. rotunda* and specimens later referred to it by Allcock *et al.* (2004) are in radular morphology; the type is described and illustrated with 7 well-developed teeth across in a transverse row along the radula, in addition to possessing a row of acutely pointed marginal blocks on either side of these teeth (Robson 1932: Fig. 74), whereas their specimens possessed 5 rows only and lacked marginal blocks (Allcock *et al.* 2004: Fig. 8A); the shape of individual teeth also differed considerably. As the radula was lost from the type material of this species (in addition to other parts of the anatomy), Allcock *et al.* (2004) could not confirm the accuracy of Robson's illustrations of same, and chose to disregard them in their redescription of this taxon.

Both species, *B. rotunda* and *B. albida*, have high arm sucker counts relative to other species of *Thaumeledone*, a character shown to be important for separating genera (Fig. 26). Both taxa also possess a more conventional octopodid radula comprising 7 teeth across in a transverse row, with marginal blocks (although the rachidian of neither possesses lateral cusps). These two features alone differ markedly from those described for specimens referred to *T. rotunda* (not Hoyle, 1885) by Allcock *et al.* (2004), or any species presently accommodated in the genus *Thaumeledone*; they differ also from radular detail described for the sole species of *Praealtus*. Although radular morphology herein is recognised to vary at both species and generic levels,

given obvious anatomical differences between this unique specimen and those referred to both *Thaumeledone* and *Praealtus*, the attribution of it to either genus is unacceptable. As the redescription of *B. rotunda* by Allcock *et al.* (2004) is inconsistent with the descriptions of type material made by Hoyle (1885) and Robson (1932), and the latter two are entirely consistent with that proffered herein for this unique specimen, it is referred to *B. albida* (Berry). Moreover, the proximity of capture (depth, latitude and longitude) of this unique specimen is far closer to the type localities of both *Bentheledone* species thus far described than it is to any material referred to by Allcock *et al.* (2004). The course of action followed here is to remove the genus *Bentheledone* from synonymy of *Thaumeledone*, and recognise those specimens referred to *T. rotunda* (Allcock *et al.* 2004, not Hoyle, 1885) as a new undescribed species, *Thaumeledone* sp. nov. As a consequence of this decision, the genera *Praealtus*, *Thaumeledone* and *Bentheledone* are recognised as valid Southern Ocean genera, one new species of *Thaumeledone* awaits description, that formerly referred to as *T. rotunda* (Allcock *et al.* 2004, not Hoyle, 1885), *B. rotunda* awaits redescription based on new material collected from or proximal to the type locality, and *B. albida* (Berry) is redescribed.

The relationships between taxa that were identified by PCA are not appropriate to use for phylogenetic reconstruction, given that many of the morphological characters used in descriptions of taxa may reflect environmental pressure more than evolutionary history (Strugnell *et al.* 2008). For instance, a closer relationship has been suggested between the genus *Benthooctopus* (= *Muusoctopus* Gleadall), typically a deep-dwelling taxon, and the generally shallower-dwelling taxon *Enterooctopus*. The genus *Enterooctopus*, known from 0–1500 m (Strugnell *et al.* 2010) shares a number of categorical characters and states with deeper-dwelling taxa; however, these have not been assessed in multivariate analysis. They include reduction in number of lateral cusps on the rachidian tooth of the radula, reduction (to absence) of a crop diverticulum, lack of connective tissue membranes between renal and reproductive tissues and the inner ventral surface of the mantle cavity, and the position of the female genital apertures on the face of the viscera (opening proximal to the base of the gills). These are all characters common to taxa referred to *Benthooctopus* (= *Muusoctopus*). However, from typical *Benthooctopus* (= *Muusoctopus*) taxa they differ in having a well-developed ink sac, large size, very small eggs and planktonic young for all but the type species of this genus, and a greatly elongated ligula — all characters more typical of littoral octopuses. The phylogenetic position of *Enterooctopus* is unclear, but in the event that all taxa presently referred to it are related, then this genus may prove to be a somewhat early (basal) evolutionary branch from littoral to deep-sea forms attributed to *Octopus* (s.l.) and *Benthooctopus* (= *Muusoctopus*), as earlier postulated (Robson 1929: 182, O’Shea 1999: 268), and most recently,

independently supported using molecular data by Strugnell *et al.* (2010). However, on grounds of counts, measures and indices, *E. zealandicus* does not differ greatly from littoral octopodid genera (Fig. 26), and thus, if a phylogenetic relationship were drawn on the bases of these similarities then its potential relationship with other taxa would be obscured.

