

**A systematic review of the squid family Cranchiidae  
(Cephalopoda: Oegopsida) in the Pacific Ocean**

Aaron Boyd Evans

A thesis submitted through the Institute for Applied Ecology New Zealand  
and the AUT Lab for Cephalopod Ecology and Systematics (ALCES),  
Auckland University of Technology

in fulfilment of the requirements for the degree of  
Doctorate of Philosophy (PhD)

Supervised by Dr Kathrin Bolstad and Dr Mandy Reid

2018

**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.

A handwritten signature in black ink, appearing to read 'A. Boyd Evans', written over a horizontal line.

Aaron Boyd Evans

## Table of Contents

List of Figures .....	ii
List of Tables .....	iv
Abstract .....	v
Foreword .....	vii
Introduction .....	1
Materials and Methods .....	10
Systematics	
Cranchiinae .....	18
1. <i>Cranchia</i> .....	19
2. <i>Leachia</i> .....	27
3. <i>Liocranchia</i> .....	60
Taoniinae .....	73
4. <i>Bathothauma</i> .....	74
5. <i>Galiteuthis</i> .....	89
6. <i>Helicocranchia</i> .....	113
7. <i>Liguriella</i> .....	124
8. <i>Megalocranchia</i> .....	134
9. <i>Sandalops</i> .....	152
10. <i>Taonius</i> .....	160
11. Genetic Analysis of the Cranchiidae .....	186
Concluding Discussion .....	195
Acknowledgements .....	204
References .....	205
Appendices	
Appendix A: Checklist of Pacific Cranchiid Taxa .....	217
Appendix B: Measures and Counts .....	218
Appendix C: Data for Molecular Analysis .....	230

## Index of Figures

0.1: Distribution of cranchiid material examined in this study	13
0.2–0.4: Cranchiid morphological characters	14–15
0.5: Common morphological measures	16
1.1–1.6: <i>Cranchia scabra</i>	21–25
2.1: Distribution of <i>Leachia</i> taxa in the Pacific Ocean	33
2.2–2.7: <i>Leachia danae</i>	35–38
2.8–2.13: <i>Leachia dislocata</i>	41–44
2.14: <i>Leachia pacifica</i>	45
2.15–2.18: <i>Leachia separata</i> sp. nov.	48–51
2.19–2.21: <i>Leachia</i> sp. NZ	53, 54
3.1: Distribution of <i>Liocranchia</i> taxa in the Pacific Ocean	62
3.2–3.7: <i>Liocranchia reinhardti</i>	65–68
3.8–3.11: <i>Liocranchia valdiviae</i>	70–72
4.1: Distribution of <i>Bathothauma</i> taxa in the Pacific Ocean	77
4.2: <i>Bathothauma</i> posterior gladius schematic	78
4.3–4.9: <i>Bathothauma lyromma</i>	79–83
4.10, 4.11: <i>Bathothauma</i> sp. HI	84
5.1: Distribution of <i>Galiteuthis</i> taxa in the Pacific Ocean	92
5.2–5.7: <i>Galiteuthis glacialis</i>	94–98
5.8–5.12: <i>Galiteuthis pacifica</i>	100–102
5.13–5.17: <i>Galiteuthis phyllura</i>	104–107
5.18–5.23: <i>Galiteuthis suhmi</i>	109–111
6.1: Distribution of <i>Helicocranchia</i> taxa in the Pacific Ocean	114
6.2–6.5: <i>Helicocranchia pfefferi</i>	117–119
6.6–6.8: <i>Helicocranchia</i> sp. NZ	121–123
7.1: Distribution of <i>Liguriella</i> taxa in the Pacific Ocean	125
7.2–7.6: <i>Liguriella podophtalma</i>	127–129
7.7: <i>Liguriella pardus</i>	131
8.1: Distribution of <i>Megalocranchia</i> taxa in the Pacific Ocean	137
8.2, 8.3: <i>Megalocranchia abyssicola</i>	138, 139
8.4–8.8: <i>Megalocranchia</i> cf. <i>fisheri</i>	140–143
8.9: <i>Megalocranchia maxima</i>	145
8.10, 8.11: <i>Megalocranchia</i> sp. NZ	147, 148
9.1–9.6: <i>Sandalops melancholicus</i>	154–158



10.1: Distribution of <i>Taonius</i> taxa in the Pacific Ocean	163
10.2: <i>Taonius belone</i>	164
10.3–10.7: <i>Taonius borealis</i>	167–169
10.8–10.10: <i>Taonius expolitus</i> sp. nov.	171, 172
10.11, 10.12: <i>Taonius notalia</i> sp. nov.	174, 175
10.13–10.16: <i>Taonius robisoni</i> sp. nov.	177, 178
10.17–10.21: <i>Taonius tanuki</i> sp. nov.	181–183
11.1: Maximum-likelihood phylogenetic tree for Cranchiidae	190

### Index of Tables

Table 1: Comparison of adult characters in cranchiid genera	.....17
Table 2: Morphological distinctions among cranchiid genera	.....18
Table 3: Summary of taxonomic revisions of <i>Leachia</i>	.....27–28
Table 4: Comparative characters of <i>Leachia</i> taxa	.....32
Table 5: Characters of <i>Liocranchia</i> taxa	.....61
Table 6: Morphological distinctions among taoniin genera	.....73
Table 7: Characters of <i>Galiteuthis</i> taxa	.....91
Table 8: Characters of <i>Megalocranchia</i> taxa	.....136
Table 9: Characters of <i>Taonius</i> taxa	.....162

## Abstract

The Cranchiidae, commonly known as the ‘glass squid’, are a diverse but poorly known family of deep-sea oegopsid squid. Members of the family are found in every ocean, occupying different depths throughout ontogeny, and some members are thought to make up a significant portion of the diets of large marine predators. The systematics of the family has been uncertain since its original establishment in 1817, and historic revisions have seen the creation and subsequent synonymy of numerous taxa. It has been 38 years since the systematics of the family was last revised (Voss, 1980; to genus level) and several genera are believed to contain undescribed species.

This thesis describes the cranchiid squids of the Pacific Ocean, a region selected because its cranchiid diversity remains relatively unstudied. Many of the original descriptions for this family were from early research in the Atlantic Ocean, and descriptions of Pacific species have often been a part of smaller biological surveys in specific sub-regions; therefore, a larger familial revision will provide systematic stability in this basin. Ten of the known cranchiid genera are treated: *Cranchia*, *Leachia*, *Liocranchia*, *Bathothauma*, *Galiteuthis*, *Helicocranchia*, *Liguriella*, *Megalocranchia*, *Sandalops*, and *Taonius*. Of the remaining three, *Teuthowenia* was recently treated by a previous study (Evans, 2013), *Mesonychoteuthis* occurs solely in the Antarctic, and *Egea* is presently known only from the Atlantic. Herein, 26 species are included: 20 previously known species and six species new to science, plus four additional forms that will likely prove to represent additional novel taxa (but will require additional material before full descriptions and names can be given). Diversity of the genus *Taonius*, in particular, is expanded by these results, with four new species being recognised and described herein.

Species delineations were made using both traditional morphological and molecular characters (which identified 34 unique BINs, likely representing species, from both the Pacific and Atlantic Ocean). Data were collected primarily from preserved material in museum collections around the Pacific Ocean, illustrating important physical characters, with fresh material sampled when available. Although this research focussed primarily on external morphology, when internal features (e.g. beaks) were readily available or already extracted, these were included in the description.

Using COI, a preliminary phylogeny of the family is presented, which includes over half of the family’s estimated 60+ species, including 18 sequenced herein for the first time. Genetic results support monophyly of each of the twelve genera included (no

*Egea* tissue or sequences were available), supporting the morphology-based genera hypothesised by Voss (1980).

As a result of this thesis, 26+ cranchiid species are now known to occur in the Pacific Ocean. The descriptions, illustrations, and sequences presented herein should facilitate both morphological re-identification of these taxa, and the positive identification via barcoding of damaged specimens and tissues of these taxa collected (e.g., from predator gut contents) in future studies. The characters used herein to help delineate taxa can be helpful in future research that assesses the diversity of the family. Comparative studies of Atlantic and Indian Ocean material are still badly needed, and global revisions of several genera (*Helicocranchia* and *Megalocranchia*) would greatly benefit the stability of this family.

## **Foreword**

Due to the known instability of the family Cranchiidae, this thesis has been divided into chapters based on the ten genera observed herein. As historical revisions of the taxa within each genus are numerous, each chapter begins with a short historical review and concludes with a brief discussion of how the findings of this research compare to previous systematic works. The thesis will conclude with a general discussion of the results based on the family as a whole. Hopefully, this format will enable better understanding and clarity for readers and will aid in future taxonomic research of this family.

The new nomenclature in this thesis is not issued for public and permanent scientific record, or for purposes of zoological nomenclature, and is not published within the meaning of the International Code of Zoological Nomenclature (ICZN [Article 8.2]).

This thesis is for all the children who marvel at the mysteries of the ocean.

## Introduction

The Cranchiidae are a family of deep-sea squid commonly known as ‘glass squids’ due to the near-transparent nature of their mantle tissue. Cranchiids range in mature size from about ten centimeters (mantle length) to over two meters, as seen in the colossal squid *Mesonychoteuthis hamiltoni* Robson, 1925, and have a variety of morphological characteristics that distinguish them from other families of squid. The family is distinguished from all other teuthids by the mantle and head being fused at three locations, one along the dorsal midline and two ventrally (one on either side of the funnel) (Owen, 1836; Chun, 1910). This differs from most other squid species, in which the mantle is connected to the head via separable locking cartilages. Cranchiids, like many other deep sea creatures, are bioluminescent; all genera possess light-producing photophores on the eyes (with additional photophores on the viscera in some taxa) (Herring, Dilly & Cope, 2002); however, the quantity and size of these organs differs by species and can be used for identification in some genera. Despite their abundance and presence in every ocean, knowledge remains limited on the behaviour, ecology, phylogeny and systematics of the majority of species within this family.

In this research, and taxonomy in general, each taxonomic grouping (e.g., species, genus) is treated as an individual hypothesis. Observations of extant material should reveal natural groupings, and provide evidence either confirming or showing the need to revise the nominal taxa presently reported from the Pacific Ocean.

### *Historical Overview:*

The family was originally proposed in 1849 by both Prosch and Gray independently; Prosch classified his “Cranchidae” as a sub-family of the pre-established Teuthidae, while Gray made the mistake of characterising a dermal covering over the eye as a distinguishing feature of his “Cranchiadae”, a characteristic that separates the squid sub-orders Oegopsida and Myopsida (Prosch, 1849; Gray, 1849). However, the original representative species for this family had been named several decades prior to the naming of the family itself. *Cranchia scabra* Leach, 1817, was distinguished from other loliginids by having a large saccular body with hard tubercles on the outer dermal surface (Leach, 1817), but no additional morphological details were provided. A second species, *Cranchia maculata* (= *Teuthowenia maculata* fide Voss, 1985) was also described at this time, providing equally limited details (Leach, 1817). These

descriptions were further clarified a year later when Leach explained that his had been based on the accounts of John A. Cranch, who had described the two animals in a similar fashion to Leach, but did mention that the head and the mantle were connected to each other via fused tissue (Leach, 1818). Grant (1833) reinstated Lamarck's genus *Loligopsis* (=nomen dubium, fide Voss, 1980), attributing his new species *L. guttata* (= *Leachia cyclura* fide Pfeffer, 1912) to it; however, other authors criticised this decision due to the fact that the type specimen of *Loligopsis* had not been seen by any European researcher and was based upon a single drawing (Grant, 1833). Several other taxa (e.g. *L. cyclura* and *Taonius pavo*) were also included as part of this genus throughout the early 1800's (d'Orbigny, 1845).

*Cranchia scabra* was re-described by Owen (1836), this time with greater detail regarding taxonomic characters, with specific reference to the uninterrupted connection between the mantle and the head that distinguished the genus from *Loligo* Lamarck, 1798 and *Onychoteuthis* Lichtenstein, 1818. Despite Owen's re-description of *Cranchia*, d'Orbigny (1845) made his own account of the genus, making specific mention of a dermal covering over the eyes that was believed to be the only feature separating *Cranchia* from other loligopsids, and as such placed it into a separate family. As the genus *Loligopsis* had already been re-instated by Grant (1833), d'Orbigny provided an additional description of the genus and the four taxa that had been placed in it; this was later amended by Steenstrup (1861), who determined that the inclusion of cranchiid species into the genus *Loligopsis* by d'Orbigny was erroneous. Further clarification was made regarding d'Orbigny's past description of an ocular covering on *C. scabra* that had originally separated it from the other loligopsids, despite many other morphological similarities (Steenstrup, 1861). The synonymy of *Cranchia* and *Loligopsis* combined all teuthids known at the time with heads and mantles firmly joined by three fusion points into a single genus.

By the early 1900's there were nine accepted genera in the family Cranchiidae, divided into two groups: those with chitinous strips on the ventral surface of the mantle (*Cranchia* Leach, 1817; *Leachia* Lesueur, 1821; *Liocranchia* Pfeffer, 1884; *Zygaenopsis* Rochebrune, 1884) and those without (*Taonius* Steenstrup, 1861; *Taonidium* Pfeffer, 1900; *Hensenioteuthis* Pfeffer, 1900; *Owenia* Prosch, 1849; *Desmoteuthis*, Verrill, 1881) (Pfeffer, 1900). These groups were further subdivided: those with chitinous strips were divided based on how many strips were present and the attachment of the fins to the mantle, while those without cartilaginous strips were divided based on fin size. To further subdivide this latter group, two of the genera,

*Owenia* (= *Teuthowenia* fide Chun, 1910) and *Hensenoteuthis* (= *nomen dubium*, fide Voss, 1980), were classified as having long stalked eyes and tiny fins attached to the posterior tip of the mantle, features now understood to belong to almost all paralarval members of the family (Voss, 1980; Evans, 2013). Pfeffer expanded this systematic categorisation in his 1912 publication, focussing on the axial relationship between the fin edge and the posterior end of the gladius. These relationships were termed ‘straight’, ‘split’ and ‘bent’ axes, depending on the angle at which the fin connected to the mantle (Pfeffer, 1912). Pfeffer also officially divided the family Cranchiidae into two subfamilies, Cranchiinae and Taoniinae, based on the earliest described representative taxa, characterised by the number of photophores on the eyes and the arrangement of tubercles on the mantle; these subfamilies are maintained in present classification of the cranchiids.

In 1922, Grimpe created a third sub-family in his revision of European cephalopods, which was called Teuthoweniinae and contained *Teuthowenia* Chun, 1910 and *Sandalops* Chun, 1906. Grimpe (1922) also reassigned the genus *Bathothauma* Chun, 1906 to its own family, Bathothaumatidae. He united this new family with the originally named cranchiid species into a new super-family grouping which was named Cranchina; however, these taxonomic revisions do not appear in future discussions of cranchiid systematics, as most researchers disregarded Grimpe’s revised systematics (Voss, 1980).

In his taxonomic review, Clarke (1966) listed 24 genera within the cranchiid family, but admitted that many of them, particularly from the Taoniinae, “hold little value and have been used indiscriminately in the past”, referring to the historical systematic confusion of the family. In the species-level descriptions, many were noted to have typical paralarval features, but as Clarke was not undertaking systematic revisionary work at the time, these were still retained in separate genera. *Ascocranchia* Voss (= *Helicocranchia* fide Voss, 1980), was the only genus to fall in between the two pre-determined sub-families as it was believed to have features of both Cranchiinae and Taoniinae (Voss, 1962). Roper, Young, and Voss (1969) revised the family by synonymising some of the “larval” genera with genera where species morphology of mature specimens was known, such as recognising *Pyrgopsis* Rochebrune, 1884 as a junior synonym of *Leachia*. Roper and colleagues also noted three genera characterised by enlarged sucker teeth or hooks on the tentacular club (*Mesonychoteuthis*, *Taonius*, and *Galiteuthis*) as a distinguishing characteristic to identify those genera and superficially group them together (Roper et al., 1969). This revision also placed



*Ascocranchia* in Taoniinae due to its similarities with *Helicocranchia* Massy, 1907; however, *Ascocranchia* was later recognised as a junior synonym of *Helicocranchia* (Voss, 1980).

Nesis (1974) tried to further group the genera within the sub-families based on tail length and provided descriptions for four of the genera; however, these descriptions misidentified key morphological traits that are now used to identify genera (for instance, the internal photophores in *Megalocranchia* Pfeffer, 1884). These classifications were further confused by the addition of sub-species separated by geographical range and minor differences in fin size. Nesis also proposed *Vossoteuthis* Nesis, 1974 (= *Egea* fide Voss, 1980) as a genus, despite the fact that he had not personally examined all of the species he grouped within that genus (Nesis, 1974).

Imber (1978) attempted significant revisions to the family in his overview of New Zealand teuthofauna. This revision saw the synonymy of large numbers of nominal species, the restoration and synonymy of several genera, and the naming of new species. Imber's research settled on sixteen cranchiid species living in New Zealand waters; however, his work was largely based on beak morphology, and the decisions of synonymising so many species (and retaining species that had already been named as junior synonyms by prior authors) was later heavily critiqued by Voss (1980).

Voss (1980) revised the whole family on a global scale, as opposed to only examining regional genera as had been done in many of the previous revisions of the Cranchiidae; much of this research examined type specimens. From this research, Voss supported the validity of 13 (of the nominal 41) genera in the family and intended to further clarify the systematics of the cranchiid squid by doing detailed generic investigations; however, this became limited to the genus *Teuthowenia* (Voss, 1985). Another familial revision was conducted by Nesis (1987), but with less detail. This revision differed from Voss in retaining several genera, *Belonella* Lane, 1957 (= *Taonius* fide Voss, 1980) and *Drechselia* Joubin, 1931 (= *Leachia* fide Voss, 1980), and separating the genus *Leachia* into two sub-genera based on loss of paralarval features and secondary sexual modifications. Nesis did not provide any explanation for his inclusion of these additional genera within the family, only stating characters that differed from the other described genera; these differences will be discussed in later chapters.

Voss, Stephen, and Dong (1992) reported on the morphological characteristics of many paralarval specimens from the family and clarified how paralarval features change through development. However, as Evans (2013) showed for *Teuthowenia*,

some species progress through several distinct morphological growth stages during ontogenetic development; therefore, there should be more investigation into the particular details that distinguish the species of this family throughout all developmental stages.

In the last few decades, taxonomic work on the family has been intermittent. A brief description of *Drechselia danae* (= *Leachia danae* fide Voss, 1980; valid species fide Nesis, 1987) was published, identifying this species from off the west coast of Mexico for the first time (De Silva-Dávila, Avendaño-Ibarra, García-Domínguez, & Saldierna-Martínez, 2010). A new genus, *Enigmocranchia*, was described from the waters of Japan (Kubodera & Okutani, 2014), named for the many morphological similarities it shared with the genus *Cranchia*. This research examines material from these genera and discusses their validity.

#### *A unique morphology:*

Squid from the family Cranchiidae have several features that distinguish them from other families. The three fusion points between the mantle and the head differ from all other teuthids (Leach, 1818), which have separate locking cartilage components on the mantle and funnel. Many cranchiid species exhibit cartilaginous tubercles at these connection points, with two species (*Cranchia scabra* and *Galiteuthis glacialis*) having tubercles distributed across the surface of their mantle as well (McSweeney, 1971; Roper & Lu, 1990).

In addition to the fusion between the mantle and the head, the mantle itself has connected compartments internally, not seen in other squid families. Cranchiids have a ventral and horizontal partition which connects near the middle of the animal, creating three chambers (two dorsal and one ventral) around the coelom (Clarke, 1962). The compartments are filled with ammoniacal fluid that help the squid maintain their buoyancy (Clarke et al, 1979; Voight, Pörtner & O'Dor, 1995). Although buoyancy using ammonium storage has been documented in eight families of oceanic squid (and even crustaceans), the Cranchiidae were the first cephalopod family discovered to use this method of buoyancy, and the compartmentalised internal structure is unique amongst cephalopods (Voight, Pörtner & O'Dor, 1995). The coelomic chambers also allow for a unique form of respiration in which water is pushed from chamber to chamber via a spiracle. This movement creates pressure within the mantle, thereby closing off the funnel and eliminating the need for a funnel valve in most cranchiids

(Clarke, 1962). However, much of the work done on the buoyancy of cranchiids has focussed on *C. scabra*; therefore members of the other genera may have slight alterations of this body plan.

The mantle tissue of cranchiid squids maintains transparency through to adulthood in many species. This feature benefits the squid, camouflaging it against the minimal down-welling light from the surface. Several squid families exhibit transparent tissues into adulthood (such as some chroteuthids); however, the cranchiids also possess interesting internal morphology. In most genera (e.g. *Leachia*, *Teuthowenia*) the largest internal organ, the digestive gland, is positioned vertically within the mantle coelom (Seapy & Young, 1986). The gland also pivots as the animal changes orientation, so that it is always positioned vertically, minimising the silhouette seen by predators below the squid. In the genus *Megalocranchia*, the digestive gland is further masked by a four-lobed photophore (Nesis, 1974) which creates a faint light that aids in counter illumination, and in some genera the ink sac is positioned at the posterior tip of the digestive gland, masking its profile from below when the gland is positioned vertically. Most other internal organs are either transparent or diminished in size, the small surface area (viewed from below) creating minimal shadows, while externally the silhouette of the opaque eyes is masked by ventral ocular photophores.

The presence of photophores is common in deep-sea animals. Light production in the deep sea can aid in both inter- and intra-specific communication (Herring, 2000). Fortunately for taxonomists, the diverse photophores found in the Cranchiidae are also helpful for distinguishing among genera, and were one of the major features used to differentiate between the sub-families Cranchiinae and Taoniinae. Cranchiinae contains three genera, all of which have more than three eye photophores (which are circular), while those of Taoniinae have three or fewer (which are often more linear). The photophore pattern further varies by genus, and in some cases by species as well. Photophores are not just limited to the eyes, as the previously mentioned *Megalocranchia* has an internal photophore and six of the genera are known to have photophores on the distal tips of the arms in mature females (Herring, Dilly & Cope, 2002).

#### *An important trophic link:*

Many members of the family have been shown to undergo ontogenetic descent, whereby the paralarvae of the squid live in epipelagic waters, and move deeper into the

mesopelagic zone during maturation (Voss, 1985; Evans, 2013). Therefore, cranchiid squid form part of several trophic systems across their lifespan, making them a potentially important food group for many apex predators. Given that several of the species can attain large sizes at maturity (*Taonius*, *Megalocranchia*, *Mesonychoteuthis* etc.) these squid also make up a large portion of the biomass eaten by certain predators. For example, the colossal squid, *Mesonychoteuthis hamiltoni*, has been recorded to comprise at least 75% of the diet of sperm whales, *Physeter macrocephalus*, in Antarctic waters (Clarke, 1980). This is a particularly strong example, and it should be noted that these large squid act as both predators and prey at different life stages, sometimes of the same species, such as the Patagonian toothfish, *Dissostichus mawsoni* (Remeslo, Yakushev, & Laptikhovsky, 2015). Although large *Mesonychoteuthis* specimens have been captured when tangled in the hooks of toothfish longlines (and are believed to have been feeding on the hooked fish), they are also an important part of the diets of several pelagic predators (e.g. swordfish) and considered to be the second most important food item for some species (Hernández-García, 1995; Petrov & Tatarnikov, 2011). Other genera, such as *Egea* Joubin, 1933, or *Helicocranchia*, of which less is known, may yet prove to play an equally important role in other deep-sea ecosystems.

Although very little specific research has focussed on the role of the family Cranchiidae in ecosystems, many trophic surveys have reported their presence in the stomachs of cetaceans, pinnipeds, fish, and seabirds (Imber, 1992; Rodhouse et al., 1992; Hernández-García, 1995; Beatson, 2007) showing that these squid are eaten by predators at most depths. Many cetaceans, such as sperm whales, are able to dive down to great depths to capture their prey (large deep-sea squid); however, epipelagic marine animals are also known to eat cranchiid squid (e.g. Prince, 1980; Thomas & Friend, 1982) which may occur in shallow oceanic waters through several mechanisms. Firstly, most cranchiid squids are presently known to occur near the surface during early life stages, only later descending to mesopelagic depths. Secondly, some whales have been shown to extrude their stomach contents every few weeks (as a way to clear away all the solid, indigestible matter), so it is possible that scavengers ingest the beaks of these deep-sea foraged squid as a recycled food source (Clarke, 1980); however, this regurgitation is not well documented, and may depend on the whale's diet. Finally, some species of cranchiid squid have been shown to float to the surface after spawning has occurred (Nesis, Nigmatullin & Nikitina, 1998), and may again be scavenged by a variety of shallow-water organisms.

### *Cranchiids and genetics:*

The evolution of the family was examined by Voss (1998) who analysed phenotypic similarities between genera, suggesting several models via which the cranchiid family had evolved from their ancestral phenotype to the array of species seen in present day. She theorised that some morphological features, such as the statocyst and reproductive organs, of some genera were more complex than others, which could indicate a more derived structure; however, some of her phylogenetic radiations contradicted this. Voss' research showed that the Cranchiinae (*Cranchia*, *Leachia*, and *Liocranchia*) had diverged from the other cranchiids quite early during their evolution, supporting the supposition that the Cranchiinae and Taoniinae were evolutionarily distinct enough to warrant systematic separation as sub-families (Voss, 1988). Although Voss theorized several plausible pathways for cranchiid evolution, many questions remained about their evolutionary lineage.

However, with modern advances in genetic technologies, it has become easier to understand relationships among genera and species. Genetic analysis has become vital to the differentiation of species, and integrative taxonomy has helped in the delineation of many new species. For a family of squid that has a notoriously unstable systematic history, genetic analysis is an important resource that can be used to assist in unravelling the relationship among taxa of this family. And yet, with the genetic analysis of cephalopods being a relatively new field of exploration, little work has been done on this particular family. One study (Bolstad, Perez, Strugnell, & Vidal, 2015) surveyed Atlantic cranchiid fauna and confirmed that the general taxonomic separation of Cranchiinae and Taoniinae was supported to an extent, and that the 'hooked genera' of taoniins also group together. However, this appears to be one of the only examples of this type of molecular analysis available for the Cranchiidae, and further molecular analysis would strengthen the systematics of this family considerably.

### *Aims of this study:*

Taxonomic research underpins all biological and ecological studies. Accurate understandings of squid morphology and zoogeography are prerequisites for characterising these animals' trophic roles within epi- and mesopelagic communities, but have remained elusive for many oegopsid families, and the cranchiids in particular. The problematic nature of this family has led to its many taxonomic uncertainties being

filed in the ‘too hard’ basket for decades; it is true that a general lack of material and the poor condition of many preserved specimens have made progress historically quite challenging. However, it should be possible to stabilise many of the locally occurring taxa, through a thorough review of Pacific cranchiid material.

This region was selected because its cranchiid diversity remains relatively unstudied. Many of the original descriptions for this family were from early research in the Atlantic Ocean, and descriptions of Pacific species have often been a part of smaller biological surveys in specific sub-regions. A careful review of all locally occurring cranchiid fauna should provide much-needed systematic stability in this basin.

This thesis aims therefore to:

- (1) provide detailed redescriptions of each known Pacific species based on morphology, illustrating and comparing key morphological features throughout ontogeny (as far as available material permits);
- (2) identify and describe new Pacific cranchiid species encountered, where there is sufficient evidence of their novelty;
- (3) collect and sequence Pacific cranchiid tissue wherever possible, in order to incorporate molecular characters into taxonomic decisions, and facilitate future comparisons/identifications of fresh cranchiid specimens and prey tissues; and
- (4) provide a much updated account of cranchiid diversity and zoogeography in the Pacific ocean, supporting and setting standards for an eventual global revision of the family.