Description of a taxon as having or lacking an ink sac has likely obscured relationships between taxa, resulting in the confused subfamilial classifications proposed for the family Octopodidae by Robson (1929, 1932) and Voss (1988a, b). Subsequent descriptions of taxa should examine whether an ink sac artery is present or a vestige of the ink sac itself exists, or whether an apparent ink sac duct remains proximal to the anus. On the basis of evidence presented herein, it cannot be determined which structure is lost first (the ink sac artery, ink sac itself, or duct), but at least the one *Thaumeledone* taxon described herein that lacked any apparent ink sac or vestige of a duct retained a branch from the arterial system that was positionally homologous with the ink sac artery as described for more littoral forms. Examination of additional deep-sea taxa historically referred to genera considered to lack an ink sac might shed more light on the chronology of atrophy of these three structures.

The presence or absence of a functional ink sac should not be used as a character upon which to reconstruct phylogenies at the level of subfamily, and its value as an informative phylogenetic character at the level of genus and species is also questionable. Of those characters proposed by Voss (1988a, b) for apportioning genera to higher systematic groups, biserial/uniserial sucker arrangement has also been reported to be of dubious phylogenetic value (Voight 1997). It seems that characters and their states conventionally used to divide genera in the family Octopodidae are not evolutionary meaningful for creating subfamilial groups. That is not to say that these characters have no taxonomic value, because they do have obvious value for identifying taxa. It simply means that additional characters and states should be examined, and independently compared and contrasted with molecular data in order to reconstruct phylogenies within this morphologically diverse group of octopuses.

Of those characters cited by Hochberg *et al.* (2005) as appropriate for differentiating genera and species from a taxonomic, as opposed to phylogenetic perspective, the following prove to be of value:

- Generic-level differentiation:
 - Arm to body ratio (ALI) (Figs 14, 26)
 - Gill lamellae number (GilC) (Figs 16, 26)
- Species-level differentiation:

- Funnel length (FUL) (Figs 15, 27)

Those that prove to be of limited value for differentiating genera include:

- Funnel length (FUL) (Figs 14, 26)
- Ink sac presence (ISP) (Figs 16, 26)

Those that prove to be of limited value for differentiating species, at least those of the genus *Pareledone* (for which five species were available for comparison as reported herein) include:

- Arm sucker counts (ASC) (Figs 15, 27)
- Relative length of arms to each other (ALI I–IV) (Figs 15, 27)
- Individual web sector depths (Tables 148, 158, 167, 177, 186)
- Ink sac presence (ISP) (Figs 17, 28)

CONCLUSION

This thesis evaluated the usefulness of morphological and anatomical characters conventionally used in systematics of octopuses. The exclusive use of external characters only is not recommended for octopodid classification; instead, a combination of external and internal characters is highly recommended. Beaks have proven to be of limited taxonomic value for discriminating closely related species, but in some cases they do add information and their continued description is recommended.

Those characters historically used to define subfamilies (ink sac presence or absence, and the number of sucker rows) provide limited phylogenetic information, and until more informative characters and their states are identified, and these are corroborated with molecular support, the concept of the subfamily in the Octopodidae should be abandoned.

REFERENCES

- Adams H., & A. Adams 1858. *The genera of Recent Mollusca; arranged according to their organization*, London.
- Allcock, A. & S. B. Piertney. 2002. Evolutionary relationships of Southern Ocean Octopodidae (Cephalopoda: Octopoda) and a new diagnosis of *Pareledone*. *Marine Biology*, **140**(1), 129–135.
- Allcock, A. 1997. The genetics and taxonomy of Southern Ocean Octopodidae, with special reference to the genus *Pareledone*. PhD Thesis thesis. University of Liverpool, Liverpool, UK.
- Allcock, A. 2005. On the confusion surrounding *Pareledone charcoti* (Joubin, 1905) (Cephalopoda: Octopodidae): endemic radiation in the Southern Ocean. *Zoological Journal of the Linnean Society*, **143**(1): 75–108.
- Allcock, A., A. Brierley, J. Thorpe & P. Rodhouse. 1997. Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turqueti*. *Marine Biology*, **129**(1): 97–102.
- Allcock, A., F. Hochberg & T. Stranks. 2003c. Re-evaluation of *Graneledone setebos* (Cephalopoda: Octopodidae) and allocation to the genus *Megaleledone*. *Journal of the Marine Biological Association of the UK*, **83**(2): 319–328.
- Allcock, A., F. Hochberg, P. Rodhouse & J. Thorpe. 2003b. *Adelieledone*, a new genus of octopodid from the Southern Ocean. *Antarctic Science*, **15**(4): 415–424.
- Allcock, A., J. Strugnell & M. Johnson. 2008. How useful are the recommended counts and indices in the systematics of the Octopodidae (Mollusca: Cephalopoda). *Biological Journal of the Linnean Society*, **95**: 205–218.
- Allcock, A., J. Strugnell, P. Prodöhl, U. Piatkowski & M. Vecchione. 2007. A new species of *Pareledone* (Cephalopoda: Octopodidae) from Antarctic Peninsula Waters. *Polar Biology*, **30**(7), 883–893.
- Allcock, A., M. Collins & M. Vecchione. 2003a. A redescription of *Graneledone verrucosa* (Verrill, 1881) (Octopoda: Octopodidae). *Journal of Molluscan Studies*, **69**(2): 135–143.
- Allcock, A., M. Collins, U. Piatkowski & M. Vecchione. 2004. *Thaumeledone* and other deep water octopodids from the Southern Ocean. *Deep-Sea Research Part II*, **51**(14–16): 1883–1901.

- Anderson, M. J., R. N. Gorley & K. R. Clarke. 2008. *PERMANOVA + for PRIMER. Guide to software and statistical methods*. PRIMER-E Ltd, Plymouth, UK.
- Anderson, T. J. (1999) Morphology and biology of *Octopus maorum* Hutton 1880 in northern New Zealand.
- Anderson, T. J. 1999. Morphology and biology of *Octopus maorum* Hutton 1880 in northern New Zealand. *Bulletin of Marine Science*, 63(3): 657–676.
- Batham EJ 1957. Care of eggs by *Octopus maorum*. *Transactions of the Royal Society of New Zealand*, 84: 629–638.
- Benham, W. B. 1943. The octopodous Mollusca of New Zealand – III. The giant octopus, *Macropus maorum* (Hutton) – in youth, adolescence and maturity *Transactions of the Royal Society of New Zealand*, 73, 139–153.
- Berry, S. S. 1917. Cephalopoda. Australasian Antarctic Expedition 1911–1914. *Scientific reports. Series C*, 4(2): 1–38, pl. 10–14.
- Bizikov, V. A. 2004. The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution. *Ruthenica*, 3, 1–88.
- Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. J. Humphries, S. G.R. Smith & R. E. Strauss. 1985. *Morphometrics in evolutionary biology*. Academy of Natural Sciences of Philadelphia, Philadelphia.
- Brusca, R. & J. Brusca. 2003. *Invertebrates*. Sinauer Associates, Sunderland, Massachusetts.
- Carlini, D., R. E. Young & M. Vecchione. 2001. A molecular phylogeny of the Octopoda (Mollusca: Cephalopoda) evaluated in light of morphological evidence. *Molecular Phylogenetics and Evolution*, 21(3): 388–397.
- Chenu J. C. 1859. *Manuel de Conchyliologie et de Paléontologie conchyliologique, parts 1 & 2*, Paris, France.
- Clarke, A. 1986. *A handbook for the identification of cephalopod beaks*. Clarendon, Oxford, UK.
- Clarke, K. R. & R. M. Warwick. 2001. *Change in marine communities, an approach to statistical analysis and interpretation*. PRIMER-E Ltd., Plymouth, UK.
- Clarke, M. 1998. The value of statolith shape for systematics, taxonomy, and identification *In* N. Voss, M. Vecchione, R. Toll & M. Sweeney (eds.), *Systematics and biogeography of cephalopods*. *Smithsonian Contributions to Zoology*, 586 (1): 69–76.
- Clarke, M. R. 1980. *Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology*. Marine Biological Association of the United Kingdom, Plymouth.
- Clarke, M. R. 1980. *Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology*. Marine Biological Association of the United Kingdom, Plymouth.