## Material and Methods

### *Taxonomic Conventions:*

The Cranchiidae have been a systematically unstable family and, as such, many of the junior names used historically to refer to both genera and species are discussed in this research. When discussed, the senior name follows the junior name in parenthesis, with an equal sign and the attributing author: e.g. *Loligopsis pavo* (= *Taonius pavo* fide Steenstrup, 1861).

The synonymy for individual taxa is limited to previous taxonomic descriptions providing adequate morphological detail. In some instances, previous literature lacked sufficient detail to identify a specimen to species level, but occasionally the included illustrations provided details the text did not.

### *Material examined:*

Specimens were examined from museums and natural history collections from around the Pacific Ocean, and further abroad for certain type specimens. The following institutions were visited:

- Australian Museum (AMS), Sydney, Australia
- Museum of Natural History (BMNH), London, United Kingdom
- California Academy of Sciences (CAS), San Francisco, United States
- Muséum National d'Histoire Naturelle (MNHN), Paris, France
- Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington, New Zealand
- National Museum of Victoria (MV), Melbourne, Australia
- National Institute of Water and Atmospheric Research, Ltd (NIWA), Wellington, New Zealand
- Smithsonian National Museum of Natural History (NMNH), Washington, D.C., United States (previously known as United States National Museum [USNM])
- National Museum of Nature and Science (NSMT), Tokyo, Japan
- Royal British Columbia Museum (RBCM), Victoria, Canada
- Rosenstiel School of Marine and Atmospheric Science (RSMAS), Miami, United States
- Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, United States

- Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität (ZMB), Berlin, Germany

Distribution maps for each genus were created based on the material examined herein (Fig. 0.1). Material was available from most coastal areas of the Pacific Ocean, apart from the coast of South America, and some material was available from the central Pacific Ocean. Material from the Southern Ocean and Antarctic waters were relatively scarce. The term “non-localised specimens” were those that lacked specific geographic co-ordinates and were usually from a general area (ex. “sub-Antarctic”).

Some material could not be confidently identified due to either material condition, age, or size and has therefore been excluded from systematic treatment.

Prior to examination, most specimens had been fixed in ~4% formalin and stored in 70–80% ethanol or ~40% isopropyl. Examinations and illustrations were made using a dissecting microscope and a camera lucida was used to illustrate small specimens or characters. Morphological measures and counts were taken as per Roper and Voss (1983). Measurements and counts for symmetrical features (those appearing on both sides of the midline, e.g. arms, eyes) were taken from the more complete side of the specimen. Ranges of indices are provided in text as X–Y–Z, where X is the lowest observed value, Y is the mean, and Z is the highest observed value. If both sides of the specimen were equally damaged, a ‘minimal estimation’ value was taken and noted; however, these values were not included in the mean value calculation. Mean values were not calculated for sucker counts (on both arms and tentacle clubs) as the presence of suckers, particularly on the distal portion of the arms, was variable due to damage.

Arm and tentacle club suckers were imaged using a traditional microscope or a scanning electron microscope (SEM) if available, after being critical-point dried and then sputter-coated in gold–palladium. When possible, beaks were extracted from preserved specimens, and soft tissues removed. Beak description terminology follows Clarke (1986). Due to restrictions on destructive sampling, beaks and gladii could not be removed from most specimens housed in overseas collections. This was a limitation of this research, as the beak in particular is a vital component of identification in trophic and ecological research.

When sufficient material was present, paralarval and juvenile developmental stages were identified based on morphological differences, with divisions made when several physical features changed markedly, or developed where absent in the previous stage (as for *Teuthowenia pellucida*; see Evans & Bolstad, 2014). In most species the sub-adult (or juvenile) form was characterised by the stalked eyes becoming sessile, and



was deemed an adult when primary and secondary sexual characteristics were fully developed. When sufficient material allowed, an ontogenetic stage (ex. adult, juvenile) has been identified for a given range of mantle lengths.

*Additional instruments used:*

Illustrations were made by hand or using a camera lucida attachment and Leica WILD M3B microscope when the specimen was too small. Absent or damaged features were represented using a dashed line. Inked images were scanned and then digitally compiled using Adobe Photoshop. Global distribution maps were made using ArcMap 10.5 to plot geographic co-ordinates (when available) and vertical distribution graphs were plotted in Microsoft Excel. A neighbour-joining phylogeny was created using all currently available public cranchiid data for cytochrome *c* oxidase subunit I (COI) data. This phylogenetic tree was created using MEGA7.0.26 (Kumar, Stecher, & Tamura, 2015); further explanation of the methods of the molecular analysis are detailed in chapter 11.

*Useful characters and character states for the Cranchiidae:*

1. Mantle: Mantle tissues are frequently gelatinous; however, several taxa have tubercles on their mantle while in others the tissue becomes reticulated in mature adults. Mantle shape is often conical, tapering posteriorly to fins, or rotund. Visibility of gladius through dorsal midline can be a useful character, including conus shape and visible rachis shape through tissue.
2. Fins: Fin shape may be lanceolate, sagittate, ovate, individually or together circular or paddle-shaped. Anterior fin margin may attach to mantle at the conus' widest point or elsewhere on mantle.
3. Eyes: Proportional size of eyes in adults, e.g. large bulbous eyes, exterior to head cavity (*Taonius*), smaller eyes within head (*Liocranchia*). Eye stalks can help differentiate among taxa at differing ontogenetic stages, e.g. long, slender eye-stalks supporting larger spherical eye (*Bathothauma*), short, stout stalks subequal in diameter to eyeball (*Helicocranchia*). Eye photophores: circular (Cranchiinae) or linear (Taoniinae); number and pattern can vary among taxa; presence/absence of internal photophores (*Megalocranchia*).
4. Arms: Presence/absence of keel on arms (located aborally, directed either away from arms or along oro-medial margin on Arms IV). Presence/absence and size

of trabeculated membranes along oral margins of arms; membranes are wide (greater than arm diameter) or low (less than arm diameter).

5. Tentacles: Most cranchiids lack well-defined regions of the club; only the hooked taxa (*Galiteuthis* and *Mesonychoteuthis*) have obvious regions differentiated. Suckers generally increase in size slightly mid-club and then decrease again distally. Proportional length of tentacle club to overall tentacle length (including stalk and club) can be a useful generic character.

Due to this family's unique morphology, with the head and mantle fused at three places and compartments within the mantle to store ammonical fluid, some specialised terms have been used to refer to specific parts of the cranchiid anatomy. The dorsal fusion between the head and the mantle is referred to as the nuchal fusion, while the two ventral fusion points (which are almost always identical to each other morphologically) are referred to as the funnel–mantle fusions. Other diagnostic characters for each genus are summarised in Table 1.

There are always cartilaginous connections at the ventral fusion points, which are thought to provide some structure for the otherwise gelatinous mantle. The shape of these cartilaginous areas is genus specific, and can help to distinguish between the sub-families Cranchiinae and Taoniinae. All cranchiid taxa possess long cartilaginous lines referred to herein as “strips”; these strips are often studded with a series of cartilaginous tubercles (Fig. 0.2a). In the Taoniinae, these cartilaginous areas are small and vary in shape (linear, ovate, triangular, etc.); tubercles can be present or absent.

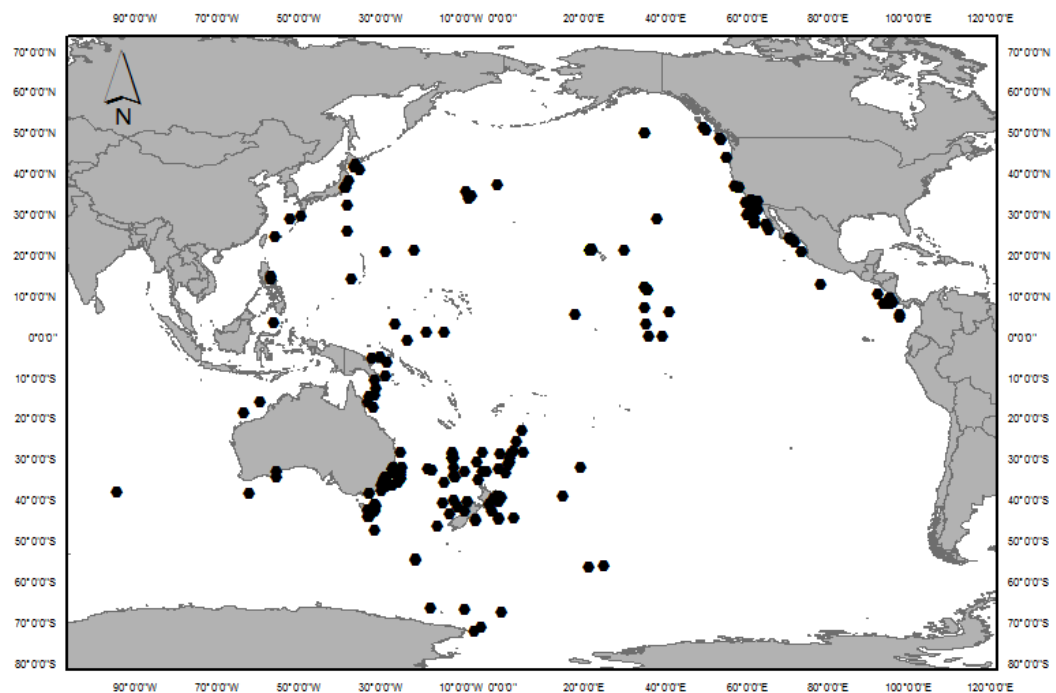


Fig. 0.1—Locality data of all cranchiid material examined.

The cartilaginous areas at the funnel–mantle fusions have not been frequently described in previous literature, and herein have been referred to as “ventral windows”, as the cartilaginous area is often more translucent than the surrounding preserved tissue.

In addition to the funnel–mantle fusions in most genera, tubercles can be found in several other locations on certain cranchiid taxa. Tubercles can be found at the nuchal fusion (in *Galiteuthis glacialis*), along the dorsal midline (in *Liocranchia reinhardti*), or covering the surface of the mantle (in *Cranchia scabra* and *Galiteuthis glacialis*). Tubercles can range from simple conical protrusions (Fig. 0.3a), to complex clusters of protrusions (Fig. 0.3b), to the highly complex stellate clusters of primary and secondary cusps (or protrusions) present in *C. scabra* (Fig. 0.3c). In some species (such as *Leachia dislocata*), complex tubercles can also be antero-posteriorly compressed (Fig. 0.3d).

Sucker ring/hook dentition (on both arms and tentacles) varies widely among cranchiids and is useful for identification, sometimes at the species level. Arm suckers are usually blunt, rounded, angular (Fig. 0.4a, d, e) or absent, while tentacle club sucker ring teeth are most often pointed (Fig. 0.4b, c). In most specimens, only one tooth shape was observed within a single sucker ring margin; however, in some instances,

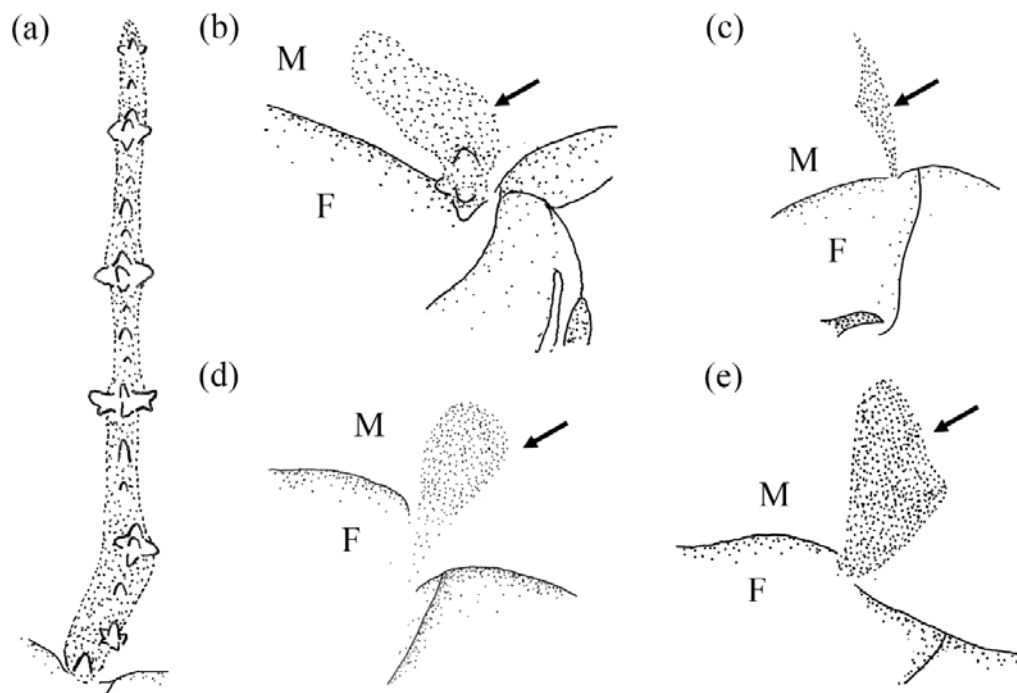


Fig. 0.2—Ventral cartilaginous shapes at left funnel–mantle fusion (a) cartilaginous strip [*Leachia*], (b) oval window with tubercles [*Galiteuthis*], (c) wing-shaped window [*Megalocranchia*], (d) rounded window [*Taonius*], (e) triangular window [*Galiteuthis*]. (Arrow = cartilaginous window, M = mantle, F = funnel)

both angular and rounded teeth were present, likely due to ontogenetic development of dentition, and/or natural wear. Where multiple tooth shapes co-occurred, the most common shape (usually seen in the distal medial teeth, and the overall majority of teeth on a given ring) is reported, from the largest suckers on the arm (usually located medially on the arm).

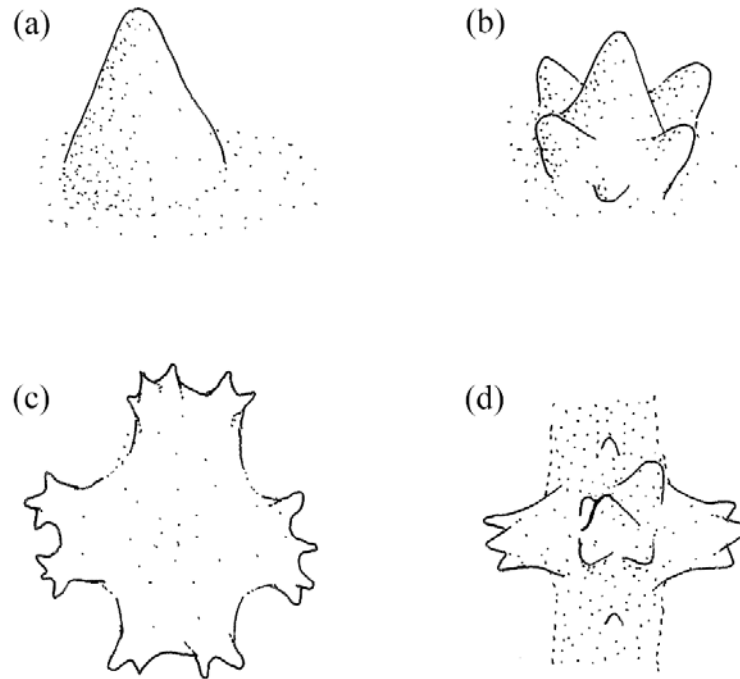


Fig. 0.3—Cranchiid tubercles: (a) simple, (b) complex, (c) stellate (*C. scabra*), and (d) antero-posteriorly compressed cluster.

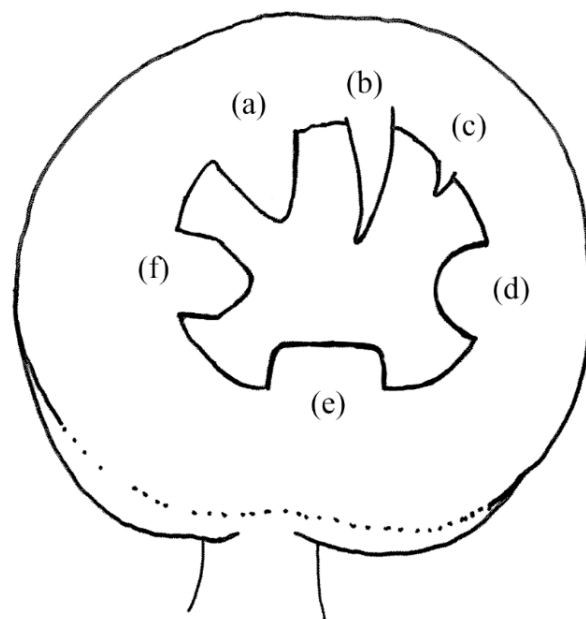


Fig. 0.4—Stylised sucker dentition morphology of the Cranchiidae: (a) angular, (b) long, pointed, (c) short, pointed, (d) rounded, (e) blunt/square, (f) turret-shaped.

*Commonly Used Morphological Abbreviated Terminology (Fig. 0.5):*

CL—Tentacle club length

ED—Eye diameter

FA—Funnel Aperture Width

FB—Funnel Base Width

FL—Fin Length

FW—Fin Width

HL—Head Length

HW—Head Width

LRL—Lower Rostral Length (of beak)

ML—Mantle Length

MW—Mantle Width

TnL—Tentacle length (including stalk and club)

*Non-morphological Abbreviations:*

BT—Bottom Trawl

MWT—Mid-water trawl

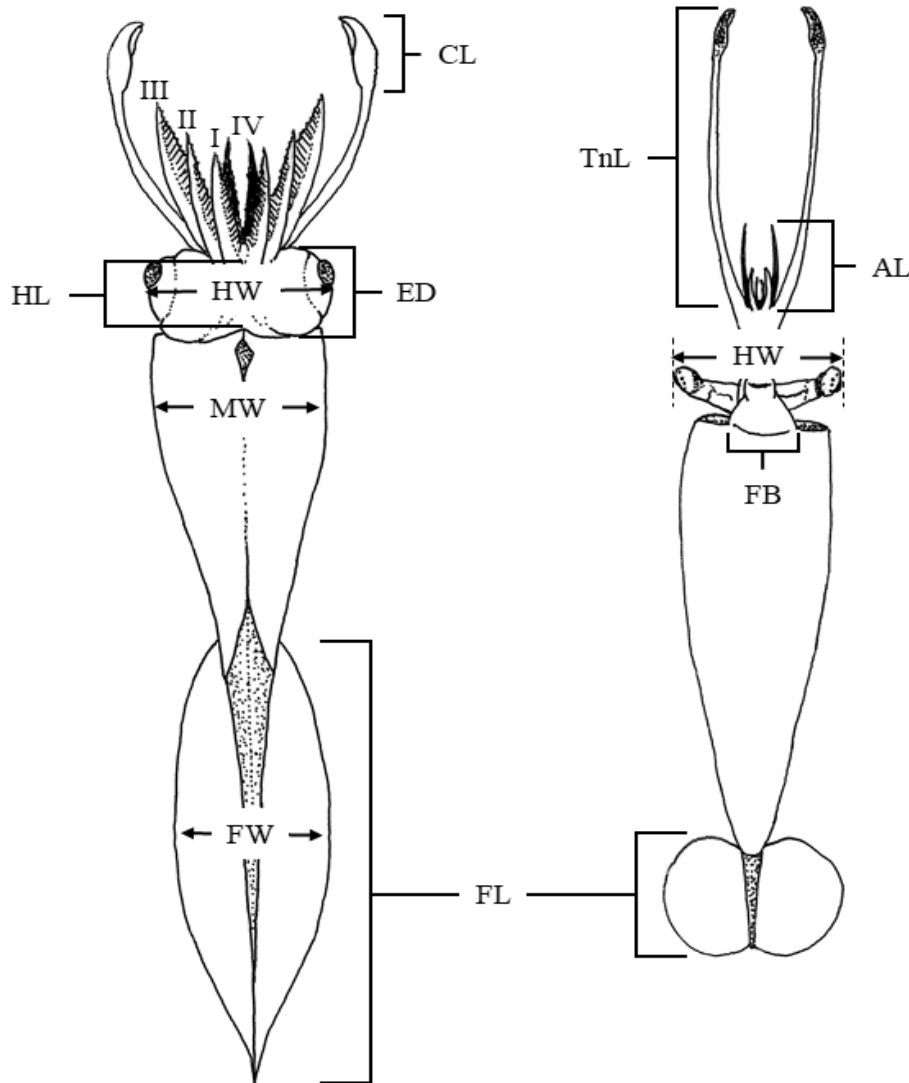


Fig. 0.5—Common morphological measures used in this research. Examples of both adult (left) and paralarval (right) squid.

Table 1–Comparison of adult characters in Pacific cranchiid genera.

<b>Character Genus</b>	<b>Adult mantle shape</b>	<b>Adult fin shape</b>	<b>Funnel–mantle fusion tubercles</b>	<b>Arm sucker dentition</b>	<b>Tentacle club armature</b>	<b>Eye photophores</b>
<i>Cranchia</i>	Stout, ovate/spherical	Individually circular	Present	Present	Suckers	Circular
<i>Leachia</i>	Slender, conical	Together circular/rhombic	Present	Present	Suckers, mid- manus enlarged	Circular
<i>Liocranchia</i>	Conical	Together circular	Present	Taxon dependent	Suckers	Circular
<i>Bathothauma</i>	Cylindrical	Individually circular/lobed	Absent	Present	Suckers	Crescent
<i>Galiteuthis</i>	Slender, conical	Lanceolate	Taxon dependant	Taxon dependent	Suckers, hooks	Linear/crescent
<i>Helicocranchia</i>	Stout, ovate	Paddle-shaped	Absent	Present	Suckers	Crescent
<i>Liguriella</i>	Conical	Together ovate	Present	Present	Suckers	Linear/crescent
<i>Megalocranchia</i>	Conical, variably stout or slender	Lanceolate	Absent	Present	Suckers	Linear/crescent, also present internally
<i>Sandalops</i>	Stout, ovate	Rounded	Absent	Absent	Suckers	Crescent/circular
<i>Taonius</i>	Slender, elongated, conical	Lanceolate	Absent	Present	Suckers, enlarged teeth	Linear/crescent

### Cranchiinae Pfeffer, 1912

In 1912, Pfeffer divided the family Cranchiidae into two sub-families, Cranchiinae and Taoniinae, based on morphological differences suggested by Chun in 1910 (who originally grouped cranchiid squid together based on the presence of ventral cartilaginous supports at the funnel–mantle fusion). The sub-family Cranchiinae was distinguished by Pfeffer (1912) as having several round light-producing organs on the ventral surface of the eye, as well as several other luminous organs arranged closer to the edge of the pupil (in contrast to Taoniinae, which had one or two crescent or linear photophores on the ventral surface of the eye). The other defining feature mentioned by Pfeffer was the presence of cartilaginous strips on the ventral surface of the mantle that supported tubercles (whereas Taoniinae either lack tubercles or possess a single cluster at the ventral fusion points). These strips originate from or ‘emphasize’ the ventral fusions on either side of the funnel.

Pfeffer further divided this sub-family into three tribes: *Leachia*-like Cranchiinae, *Cranchia*-like Cranchiinae and *Liguriella*-like Cranchiinae. *Leachia*-like Cranchiinae contained the genera *Leachia* and *Pyrgopsis* Rochebrune, 1884 (= *Leachia*, *vide* Nesis, 1987), *Cranchia*-like Cranchiinae contained the genera *Liocranchia* and *Cranchia*, and the *Liguriella*-like Cranchiinae contained only the genus *Liguriella*. Despite *Liguriella* lacking cartilaginous strips, which had been described as a unifying feature of the sub-family, it was placed in the Cranchiinae because Pfeffer decided that, given the lack of understanding of this genus, it seemed a logical default placement.

This division between the sub-families in Cranchiidae has been maintained through to our current understanding of the cranchiids, even with advances in our understanding of systematics and molecular technology (Voss, 1988; Lindgren, 2010; Lindgren, Pankey, Hochberg, & Oakley, 2012). Presently, Cranchiinae is considered to comprise three genera: *Cranchia*, *Leachia*, and *Liocranchia* (Table 2). These three genera remain united (and are distinguished from the Taoniinae) by the presence of the placement of tubercles on the mantle and the arrangement of photophores on the ventral orbital surface.

Table 2— Distinguishing characters of the Cranchiinae.

Genus	Mantle	Tubercles	Juvenile Eyes	Photophores
<i>Cranchia</i>	Stout (min MW 38% ML)	Mantle covered in complex tubercles	Sessile	14
<i>Leachia</i>	Slender (max MW 35% ML)	Single line of tubercles at funnel- mantle fusion	Stalked	4–21
<i>Liocranchia</i>	Slender (max MW 45% ML)	Ventral ‘V’ arrangement of tubercles; variably also present on dorsal midline	Sessile	4–14

Each of these genera is discussed in more detail below.

## *Cranchia* Leach, 1817

### Historical Review

The genus *Cranchia* was originally described by Leach (1817) to accommodate two new species: *C. scabra*, with a roughly tuberculate ‘sac’ [mantle]; and *C. maculata* (= *Teuthowenia maculata*, *fide* Voss, 1985), with a smooth sac with distinct dark oval spots. A year later, Leach (1818) provided a revised genus description with slightly more detail, mentioning the three connections between the head and mantle in both species. The presence of a corneal opening was first described by Owen (1836), a feature used to support the generic separation of *Cranchia* and the genus *Loligo*. *Cranchia* was later placed into the newly formed myopsid family ‘Sepidae’ by d’Orbigny (1834), who erroneously believed the eye to be covered by tissue. D’Orbigny also described a juvenile member of *Cranchia*, mistaking it for a species of warty octopod which he described as *Octopus (Philonexis) eylais* (d’Orbigny, 1834 [= *C. scabra*, *fide* Hoyle, 1904]); however, he admitted that it may have been a damaged *C. scabra* specimen.

*Cranchia* was the first genus to be placed in the family Cranchidae (Prosch, 1849) and (independently in the same year) Cranchiadae [sic] (Gray, 1849). These were the precursors of the modern cranchiid family. Gray and Prosch both retained the two species of *Cranchia* described by Leach (1817), but Prosch also described a new third species *C. (Owenia) megalops* (= *Teuthowenia megalops*, *fide* Voss, 1985). In his revision of the family, Pfeffer (1884) named two more species of *Cranchia*: *C. tenuitentaculata* and *C. hispida* (both = *C. scabra*, *fide* Pfeffer, 1912). *Cranchia tenuitentaculata* was distinguished by being slightly larger and having long thread-like tentacles, although examination of the illustration makes it clear that the elastic tentacular tissues were simply stretched to their maximum length.

*Cranchia scabra* (the sole species currently accepted in the genus) has remained systematically stable through to modern times and has been used to study the specialised cranchiid buoyancy system. *Cranchia scabra* was found to control its buoyancy using three ammonium-filled coelomic chambers connected via spiracles (Clarke, 1962). Clarke also explained how these chambers assist with a style of respiration specialised in many cranchiids, allowing the animals to move water from one chamber to another, in the absence of a funnel valve preventing backflow. Pearson (1969) reported on the microstructure of the cartilaginous ‘tubers’ found on the mantle and fins. He concluded that the tubercles were similar in structure to the cartilaginous dermal scales of *Lepidoteuthis*, and drew parallels between these cartilaginous structures and outer dermal scales that have developed in vertebrates such as bony fish. This research was continued in greater detail by Roper and Lu (1990) who compared tubercles in *Cranchia* to those of the other Cranchiinae and found that the tubercles of all genera were histologically similar, and differed only in shape. Arkhipkin (1996a) examined statolith rings in *C. scabra* and extrapolated from this the general life history of the species, reporting that *C. scabra* grows quickly over the first 4–5 months, attaining a large mantle size (~120 mm ML), and then descends to live in deeper waters. These findings differ from those described for many other cranchiids, which usually move into deeper waters over the course of their development, often beginning their descent at sizes of around 50 mm ML (e.g. *Teuthowenia pellucida*, Evans & Bolstad, 2014).