- Clarke, M. R. 1986. *A handbook for the identification of cephalopod beaks*. Clarendon Press, Oxford, UK.
- Collins, M. A. (2003) The genus *Grimptoteuthis* (Octopoda: Grimptoteuthidae) in the north-east Atlantic, with descriptions of three new species. *Zoological Journal of the Linnean Society*, **139**(1): 93–127.
- Cotton, B. C. 1932. Notes on Australian Mollusca, with descriptions of new genera and new species. *Records of the South Australian Museum*, **4**(537–547).
- Cuvier, G. 1797. *Tableau élémentaire de l'histoire naturelle des Animaux*. Paris.
- d'Orbigny A. 1845. *Mollusques vivants et fossiles, ou description de toutes les espèces de coquilles et de mollusques*. Adolphe Delahays, Paris. 605 pp.
- Daly, H. & P. Rodhouse. 1994. Comparative morphology of two sympatric *Pareledone* species from South Georgia. *Antarctic Science*, **6**(2): 163–169.
- Dell R. K. 1951. The New Zealand Cephalopoda. *Tuatara*, **4**: 91–102.
- Dell R. K. 1952. The Recent Cephalopoda of New Zealand. *Dominion Museum (New Zealand) Bulletin*, **16**: 1–157.
- Dell, R. K. 1952. The recent Cephalopoda of New Zealand. *Dominion Museum [N.Z.] Bulletin*, (16): 1–157.
- Filhol H. 1885. Mollusques marins. In "Mission de l'île Campbell." Recueil de Mémoires, Rapports et Documents relatives a l'observation du passage de Vénus sur le Soliel. *Comptes rendus hebdomadaire des Séances de l'Academie des Sciences, Paris 3, Pt, 2*: 517–571.
- Filhol, H. 1885. Mollusques marins. In: "Mission de l'île Campbell". *Recueil de mémoires, rapports et documents relatifs a l'observation du passage de vénus sur le soleil, Paris 3, Pt. 2*, 517–571.
- Gleadall, I. G. 2004. Some old and new genera of octopus. *Interdisciplinary Information Sciences*, **10**(2): 99–112.
- Gleadall, I. G., J. Guerrero-Kommritz, F. G. Hochberg & V. V. Laptikhovsky. 2010. The inkless octopuses (Cephalopoda: Octopodidae) of the southwest Atlantic. *Zoological Science*, **27**(6): 528–553.
- Grubert, M. A. & V. A. Wadley. 2000. Sexual maturity and fecundity of *Octopus maorum* in Southeast Tasmania. *Bulletin of Marine Science*, **66**(1): 131–142.
- Guerra, A., A. González & Y. Cherel (2000) *Graneledone gonzalezi* sp. nov.(Mollusca: Cephalopoda): a new octopod from the Iles Kerguelen. *Antarctic Science*, **12** (1): 33–40.
- Guzik, M., M. Norman & R. Crozier. 2005. Molecular phylogeny of the benthic shallow-water octopuses (Cephalopoda: Octopodinae). *Molecular Phylogenetics and Evolution*, **37**(1): 235–248.
- Hanlon, R. & J. Messenger. 1996. *Cephalopod Behaviour*. Cambridge University Press, New York.
- Hochberg, F. G. 1998. Class Cephalopoda. In P. V. Scott & J. A. Blake (eds.), *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Vol.8 – The mollusca, part 1. Santa Barbara Museum of Natural History, Santa Barbara, California. 175–218.
- Hochberg, F. G., M. Nixon & R. Toll. 1992. Order Octopoda. In M. J. Sweeny, C. F. E. Roper, K. M.

- Mangold, M. R. Clarke & S. v. Boletzky (eds.), "Larval" and juvenile cephalopods: a manual for their identification, *513*, 1-282.
- Hochberg, F., M. Norman & C. Huffard. 2005. Summary of CIAC Octopus Workshop. *Phuket Marine Biological Center. Research Bulletin*, **66**, 5–9.
- Hoyle, W. E. 1886. Report on the Cephalopoda collected by the HMS Challenger during the years 1873–1876. *Report of the Scientific Results of the Exploring Voyage of HMS Challenger 1873–1876*, **16**: 1–245.
- Hoyle, W. E. 1888. A catalogue of Recent Cephalopoda. *Proceedings of the Royal Physical Society of Edinburgh* **9**: 205–267.
- Hoyle W. E. 1909. A catalogue of Recent Cephalopoda. Second supplement, 1897–1906. *Proceedings of the Royal Physical Society of Edinburgh*, **17**: 254–299.
- Hoyle W. E. 1910. A list of the generic names of dibranchiate Cephalopoda. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **32**: 407–413.
- Huffard, C. L. 2007. Ethogram of *Abdopus aculeatus* (d'Orbigny, 1834) (Cephalopoda: Octopodidae): can behavioural characters inform octopodid taxonomy and systematics? *Journal of Molluscan Studies*, **73**: 185–193
- Hutton F. W. 1880. Manual of the New Zealand Mollusca. James Hughs, Wellington. 224 p.
- ITIS. 2010. ITIS Report. [online]. <http://www.itis.gov> [accessed 11/01/2010]
- J. R. C, Gaimard J. 1832. Mollusques. In *Voyage de découvertes de l'Astrolabe pendant les années 1826–1829, Zoologie*, **2**: 1–320. Paris.
- Joubin, L. 1918. Etudes préliminaires sur les Céphalopodes recueillis au cours des coisières de S.A.S. le Prince de Monaco, 6ème, Note: *Vitreledonella richardi* Joubin. *Bulletin de l'Institut Oceanographique de Monaco*, **340**: 1–40.
- Kaneko, N. & T. Kubodera. 2007. First records of two *Abdopus* octopuses, *A. abaculus* (Norman and Sweeney, 1997) and *A. aculeatus* (d'Orbigny, 1834) from Japan. *Proceedings of the Japanese Society of Systematic Zoology*, (22): 38–43.
- Kubodera, T. & T. Okutani. 1986. New and rare cephalopods from the Antarctic waters. *Memoirs of National Institute of Polar Research. Special issue*, (44): 129–143.
- Kubodera, T. & T. Okutani. 1994. Eledoninae octopods from the Southern Ocean: systematics and distribution. *Antarctic Science*, **6**(2): 205–214.
- Kubodera, T. 1990. Fishes collected by the R/V *Shinkai Maru* around New Zealand. *Japan Marine Fishery Resource Centre*, 349–351.
- Lamprell, K. L., J. M. Healy, A. M. Scheltema, K. Gowlett-Holmes & C. C. Lu. 2001. *Zoological Cata-*