## Systematics

***Cranchia scabra* Leach, 1817** (Figs 1.1–1.6, Table B1).

*Cranchia scabra* Leach, 1817: 140; Leach, 1818: 13, Pl. 18; Owen 1836: 103–108, Pl. XXI fig. 1–5; Férussac & d'Orbigny, 1834: 222–224, Pl. I fig. 1; d'Orbigny, 1845: 239–240, Pl. 8; Steenstrup, 1861: 28–31; Chun, 1910: 257–262, Pl. XLVIII fig. 1–2, Pl. XLIX, L, LX fig. 1–6; Pfeffer, 1912: 678–689; Robson, 1924: 10; Young, 1972: 78–80; Imber, 1978: 448–449, fig. 1a; Voss, Stephen, & Dong, 1992: 188–189, fig. 217; Reid, 2016: 82–83.

*Loligo cranchii* d'Blainville, 1823: 123.

*Octopus (Philonexis) eylais* d'Orbigny, 1834: 20, Pl. I fig. 8–14.

*Cranchia hispida* Pfeffer, 1884: 27, fig. 37.

*Cranchia tenuitentaculata* Pfeffer, 1884: 26–27, fig. 36.

*Cranchia scabra hispida* Pfeffer, 1912: 690–691, Pl. 48 fig. 27.

*Cranchia scabra tenuitentaculata* Pfeffer, 1912: 689–690, Pl. 48 fig. 28.

**Diagnosis:** Cranchiian with a stout mantle covered in multi-pointed, stellate tubercles; fins small, individually circular, dorsally tuberculate; eyes with 14 spherical ocular photophores.

**Type material:** (examined) *Cranchia scabra* **BMNH Holotype 1986265** [*fide* Lipinski *et al.* (2000: 108)]. Type locality not designated; Africa.

**Material examined (20 specimens):** **NSMT-Mo. 71608**, ML 50 mm, ♂, 36.66°N, 141.43°E, 646 m, off Tohoku, 07/06/1999; **NSMT-Mo. 85213**, ML 4 mm, sex indet., 1.02°S, 156.82°E, Northeast of Papua New Guinea, Pacific, 190 m, 08/09/1995; **NIWA 95894**, ML 11.5 mm, sex indet., 14.80°S 0.13°E, Stn.TAN9101/3, 18/06/1991; **NMNZ M.074464**, ML 28, 25, 25 mm, sex indet., 28.70°S, 179.38°E, New Zealand, 20 m over 1700 m, RV *James Cook*, MWT, Stn. J09/58/76, 19/06/1976; **NMNZ M.074331**, ML 19 mm, sex indet., 28.83°S, 177.81°W, New Zealand, RV *James Cook*, surface, Stn. J09/31/76, 17/06/1976; **NMA C399127**, ML 46 mm, sex indet., 31.82°S, 153.17°E–31.87°S, 153.17°E, off Crowdy Head, MWT, 292–300 m, 15/08/1985; **NMV F51851**, ML 8 mm, sex indet., 32.02°S, 155.02°E, 05/02/1983; **NMA C399163**, ML 21 mm, sex indet., 32.32°S, 152.98°E–32.25°S, 153.02°E, Off Cape Hawke, MWT, 365–370 m, FRV *Kapala*, 13/08/1985; **NMNZ M.091605**, ML 70, 62, 59 mm, sex indet., 33.17°S, 170.79°E, New Zealand, 75–80 m over 1900 m, RV *James Cook*, MWT, Stn.J16/26/85, 24/10/1985; **NMNZ M.287288**, ML 127 mm, ♀, 34.01°S, 168.03°E, New Zealand, 626–920 m, FV *Seamount Explorer*, SL *Thickpenny*, BT, Stn.1828/53, 23/10/2003; **NMV F163438**, ML 69 mm, sex indet., 34.28°S, 124.52°E–34.32°S, 124.52°E, Western Australia, 88 km South East of Point Malcolm, CSIRO RV *Soela*, 28/11/1981; **NMV F163416**, ML 73 mm, sex indet., 34.34°S, 154.53°E, Australia off NSW, 20 m, CSIRO RV *Soela*, 01/10/1981; **NMV F163415**, ML 56 mm, sex indet., 36.42°S, 150.37°E, New South Wales, CSIRO RV *Soela*, 01/04/1981; **NMV F163466**, ML 64 mm, ♂, 36.50°S, 153.11°E–36.35°S, 151.72°E, RV *Courageous*, 20/01/1978; **NMNZ**

**M.286145**, ML 41 mm, sex indet., 40.53°S, 178.99°E, New Zealand, E of Cape Turnagain, 17–107 m over 3000 m, RV *Tangaroa*, MWT, Stn.TAN9503/59, 30/03/1995; **NMV F80426**, ML 91 mm, sex indet., 47.50°S, 148.50°E–42.53°S, 148.47°E, 498 m, 13/12/1983.

**Non-localised material examined (8 specimens):** **SBMNH 60321**, ML 86 mm, sex indet., **SBMNH 60320**, ML 71 mm, sex indet.; **CAS 144135**, ML 69 mm, ♂, Gulf of Mexico, 1066 m, RV *Oregon II*, 07/02/2001; **NSMT-Mo. 75946**, ML 64 mm, sex indet, 18/06/2005; **NSMT-Mo. 68168**, ML 60 mm, sex indet, 07/06/1990; **NIWA 90024**, ML 39 mm, sex indet. NZOI Z8343, 23/11/2002; **NIWA 90022**, ML 15 mm, sex indet., Stn. Z8349, 29/05/2004; **NIWA 90026** ML 14 mm, sex indet., Stn. Z8348; **NMV F163470**, ML 8 mm, sex indet., SP7/80/17, 02/03/1981.

### Description:

**Adult** (ML 60–160 mm; Fig. 1.2)—Mantle stout, ovate to spherical in shape; widest point around anterior 40% ML, MW 38–62–70% ML. Mantle covered in multi-pointed, star-shaped tubercles with 3–6 primary cusps and 2–4 secondary cusps (Fig. 1.3a). Fins individually circular to oval shaped, FL 10–17–24% ML (>20% at ML > 100 mm), FW 22–31–45% ML (often double FL). Fins with tubercles on dorsal surface, radiating from gladiol midline. Head with sessile eyes, HL 6–15–21% ML; HW 20–29–45% ML. Relative eye diameter varies with size (ED 12–18–25); ED<HL at ML<40 mm, ED>HL at ML>40 mm; eye with 14 spherical photophores in adults, 12 located on ventral surface, two dorsal to lens (Fig. 1.3b). Funnel stout, FB >50% HW, aperture large; FA–FB ratio decreases with size. Ventral mantle with cartilaginous strips (10–15% ML) in ‘V’ shape originating from ventral fusion points.

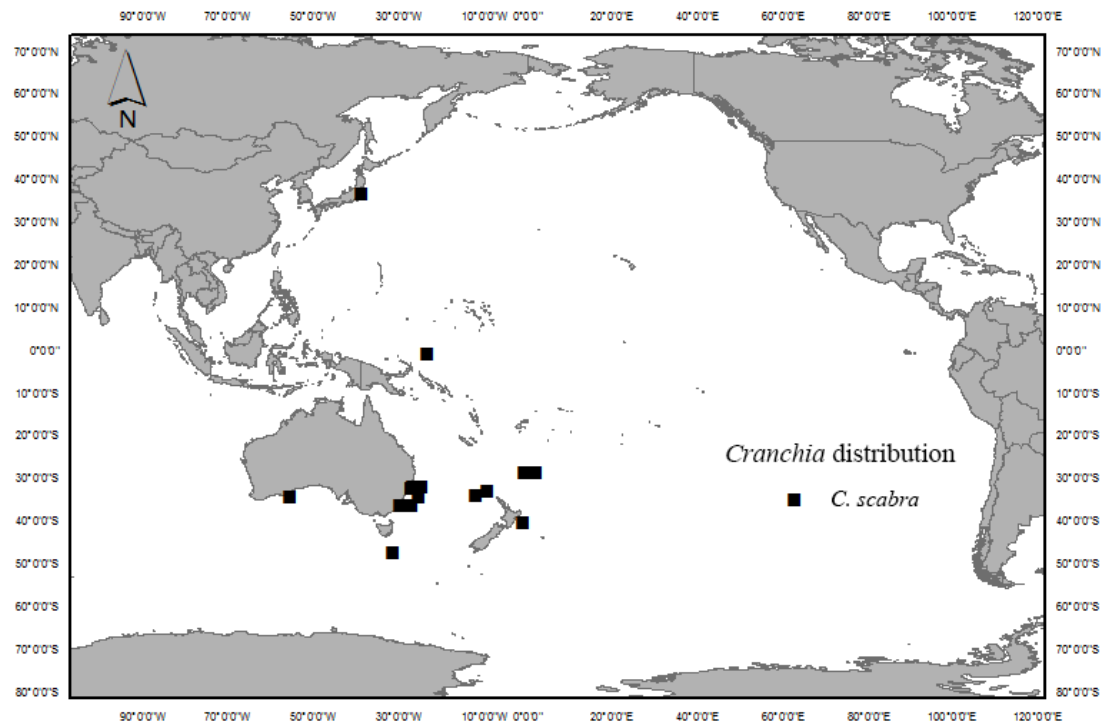


Fig. 1.1—Distribution of examined *Cranchia* material in the Pacific Ocean.

Arms robust in appearance but tissue often gelatinous; formula  $\text{III} > \text{II} \approx \text{IV} > \text{I}$ ; Arm I 8–14–30% ML, Arm II 14–24–38% ML, Arm III 22–36–60% ML, Arm IV 13–24–38% ML; arms with low protective membranes, keel present on Arms III. Arm suckers biserial, spherical, slightly larger medially, steadily decreasing in size to distal arm tip; longest arm with 40–70 suckers. Basal arm suckers (Fig. 1.4a) with 3–8 blunt/rounded teeth on distal margin; median to distal suckers (Fig. 1.4b) with 6–10 angular teeth on distal half of ring margin. Tentacles 75–85–110% ML, 0–20 paired suckers on tentacular stalk. Clubs (Fig. 1.5a) slightly expanded, with wide dorsal membrane and low ventral membrane; CL 9–15–24% ML (7–17–23% TnL). Club with 75–100 subequal suckers; little distinction among carpus, manus and dactylus suckers; sucker ring margins wide with rough texture, largest manus sucker (Fig. 1.4c) with 15–19 small pointed teeth around entire margin.

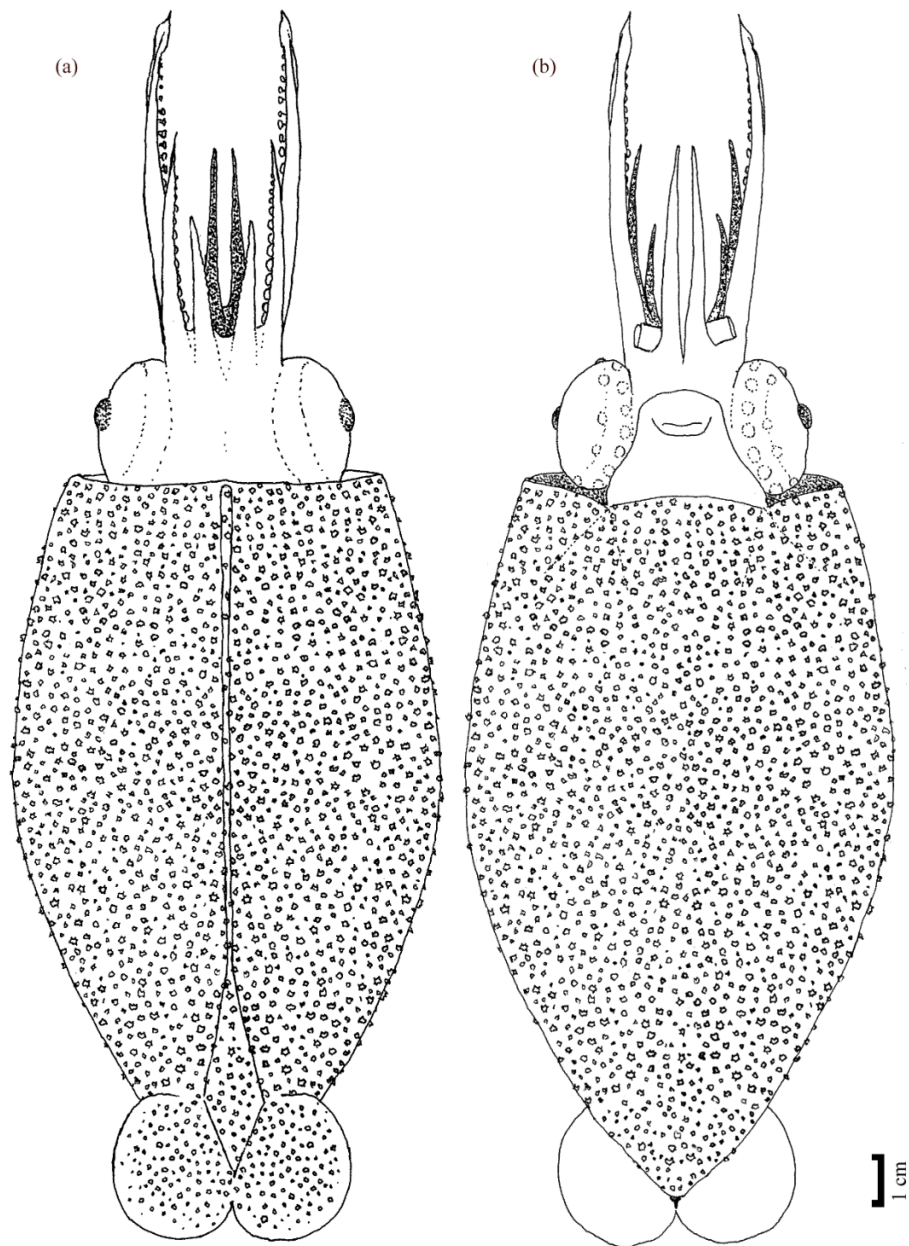


Fig. 1.2—Mature female *C. scabra*: (a) dorsal and (b) ventral view (M.287288, ML 127 mm)

Mature females with secondary sexual modifications on all arms (Fig. 1.5b): protective membranes on oral surface are enlarged at distal tips of the arms, pigmented dark red, and called 'brachial organs'; Arm III organ significantly larger than others. Males with four series of small suckers on distal 1/3 of Arms III; Arms IV also modified, curving dorsally with two sucker series along outer edge of oral surface. Mid arm with four series of smaller suckers in approximate transverse rows, arm base with ~12 pairs of regularly sized suckers in two series. Female sexual modifications appear at larger sizes (ML>120 mm) than in males (develops ~60 mm ML).

**Juvenile** (15–60 mm ML; Fig. 1.6a,b)—Mantle broadly ovoid, MW 57–67–89% ML. Fins individually circular, FL 10–15–20% ML, FW 24–28–32% ML (FW 150–192–250% FL); tubercles (lacking secondary cusps) on inner 2/3 of dorsal surface of fins or nearly covering fins, radiating from glacial midline. Head length 5–15–21% ML; HW 20–24–31% ML. Eyes 8–12–20% ML; larger photophores developed by ML 40–50 mm, up to 12 visible. Funnel stout, aperture large; FA 21–51–75% FB. Ventral mantle surface with cartilaginous strips, 5–12 % ML, in 'V' shape originating from ventral fusion points.

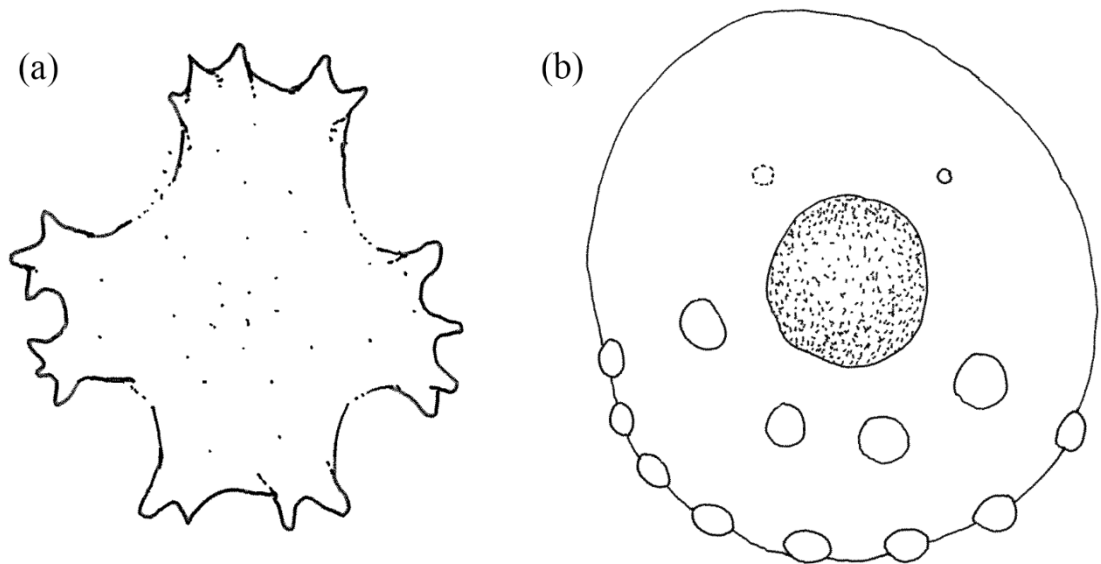


Fig. 1.3—(a) Schematic stellate mantle tubercle (b) schematic left eye of *C. scabra*.

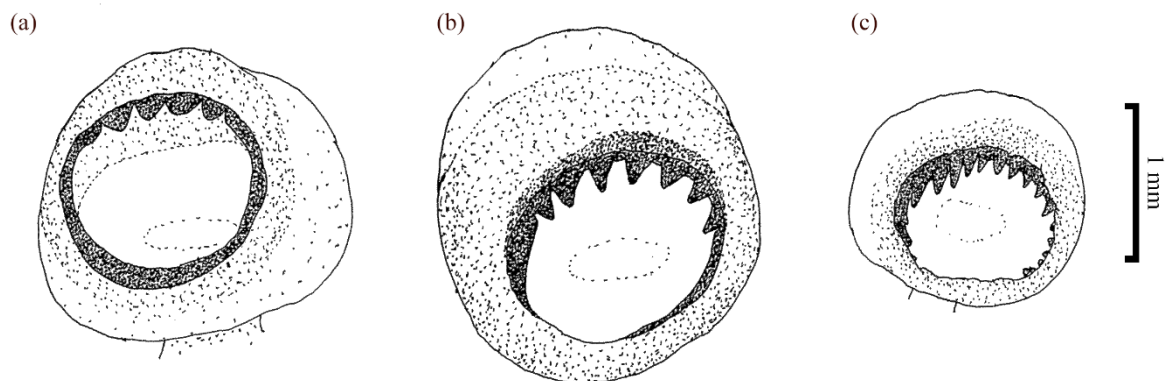


Fig. 1.4—Suckers of *C. scabra*: (a) basal Arm III sucker, (b) mid-Arm III sucker, and (c) largest manus sucker.

Arm formula  $\text{III} > \text{II} \geq \text{IV} > \text{I}$ ; Arm I 5–9–12% ML, Arm II 11–16–21% ML, Arm III 19–25–36% ML, Arm IV 10–15–23% ML; with low protective membrane on oral surface of most arms. Arm suckers biserial, spherical, subequal; arms with 16–34–60 suckers. Tentacle length 43–81–116% ML; club slightly expanded; CL 10–16–21% TL; club with 76–95 suckers.

**Paralarva** (5–15 mm ML; Fig. 1.6c,d)—Morphology as in juvenile with the following exceptions. Mantle width 60–76–110% ML, multi-pointed tubercles developing, sparsely but evenly spaced (tubercle coverage density increases with size). Fin length 8–15–25% ML, FW 25–34–47% ML (FW 110–244–350% FL); tubercles on inner 1/3 dorsal surface of fins, radiating from gladiol midline. Head length 6–15–30% ML; head width (HW) 20–29–45% ML. Eyes 7–11–17% ML; eye photophores not apparent. Cartilaginous strips difficult to discern in smaller specimens. Arm formula  $\text{III} > \text{II} \approx \text{IV} \approx \text{I}$ ; Arm III 13–17–25% ML, other arms 3–8–13% ML; protective membrane and keels absent. Arm suckers biserial, spherical, subequal; 6–30 suckers (number increasing with size). Tentacles 22–72–100% ML; club poorly differentiated from stalk; CL 13–19–23% TL; with 50–75 suckers.

**Known distribution:** Tropical, cosmopolitan species. Known depth from surface to ~1000 meters.

**Remarks:** Little ontogenetic variation in morphometrics was observed in this species. The paralarval size class is distinguished by having 1/3 of the fins covered in small tubercles, arm lengths sub-equal, and photophores not yet present or just developing, while the adult is recognised when all 14 photophores are fully developed and secondary sexual modifications are present.

Very few mature specimens were encountered in collections. Voss (1980) described the hectocotylus of male *Cranchia scabra*, based on an individual of 120 mm ML. Few of the specimens available for examination in this study were over 100 mm ML, and none were mature enough to have developed this modification.

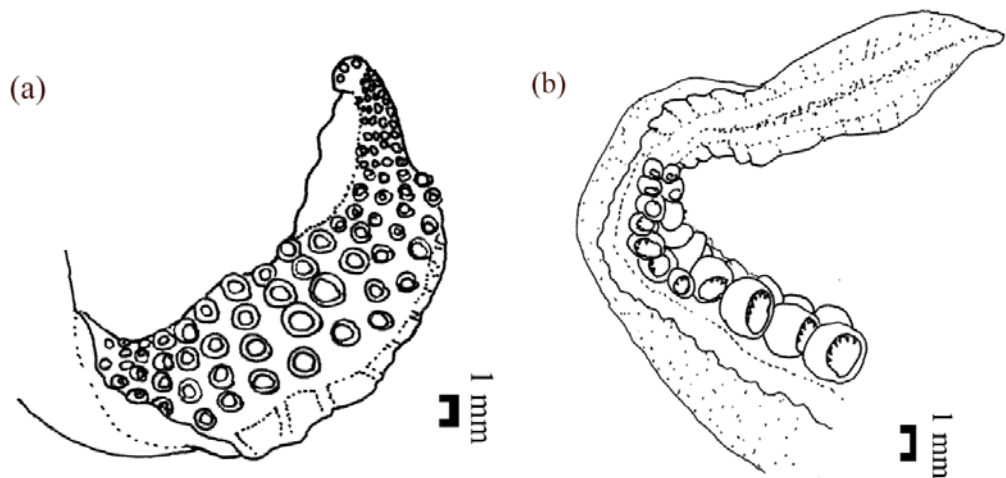


Fig. 1.5— (a) *C. scabra* left tentacular club and (b) female brachial organ, Arm III (M.297299; ML 127 mm).



## Discussion

*Cranchia*, the first recognised cranchiid genus, has historically also been one of the most systematically stable of the family. It has long been thought to be monotypic, both by traditional morphological taxonomists and more recently through genetic analysis, as sequences collected from specimens from Japanese to New Zealand waters all fall within a single BIN for CO1 (BOLD: AAJ6514). Based on the morphology observed herein, a single species appears to occur throughout the Pacific; however, Kubodera and Okutani (2014) published a description of a new genus in the Cranchiinae based on three specimens found in Japanese waters. This new genus was named *Enigmocranchia* because of its morphological similarities to *Cranchia scabra*; however, it was distinguished from *Cranchia* by having round cutaneous dermal structures and brachial end organs on all arms in females. Fully developed *C. scabra* have been reported to have a maximum of 14 photophores (Voss, 1980), while Kubodera and Okutani (2014) found *E. nipponica* to have ‘at least’ 14 photophores (possibly up to 16, with uncertainty owing to the specimens being damaged). Kubodera and Okutani stated that the dermal sculpture on *Enigmocranchia* was cutaneous, not cartilaginous, producing round bumps instead of cusped tubercles; however, examination of the paratype NSMT-Mo:85540 (ML 157 mm) showed that the skin structure was similar to *Cranchia*’s mantle tubercles, although these surfaces had been worn down, making them appear more rounded in nature. When viewed in profile, the mantle had many pronounced, multi-cusped tubercles, like those seen on *C. scabra*.

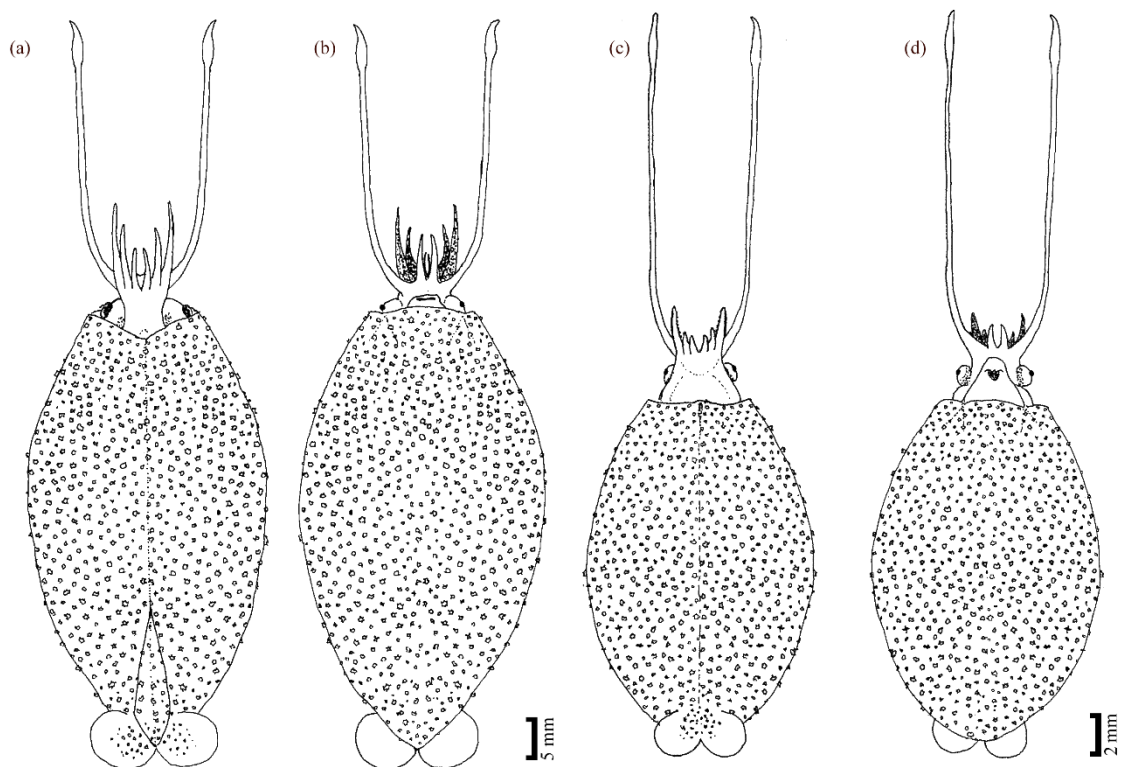


Fig. 1.6—Immature *C. scabra*: (a) dorsal and (b) ventral view of juvenile (NMNZ M.286145, ML 41 mm), and (c) dorsal and (d) ventral view of paralarva (NIWA 90026, ML 14 mm).

Another feature used to distinguish the two genera was female brachial organs. Kubodera and Okutani (2014) did not believe that the presence of these organs had been reported on all arms, despite the fact that Voss (1980) did so. The largest *C. scabra* specimen examined in New Zealand collections (NMNZ M.287288, ML 127 mm) possessed brachial end organs on all arms, with the third pair noticeably enlarged (as was reported in *Enigmocranchia*); however, those of *E. nipponica* comprised nearly half the length of Arm III (making Arm III 60% ML). This index was higher than any seen in other material from around the Pacific; however, *C. scabra* of similar size were not available, and should be examined to see whether this ratio is similar. Thus, it appears that all of the features reported to characterise *Enigmocranchia* also occur in *Cranchia*. When possible *E. nipponica* should be compared genetically with *C. scabra*; if *E. nipponica* proves genetically distinct, I suggest it be placed within *Cranchia* as the second known species in the genus (and if not, it will prove a junior synonym of *C. scabra*).

The development of tubercles on *Cranchia scabra* was interesting to examine. The tubercles on the dorsal fin surface were often simpler than those on the mantle, with most tubercles being simple (Fig. 0.4a). More complex tubercles (with additional cusps; Fig. 1.3a) were seen on larger individuals, albeit rarely. The smallest specimens showed only minimal sculpture on the fin surface, near the conus midline. Tubercles radiated outward from the midline as specimens increased in size (the word radiated is used here since the fin tubercles always appeared to cover an approximately circular area). This tubercle pattern only reached the outer fin margin in larger specimens of 70–80 mm ML. Tubercles on the mantle were mostly complex, with most tubercles having secondary cusps and larger tubercles having a tertiary set of cusps. These structures become more complex and more densely set with age; however, there always appeared to be an even distribution of dermal tubercles at all size ranges. In contrast, Voss (1980) illustrated a paralarval specimen of *C. scabra* with a sparse covering of tubercles that do not uniformly cover the entirety of the mantle, but are more densely concentrated around the mantle's widest point. Even within specimens of a similar size (8 mm ML), the material examined herein showed a more uniform distribution of tubercles on the mantle surface (although the overall tubercle density compared to larger specimens was decreased). At this small size, paralarval individuals probably develop tubercles at varying rates, so examining additional paralarval specimens would most likely show some variation in the rate of tubercle development and overall density of mantle coverage.

## *Leachia* Lesueur, 1821

### Historical Review

The genus *Leachia* has had a systematically unstable history (see Table 3). *Leachia* was first described by Lesueur (1821) from a voyage exploring Western Australia; however, the type specimen of the genus (*L. cyclura* Lesueur, 1821) was never actually examined by Lesueur himself, as the description was based on an illustration by Mr. Nicolas-Martin Petit (in Grant, 1833). Lesueur (1821) placed *Leachia* into the family Loliigoidea Lesueur, 1821, and described the genus as having an elongated cylindrical body, transparent tissue, and third arms that were longer and more robust than other arm pairs. Lesueur also described *Leachia* as being an ‘octopod’, because the illustration (and presumably the specimen) lacked tentacles; however, as the specimen was not systematically placed with other octopuses, this term was used superficially.

Table 3—Summary of taxonomic revisions of *Leachia*.

Reference	Summary	Characters discussed	Present status of taxa
Lesueur (1821): report of novel taxa	Described genus <i>Leachia</i> and its type species <i>L. cyclura</i> based on illustrated material from Western Australia.		<ul style="list-style-type: none"> <li>• <i>Leachia</i> (valid)</li> <li>• <i>L. cyclura</i> (valid)</li> </ul>
Grant (1833): report of novel taxa	Considered <i>Leachia</i> junior synonym of <i>Loligopsis</i> Lamarck, 1812 (type species: <i>Lol. peronii</i> ). Resurrected <i>Loligopsis</i> to include <i>L. cyclura</i> and his new species <i>L. guttata</i> .	Series of ~12 cartilaginous tubercles spanning ~50% ventral mantle length	<ul style="list-style-type: none"> <li>• <i>L. guttata</i> = <i>L. cyclura</i> (fide d’Orbigny, 1845)</li> </ul>
Rathke (1833)	Described genus <i>Perothis</i> for new species <i>P. eschscholtzii</i> and <i>P. dubia</i> based on small specimens from Western Indian Ocean.	Five or six tubercles on ventral mantle surface; ‘threadlike’ organ under the eyes, stubs of ‘fifth arm pair’ (tentacles)	<ul style="list-style-type: none"> <li>• <i>Perothis</i> = <i>Leachia</i></li> <li>• <i>P. eschscholtzii</i> and <i>P. dubia</i> = <i>L. cyclura</i> (fide Nesis, 1987)</li> </ul>
Adams and Reeve (1848)	Described <i>L. ellipsoptera</i> from North Atlantic; illustrated mantle–head fusion.	Eight arms, fins large and round, four ventral eye photophores	<ul style="list-style-type: none"> <li>• <i>Leachia ellipsoptera</i> (? Valid)</li> </ul>
Rochebrune (1884): family revision	Genera <i>Loligopsis</i> and <i>Perothis</i> placed into family Loliopsidae; described new genus <i>Dyctydiopsis</i> for ‘D.’ ellipsoptera; described new genus and species <i>Pyrgopsis rhynchophorus</i> ; described <i>Zygaenopsis zygaena</i>	<i>P. rhynchophorus</i> : Fins together form equilateral triangle, ventral line of four tubercles, eyes stalked, arm pair I shorter than others.	<ul style="list-style-type: none"> <li>• <i>Pyrgopsis</i> = <i>Leachia Dyctydiopsis</i> = <i>Leachia</i> (fide Voss, 1980)</li> <li>• <i>L. rhynchophorus</i> (= valid species?)</li> <li>• <i>Zygaenopsis zygaena</i> = <i>nomen dubium</i> (fide Pfeffer, 1912)</li> </ul>
Pfeffer (1884): report of museum taxa	Described <i>Lol. schneehagenii</i> .	square fins, ¼ mantle length, arm suckers lacking dentition.	<ul style="list-style-type: none"> <li>• <i>Loligopsis schneehagenii</i> = ?<i>Leachia pacifica</i> (fide Nesis, 1987)</li> </ul>
Hoyle (1885)	Discussed the state of the type specimen of		<ul style="list-style-type: none"> <li>• <i>Loligopsis peronii</i> = <i>nomen dubium</i> (fide</li> </ul>



	<i>Loligopsis</i> , and that should it ever be re-discovered, it would be unrecognisable from prior descriptions.		Sweeney & Vecchione, 1998)
Pfeffer (1900): familial revision	Re-described <i>Zygaenopsis zygaena</i>	Holotype described as having ‘bars of chitinous granules’ on mantle, stalked eyes and small ‘embryonic’ arms. ‘Expanded lobes’ (clubs) reported at the end of the tentacular stalk.	<ul style="list-style-type: none"> <li>• <i>Zygaenopsis</i> = <i>Leachia</i> (fide Pfeffer, 1912)</li> </ul>
Issel (1908)	Described <i>Zygaenopsis pacifica</i>	Cartilaginous strip 1/7 ML, with six tubercles (with 2–4 points); FL 25% ML.	<ul style="list-style-type: none"> <li>• =<i>Leachia pacifica</i> (fide Nesis, 1987).</li> </ul>
Pfeffer (1912)	Divided cranchiid squid in Cranchiinae and Taoniinae; <i>Perothis</i> was recognised as junior synonym of <i>Leachia</i> ; <i>Zygaenopsis</i> recognised as junior synonym of <i>Pyrgopsis</i>	<i>L. cyclura</i> : five or six photophores, ‘short’ cartilaginous strip. <i>L. eschscholtzii</i> : eight photophores, ‘long’ cartilaginous strip.	<ul style="list-style-type: none"> <li>• <i>Leachia cyclura</i> (valid)</li> <li>• <i>Leachia eschscholtzii</i> = <i>L. cyclura</i> (fide Nesis, 1987)</li> </ul>
Berry (1920): diagnosis of the Western Atlantic fauna	Described new species from Atlantic, <i>Pyrgopsis lemur</i> , but gave no measurements	Fins together create ellipse; arms short; ventral cartilaginous strip present.	<ul style="list-style-type: none"> <li>• <i>Pyrgopsis lemur</i> (status unknown)</li> </ul>
Joubin (1931): Tropical Pacific expedition	Described <i>Drechselia danae</i>	Both males and females with three teeth on arm suckers, females’ central tooth more pronounced.	<ul style="list-style-type: none"> <li>• =<i>Leachia danae</i> (fide Voss, 1980)</li> </ul>
Young (1972): diagnosis of Southern Californian fauna	Considered <i>Pyrgopsis</i> a junior synonym of <i>Leachia</i> ; described new species <i>L. dislocata</i>	Cartilaginous strip ~15% ML; anterior tubercle displaced towards median line; FL 20–25% ML, arm suckers with 10–14 teeth.	<ul style="list-style-type: none"> <li>• <i>Pyrgopsis</i> = <i>Leachia</i> (Young, 1972)</li> <li>• <i>L. dislocata</i> (valid)</li> </ul>
Nesis (1987): global summary	Divided the genus into two sub-genera: <i>Leachia</i> and <i>Pyrgopsis</i> . <i>Leachia</i> had sessile eyes by 40 mm ML, <i>Pyrgopsis</i> eyes were stalked until 100 mm ML.	<i>L. (L.)</i> sp. A: cartilaginous strips 40–60% ML, eight photophores on eyes. <i>L. (P.)</i> sp. B: cartilaginous strips 20% ML, Tropical Atlantic. <i>L. (P.)</i> sp. C: develops female brachial organs by 40 mm ML, Indian Ocean.	<ul style="list-style-type: none"> <li>• No further information available on these taxa as this reference represents the most recent taxonomic work on the family</li> </ul>

Some authors rejected the generic status of *Leachia* (ex. d’Blainville, 1823) due to its description being based on imperfect illustrations, but Grant (1833) believed it to represent the same taxon as *Loligopsis* Lamarck, 1812 (another genus described solely from illustrations, which had also received little support from other authors). Grant resurrected *Loligopsis*, placing *L. cyclura* within it, and added his new species, *L. guttata* (= *L. cyclura*, fide Pfeffer, 1912), with the type specimen of the genus being *L. peronii* (= *nomen dubium*). In the description for this new species, Grant mentioned lines of approximately twelve rough cartilaginous tubercles on the ventral surface, extending

halfway down the mantle from the funnel (Grant, 1833) but did not mention the presence of the cartilaginous line on which the tubercles are found. In the same year, Rathke also created a new genus, *Perothis* (= *Leachia*, *fide* Voss, 1980), which was based on specimens caught in the Western Indian Ocean (Rathke, 1833).

In order to distinguish taxa lacking a membrane covering the eye (now known as oegopsids) from those possessing it (myopsids), d'Orbigny (1845) created the family Loliopsidae, into which he placed *Loligo pavo* (= *Taonius pavo*) and *Leachia cyclura*. In this revision, d'Orbigny considered *Loligopsis guttata* (Grant, 1833) and *Perothis pellucida* (Rathke, 1833; which had been originally described by Eschscholtz, but was never published) as junior synonyms of *L. cyclura*.

Adams and Reeve (1848) illustrated their new species, *Loligopsis ellipsoptera* (current taxonomic status unknown), and clearly showed the fusion between the head and the mantle at the nuchal midline and on either side of the funnel for the first time. These illustrations lacked the ventral cartilaginous strips characteristic of *Leachia*; however, the fins were wide and oval in shape and the authors noted it was most similar to a specimen of '*Loligopsis*' *pavo* described by d'Orbigny. Adams and Reeve included this specimen as an octopod; however, Steenstrup (1861) later pointed out that the tentacles were not altogether absent, simply damaged, therefore making it a decapod. Steenstrup also resurrected Lesueur's genus *Leachia*, stating that although the original description was minimal and based on an illustration, it was the oldest available generic name for the species *L. cyclura*, thereby returning *cyclura* to its original genus.

Rochebrune (1884) disregarded Steenstrup's designations, instead returning to and critiquing d'Orbigny's work from forty years earlier. Rochebrune agreed that *Cranchia* and *Loligopsis* should be placed in separate families; however, he disagreed with some of the characteristics d'Orbigny had used in his delineation of species. In his revision of the family Loliopsidae, Rochebrune (1884) united species from the previously described genera *Loligopsis* and *Perothis* (Rathke, 1833) and his own genera *Pyrgopsis* and *Dyctydiopsis* (all three of which were later placed into synonymy with *Leachia*; Voss, 1980). Hoyle (1885) discussed how the minimal details of the original *Leachia* genus description made the distinction of *Leachia* challenging, adding that comparing the illustrations for *L. cyclura* and *L. guttata* showed them to be similar and, due to a lack of further information, synonymous, as had been concluded by Rochebrune the previous year. While discussing these previous controversies of the genus, Hoyle noted that the lack of tentacles (which had been mentioned by Adams and Reeve [1848]) was common in the genus and that no specimen of *Leachia* had been identified with whole tentacles up until that point.

Several years later, Pfeffer (1900) erected a new genus which was named *Zygaenopsis* (= *nomen dubium*, Voss, 1980). The holotype was described as having 'bars' of chitinous granules on the mantle, stalked eyes, and small 'embryonic' arms. The specimen also had 'expanded lobes' (clubs) at the end of the tentacular stalk. This new genus was later grouped alongside *Leachia* as part of the modern Cranchiinae by Chun (1906) who could not justify synonymising the two genera as specimens of *Zygaenopsis* lacked eye photophores despite nearing maturity (maturity was assumed as Chun noted the presence of a hectocotylied third arm in some specimens.).

While researching in the Azores in 1905, Joubin found four female specimens of *Leachia cyclura* that had floated to the surface. As the specimens had some damage, Joubin used them to examine the ocular photophores of *L. cyclura*. Joubin found that all specimens had five silver orb-shaped organs along the ventral surface, and another smaller organ on the ‘face’ of the eyeball. Joubin found that tissue areas between the photophores and the eye were deeply saturated with black chromatophores, preventing irradiance from the luminous organs from entering the retina. Joubin acknowledged how little was known on this topic, and mentioned a handful of authors who had researched luminous organs in cephalopods.

In the early 1900’s the cranchiid family was divided into two sub-families, Cranchiinae and Taoniinae (Pfeffer 1912). Pfeffer’s revision included placing *Perothis* into synonymy with *Leachia*, and *Zygaenopsis* with *Pyrgopsis*. Although the latter was not the oldest generic name, *Pyrgopsis* was chosen as the continuing sub-designation within the family as *Zygaenopsis* was preoccupied by a lepidopteran genus (Pfeffer, 1912). Pfeffer also synonymised several species; for example, he considered *L. ellipsoptera* to be a junior synonym of *L. cyclura*, due to Adam and Reeve’s (1848) described differences in morphological ratios still being within accepted variation for oegopsids.

In the Pacific, Joubin (1931) described *Drechselia danae*. The description included both an adult female and male, although Joubin acknowledged that neither was in pristine condition. However, the description did include a detailed explanation of the secondary sexual arm modifications for the species, along with clearly illustrated features. In both sexes, arm sucker rings showed three pointed teeth, with a central tooth enlarged in females. Joubin mentioned several differences between this new species and known Cranchiidae, including the shape of the conus, fin size, novel hectocotylus morphology, and the absence of suckers on the club surface (most likely from specimen damage).

Little attention was subsequently paid to *Pyrgopsis* or *Leachia* for many years, as advancing knowledge in other cranchiid genera was prioritised; however, after several decades Young (1972) concluded that *Pyrgopsis* was a junior synonym of *Leachia*, representing the paralarval stages of the genus. Young named a new species (*L. dislocata*) from off the Californian coast. In his survey of the Pacific diversity, Young discussed the unstable systematics of the genus, acknowledging it as one of the most taxonomically tumultuous of any oegopsid genus. Young mentioned how important the number of eye photophores was for distinguishing among species; and noted that his new species, *L. dislocata*, had the most eye photophores (15) of any known species within *Leachia*. Voss *et al.* (1992) later determined *L. danae* had a greater number of ocular photophores (21). Three years later, Young published research regarding the maturation and spawning habits of *L. pacifica*. In this paper, Young mentioned that many species of *Leachia*, which up until that time had been presumed an epipelagic species, grow to 80% of their maximum size in near-surface waters, and then migrate to depth (~2000 m) to mature and spawn (Young, 1975).

Several years later, Imber (1978) undertook a revision of the teuthofauna from New Zealand waters, reporting two locally occurring species of *Leachia* (*cyclura* and *eschscholtzii*) and synonymising several geographically distant species to fit within those two. This decision was later refuted by Voss (1980) who criticized the ‘lumping’

of geographically separate and morphologically distinct species. Voss, in her comprehensive review of the cranchiid genera, confirmed the synonymy of previous generic names already proposed by previous authors, adding the genus *Drechselia* to the long list of *Leachia*'s junior synonyms (Voss, 1980). Voss provided a detailed generic description of *Leachia*, summarising many of the adult features that had historically caused identification issues.

Nesis (1987) provided a taxonomic overview of the genus, prefacing his work by stating that this was only a preliminary key for this genus, as only *L. pacifica* had been described throughout its ontogeny to date. In total, Nesis reported eight species, but divided the genus into two sub-genera: *Leachia* and *Pyrgopsis*; *Drechselia danae* was retained as its own monotypic genus. Species of *Leachia* had sessile eyes earlier in development and female specimens lacked brachial organs on the distal portion of the third arms, while *Pyrgopsis* retained stalked eyes until about 100 mm mantle length (Nesis, 1987).

Sweeney *et al.* (1992) examined paralarval members of all nominal species within the genus. Of the 14 nominal species, the authors agreed that six appeared valid, but admitted that the number might be revised upward to 11. Out of the six found to be valid, they examined morphometric features of five, focussing on eye development, tubercle patterns and maturation size. Sweeney *et al.* (1992) found that the species usually had discrete, but adjacent geographic distributions, although some overlap was also noted. However, this review of distributions lacked several key geographic areas, such as the southern Pacific. It was explained that further research on this genus was forthcoming; however, that information was never published. The five species of *Leachia* considered valid were: *L. lemur*, *L. atlantica*, *L. dislocata*, *L. danae*, and *L. pacifica*. The sixth valid species would have been *L. cyclura*; however, no description was provided by the authors for that species.

Most recently, the presence of '*Drechselia danae*' was reported from off the coast of Mexico (De Silva-Dávila, Avendaño-Ibarra, García-Domínguez, & Saldierna-Martínez, 2010). The three specimens reported in this study were attributed to the genus *Drechselia* for the sole reason that it is considered to be the valid generic name according to the Integrated Taxonomic Information System (ITIS). This was the first instance of *L. danae* being recorded in these waters, and all three specimens were caught at shallow depth (less than 200 meters). De Silva-Dávila *et al.* (2010) also described the general morphology of the specimens (all of which were mature) and how they differed from co-occurring species *L. dislocata* and *L. pacifica*. As researchers continue to gain a better understanding of taxonomic differences, we may likely find that these geographic distributions continue to expand.

## Systematics

*Leachia* Lesueur, 1821 (Table 4)

*Leachia* Lesueur, 1821: 12–13, Pl. VI; Steenstrup, 1861: 34–37; Hoyle, 1885: 326–329; Chun, 1910: 271–276, Pl. LII 4–7; Pfeffer, 1912: 650–656, Pl. 47 fig. 2–13; Voss, 1960: 429–433; Young, 1972: 80–83; Voss, Stephen, & Dong, 1992: 189–192, fig. 218a–j, fig. 219a–e; Reid, 2016: 83–85.

*Dyctydiopsis* Rochebrune, 1884: 16–17.

*Pyrgopsis* Rochebrune, 1884: 23–24, Pl. II, fig. 1–6; Pfeffer, 1912: 656–664, Pl. 47 fig. 14–17; Berry, 1920: 298–299, Pl. 16, fig. 5; Robson, 1924: 5–6.

*Zygaenopsis* Rochebrune, 1884: 20; Pfeffer, 1900: 193; Chun, 1906: 84; Issel, 1908: 223–228, Pl. 10, fig. 33–44.

*Perothis* Rathke, 1883: 1–28; Rochebrune, 1884: 25.

*Euzygaena* Chun, 1910: 276–277.

*Drechselia* Joubin, 1931: 197–208, fig. 33–46; De Silva-Dávila, Avendaño-Ibarra, García-Domínguez & Saldierna-Martínez, 2010: 89–93, fig. 2–3.

**Diagnosis:** A small to medium-sized cranchiid (ML to 120 mm in examined material), body slender, with fins together ovoid or circular. Ventral mantle surface with a single longitudinal series of cartilaginous tubercles extending posteriorly from each ventral funnel fusion point. Eyes each with five or more circular photophores. Third arm pair more robust and over twice the length of other pairs; tentacles slender with proportionally small club.

Table 4—Characters used herein to distinguish Pacific species. \*, this research.

Species	Ventral tubercles	Strip length	Eye photophores	Arm sucker dentition	Manus sucker teeth
<i>L. danae</i>	8 complex, with occasional simple in between.	9–11–15% ML	20	3 angular (curved in larger individuals)	15–22
<i>L. dislocata</i>	~7 complex (3 simple in between), dislocated tubercle at anterior margin	13–16–21% ML	15	6–12 angular	15–28
<i>L. pacifica</i>	~ 15 (6 complex with 1 or 2 two simple in between)	15–20%	~5	~10 rounded	12
<i>L. separata</i> *	10 complex and 9–11 individual tubercles posteriorly	15–16–20% (up to 45% with extra tubercles)	16	7–10 angular	24
<i>L. sp. NZ</i> *	6 complex tubercles, simple tubercle at fusion.	18–20% ML	10 or 11	6–12 pointed	~24

***Leachia danae* (Joubin, 1931)** (Figs 2.2–2.7, Table B2)

*Drechselia danae* (Joubin, 1931): 197–208, fig. 33–46; De Silva-Dávila, Avendaño-Ibarra, García-Domínguez & Saldierna-Martínez, 2010: 89–93, fig. 2–3.

*Leachia danae* (Joubin, 1931): Voss, Stephen, & Dong, 1992: 192, fig. 219d.

**Diagnosis:** Sucker rings on third arm pair with three angular teeth (and 2–4 smaller cusps), central tooth enlarged; eyes with 20 photophores: 12 sub-orbital, 7 dorsal to lens, one on posterior of eye; cartilaginous strip ~10% ML.

**Type material:** (not examined) *Drechselia danae* **ZMUC Syntypes (2)** [fide Kristensen and Knudsen (1983:221)]. Type Locality: 6°40'N, 80°47'W (Pacific Ocean).

**Material examined (10 specimens):** **SBMNH 464519:** ML 159 mm, ♀, 24.02°N, 108.87°W, Mexico, Baja California Sur, 2615 m, 16/11/1967; **SBMNH 464440:** ML 154 mm, ♂, 23.23°N, 108.16°W, Mexico, Baja California Sur, 2505 m, 15/11/1967; **SBMNH 464531:** ML 44, 84 mm, ♂, 21.04°N 106.65°W, Mexico, Jalisco, 3291 m, 8/11/1967; **SBMNH 464442:** ML 112 mm, ♂, 20.82°N 106.40°W, Mexico, Nayarit, Islas Marias, Isla Maria Cleofas, 4078 m, 8/11/1967; **NMNH 729787:** ML 74 mm, sex indet., 13.00°N, 102.00°W, North Pacific Ocean, Mexico, 64–435 m, *Minox III*, 16/10/1973; **NMNH 814874:** ML 70 mm, sex indet., 12.03°N, 144.90°W, North Pacific Ocean, Kiribati, Line Islands, 50 m, *Townsend Cromwell R/V*, midwater trawl, sta. 47-16, 23/01/1970; **NMNH 814880:** ML 62 mm, sex indet., 12.03°N 144.90°W, North Pacific Ocean, Kiribati, Line Islands, 50 m, *Townsend Cromwell R/V*, midwater trawl, sta. 47-16, 23/01/1970; **NMNH 814879:** ML 104 mm, sex indet., 11.47°N, 144.46°W, North Pacific Ocean, 50 m, *T. Cromwell R/V*, 31/03/1970; **SBMNH 49616:** ML 103 mm, sex indet., 8.60°N, 84.43°W, Costa Rica, Puntarenas, Velero 19021-73, 25/05/1973.

**Non-localised material examined (1 specimen):** **CAS 030995:** ML 70 mm, sex indet., Guerrero; off Acapulco, 274 m, *Templeton Crocker*, 16/07/1932.

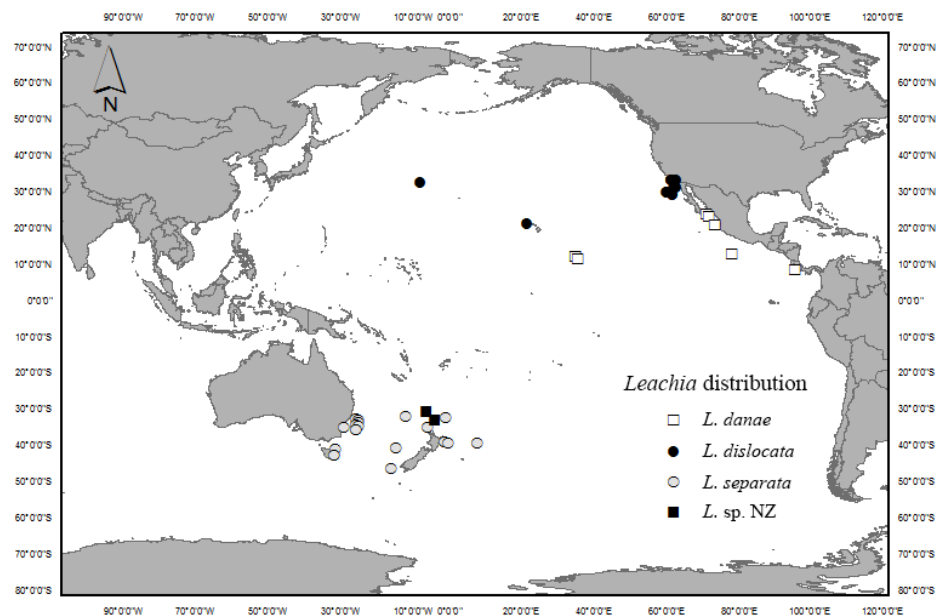


Fig. 2.1— Distribution of examined *Leachia* material in the Pacific Ocean.

**Description:**

**Adult** (70–160 mm; Figs 2.2, 2.3)—Mantle elongate conical, MW 15–20–30% ML; mantle lumen ends midway through fin length. Fins large, FL 30–37–42% ML, FW 38–44–55% ML (FW 105–115–130% FL). Cartilaginous strip ~10% ML, with approximately 10 complex tubercles, one or two simple tubercles interspersed between (Fig. 2.3c). HL 5–10–12% ML, HW 16–19–22% ML. Eye with 20 (or 21?) circular photophores (Fig. 2.4), all photophores developed by 100mm ML, ED 7–11–13% ML; eyes becoming sessile around 80mm ML; however, even by 40 mm ML, stalked eyes have become fairly bulbous and stalks diminished in size. Funnel ~10% ML, base ~30–50–70 MW, narrowing to aperture 30–40–60% FB.

Arms robust at bases, quickly attenuating to tip. Arm formula in adults III>II=IV>I. Arm I 10–16–27% ML, Arm II 17–22–32% ML, Arm III 30–38–50% ML, Arm IV 15–21–29% ML. Arms with low protective membrane along entire length; buccal web minimal or absent, keel present on Arm IV. Suckers spaced widely on arms, those on arm pairs I, II, and IV small, with diameter of Arm III suckers approximately twice as large; basal-most sucker pairs slightly enlarged. Sucker counts on longest arm 26–180; Arm III suckers with 3–7 pointed teeth (Fig. 2.5a), with central tooth enlarged into hook from 7<sup>th</sup> sucker pair in larger individuals (less pronounced in males); sucker rings on Arms I, II and IV also with 3–7 teeth on distal margin, remainder of ring crenulated; mid-arm suckers with sharp teeth, those toward tips generally with fewer, blunter teeth. In mature males, Arm IVR dorsoventrally compressed and enlarged, curling distally, forming disc-shaped hectocotylus (Fig. 2.3b), with thin protective membrane along outer margin; suckers elongated in proximal portion of hectocotylus, with nine angular teeth protruding orally from sucker ring margin; remaining suckers around outer edge of appendage with ~14 small sharp teeth. Females with pigmented brachial organs on all arms, developing from around 110 mm ML.