- logue of Australia Volume 17.2: Mollusca: Aplacophora, Polyplacophora, Scaphopoda, Cephalopoda* (Zoological Catalogue of Australia Series). CSIRO Publishing, Melbourne.
- Lu, C. & T. Stranks. 1994. Synopsis of *Pareledone* and *Megaleledone* species, with description of two new species from East Antarctica (Cephalopoda: Octopodidae). *Memoirs of the Museum of Victoria*, **54**, 221–242.
- Mangold, K. & R. Young. 1998. The systematic value of the digestive organs In N. Voss, M. Vecchione, R. Toll & M. Sweeney (eds.): *Systematics and biogeography of cephalopods*. *Smithsonian Contributions to Zoology*, **586**(1): 21–30.
- Mangold, K. & R. Young. 2008. Incirrata Grimpe, 1916. Common octopods, octopuses or devilfishes [online]. <http://tolweb.org/Incirrata/20087/2008.04.28> in The tree of life web project. <http://tolweb.org/> [accessed 28/04/2010]
- Melzner, F., J. W. Fosythe, P. G. Lee, J. B. Bood, U. Piatkowski & C. Clemmesen. 2005. Estimating recent growth in the cuttlefish *Sepia officinalis*: are nucleic acid-based indicators for growth and condition the method of choice? *Journal of Experimental Marine Biology and Ecology*, **317**(1): 37–51.
- Naef, A. 1923. *Fauna and flora of the Bay of Naples. Cephalopoda (systematics)*. Monograph 35. Part I. Vol. I. Zoological Station, Naples. Translated from German by A. Mercado. Jerusalem, Israel: Israel Program for Scientific Translations.
- Nixon, M. & J. Young. 2003. *The brains and lives of cephalopods*. Oxford University Press, Oxford, UK.
- Nixon, M. 1998. The radulae of Cephalopoda. In N. Voss, M. Vecchione, R. Toll & M. Sweeney (eds.): *Systematics and biogeography of cephalopods*. *Smithsonian Contributions to Zoology*, **586**(1): 39–53.
- Norman, M. & F. Hochberg. 2005. The current state of octopus taxonomy. *Phuket Marine Biological Center. Research Bulletin*, **66**: 127–154.
- Norman, M. D., F. G. Hochberg, C. Huffard & K. M. Mangold. 2009. Octopodidae D'Orbigny, 1839. Octopods, octopuses, devilfishes [online]. <http://tolweb.org/Octopodidae/20194/2009.12.29> in The tree of life web project. <http://tolweb.org/> [accessed 01/02/2010]
- O'Shea, S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). *NIWA Biodiversity Memoir* **112**: 1–280.
- O'Shea, S. 2006. *Pinnoctopus*, *Enteroctopus* or *Octopus* [online]. <http://www.tonmo.com/forums/show-thread.php?6808-Pinnoctopus-Enteroctopus-or-Octopus?s=> [accessed 05/07/10]
- Ogden, R. S., A. L. Allcock, P. C. Wats & J. P. Thorpe. 1998. The role of beak shape in octopodid taxonomy. *South African Journal of Marine Science*, **20**: 29–36.
- Palacio, F. J. (1978) *Vosseledone charrua*: A new patagonian cephalopod (Octopodidae) with notes on related genera. *Bulletin of Marine Science* **28**(2): 286–296.
- Park, J. 1885. Description of a new *Octopus*. *Transactions and Proceedings of the Royal Society of New*