Tentacles 35–45–52% ML, club 5–8–10% ML (~20% TnL) remaining proportionally small throughout development. Tentacles with 13–18 small suckers along stalk length, distal locking apparatus at distal end of stalk, 4–8 suckers and pads alternating. Clubs with 60–80 suckers; carpus poorly defined, variably present, several greatly enlarged suckers mid-manus with 15–22 small pointed teeth on inner ring margin (Fig. 2.5b); dactylus suckers with 17–22 angular teeth distributed around entire ring margin. In mature males tentacles atrophied, reduced to short transparent appendages lacking clubs or suckers.

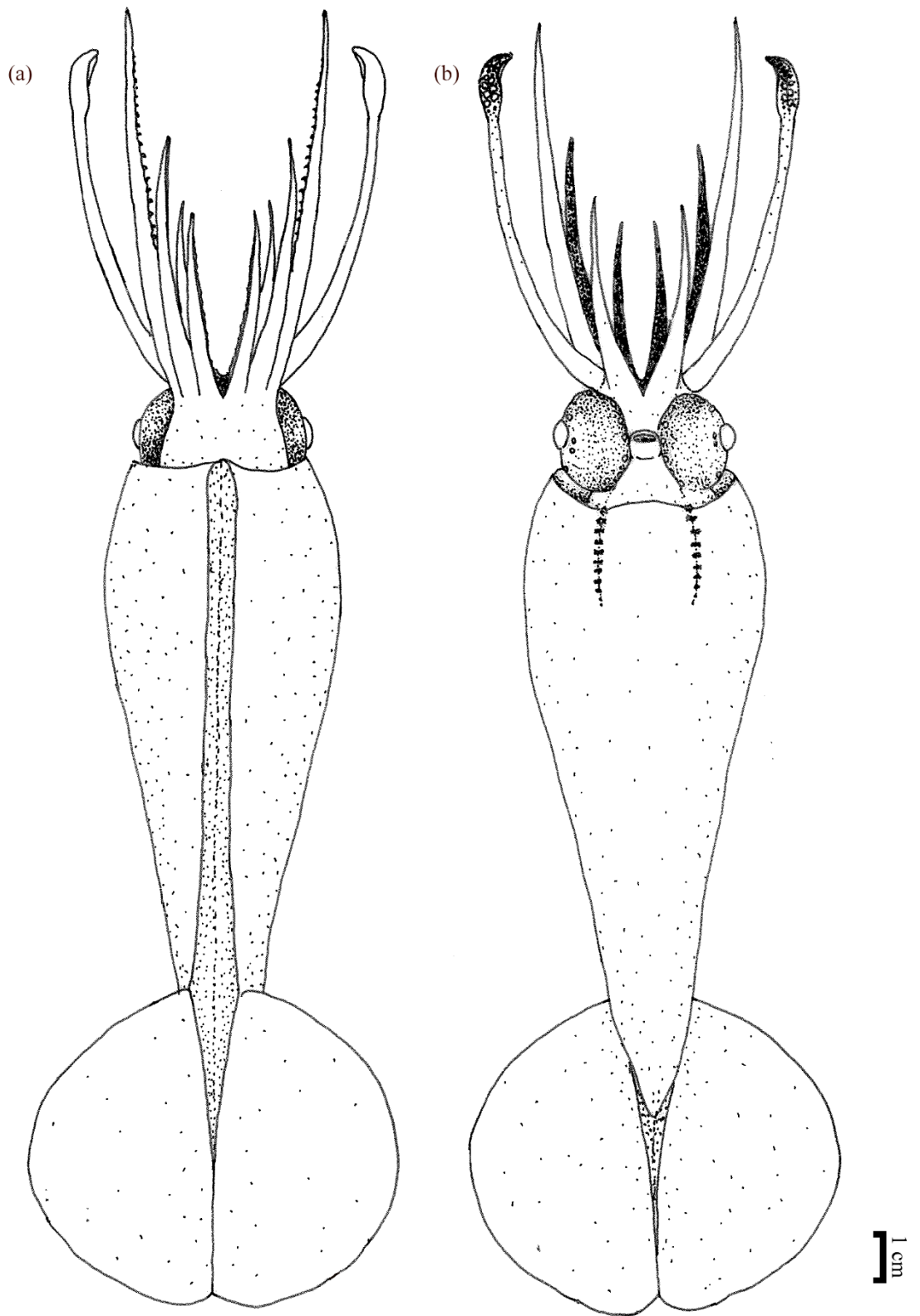


Fig. 2.2—Adult female *L. danae* (a) dorsal and (b) ventral view (SBMNH 464519, ML 159 mm).



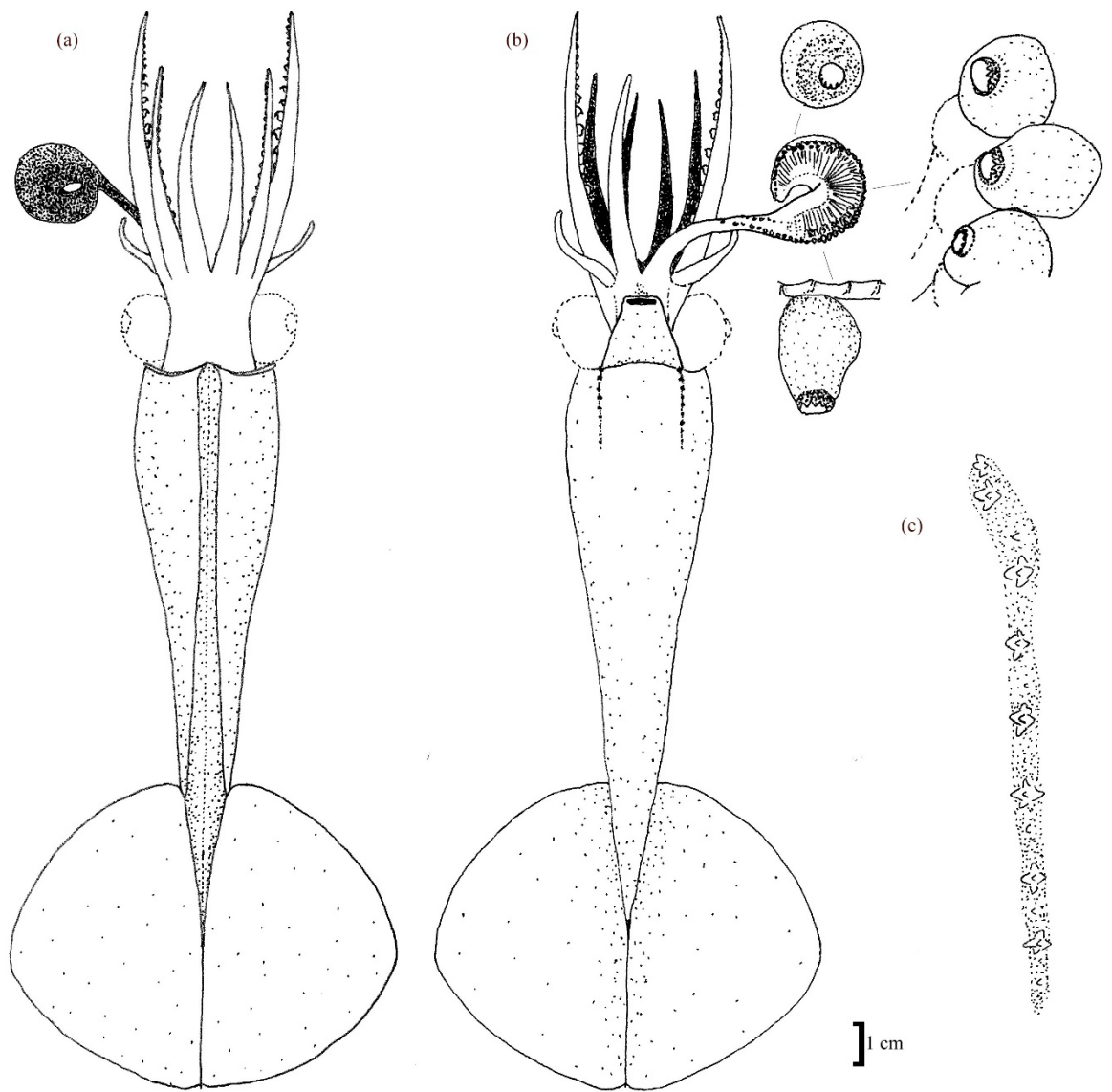


Fig. 2.3—Adult male *L. danae* (a) dorsal, (b) ventral, (c) left cartilaginous strip (SBMNH 464440, ML 157 mm).

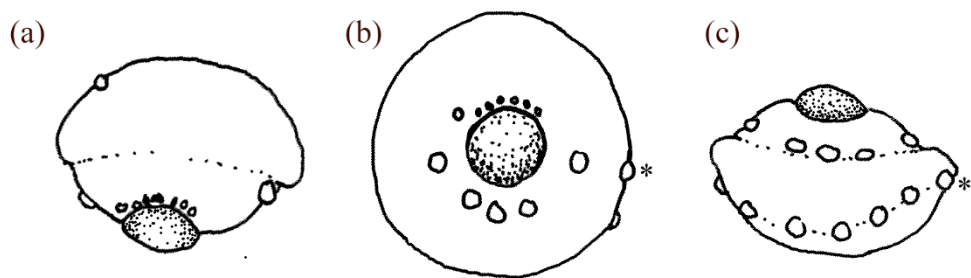


Fig. 2.4—Schematic for right eye of *L. danae* showing (a) dorsal view, (b) lateral view, and (c) ventral view. \* indicates reference photophore.

**Juvenile** (Up to 70 mm ML; Fig. 2.6)—Mantle conical, MW 17–20–24% ML; mantle lumen ends midway through fin length. Fin length 35–38–40% ML, FW 37–42–47% ML (FW 90–112–120% FL). Cartilaginous strip 10–13–14% ML, with approximately eight complex tubercles, one simple tubercle interspersed between. HL 5–11–14% ML, HW 15–20–26% ML. Eyes stalked, stalks diminish with size, eye with 15–19 circular photophores, ED ~6% ML.

Arm formula III>IV>II>I: Arm I 3–6–10% ML, Arm II 6–8–13% ML, Arm III 20–25–30% ML, Arm IV 10–12–17% ML. Sucker counts 60–90 on longest arm; Arm III suckers with three blunt or rounded teeth, the central tooth slightly enlarged; sucker rings on other arms with three or four small blunt teeth or crenulations. Tentacles 34–41–50% ML (Fig. 2.6c), club 6–8–9% ML (~20% TNL) club slightly expanded. Clubs with 60–76 suckers, several enlarged suckers mid-manus with 21–25 small pointed teeth on inner ring margin.

**Known distribution:** Baja California to Costa Rica (Fig. 2.1). Present material collected from surface to 4,078 meters (Fig. 2.7); elsewhere reported from 2,680 meters (Joubin, 1931) and 200 meters (De Silva-Dávila *et al.*, 2010).

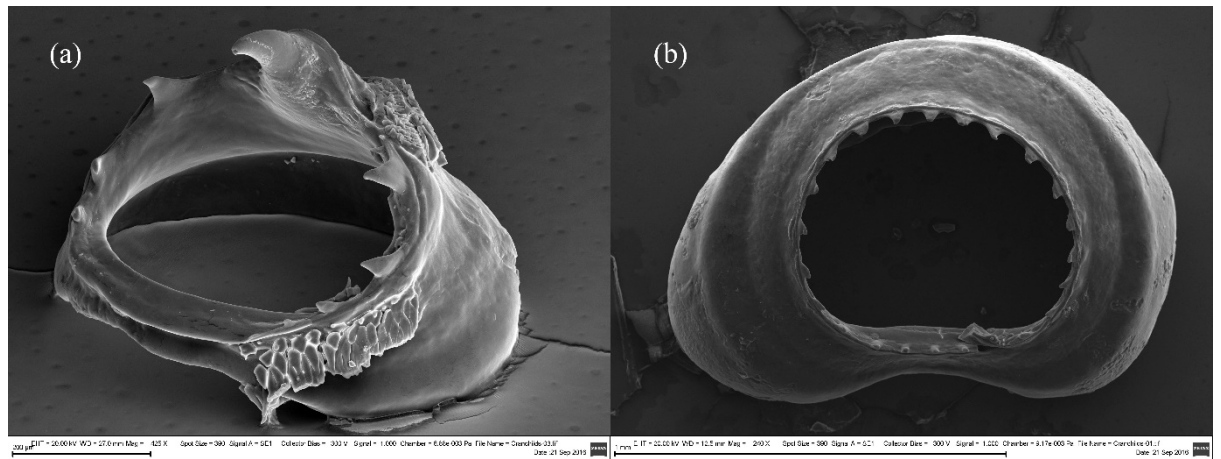


Fig. 2.5—(a) largest sucker ring from Arm III, (b) largest manus sucker ring (SBMNH 464437).

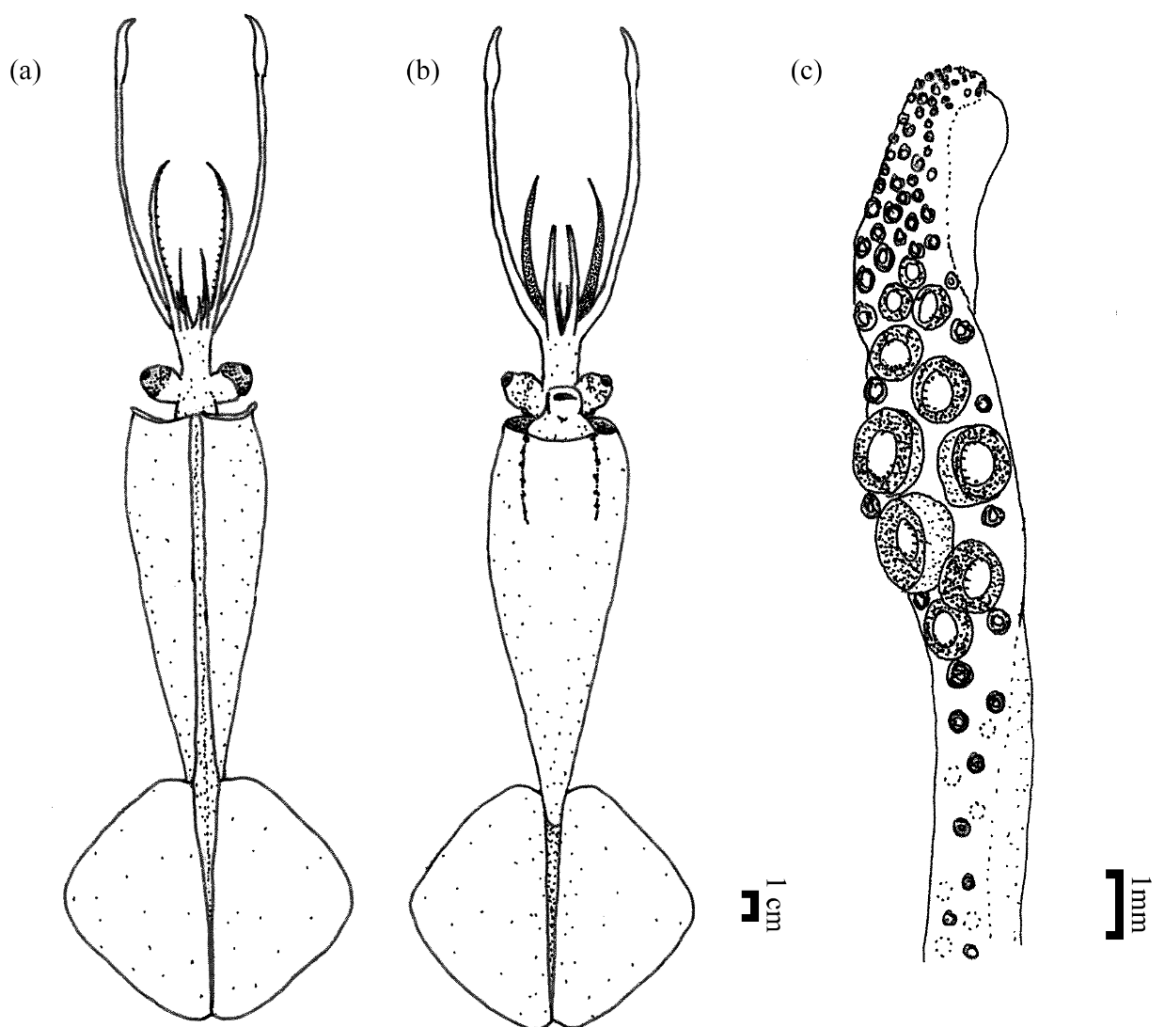


Fig. 2.6—Juvenile *L. danae* (SBMNH 464531, ML 44 mm) (a) dorsal, (b) ventral, (c) right tentacle club.

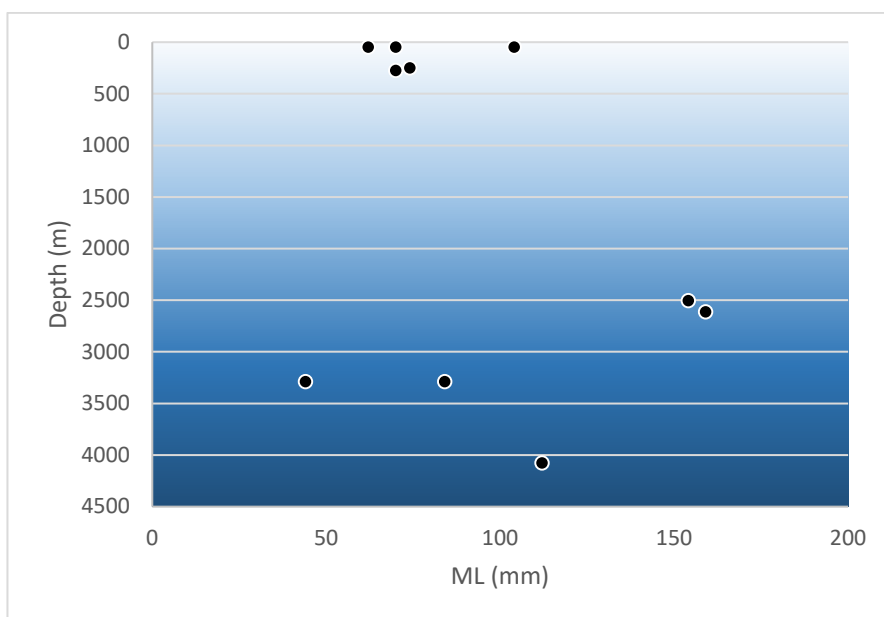


Fig. 2.7—Vertical distribution of *L. danae* specimens examined herein.

**Remarks:** *Leachia danae* and *L. dislocata* are sympatric in the North Pacific, and younger individuals can be difficult to differentiate. In general, the fins of *L. danae* are noticeably larger (FL 30–38–42% ML) than in *L. dislocata* (FL 20–27–35% ML). Overall, the eye diameter of *L. danae* is also generally larger (ED 110–158–238% HL) in adults than was observed in *L. dislocata* (ED 85–115–180% HL); however, this is often not a helpful measurement because eyes are easily damaged. Perhaps most reliably, most specimens can easily be distinguished by the Arm III sucker rings, as *L. danae* develop three distinct teeth from about 40 mm ML. In *L. dislocata* there are often 6–12 angular teeth, although several mature males examined in this study had elongated suckers on Arm III with small apertures and three or four small sharp teeth. The ventral surface of *L. danae* lacks the anterior dislocated tubercle seen in juveniles of *L. dislocata* (appearing by 20 mm ML). The great variation in sucker counts (26 to 180 in mature individuals) appears to represent sexual dimorphism, as SBMNH 464440, a mature male, had the lowest sucker counts of all specimens despite being the second largest specimen examined.

It is possible that the adult description of *L. danae* will resolve in the future to be two separate life stages, possibly a sub-mature and mature stage, as larger specimens show some variation. At ML ~150 mm, Arms I, II, and IV are proportionally longer than those in the next-largest specimen (115 mm ML). It is possible that as sexual modifications develop on the tips of the arms, the average rate of arm growth is reduced, and then continues once the secondary sexual modifications have fully developed. However, no material was available of intermediate size, so it remains unknown at present whether this change in proportions takes place gradually, or suddenly.

***Leachia dislocata* Young, 1972** (Figs 2.8–2.13, Table B3)

*Leachia dislocata* Young, 1972: 80–83; Voss, Stephen, & Dong, 1992: 191, fig. 218c–j, fig. 219c.

*Leachia pacifica* (not Issel, 1908): Nesis, 1987: 270–271, fig. 69O, Q.

**Diagnosis:** Ventral cartilaginous strip (12–16–21% ML) with second anterior tubercle displaced toward midline; complex tubercles with antero-posteriorly compressed shape; eyes with 15 circular photophores.

**Type material:** *Leachia* (*Pyrgopsis*) *pacifica* **SBMNH Holotype 34999** [*fide* Scott *et al.* (1990:20)]. Type locality: 32°35'N, 118°06'W, eastern North Pacific Ocean; **SBMNH 35001**, paratype, ML 91 mm, sex indet., 33.32°N 118.73°W, USA, California, Velero Sta. 8116, 1385 m, 23/08/1962; **SBMNH 35000**, paratype, ML 99 mm, sex indet., 33.25°N 118.53°W, USA, California, Santa Catalina Island, Velero Sta. 8028, 2000 m, 8/08/1962; **SBMNH 35006**, paratype, ML 96 mm, ♂, 31.30°N 117.37°W, Mexico, Baja California, Velero Sta. 10985, 3090 m, 18/02/1966; **SBMNH 35005**, paratype, ML 107 mm, ♀, 30.38°N 118.48°W, Mexico, Baja California, Isla Guadalupe, Velero Sta. 10840, 4000 m, 25/11/1965.

**Material examined (8 specimens):** NMNH 729791, ML 66 mm, sex indet., 33.28°N 117.29°W, North Pacific Ocean, USA, California, San Diego Trough, 0–800 m, 26/08/1948; NMNH 729790, ML 121 mm, sex indet., 30.00°N 120.00°W, North

Pacific Ocean, Mexico, 85–110 m, *Westfall*, Stn: 72-4, 21/08/1972; **NMNH 729792**, ML 90 mm, sex indet., 30.00°N 120.00°W, North Pacific Ocean; Mexico, 40–54 m, 12/07/1972; **NMNH 729793**, ML 76 mm, sex indet., 30.00°N 120.00°W, North Pacific Ocean, Mexico, 58–78 m, *Westfall*, 2 m Tucker trawl, Sta: 72-15, 14/07/1972; **SBMNH 45765**: ML 134, 107 mm, ♂, 29.13°N 118.37°W, Mexico, Baja California, Isla Guadalupe, N. of Guadalupe, 0–2500 m, 25/04/1967; **SBMNH 464505**, ML 106 mm, ♀, 29.15°N, 118.21°W, Mexico, Baja California, Isla Guadalupe, 1792 m, 15/03/1969; **NMNH 814864**, ML 46, 31 mm, ♀, 21.20°N 158.30°W, North Pacific Ocean, Hawaiian Islands, off Kailua, 40 m, *T. Cromwell R/V*, Sta. 7-21, 21/08/1964.

**Non-localised material examined (1 specimen):** **CAS 085043**, ML 104 mm, sex indet., W of Point Arena, 0–106 m, Stn. 3880, 26/03/1979.

### **Description:**

**Adult** (ML 70–140 mm; Fig. 2.8)—Mantle width 14–21–27% ML, anterior glacial terminus with 2–5 small protrusions at tip (Fig. 2.8a). Cartilaginous strips 12–16–21% ML, curving slightly in towards midline near anterior mantle margin; approximately eight complex tubercle clusters on line, often with seven to nine points, and several single- or double-pointed tubercles interspersed between each complex cluster; single complex dislocated tubercle near the anterior mantle, offset toward midline (Fig. 2.8b, c). Fins together circular, FL 20–27–35% ML, FW 33–36–46% ML, attaining greatest width at posterior third. Head rectangular, HL 4–7–12% ML, HW 12–17–21% ML; ED 5–8–11% ML, eyes becoming sessile (~70–100 mm ML) and proportionally larger (85–115–180% HL). Adult eyes with 15 photophores: eight in ventral outer series, five in ventral inner series (three large ocular organs separated by two smaller organs), two small photophores dorsal to lens (Fig. 2.9).

Arms variably with low protective membrane, extending along full arm length. Arm formula III>II=IV>I: Arm I 2–10–22% ML, Arm II 5–16–25% ML, Arm III 16–33–53% ML, Arm IV 5–13–21% ML. Suckers spherical or oblong, often with small apertures. Sucker counts vary among specimens, Arms III often with twice as many suckers as Arms I; however, some specimens with little variation among arms; longest arm with 50–70 suckers, mid-arm sucker diameter three times that of basal suckers, 6–12 angular teeth on distal third of sucker ring (Fig. 2.8d, 2.10c). Secondary sexual modifications present in both males and females: males with right fourth arm dorsoventrally compressed and enlarged, distally curled to form disc-shaped hectocotylus, thin protective membrane along outer margin; suckers elongated slightly, primarily positioned along outer edge of appendage; sucker rings with narrow apertures. Left fourth arm occasionally also slightly modified, with two series of small distal suckers widely spaced from each other. Female modifications found on third arm pair, appearing as pigmented membranes at tip of arm (Fig. 2.10e).

Tentacles 28–34–39% ML (Fig. 2.10a), often only slightly longer than Arms III, with four or five pairs of suckers along stalk length, CL 4–6–8% ML (13–17–21 % TnL) remaining proportionally small throughout maturity. Clubs with 55–65 suckers in four series, 8–10 alternating suckers and pads on carpal locking apparatus, ~20 manus suckers, 5–8 mid-manus suckers enlarged, 40–50 dactylus suckers. Largest manus sucker rings with 15–28 small pointed teeth (Fig. 2.10b), smaller manus suckers with

~eight pointed teeth, dactylus suckers with eight pointed teeth, dentition decreasing towards distal club tip.

Beak (Fig. 2.11): Lower rostral length (LRL) of largest specimen 1.3 mm. Wings and lateral wall not fully darkened, 0.8 mm clear margin remaining around wing periphery, ~3 mm clear at wall margin. In lateral profile (Fig. 2.11a), crest-to-base ratio 0.8; baseline length greater than height. Rostral tip straight, ending in sharp point. Jaw angle and wing angle both obtuse; rostral edge forms shallow, continuous curve. Small rounded wing fold covers jaw angle; wing-to-LRL ratio 0.4. Hood and wings narrow, narrowing further at jaw angle; wing fold appears un-thickened. Hood slightly curved; hood-to-LRL ratio 1.91; hood just above crest. Crest narrow, not thickened, slight curve in profile. Lateral wall with low ridge running horizontally, slightly below crest. Free corners of lateral wall (along baseline) angled slightly outward in ventral view.

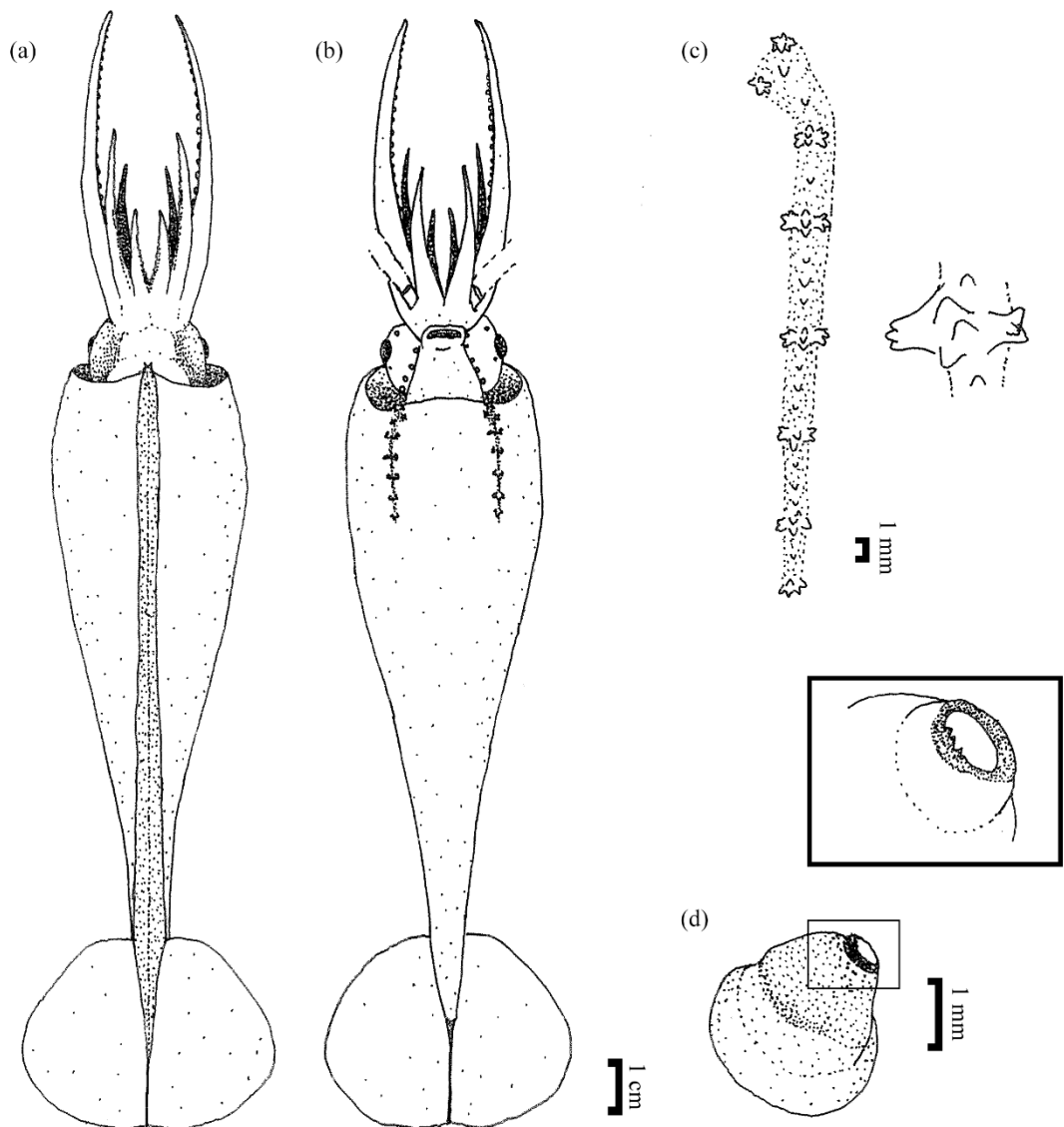


Fig. 2.8—Adult *Leachia dislocata* (SBMNH 45765, ML 134 mm) (a) dorsal, (b) ventral, (c) left cartilaginous strip, (d) Arm III sucker with magnified ring margin [inset].

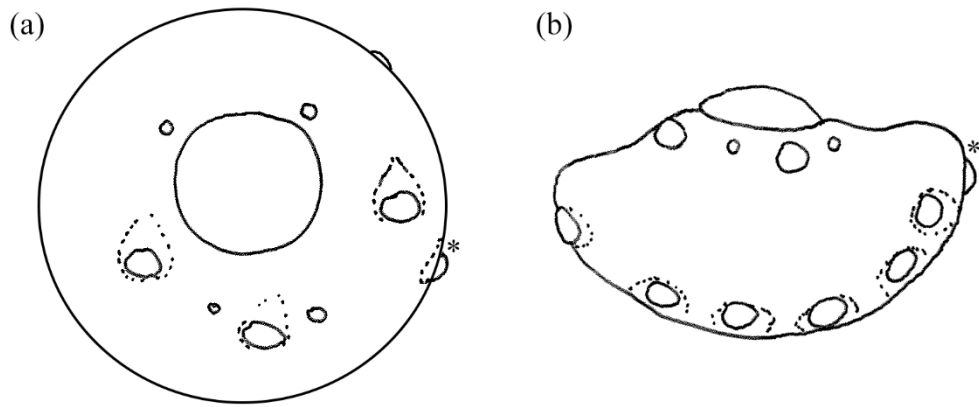


Fig. 2.9—*L. dislocata* left eye schematic showing (a) lateral surface and (b) ventral surface. (\*reference photophore).

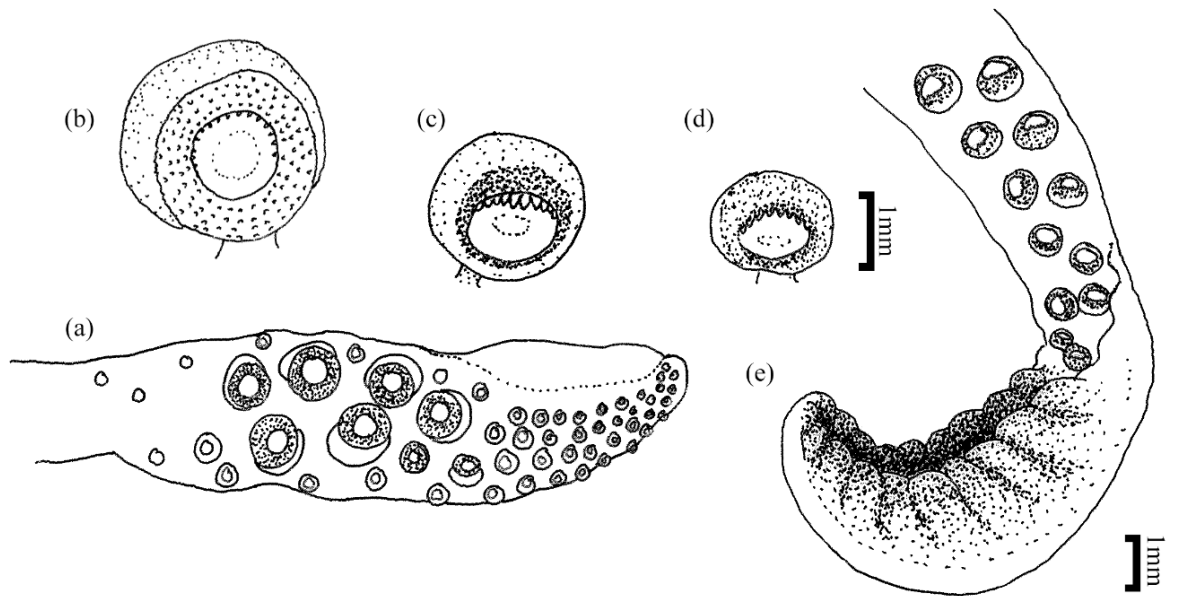


Fig. 2.10—(a) *L. dislocata* left tentacle club (a: NMNH 814864, ML 46 mm), (b) largest manus sucker, (c) mid-arm sucker, (d) distal arm sucker, and (e) female brachial organ (b-e: SBMNH 464505, ML 106 mm).

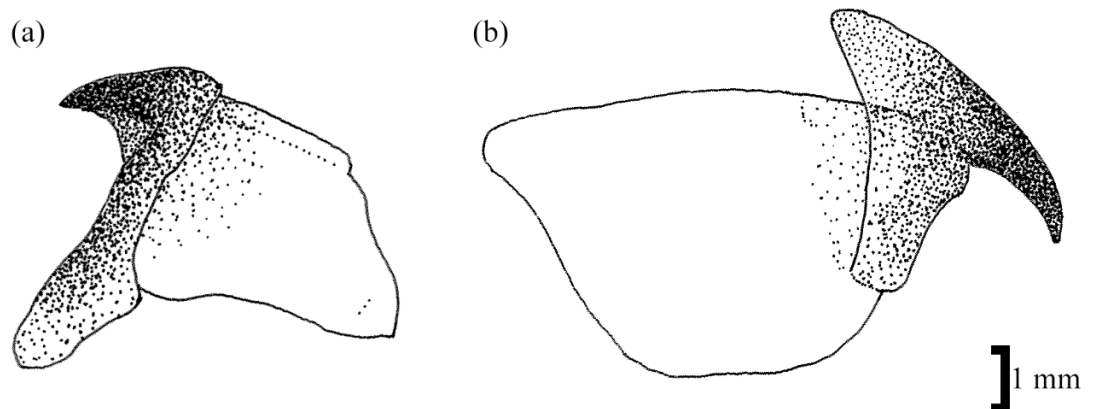


Fig. 2.11—*L. dislocata* beak (SBMNH 45765) (a) lower beak and (b) upper beak.

**Juvenile** (ML ~30–70 mm; Fig. 2.12)—Mantle spindle shaped, MW 16–23–31% ML, anterior glacial terminus with two small protrusions at tip. Cartilaginous strip 13–14–16% ML, approximately six complex tubercle clusters on strip, single complex dislocated tubercle near the anterior margin. Fins oval, FL 23–27–32% ML, FW 31–38–43% ML, widest point mid-fin. Head length 8–11–15% ML, HW 11–18–29% ML; eyes on stout stalks, ED 1–4–6% ML. Photophores in varying stages of development, larger organs becoming visible during this stage.

Arm formula III>IV>II>I: Arm I 4–6–7% ML, Arm II 6–9–11% ML, Arm III 16–24–33% ML, Arm IV 8–11–13% ML. Suckers spherical with about seven angular teeth on distal margin; sucker counts vary between specimens, Arm III often with twice as many suckers as Arm I; longest arm with 40–50 suckers. Secondary sexual modifications developing on females: small brachial organ on third arm pair, tissue not darkened. Tentacles 47–55–65% ML, significantly longer than Arm III, CL 6–8–9% ML (12–14–18 % TnL) remaining proportionally small throughout maturity. Clubs with ~55 suckers in four series, mid manus suckers slightly enlarged; largest manus suckers with 13 small pointed teeth, smaller manus suckers with ~eight pointed teeth.

**Known distribution:** From California to Mexico, Hawaiian Islands (Fig. 2.1). Examined material collected from surface to 4000 meters (Fig. 2.13).

**Remarks:** Despite younger life stages having an elongated buccal pillar, HL ratio remains constant throughout development, which is unusual, as one might expect a trend of decreasing proportional length as the buccal pillar resorbs into the head. This species most closely resembles *L. pacifica* (which also has a dislocated tubercle near the fusion); however, these species can be distinguished by the number of ocular

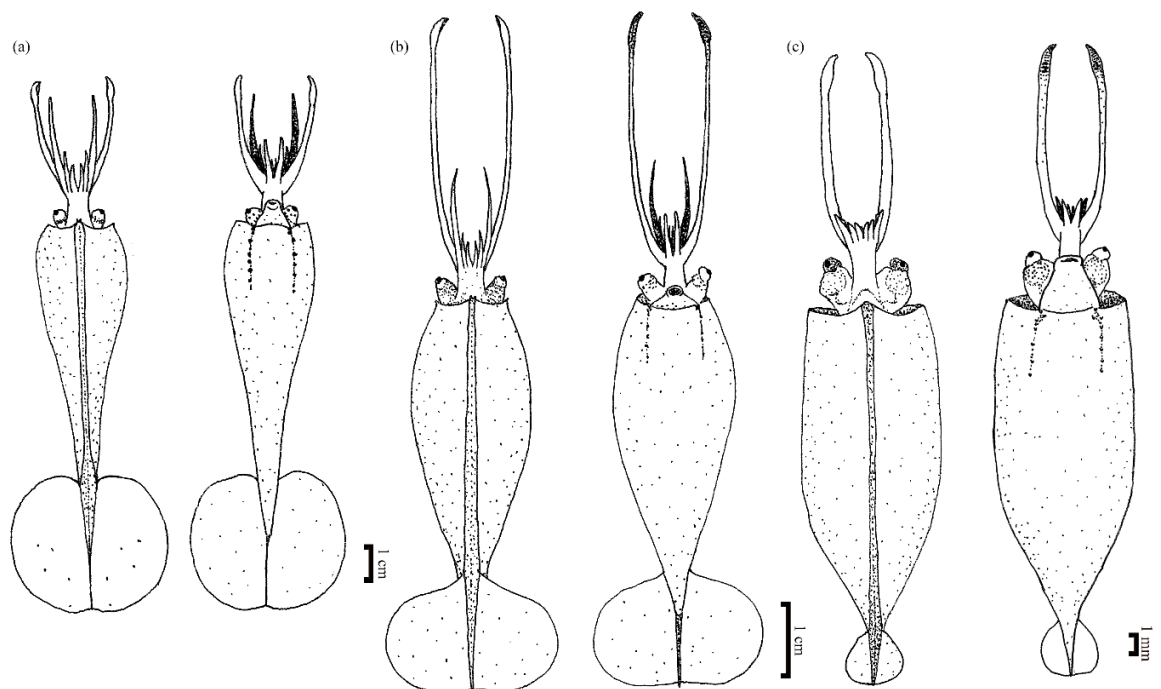


Fig. 2.12—Ontogenetic development of *L. dislocata*: dorsal and ventral views of (a) sub-adult (CAS 85043, ML 104 mm), (b) juvenile (SBMNH 464398; ML 51 mm), and (c) paralarva (SBMNH 464398; ML 20 mm).



photophores (*L. dislocata* with 15 and *L. pacifica* with five or six). The geographic range of *L. dislocata* overlaps with that of *L. danae*, which can again be distinguished by the number of eye photophores (*L. danae* with 20 photophores) or by examining arm sucker dentition (*L. danae* with three angular teeth on sucker ring margin, the central one noticeably enlarged). Unfortunately, small paralarval specimens (below 20 mm ML) could not be examined in this study, so further research is needed in order to complete the ontogenetic series.

***Leachia pacifica* (Issel, 1908) (Fig. 2.14)**

*Zygaenopsis pacifica* Issel, 1908: 223–228, Pl. 10 fig. 33–44.

*Euzygaena pacifica* (Issel, 1908): Chun, 1910: 276–277, Pl. LII fig 1–3.

*Pyrgopsis pacificus* (Issel, 1908): Pfeffer, 1912: 661–664; Sasaki, 1929: 338–340, Pl. XXVII fig. 7–17.

*Pyrgopsis pacifica* (Issel, 1908): Robson, 1924: 5–6.

*Leachia pacifica* (Issel, 1908): Young, 1975: 19–25, fig. 1; Voss, Stephen, & Dong, 1992: 192, fig. 219.

**Diagnosis:** Ventral cartilaginous strip (15–20% ML) usually with an anterior dislocated tubercle; eyes with five ventral photophores.

**Type material:** (not examined) *Zygaenopsis pacifica* **Type repository unresolved.**

**Type locality:** between Tahiti Island and Pago Pago Island (14°32'S, 167°43'W).

**Material examined (1 specimen):** NSMT Mo:72209: ML 31 mm, sex indet., 24.60°N, 124.10°E, Japan, off Ishigaki Island, surface tow, 10/03/1998.

**Non-localised material examined (2 specimens):** two un-catalogued specimens (ML 45, 46 mm) from Hawaiian waters, sent to me via Dr. Richard Young.

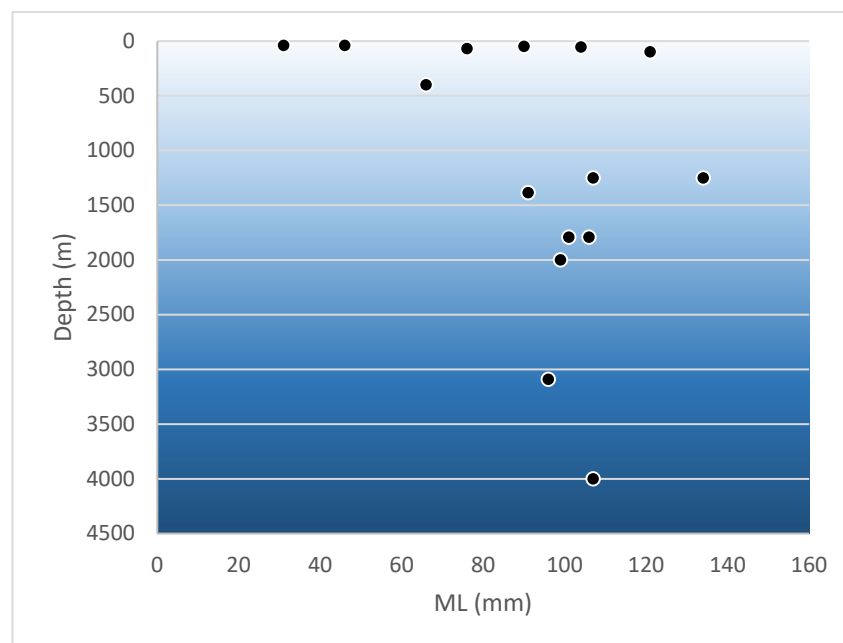


Fig. 2.13—Vertical distribution of *L. dislocata* specimens examined herein.

### Description:

**Paralarva** (30–45 mm ML; Fig. 2.14)—Mantle conical, MW 25–30% ML; ventral cartilaginous strip 15–20% ML, with ~eight complex tubercles, single complex tubercle offset at anterior end, tubercle at ventral fusion simple (Fig. 2.14c). Fins oval, FL 24–27%, FW 30–40% ML. Eyes stalked, ED 4% ML, with five ventral photophores, median photophore largest (Fig. 2.14d). Arms slender, formula  $\text{III} > \text{II} \approx \text{IV} > \text{I}$ : Arm I 7% ML, Arm II 9–11% ML, Arm III 26–29% ML, Arm IV 11% ML; Arm IV with low aboral keel. Arms with up to 52 suckers (Arm IV), suckers sub-equal, increasing in size slightly mid arm. Tentacles 40–48% ML, stalks with ~14 small suckers, clubs 7% ML (14–17% TnL) with ~68 suckers; central manus suckers enlarged.

**Known distribution:** All examined material is from the Hawaiian Islands and Japanese waters; depth previously reported between 30–1800 meters (Young, 1978).

**Remarks:** I examined two uncatalogued paralarval specimens from Dr Richard Young. These specimens seemed to agree with a description of '*P.* *pacificus*' by Sasaki (1929); however, few other historical descriptions of this species provide enough detail to distinguish it from other immature *Leachia*. That being said, no other *Leachia* taxa examined in this study displayed this eye photophore pattern at this size, suggesting that

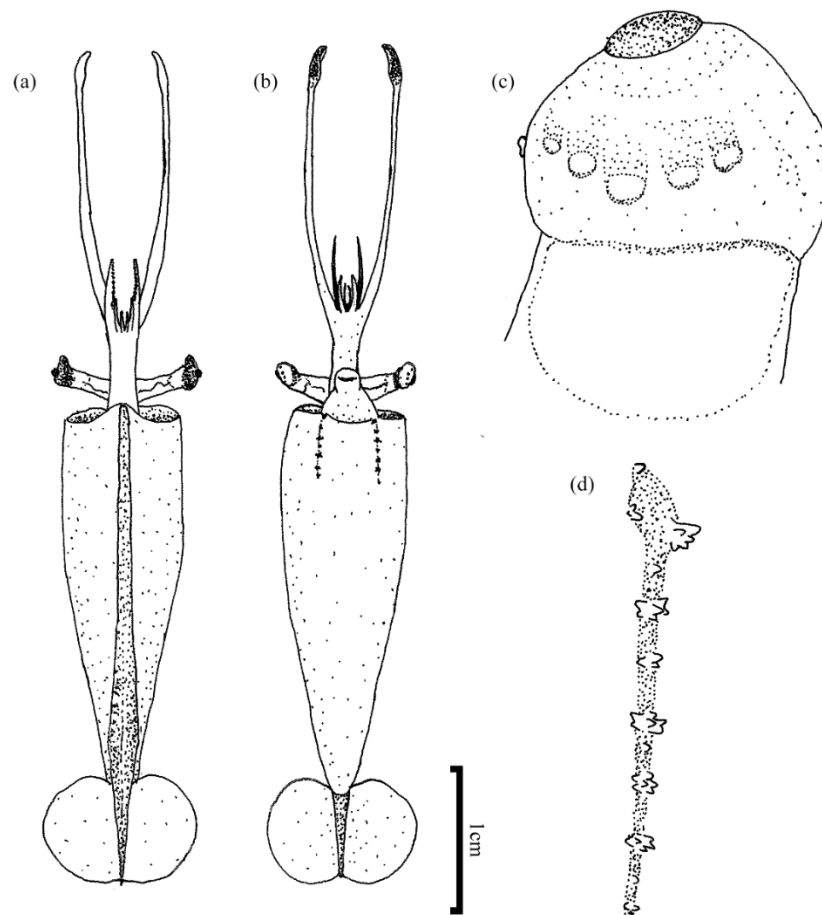


Fig. 2.14—Paralarva *Leachia pacifica* (a) dorsal view, (b) ventral view (NSMT Mo.72209, ML 31 mm), (c) ventral eye photophores, (d) left cartilaginous strip (uncatalogued specimen, ML 46 mm).

these specimens represent a separate taxon. The most morphologically similar species is *L. dislocata*, which has a sympatric distribution and also has an offset tubercle at the anterior end of the ventral cartilaginous strip. These two species can be distinguished based on eye photophore pattern (*L. dislocata* has 15 photophores compared to the five shown above). *Leachia dislocata* also often has two tubercle-like protrusions at the anterior end of the gladius, which are absent in *L. pacifica*.

***Leachia separata*, sp. nov.** (Figs 2.15–2.18, Table B4)

*Leachia eschscholtzii* (not Rathke, 1833): Chun, 1910: 271–276, Pl. LII fig. 4–7; Pfeffer, 1912: 654–656, Pl. XLVII fig. 11–13.

*Leachia pacificus* (not Issel, 1908): Allan, 1945: 338–339, Pl. XXVII fig. 5–11; Reid, 2016: 84–85.

*Leachia cyclura* (not Pfeffer, 1912): Imber, 1978: 449–451, fig. 1C, D.

*Leachia* (*P.*) *rynchophorus* (not Rochebrune, 1884): Nesis, 1987: 270, fig. 69R.

**Diagnosis:** Cartilaginous strip 12–20% ML with additional tubercles extending to 45% ML; eyes with 16 photophores.

**Type material:** *Leachia separata* **NMNZ 5 Syntypes M.067263**, Type locality: New Zealand (39.15°S, 178.83°E).

**Material examined (32 specimens):** **NMNZ M.067263** (5 syntypes), ML 112, 91, 80, 61, 54 mm, ♀/♂, 39.15°S, 178.83°E, New Zealand, 30 m over 1700 m, RV *James Cook*, Stn. J13/19/79, 01/10/1979, MWT; **NMNZ M.074202**, ML 16 mm, 32.40°S, 179.00°E, New Zealand, 274 m, RNZFA *Tui*, Stn.1962095, 25/07/1962; **NMNZ M.091514**, ML 74 mm, sex indet., 32.17°S, 167.91°E, New Zealand, 60 m over 750–1125 m, RV *James Cook*, MWT, Stn.J16/23/85, 24/10/1985; **NMV F163519**, ML 49 mm, sex indet., 32.82°S, 154.17°E–35.81°S, 155.14°E, New South Wales, 20–425 m, CSIRO RV *Soela*, 30/09/1981; **NMV F163601**, ML 94 mm, sex indet., 33.14°S 154.87°E, New South Wales, East of Newcastle, 20 m, CSIRO RV *Soela*, 12/10/1981; **NMV F163558**, ML 97 mm, sex indet., 33.80°S, 154.87°E, New South Wales, 20 m, CSIRO RV *Soela*, 10/10/1981; **NMV F163533**, ML 55 mm, sex indet., 34.46°S, 154.49°E, New South Wales, 20 m, CSIRO RV *Soela*, 30/09/1981; **NMV F163563**, ML 81 mm, sex indet., 34.67°S, 155.01°E, New South Wales, 210 m, CSIRO RV *Soela*, 08/10/1981; **NMNZ M.091689** (2 specimens), ML 42, 41 mm, sex indet., 34.95°S, 173.95°E, New Zealand, North Island off Cavalli Islands, 04/09/1977; **NMV F163526**, ML 35 mm, sex indet., 34.95°S, 151.13°E–35.00°S, 151.12°E, New South Wales, off Nowra, MWT, 0–250 m, CSIRO RV *Franklin*, 14/07/1986; **NMV F163576**, ML 42 mm. sex indet., 35.63°S, 154.24°E, New South Wales, 40 m, CSIRO RV *Soela*, 05/10/1981; **NMV F163577**, ML 81 mm, sex indet., 35.64°S 154.35°E, New South Wales, 20 m, CSIRO RV *Soela*, 05/10/1981; **NMNZ M.070963**, ML 102 mm, sex indet., 39.15°S, 178.85°E, New Zealand, 60 m over 1700 m, RV *James Cook*, MWT, Stn. J13/27/79, 02/10/1979; **NMNZ M.091573** (2 specimens), ML 108, 107 mm, sex indet., 39.23°S 179.67°E, New Zealand, North Island, East of Mahia Peninsula, 30 m over 3595–3604 m, RV *James Cook*, MWT, Stn. J12/19/87, 15/09/1987; **NMNZ M.091560**, ML 72, 61 mm, sex indet., 39.23°S, 179.83°E, New Zealand, 30 m over

3600 m, RV *James Cook*, MWT, Stn. J12/16/87, 14/09/1987; **NMNZ M. 091543**, ML 83 mm, sex indet., 39.25°S, 187.59°E, New Zealand, 30 m, RV *James Cook*, 13/09/1987, midwater trawl, Stn. J12/09/87; **NMNZ M.091568** (3 specimens), ML 113, 93, 74 mm, sex indet., 39.26°S, 179.84°E, New Zealand, 30 m over 3600 m, RV *James Cook*, MWT, Stn. J12/18/87, 14/09/1987; **NIWA 90004**, ML 102 mm, sex indet., 40.76°S 165.31°E, 4215 m, Station: TAN1311/33, 13/10/2013; **NMV F163518**, ML 31 mm, sex indet., 41.14°S, 148.75°E–41.14°S, 148.75°E, 1000 m, 18/07/1991; **NMV F52269**, ML 24 mm, sex indet., 42.67°S, 148.30°E, South Eastern Tasmania, 10–12 m over 104 m, RV *Soela*, 20/06/1984; **NMV F52113**, ML 90 mm, sex indet., 42.71°S, 148.42°E, Eastern Tasmania, RV *Soela*, Stn.84/20, 18/08/84; **NMNZ M.091657**, ML 117 mm, ♀, 46.56°S, 164.06°E, New Zealand, 75–495 m over 4793m, RV *Kaiyo Maru*, Bongo Nets, Stn. KM/111A/85, 29/07/1985.

**Non-localised material examined (4 specimens):** **NMV F163592**, ML 27 mm, sex indet., RV *Sprightly*, SP8/82/34, 29/08/1982; **NZB 110359**, ML 64 mm, Borneo, 1875; **NMNZ M.074350**, ML 78 mm, sex indet., New Zealand, RV *W. J. Scott*, 08/05/1976; **NMNZ M.074228**, ML 74 mm, New Zealand, South Island, Cloudy Bay, 27–37 m, RV *W. J. Scott*, 20/09/1971.