- Zealand* 17, 198–199.
- Parker T. J. 1885. On the size and the external sexual characters of the New Zealand *Octopus* (*Octopus maorum*, Hutton). *Nature*, London, 32: 586.
- Phillips, K., P. Nichols & G. Jackson 2003. Dietary variation of the squid *Moroteuthis ingens* at four sites in the Southern Ocean: stomach contents, lipid and fatty acid profiles. *Journal of the Marine Biological Association of the United Kingdom*, 83(3): 523–534
- Piertney, S., C. Hudelot, F. G. Hochberg & M. Collins. 2003. Phylogenetic relationships among cirrate octopods (Mollusca: Cephalopoda) resolved using mitochondrial 16S ribosomal DNA sequences. *Molecular Phylogenetics and Evolution*, 27(2): 348–353.
- Powell, A. W. B. 1937. *The shellfish of New Zealand*. The Unity Press Ltd, Auckland, New Zealand
- Powell, A. W. B. 1946. *The shellfish of New Zealand*. Second edition. Whitcomb & Tombs Ltd, Christchurch.
- Powell, A. W. B. 1957. *Shells of New Zealand*. Third edition. Whitcomb & Tombs Ltd, Christchurch.
- Powell, A. W. B. 1962. *Shells of New Zealand*. Fourth edition. Whitcomb & Tombs Ltd, Christchurch.
- Powell, A. W. B. 1979. *New Zealand Mollusca*. Collins, Auckland.
- Powell, A. W. B. 1976. *Shells of New Zealand*. Fifth revised edition. Whitcoulls Ltd, Christchurch.
- Powell, A. W. B. 1937. *The shellfish of New Zealand*. The Unity Press, Ltd., Auckland.
- Quinn, G. P. & M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- Ré, M. E. 1980. Estudio taxonómico de *Enteroctopus megalocyathus* (Gould) (Cephalopoda, Octopoda) con notas sobre su biología y pesca. *Centro Naconal Patagónico*, 53: 1–34.
- Robson G. C. 1929a. Notes on the Cephalopoda, part 8. The genera and subgenera of the Octopodinae and Bathypolypodinae. *Annals and Magazine of Natural History*, 3: 607–608.
- Robson, G. C. 1928. On the giant octopus of New Zealand, part 13. *Proceedings of the Zoological Society of London*, 17: 257–264.
- Robson, G. C. 1929. *A monograph of the Recent Cephalopoda. Part I. Octopodinae*. British Museum (Natural History), London, UK.
- Robson, G. C. 1932. *A monograph of the Recent Cephalopoda. Part II. The Octopoda*. British Museum (Natural History), London, UK.
- Rochebrune, A. T. & J. Mabile. 1889. *Zoologie. Mollusques*. Mission scientifique du Cap Horn 1882–1883. Vol. 6. Ministere de la Marine et de l'Instruction Publique, Paris.
- Roper, C. & G. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum Victoria*, 44: 49–63.
- Samuel, D. & J. Patterson. 2003. A comparative study on the radula of three coleoid cephalopods.

- South Pacific Study*, **24**(1): 33–38.
- Smale, M. J., M. R. Clarke, N. T. W. Klages & M. A. C. Roeleveld. 1993. Octopod beak identification – resolution at a regional level (Cephalopoda, Octopoda: southern Africa). *South African Journal of Marine Science*, **13**: 269–293.
- Spencer H. G., Willan R. C. 1995. The marine fauna of New Zealand. Index to the fauna: 3. Mollusca. *New Zealand Oceanographic Institute Memoir*, **105**: 1–125.
- Spencer, H. G. & R. C. Willan. 1995. The marine fauna of New Zealand. Index to the fauna: 3. Mollusca. Memoirs. N.Z. Oceanographic Institute, 105, 1–125.
- Stanks, T. N. 1988. Systematics of the Family Octopodidae (Mollusca: Cephalopoda) of south–eastern Australia. M.Sc Thesis thesis. University of Melbourne, Victoria, Australia.
- Strauss, R. E. 1985. Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). *Systematic Zoology*, **34**: 381–396.
- Strugnell, J. M., A. Lindgren & A. L. Allcock. 2009a. Cephalopod mollusks (Cephalopoda). In Hedges S. B. & S. Kumar (eds.), *The Timetree of Life*. Oxford University Press. 242–246.
- Strugnell, J. M., J. R. Voight, P. C. Collins & A. L. Allcock. 2009b. Molecular phylogenetic analysis of a known and a new hydrothermal vent octopod: their relationships with the genus *Benthoctopus* (Cephalopoda: Octopodidae). *Zootaxa*, **2096**, 442–459.
- Strugnell, J. M., M. A. Collins & A. L. Allcock. 2008. Molecular evolutionary relationships of the octopodid genus *Thaumeledone* (Cephalopoda: Octopodidae) from the Southern Ocean. *Antarctic Science*, **20**(3): 245–251.
- Strugnell, J., Y. Cherel, I. R. Cooke, I. G. Gleadall, F. G. Hochberg, C. M. Ibáñez, E. Jorgensen, V. V. Laptikhovskiy, K. Linse, M. Norman, M. Vecchione, J. R. Voight & A. L. Allcock. 2010. The Southern Ocean: source and sink? *Deep-Sea Research Part II* (in press).
- Suter H. 1913. *Manual of the New Zealand Mollusca*. Government Printer, Wellington.
- Suter H. 1915. *Manual of the New Zealand Mollusca*. Government Printer, Wellington.
- Sweeney, M. & C. Roper. 1998. Classification, type localities, and type repositories of recent Cephalopoda. *Smithsonian Contributions to Zoology*, **586**(2): 561–599.
- Swift, K., D. Johnston & N. Moltschanivskyj. 2005. The digestive gland of the southern dumpling squid (*Euprymna tasmanica*): structure and function. *Journal of Experimental Marine Biology and Ecology*, **315**(2): 177–186.
- Taki, I. 1961. On two new eledonid octopods from the Antarctic Sea. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima* **3**(2): 297–316.
- Toll, R. B. 1988. The use of arm sucker number in octopodid systematics (Cephalopoda: Octopoda). *American Malacological Bulletin*, **62**(2): 207–211.