### Description:

**Adult/(sub-adult?)**(ML 35–117 mm; Fig. 2.16)—Mantle width 10–21–35% ML; ventral cartilaginous strip 12–16–20% ML with 5–10 complex tubercles (each tubercles with 5–7 points), several single-pointed tubercles interspersed between each; series of 7–12 complex tubercles continuing posterior to the termination of the ventral cartilaginous strip (Fig. 2.16c), up to 45% ML (starting from anterior mantle fusion). Fins together rhombic in shape, FL 20–29–42% ML, FW 17–38–55% ML (FW 110–132–157% FL), attaining greatest width at posterior third. Head with extended brachial pillar, ventral surface of head appears as a flat rectangular surface; HL 8–13–20% ML, HW 10–15–25% ML; however, HL proportionally shorter as ML increases while HW varies with ontogeny. Eyes small, ED ~5% ML in specimens with stalked eyes (but see Remarks), most specimens with stalked eyes (Fig. 2.17); 16 photophores: eight sub-equal, round photophores on ventral surface, five elliptical photophores on ventral surface, three circular photophores closer to lens; olfactory papilla appears as rounded or cup-shaped protrusion on ventral surface of eye or on eye stalk. Funnel base ~30% MW with aperture size varying greatly with preservation of specimen. Dorsal pad of funnel organ appears as inverted ‘V’ with large angular flaps at lateral arms and single small papilla at anterior midpoint; ventral pads appear as elongated ovals, pointed slightly at anterior end.

Arms tapering rapidly to tip, arm formula III>II≈IV>I: Arm I 4–7–15% ML, Arm II 7–13–20% ML, Arm III 20–30–45% ML, Arm IV 5–11–18% ML. Low protective membrane along entire length, webbing absent. Up to 50 suckers on arms in most specimens (two immature male specimens with 70 suckers on third arms), suckers spherical, slightly larger at arm base, on slender peduncles, with 7–10 pointed teeth (2.14a); proximal margin of sucker ring with wide lip. Female modifications on Arm III, fleshy membrane around distal tip of arm, lacking pigmentation (Fig. 2.18b). Male Arm IVR, sucker series separated to outer edge of arm on distal 25%, membranous keel along ventral margin of arm.

Tentacles slender, TnL 42–55–74% ML, CL 4–7–10% ML; tentacular stalk with 10 small suckers; carpal-locking apparatus present at distal end with five suckers and pads alternating; 10–12 mid-manus suckers enlarged (~3x larger than remaining manus suckers), dactylus with ~50 suckers (Fig. 2.18d). Manus sucker rings with ~24 minute peg-like teeth around entire margin, distal 12–16 teeth easiest to distinguish (Fig. 2.18c); sucker ring wide with rough texture; protective membrane on dorsal surface of club, large keel on ventral surface.

**Known distribution:** New Zealand to Northern Australia (Fig. 2.1). Present material collected from surface to 4215 meters (Fig. 2.15).

**Remarks:** This taxon was challenging to resolve due to the systematic instability of the genus; *L. separata* specimens have previously been attributed to several other names, but careful examination shows that published descriptions of these taxa do not match the present material. For instance, *Leachia cyclura* was originally described from an illustration of the dorsal surface of the type specimen; however, several sources (Joubin, 1905; Pfeffer, 1912) mentioned the presence of six eye photophores (whereas *L. separata* sp. nov. has 16). Both *L. rhynchophorus* and *L. schneehagenii* were described from small, damaged specimens, and it is challenging to compare current material to these descriptions; however, Pfeffer (1912) did describe the cartilaginous strip of *L. schneehagenii* as being <25% of the mantle length and no additional cartilaginous tubercles were noted posterior to this strip.

The type specimen of *Pyrgopsis rhynchophorus* also has a short (3 mm; ML damaged) ventral cartilaginous strip, with no additional ventral tubercles occurring posterior to it, and examination of the eye revealed only four photophores present (although the eyes were both extremely damaged). Based on existing descriptions and type material, both of these species differ morphologically from *L. separata*. The final possible identification for this species was *L. eschscholtzii*; however, the holotype is no longer extant, although a ‘syntype’ (ZMB 110359) described by Chun (1910) is

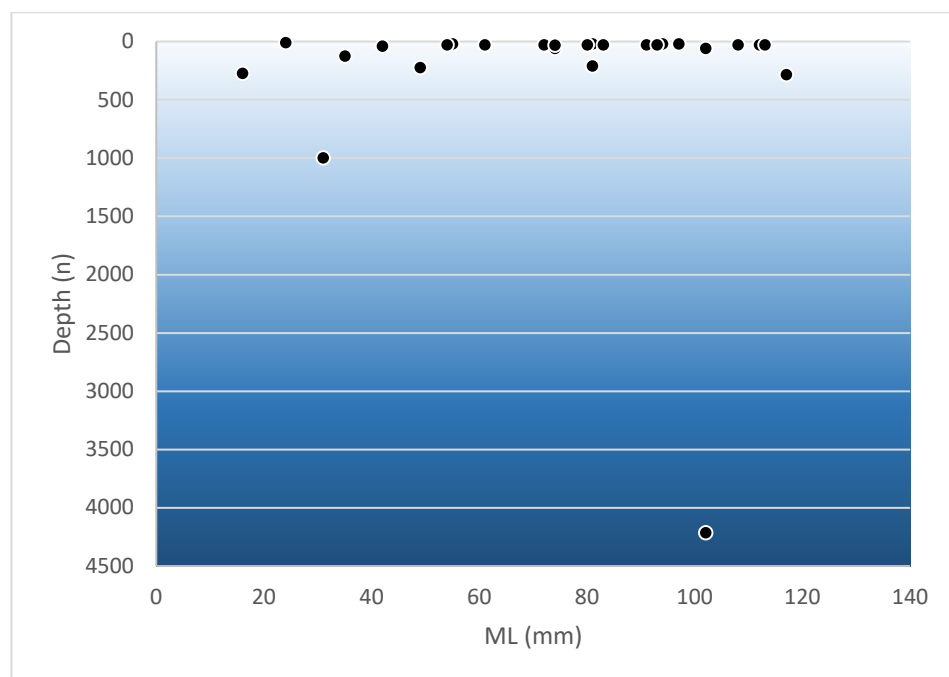


Fig. 2.15—Vertical distribution of *L. separata* material examined herein.

believed to represent this species. This specimen is morphologically similar to *L. separata*, but differs from the original type specimen described by Rathke (1835) which had eight simple tubercles and about four eye photophores. The two specimens were caught 40 years apart and the locality of Rathke's and Chun's specimens also differed, as Rathke's holotype was caught near Madagascar and Chun's 'syntype' was caught off Borneo. Based on this information, it is apparent that Chun's specimen is the same species as *L. separata*; however, due to the differing characters in the type description, this specimen should not be attributed to *L. eschscholtzii*. Therefore, upon reviewing historical descriptions of named *Leachia* taxa, and after examining several types, the more common New Zealand taxon appears to represent a novel species, herein named *L. separata*. Little molecular information is available for *Leachia*; however specimens of *L. separata* all fall within a single BIN for CO1 (BOLD: ADH5276), which is distinct from sequenced *Leachia* material from the Atlantic Ocean (Fig. 11.1).

This species matures at a larger size than other *Leachia* species; among the material examined, only one specimen, a female (ML 112 mm), possessed sessile eyes (a character state normally attained by ML 40 mm in most Pacific congeners). Male modifications appeared to be developing on several mid-size specimens (ML 91, 94 mm), producing the unusual combination of stalked eyes and sub-mature arm characters. Males may mature at smaller sizes than females, as those on the largest female specimen were only just beginning to develop. Because of this combination of immature and mature characters, the largest specimens examined may not be fully developed adults; this is noted at the beginning of the description.

*Leachia separata* occurs sympatrically with *L. sp. nov.* but can be distinguished by the number of photophores on the eyes (16 in *L. separata* and 10–11 in *L. sp. nov.*). In addition, the cartilaginous tubercles in *L. separata* are unique among Pacific *Leachia* in that they continue past the posterior terminus of the cartilaginous strip (Fig. 2.16c). This feature was the basis for deriving the name *L. separata*, as these tubercles are not connected to the rest, as is seen commonly in other *Leachia* taxa.

**Etymology:** This species is named for the separate cartilaginous tubercles, found posterior to the cartilaginous strip, on the ventral mantle (from the Latin 'separata' meaning 'separated'). This feature appears to be unique amongst the Pacific *Leachia* taxa.

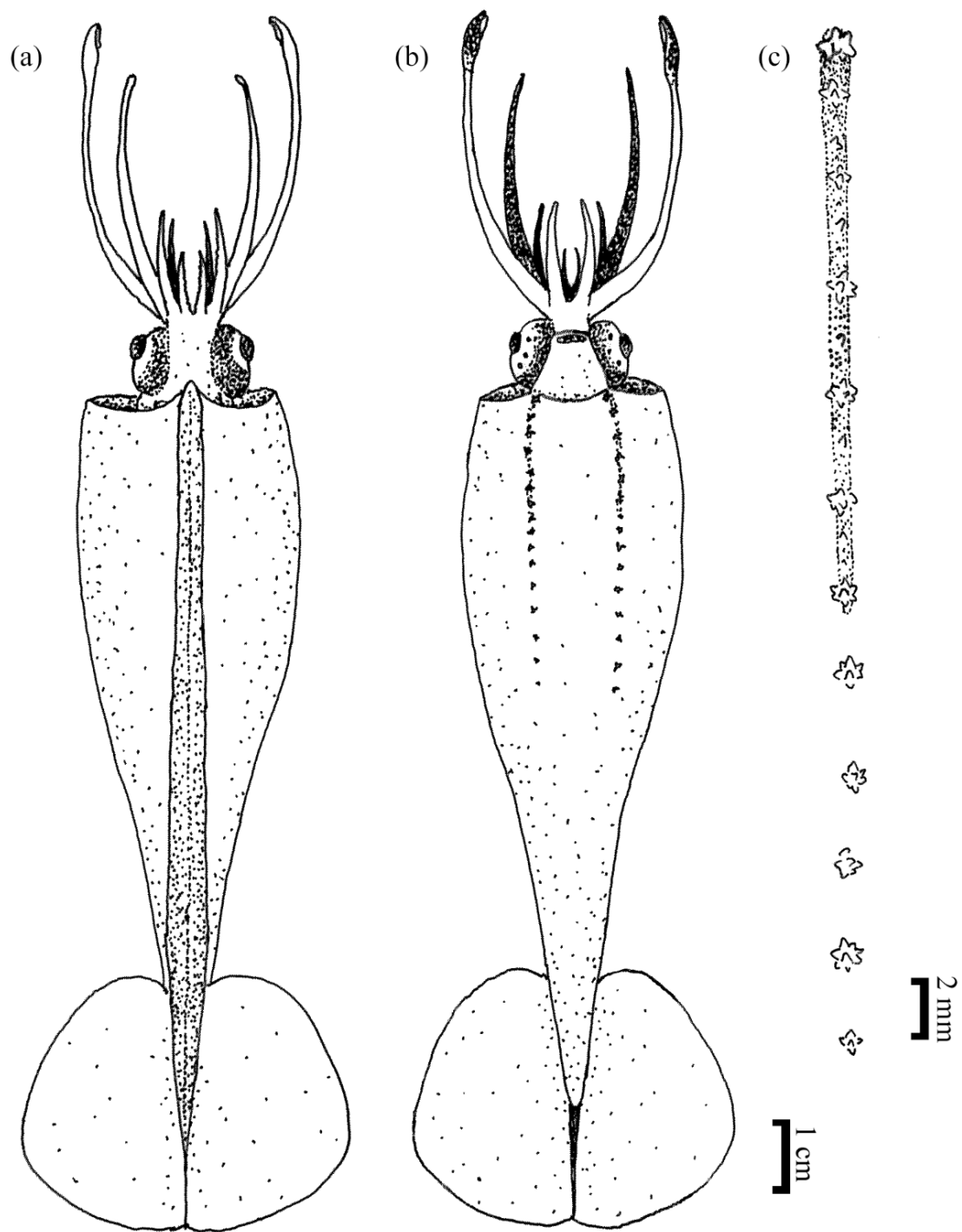


Fig. 2.16—Sub-adult(?) *L. separata* (a) dorsal view, (b) ventral view, (c) left cartilaginous strip (NMNZ M.067263, ML 112 mm).

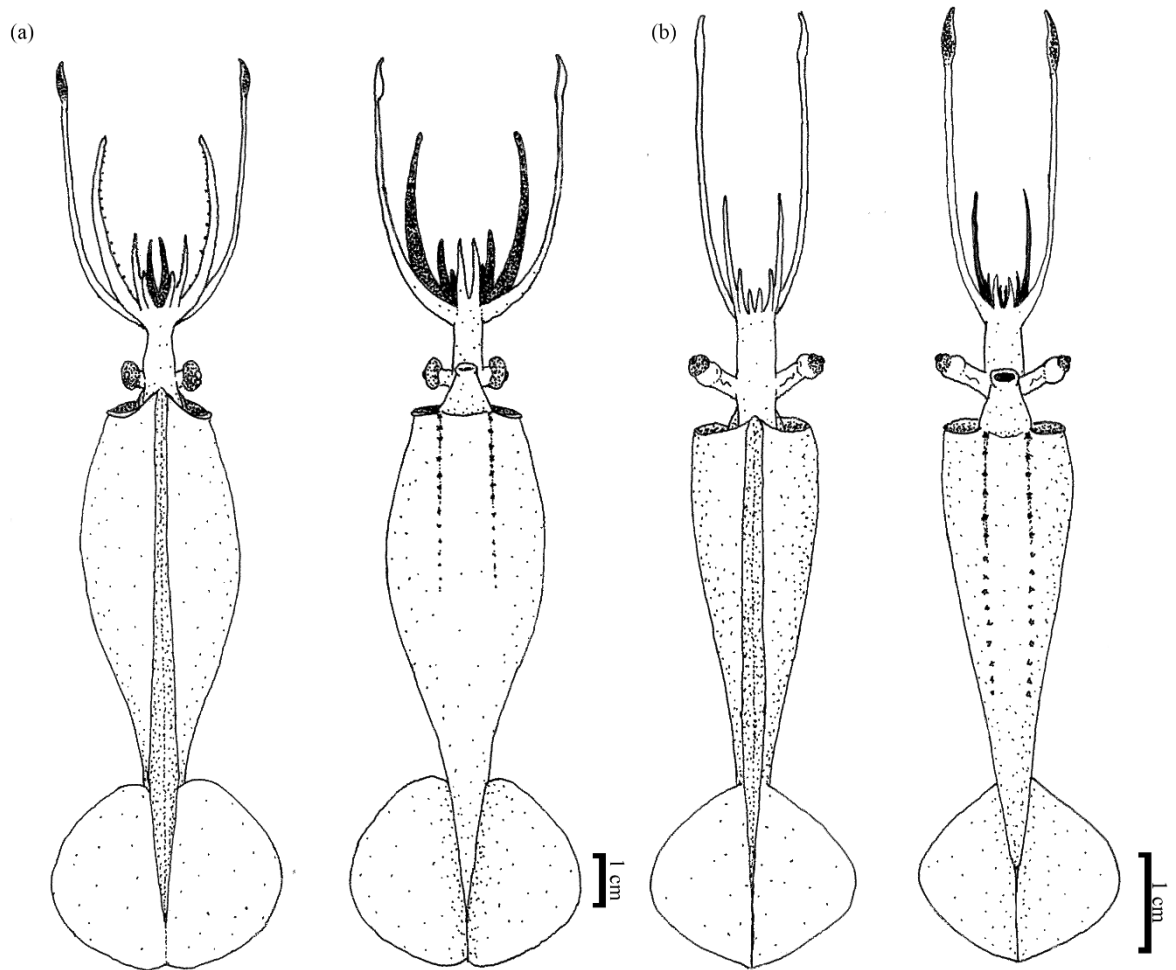


Fig. 2.17—*Leachia separata* ontogenetic growth: dorsal and ventral views of (a) sub-adult (NMNZ M.091657, ML 117 mm), (b) juvenile (NMNZ M.091554, ML 53 mm).

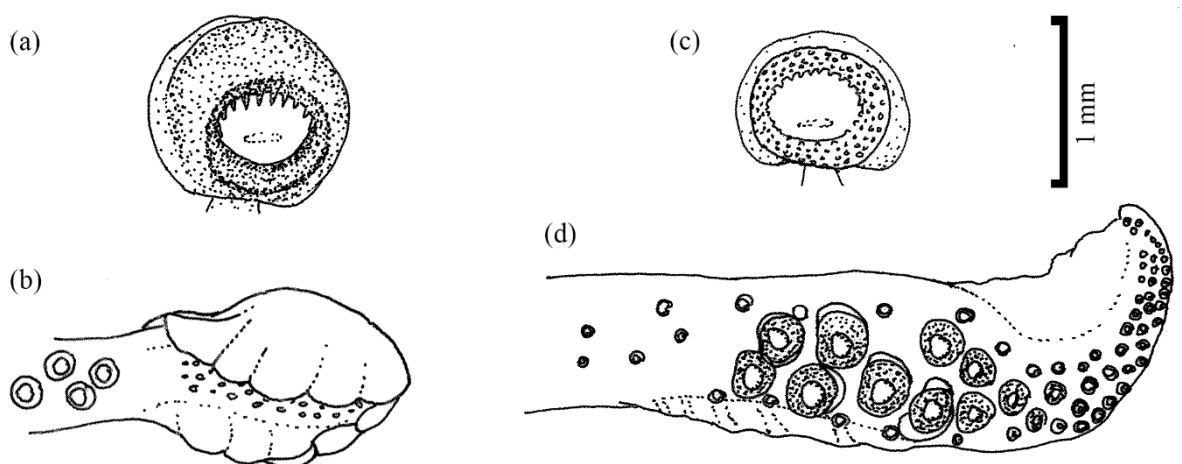


Fig. 2.18—Armature for *L. separata*: (a) mid-Arm III sucker, (b) female brachial organ, (c) largest manus sucker on (d) left tentacular club (NMNZ M.067263, ML 112 mm).



***Leachia* sp. NZ, sp. nov.** (Figs 2.19–2.21)

*Leachia eschscholtzii* (not Rathke, 1833): Imber, 1978: 452–453.

**Diagnosis:** Cartilaginous strips ~20% ML, eyes sessile around 50 mm ML with 10 or 11 round photophores on eyes.

**Material examined (2 specimens):** NMNZ M.074174, ML 56 mm, sex indet., 33.15°S, 176.10°E, New Zealand, 732–869 m over 3508 m, RNZFA *Tui*, MWT, Stn. 1962078, 23/07/1962; NMNZ M.074203 ML 46 mm, ♀, 30.70°S, 173.85°E, New Zealand, Kiwi Seamount, Northern Three Kings Rise, 521 m, RNZFA *Tui*, MWT, 06/07/1962.

**Description:**

**Juvenile** (ML 46–56 mm)—Mantle width ~27% ML (Fig. 2.19a), cartilaginous strips ~20% ML, curving slightly towards ventral midline near anterior end (Fig. 2.19b), strips with ~17 tubercles: six larger complex tubercles spaced equally along line with two or three smaller, single-point tubercles interspersed between complex tubercles (Fig. 2.19c). Fins together ovate, FL 27% ML, FW 38% ML, (FW ~1.4x FL), attain greatest width midway along fins. Head small, HL 8% ML, ventral surface of head appears as a flat rectangular surface; HW 25% ML. Eyes sessile, with nine round photophores on ventral surface: five along the lower ventral surface, three in an inner orbit closer to the lens, and a single photophore located towards the base of the eye (Fig. 2.20). As the eyes were damaged, the presence of two other possible photophores (a fourth in the inner orbit, and a small one along the eyes midline situated directly beside the lens itself) is suspected but has not been confirmed. Funnel narrow (FB ~30% MW) with small aperture (FA 40% FB).

Arms robust, tips not whip-like; Arm III over twice the length of other arms; arm formula III>IV>II>I, Arm I ~7% ML, Arm II ~10% ML, Arm III ~25% ML, Arm IV ~11% ML. Protective membrane extends along full arm length, buccal webbing absent. Suckers small, sub equal, with 6–12 small pointed teeth on distal margin (Fig. 2.19e). Sucker series on Arms III spaced widely laterally. Tentacles short, around 30% ML, club 7% ML (22% TnL), only slightly expanded, with ~60 suckers: carpal locking apparatus present on tentacular stalk, three alternating suckers and pads; manus with 16 suckers, eight enlarged; dactylus with ~40 suckers in four series until distal tip, narrowing to two series; largest manus club sucker ring with ~24 small blunt peg-like teeth on inner ring margin (Fig. 2.19d); sucker ring margins wide with rough texture.

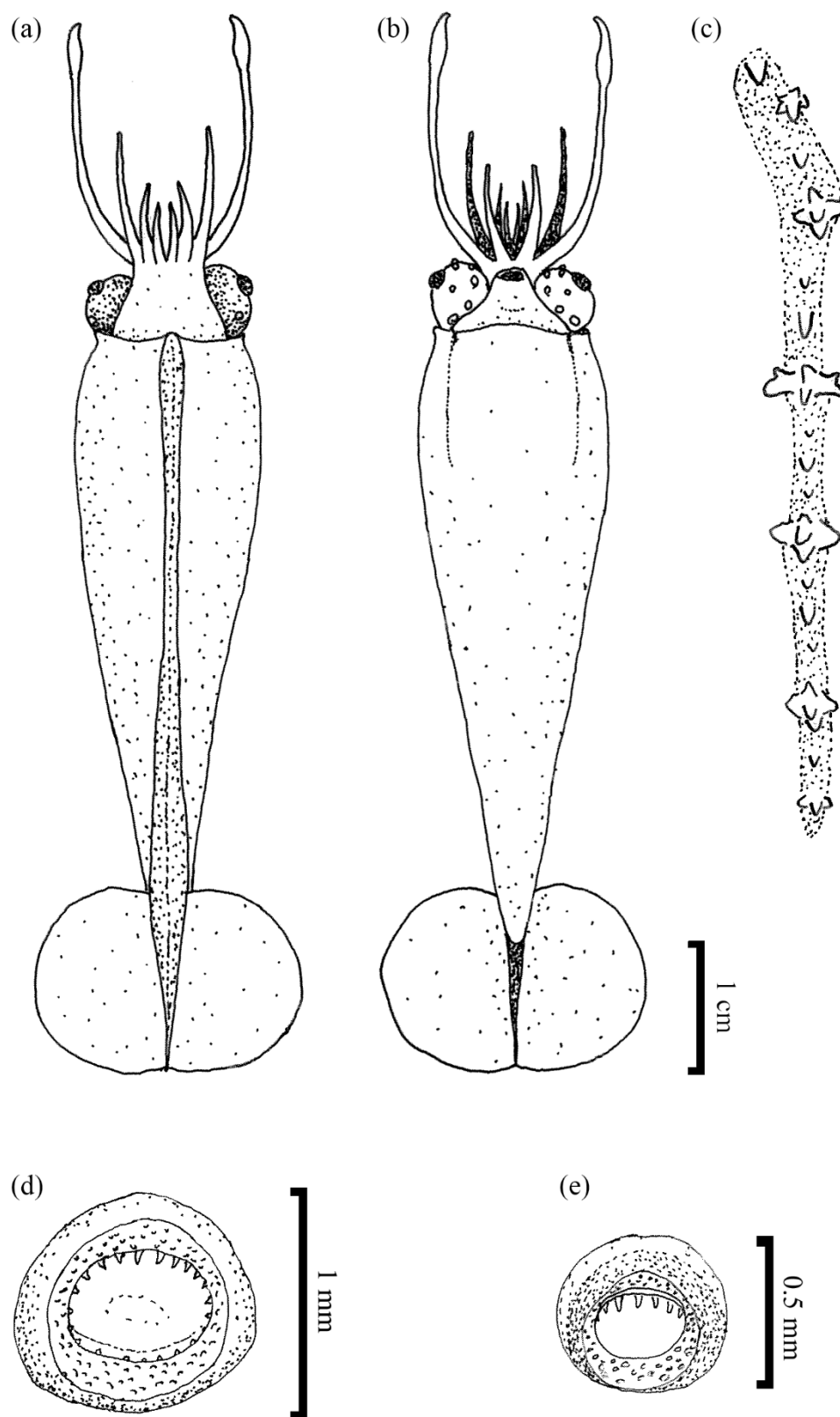


Fig. 2.19—Juvenile *Leachia* sp. NZ, sp. nov. (a) dorsal and (b) ventral view, (c) cartilaginous strip, (d) manus sucker, and (e) arm sucker (NMNZ M.074174, ML 56 mm).

**Known distribution:** Both specimens known to date were collected in northern New Zealand waters. Present material collected from 732–869 meters depth.

**Remarks:** Two specimens of *Leachia* from New Zealand collections lacked the extended ventral line of tubercles present on *L. separata*, the more commonly seen taxon in New Zealand collections. Initially, these two specimens appeared referable to *L. pacifica*, which was thought to be common throughout the Pacific Ocean and has been described as having shorter ventral cartilaginous strips; however, given the number of eye photophores it is more likely this is an undescribed taxon, as *L. pacifica* has been described as only having five or six ventral photophores, whereas the material examined from New Zealand clearly had at least ten (and possibly eleven as there seems to be a space where one photophore appeared to be missing due to damage). Of the two specimens of *L. sp. NZ* examined, one was an immature female while the other was also immature, but the sex was indeterminate due to damage. Brachial organs were forming on third pair of arms in the confirmed female specimen; however, these were not yet pigmented or developed enough to properly describe. Although a beak was removed from one of the specimens, it was too damaged for detailed morphometric reporting (Fig. 2.21); an illustration has been provided.

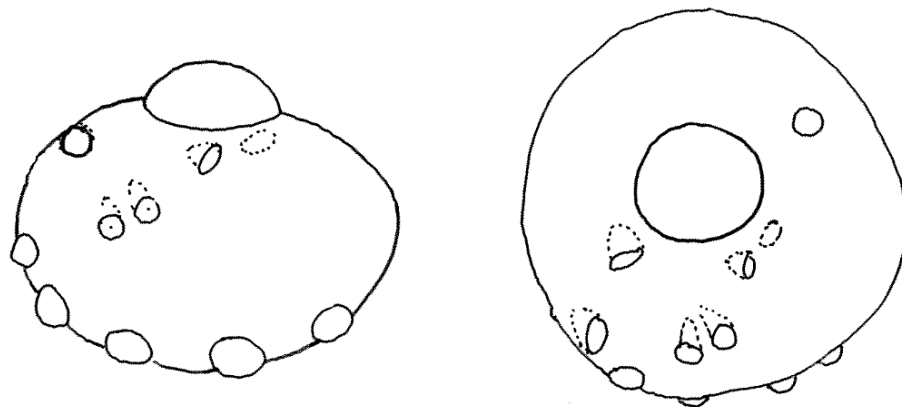


Fig. 2.20—Left eye schematic for *L. sp. NZ*, sp. nov. (M.074174; 56 mm ML).

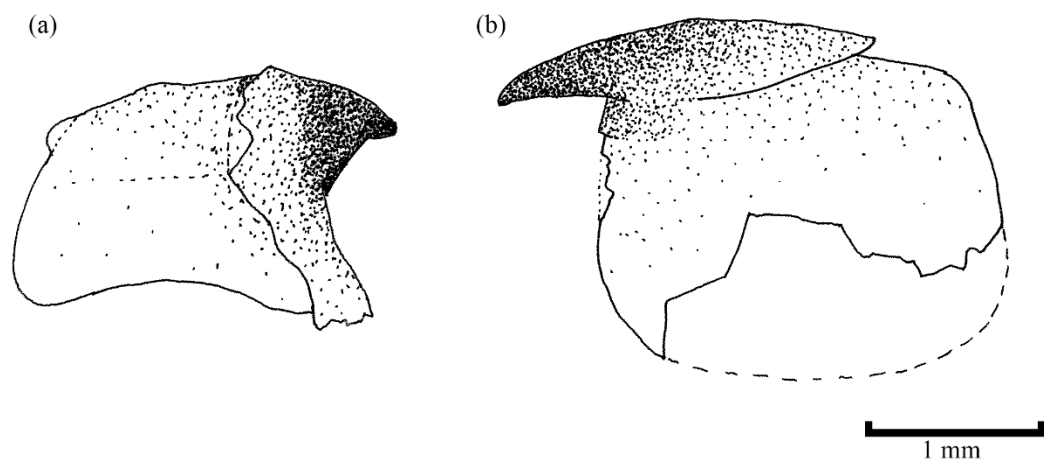


Fig. 2.21—Beaks of *L. sp. NZ*, sp. nov. (a) lower and (b) upper beak (NMNZ M.074203; ML 46 mm).