- Tryon G. W. 1879. *Manual of conchology. Vol. I. Cephalopoda*, Philadelphia.
- Väliranta, M. & J. Weckström. 2007. Applying principal components analysis (PCA) for separating wingless birch fruits – a palaeoecological case study from northern Norway. *Annales Botanici Fennici*, **44**: 213–218.
- Vecchione, M. 1994. Systematics and the lifestyle and performance of cephalopods. *Marine and Freshwater Behaviour and Physiology*, **25**: 179–191.
- Voight, J. 1993a. A cladistic reassessment of octopodid classification. *Malacologia*, **35**(2): 343–349.
- Voight, J. 1993b. The association between distribution and octopodid morphology: implications for classification. *Zoological Journal of the Linnean Society*, **108**(3): 209–223.
- Voight, J. 1997. Cladistic analysis of the octopods based on anatomical characters. *Journal of Molluscan Studies*, **63**(3): 311–325.
- Voight, J. 2002. Morphometric analysis of male reproductive features of octopodids (Mollusca: Cephalopoda). *Biological Bulletin*, **202**: 148–155.
- Voss, G. 1977. Present status and new trends in cephalopod systematics. *Symposia of the Zoological Society of London*, **38**: 49–60.
- Voss, G. 1988a. The biogeography of the deep-sea Octopoda. *Malacologia*, **29**(1): 295–307.
- Voss, G. L. & W. G. Pearcy. 1990. Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. *Proceedings of the California Academy of Sciences (USA)*, **47**(3): 47–94.
- Voss, G. L. 1976. Two new species of octopods of the genus *Graneledone* (Mollusca: Cephalopoda) from the Southern Ocean. *Proceedings of the Biological Society of Washington*, **88**(42): 117–158.
- Voss, G. L. 1988b. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In M. R. Clarke & E. R. Trueman (eds.), *The Mollusca. Vol. 12. Paleontology and Neontology of Cephalopods*. Academic Press, San Diego, California. 253–276.
- Ward, L. A. 2002. The cephalopods of Guam. *Micronesica*, **35–36**: 294–302.
- Wiens, J. J. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology*, **53**(4): 653–661.
- Wolff, G. A. (1984) Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. *NOAA Technical Reports NMFS*. U.S. Department of Commerce.
- Xavier, J. C. & Y. Cherel. 2009. *Cephalopod beak guide for the Southern Ocean*. British Antarctic Survey, Cambridge, UK.
- Young, R. E. & M. Vecchione. 1996. Analysis of morphology to determine primary sister-taxon relationships within coleoid cephalopods. *American Malacological Bulletin*, **12**(1–2): 99–112.

“A note on the plural form: Fowler’s Modern English Usage states that ‘the only acceptable plural in English is octopuses’, and that octopi is misconceived and octopodes pedantic. Octopi derives from the mistaken notion that octopus is Latin. It is not. It is (Latinized) Greek, from oktopous, gender masculine, whose plural is oktopodes. If the word were Latin, it would be octopes (‘eight-foot’) and the plural octopedes, analogous to centipedes and millipedes, as the plural form of pes (‘foot’) is pedes. In modern, informal Greek, it is called khtapodi, gender neuter, with plural form khtapodia.”

So there.