## Discussion

As in many other cranchiid genera, confusion has historically arisen from the changing appearance of *Leachia* individuals throughout ontogeny. Additionally, many early *Leachia* descriptions and revisions lacked detail, making confident diagnosis of species and detailed comparisons among taxa challenging. The detailed descriptions and illustrations provided in the present account should facilitate direct comparisons with *Leachia* taxa in other regions and in the Pacific (should further taxa be encountered in the future); however, assigning specific names to the material examined proved challenging given the systematic instability of the genus.

The type species of the genus *Leachia cyclura* Lesueur, 1821 was not included within this revision, despite being described from the ‘Pacific Ocean’ in the original text (Lesueur, 1821). Upon examining the expedition’s co-ordinates, this specimen was actually collected from off the eastern coast of South Africa, making the type locality the Indian Ocean. As Lesueur did not examine the holotype himself, writing the description based on an illustration of the dorsal surface of the type specimen, his description lacked sufficient detail to accurately attribute future material to *L. cyclura*. However, subsequent descriptions (and descriptions of currently recognized junior synonyms) may aid in the identification of characters that define this species. Grant described *L. guttata* (= *Leachia cyclura*, *fide* d’Orbigny, 1845) as having round fins, seven eye photophores, and ventral cartilaginous strips 50% ML with 11–13 tubercles. When *L. cyclura* was reported by d’Orbigny (1845) the specimen illustrated had cartilaginous strips with eleven tubercles, eight of which were connected by the strip and three that were independent of the strip, posterior to the others; however, this tubercle structure was not actually described in the text itself. The sucker armature was also illustrated by d’Orbigny, with the arms showing ~12 blunt teeth disposed around 60% of the sucker ring, and the manus suckers with four very long angular teeth that curved inwards toward the midline (d’Orbigny, 1845). Although this illustration showed an animal that had sessile eyes, neither the image nor the description elaborated on the presence or number of eye photophores. Subsequent authors noted that specimens of *L. cyclura* they examined had anywhere from five (Joubin, 1905; Pfeffer, 1912) up to eight photophores (Nesis, 1987) in specimens of ML 60–70 mm. Although the overall morphology of the taxa outlined in these descriptions is similar, there appears to be some variation in the specific details of the characters ascribed to this taxon, suggesting that a thorough review of the diagnostic characters of *L. cyclura* is needed. However, as most *Leachia* material encountered in this study had more than eight eye photophores, none of the taxa described herein can be attributed to *L. cyclura*. Hopefully future revisions of this genus will be able to provide additional description for this taxon and provide additional stability to the genus *Leachia*.

Unfortunately, within *Leachia*, disagreement has not been limited to species-level distinctions, as debate regarding generic designations also persists to the modern day. Most recently, it has been stated that Joubin’s *L. danae* should be retained as the monotypic genus *Drechselia* Joubin, 1931 (De Silva-Dávila, Avendaño-Ibarra, García-Domínguez & Saldierna-Martínez, 2010). Voss (1980) considered *Drechselia* to be a junior synonym of *Leachia*; despite this, Nesis (1987) kept the genera separate in his familial overview, based on differences in arm attenuation, fin length, sucker count, sucker dentition, and the presence of female sexual modifications on all arms. While it is true that these features separate *L. danae* from other *Leachia* species, the differences

observed appear more aligned with interspecific variation than with intergeneric variation. For example, arm attenuation is a rather subjective trait; members of *Leachia* do show considerable variation in the amount of arm-tip attenuation, but it is a challenge to quantify these differences, especially as the tips of the arms are easily damaged in most species and are prone to distortion during capture and subsequent preservation. Proportionally larger fins in adult *L. danae* (ML 70–160 mm; FL 30–42 % ML) than in other species were observed in the present study; however, there is some overlap in measurements with both *L. dislocata* (20–35 % ML) and *L. separata* (20–32 % ML).

The main feature used to justify the distinction between *Drechselia* and *Leachia* was the morphology of the sucker dentition (or hooks) (Joubin, 1931; Nesis, 1987). The sucker rings of *L. danae* usually possess three large primary cusps with several smaller cusps also visible around the ring margin at higher magnification (Fig. 2.5a). In larger individuals (most pronounced in females) the central cusp curves inwards forming a hook. Although arm hooks are rare in cranchiid squid, with *Mesonychoteuthis hamiltoni* being the only other species with this character, more evidence should be used to determine the efficacy of this character as a formal generic distinction, especially when morphology otherwise suggests close relationships with species in a known genus. Other genera show differing arm dentition among species, as both *Liocranchia* and *Galiteuthis* have species with and without sucker dentition, indicating that sucker dentition shape can vary even within a given genus. Dentition can be a useful character for species-level determination, but should be used conservatively, especially when determining generic-level distinctions. Few previous authors have reported the arm sucker dentition of *Leachia* in detail, making direct comparisons difficult. Until this trait is examined in more detail, particularly in the light of phylogenetic analyses, a cautionary approach should be taken.

In addition, the number of suckers observed in *L. danae* specimens has varied considerably among publications (although there is general agreement that females bear a greater number of suckers than males). Joubin (1931) found that one female specimen (ML 183 mm) had between 100 and 120 suckers, while the male specimen had around 50 suckers (Joubin, 1931); however, this is less than the 200+ suckers of mature specimens recorded by later authors (e.g. Nesis, 1987). The specimens examined herein had sustained some damage, but one mature female examined (SBMNH 464442) did have about 180 suckers on Arm III. It is possible that the arms on Joubin's specimens were incomplete, accounting for the lower number of suckers observed (he did acknowledge some damage on his material). In this study, the distal 40–60 suckers could only be distinguished on perfectly preserved material and under high magnification, so underreported counts in the literature would not be surprising.

Nesis (1987) stated that *Leachia danae* is the only *Leachia* species in which all arms in females show secondary sexual modifications (an observation supported by the material examined in this study); other species of *Leachia* may have brachial organs present on only the third arm pair, or they may be absent on all arms (Nesis, 1987). Brachial organs were one of the two features (the other being eye-stalk resorption) upon which Nesis delineated his sub-genera within *Leachia* (dividing taxa into *L. [Leachia]* and *L. [Pyrgopsis]*) and would indicate that this feature may be too variable to use for generic distinctions (but may be useful at the species level). When describing key generic features, Nesis did not mention the secondary modifications of males. Mature

males of *L. danae* and *L. dislocata* have very structurally similar modified 4<sup>th</sup> arms, a hectocotylus morphology not seen in other cranchiid genera. Maintaining *Leachia* as a single genus would unite the taxa sharing this unique modification, not seen in other cranchiid species (which mostly exhibit four series of diminutive suckers on arms that are not otherwise visibly modified in structure), while separating *L. danae* into its own genus emphasizes the female arm modification that can be found on all arms in some other genera (ex. *Cranchia*, *Megalocranchia*, *Teuthowenia*), but is not seen in other species of *Leachia*. Based on morphology, the observations made in this study strongly support *Drechselia* being a junior synonym of *Leachia*; and as no genetic sequences have been recovered from *L. danae*, molecular analysis will be needed to further assess this distinction.

Among the Pacific *Leachia* taxa, the most uncertainty remains around the taxonomic status of *L. dislocata*, *L. pacifica*, and *Leachia* sp. NZ. This uncertainty stems from characters that are now believed to be important for species-level identification (eye photophores and cartilaginous tubercles) not being provided in the original description of *Zygaenopsis* (= *Leachia*) *pacifica* (Issel, 1908). In particular, previous descriptions of both *L. pacifica* and *L. dislocata* have shown both species to have ventral cartilaginous strips with a dislocated tubercle near the anterior margin, as seen in figs 2.8c and 2.14d (Voss *et al.*, 1992); however, this may actually be a mistaken interpretation of the original *Z. pacifica* described by Issel (1908). When Issel originally described and illustrated the species, the description only mentioned the presence of pointed tubercles, not their arrangement on the animal's ventral surface. Although very small, the image provided in this description also does not clearly show a dislocated tubercle towards the anterior margin of the mantle (although given the image's small size, it is possible that this detail was simply lost due to poor resolution). The offset tubercle does appear in an illustration of *Euzygaena pacifica* (= *L. pacifica*, *fide* Voss, 1980) from Chun (1910) based on a specimen caught in the waters of Japan; however, Chun's identification of this specimen was not based on Issel's original description, but rather Pfeffer's (1900) description of *Zygaenopsis zygaena*. Further description of *L. pacifica* by Young (1975) also does not describe the presence of an offset tubercle, which seems odd, as Young's work described the maturation of the species through several life stages. However, the two *L. pacifica* examined herein (provided by Dr Young) did have an offset tubercle, and it is simply possible that this character was overlooked during previous descriptions of the taxon (unfortunately, type material is no longer extant). This dislocated tubercle appears to be present on several distinct taxa from across the Pacific Ocean, and might be challenging to use as a diagnostic character in this genus, although it can sometimes be useful in differentiating between taxa with overlapping distributions.

New Zealand appears to have two distinct species of *Leachia* in its surrounding waters. The taxon far more commonly seen in collections has been herein named *Leachia separata*, which is distinct from other known *Leachia* species due to the presence of additional cartilaginous tubercles posterior to the ventral strip's termination; however, this species has been described several times previously under several other names. Initially, attempts were made to attribute this material to a known taxon, which was challenging given the lack of detail in some earlier works. *Leachia separata* was previously reported by Allan (1945) under the name *Pyrgopsis pacificus*; Allan both cited and illustrated the additional posterior tubercles on specimens from off the

Australian coast. *Pyrgopsis pacificus* had been previously described from Japanese waters (Sasaki, 1929); however, Sasaki's illustrations depict an animal with comparatively short cartilaginous strips (and much rounder fins). This is clearly not the same taxon as the species described by Allan (1945) and Sasaki's material likely represents what is now considered to be *Leachia pacifica* (from the Hawaiian Islands), a separate species from *L. separata*. Chun (1910) and Pfeffer (1912) both examined material with additional tubercles on the ventral mantle, and attributed it to *L. eschscholtzii*; however, Rathke's original description and illustration of that taxon depicted an animal with only eight ventral eye photophores and did not provide detail regarding ventral tubercle patterns. *Leachia eschscholtzii* was placed into synonymy with *Leachia cyclura* by Nesis (1987), who then identified a similar-sounding species (with long ventral cartilaginous strips) as *L. rynchophorus* Rochebrune, 1884. Examination of the holotype of *L. rynchophorus* at MNHN showed that it was clearly not the same taxon as *L. separata*. The holotype of *L. rynchophorus* had only four circular photophores on the ventral surface of the eyes (although it was very damaged) and the ventral cartilaginous strips were short, lacking additional tubercles posteriorly. In addition, the original description of *L. rynchophorus* Rochebrune (1884) was from a paralarval specimen and lacked several important identifying characteristics, including the number and placement of the ventral tubercles, making attributing that name to any specimen challenging; material from near the type locality should be re-examined in order to redescribe this taxon in sufficient detail to compare it with other *Leachia*. Thus, upon reviewing historical descriptions of named *Leachia* taxa with similar morphological traits, and after examining several holotypes, the more common New Zealand taxon appears to represent a novel species, herein named *L. separata*.

The second, less commonly encountered, *Leachia* form that was found in New Zealand waters has a shorter cartilaginous strip (20% ML), bearing all of the ventral tubercles, and, despite the eyes being sessile, has fewer eye photophores (10 or 11) than most other species of *Leachia* from the Pacific (with the exception of *L. pacifica*). Currently, this material is hypothesised to represent an undescribed species (referred to simply as *Leachia* sp. NZ) because only two immature specimens are known to date, one of which is damaged. Additional material is needed, ideally from a range of ontogenetic stages, in order to establish the status of this form; in particular, tissue samples would be useful, given the frequently damaged state of many collected cranchiid specimens.

When distinguishing among species of *Leachia* in the Pacific Ocean, the character presently considered most useful is the eye photophore patterns and the ventral cartilaginous tubercles. In well-preserved material, eye photophores are the most reliable character, since each species possesses a unique pattern; however, cranchiid eyes are notoriously delicate and routinely damaged during collection, reducing the utility of this character in most cases. Ventral tubercles are a more reliable feature to use, because the ventral mantle surface is often intact in preserved specimens; however, the differences among species may be relatively minor and require a practiced eye to distinguish. *Leachia dislocata* and *L. pacifica* appear to be the only two species that have anterior displaced tubercles. These can be further differentiated when looking at the structure of the ventral tubercles present on the cartilaginous strip. Those of *L. dislocata* appear to be antero-posteriorly compressed, making the tubercle cluster appear elongated, with the outer cusps diverging away from the central cusp (Fig.

2.8c,d). Tubercles on *L. pacifica* are slightly more compact, with all cusps diverging directly from the central tubercle with very little ‘elongation’ of the cluster itself (Fig. 2.14c). The tubercles of *L. danae* are compact clusters and the cartilaginous strip lacks a dislocated tubercle at the anterior end (*L. danae* also has distinctive arm suckers as a defining feature). *Leachia separata* is the only species to have tubercles extend along the ventral mantle surface posterior to the cartilaginous strip (Fig. 2.16; see remarks for *L. separata*), making this the most helpful feature for identifying this species. The limited material available for *L. sp. NZ, sp. nov.* has not yet permitted a wide survey of tubercle structure in this taxon, but preliminarily it appears to have a combination of both compact and antero-posteriorly compressed clusters of tubercles. This could simply be because the specimens were still in early stages of development, as neither was mature, or it may be that fully developed members of this taxon show several forms of tubercles, although tubercle morphology appears to have little intraspecific variation in the other *Leachia* taxa examined to date.



## *Liocranchia* Pfeffer, 1884

### Historical Review

Steenstrup (1856), when examining material from the Atlantic Ocean, observed specimens with a unique tubercle arrangement (cartilaginous strips with tubercles on both the dorsal and ventral mantle surfaces, with the ventral strips forming acute V-shapes posterior to each head–mantle fusion); he named this new species *Leachia reinhardti* (= *Liocranchia reinhardti*, *fide* Pfeffer, 1884). Many different generic affiliations were subsequently proposed for this species (e.g., *Cranchia* in Steenstrup, 1861 and again in Lönnberg, 1896; *Loligopsis* in Tyron, 1879).

During the later 1800's there was some debate over appropriate names for genera within the family Cranchiidae. Pfeffer (1884) created a new genus, called *Liocranchia*, to hold his newly described species *L. brockii* (= *L. reinhardti*, *fide* Pfeffer, 1912). However, Hoyle (1886) was hesitant to use this new genus in systematics, as he was unsure whether some of the specimens described belonged in *Cranchia* or in the genus *Taonius* (Hoyle, 1886). Still, Hoyle retained the name *Liocranchia* as a sub-genus of *Cranchia*. Pfeffer (1900) disagreed with Hoyle's comments, but admitted that distinguishing species within the genus was challenging.

A new species was identified by Chun (1906), differing from *L. reinhardti* because it lacked tubercles along the dorsal midline. He named this species *Liocranchia valdiviae*, but did not describe it further until a familial revision in 1910. Prior to this revision two new species were named: *L. elongata* Issel, 1908 (= *Liocranchia reinhardti*, *fide* Nesis, 1987) and *L. globula* Berry, 1909 (= *Liocranchia reinhardti*, *fide* Chun, 1910). The former species was described from a paralarval specimen (mantle length of about five millimetres) reported as having dorsal and ventral tubercles; however, Issel (1908) explained that this specimen seemed different enough to warrant being distinguished as its own species. *Liocranchia globulus* was named so because of its round mantle shape (Berry, 1909), and shared similar tubercle patterns with most other described species within the genus.

Chun (1910) revised *Liocranchia* and synonymised many of the described species with *L. reinhardti*. Chun determined that *L. reinhardti* and *L. valdiviae* were the only two valid species in the genus. Two years later, Pfeffer (1912) re-assigned *Liocranchia* to be a clade of *Cranchia*, containing three species (Pfeffer included *L. globulus*), but cautioned that the three species are practically indistinguishable at smaller sizes. His key for differentiating these species was brief and mainly focussed on distinguishing *L. reinhardti* and *L. valdiviae* by discerning the presence of dorsal tubercles.

In a review of the cephalopods from the Hawaiian Islands, Berry (1914) retained his species, *L. globulus*; however, in the remarks he admitted doubt as to its validity. The description shared many similarities with *L. reinhardti*, and the only notable difference was the round shape of the mantle. Berry conceded that the specimens may have contracted their mantle muscles upon death, giving them a more rotund appearance, as was hypothesized by Chun (1910). This uncertainty continued in the 1920's, when Joubin created a new genus for a specimen of uncertain identification. *Fusocranchia alpha* (Joubin, 1920; = *Liocranchia reinhardti*, *fide* Nesis, 1987) was a small paralarval specimen that lacked many defining features; however, both Nesis

(1987) and Voss (1980) affirmed its place in the genus *Liocranchia*. Robson (1921) also described two new species during this time: *L. gardineri* (=valid species?) and *L. intermedia* (1924, [= *L. reinhardti*, *fide* Nesis, 1987]); both of these species were compared to *Liocranchia reinhardti*. The former lacked tubercles along the dorsal midline; however, Robson did not compare this specimen to *L. valdiviae*; the latter specimen was comparable to *L. reinhardti*, only larger in size.

Nesis (1987) retained *Liocranchia reinhardti* and *L. valdiviae* in the genus for his revision of the cephalopods of the world, and remarked that *L. gardineri* was not included in the key as only a single paralarval specimen had been described. Nesis did not comment on the validity of the species.

## Systematics

*Liocranchia* Pfeffer, 1884 (Table 5)

*Liocranchia* Pfeffer, 1884: 25–26; Issel, 1908: 218–223; Chun, 1910: 263–268; Pfeffer, 1912: 667–678; Robson, 1924: 6–8; Robson, 1948: 128–129; Imber, 1978: 449; Voss, 1980: 378–379; Nesis, 1987: 270, fig. 69d–g; Voss, Stephen, & Dong, 1992: 189; Reid, 2016: 85–88.

*Cranchia* (not Leach, 1817): Hoyle, 1885: 330; Steenstrup, 1861: 32.

*Perothis* (not Rathke, 1833): Rochebrune, 1884: 25–26.

*Fusocranchia* Joubin, 1920: 73–76.

**Diagnosis:** Cranchiian with two linear series of tubercles radiating from each ventral fusion points, creating a double ‘V’ shape on ventral mantle. Fins each forming 2/3 an oval; eyes with 4–14 circular photophores. Strong arm webbing around buccal crown.

Table 5 — Characters used herein to distinguish Pacific *Liocranchia* species

Species	Dorsal tubercles	Eye photophores	Arm sucker dentition	Manus sucker dentition
<i>L. reinhardti</i>	present	14	absent	15–21 pointed teeth
<i>L. valdiviae</i>	absent	4	7–10 short pointed teeth	7–11 pointed teeth

***Liocranchia reinhardti* (Steenstrup, 1856) (Figs 3.2–3.7, Table B5)**

*Leachia reinhardti* Steenstrup, 1856: 200.

*Cranchia reinhardti* (Steenstrup, 1856): Steenstrup, 1861: 32; Hoyle, 1885: 330.

*Liocranchia brockii* Pfeffer, 1884: 25–26, fig. 33a.

*Perothis reinhardti* (Steenstrup, 1856): Rochebrune, 1884: 25–26.

*Cranchia* (*Liocranchia*) *reinhardti* Hoyle, 1886: 184–187, Pl. XXXI fig. 11–14, XXXII fig. 1–4.

*Liocranchia reinhardti* (Steenstrup, 1856): Issel, 1908: 218–220, Pl. 9 fig. 24, Pl. 10 fig. 27; Chun, 1910: 263–264, Pl. LI fig. 5–7; Pfeffer, 1912: 667–674, Pl. 47 fig. 14–17; Robson, 1924: 6; Robson, 1948: 128–129; Imber, 1978: 449; Voss, 1980: fig. 2; Voss, Stephen, & Dong, 1992: 189; Reid, 2016: 85–86.

*Liocranchia elongata* Issel, 1908: 220–223, Pl. X, fig. 28–32.

*Cranchia* (*Liocranchia*) *globula* Berry, 1909: 415–416, fig. 9.

*Liocranchia globulus* Berry, 1914: 346–348, Pl. LIII fig. 2–4; Pfeffer, 1912: 674–675.

*Fusocranchia alpha* Joubin, 1920: 73, Pl. XIV, fig. 5–9.

*Liocranchia intermedia* Robson, 1924: 6–8.

**Diagnosis:** Eye with 14 circular photophores. Dorsal mantle midline with series of 30–60 simple tubercles. Arm suckers lacking dentition.

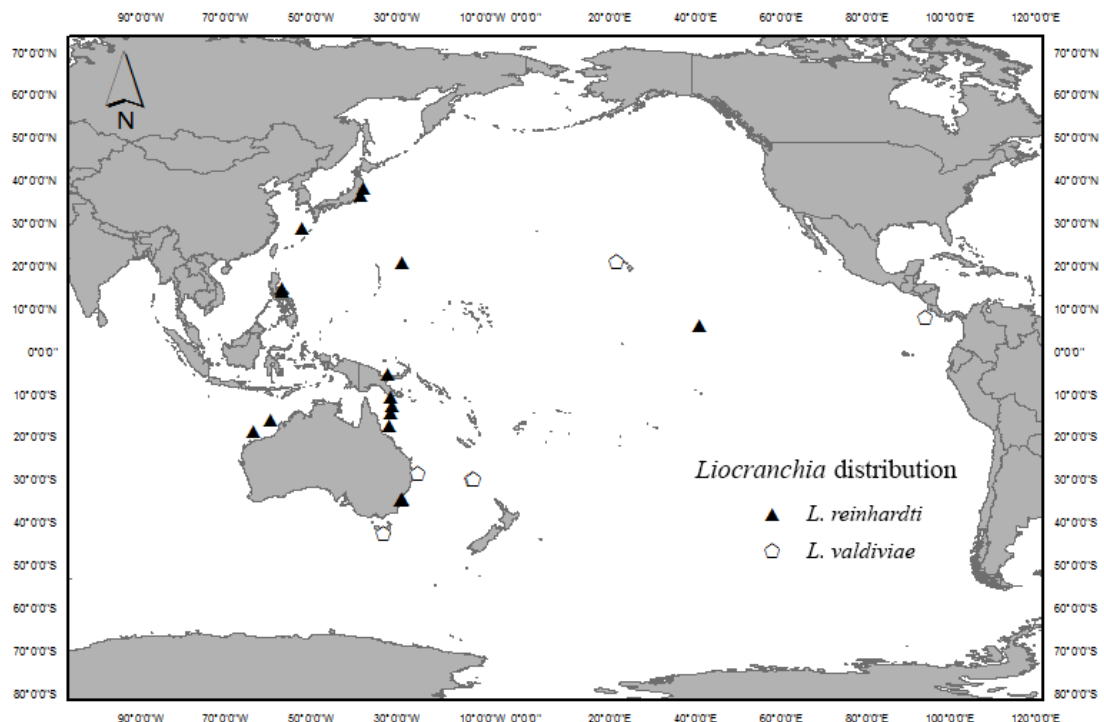


Fig. 3.1— Distribution of examined *Liocranchia* material in the Pacific Ocean.

**Type material:** (examined) *Cranchia (Liocranchia) globula* **CAS 017978 Paratype**, sex indet., 20.81°N, 51.20°E, Hawaii, off Lanai Island, Molokini Islet, USFCS *Albatross*, Stn. 282, 14/04/1902; (not examined) *Leachia reinhardti* **ZMUC Syntypes (3)** [*fide* Kristensen and Knudsen (1983:223)]. Type locality 15.19°N, 24.54°W–23°N, 32°W (Atlantic Ocean).

**Material examined (19 specimens):** **NSMT-Mo. 85459**, ML 145 mm, sex indet., 38.37°N, 142.23°E, Japan, off Sanriku, Tohoku, 750 m, 25/10/2007; **NSMT-Mo. 71607**, ML 148 mm, ♂, 36.66°N, 141.44°E, off Tohoku, 650 m, 15/10/1997; **NSMT-Mo. 63981**, ML 36 mm, sex indet., 29.02°N, 127.93°E, 175 m, Maru KH77-2 St 56, 22/07/1977; **NSMT-Mo. 62606**, ML 134 mm, ♂, 21.16°N–21.83°N, off Yui, 70–90 m, 09/05/1983; **CAS 104402**, ML 96 mm, sex indet., 14.83°N, 123.28°E, Luzon, Calagua Islands, Northeast of Calagua Islands, 760–770 m; **CAS 104401**, ML 116 mm, ♂, 14.30°N, 123.35°E, Luzon, Calagua Islands, Northeast of Calagua Islands, 648–660 m; **SBMNH 461574**, ML 38 mm, sex indet., 6.00°N, 139.00°W, Cromwell 68, Stn. 4, 12/01/1976; **NSMT-Mo. 85216**, ML 19 mm, sex indet., 3.03°N, 153.62°E, North of Papua New Guinea, Central Pacific, 200 m, 09/09/1995; **NSMT-Mo. 85215**, ML 29 mm, sex indet., 5.11°S, 147.93°E, Papua New Guinea, MWT, 29/10/1972; **NSMT-Mo. 85214**, ML 8 mm, sex indet., 10.63°S, 148.49°E, Papua New Guinea, MWT, 05/11/1972; **NMV F163639**, ML 16 mm, sex indet., 12.63°S, 148.92°E–12.50°S, 148.70°E, 1450 m, RV *Lady Basten*, 02/12/1981; **NMV F163712**, ML 59 mm, sex indet., 14.20°S, 148.70°E, Coral Sea, RV *Lady Basten*, 27/05/1981; **NMV F163702**, ML 136 mm, ♀, 17.22°S, 148.33°E–17.10°S, 148.10°E, Coral Sea, 10 m, RV *Lady Basten*, 23/06/1981; **NMV F65937**, ML 134 mm, ♂, 15.90°S, 120.37°W, Western Australia, off far North West Coast, 570–575 m, WGS84, 31/01/1990; **NMV F71691**, ML 119 mm, ♂, 18.75°S, 116.52°E–18.75°S, 116.48°E, 584–590 m, S02/82/20, 04/04/1982; **NMV F163711**, ML 71 mm, ♂, 34.25°S, 151.35°E, Tasman Sea, 250 m, RV *Soela*, S01/81/18, 26/03/1981; **NMV F163691**, ML 92 mm, sex indet., 34.60°S, 151.17°E, 200 m, RV *Soela*, S01/81/05, 24/03/1981; **NMV F163697**, ML 23 mm, sex indet., 34.10°S, 151.17°W, Australia, 200 m, S01/81/05, 24/03/1981; **NMV F163630**, ML 42 mm, sex indet., 34.80°S, 150.88°W, Australia, New South Wales, off Sydney, 60 m, Q44/920.

**Non-localised material examined (1 specimen):** **CAS 105173**, ML 91 mm, sex indet., Galapagos Islands, Roca Redonda, 548 m, 11/19/1995.

### **Description:**

**Adult** (ML 65–148 mm; Fig. 3.3)—Mantle spindle shaped, narrowing to point, MW 25–33–45% ML. Ventral surface of mantle with two cartilaginous strips (15–25% ML) originating from each ventral fusion point forming double ‘V’ shape (Fig. 3.3b), outer strip often longer than inner; each with 8–18 tubercles, mostly simple tubercles; simple tubercles present along dorsal midline, 38–50 in single series from anterior mantle margin to beginning of conus. Fins together circular or oval, 29–32–36% ML, increasing proportionally with size; FW 35–37–45% ML (FW ≥ FL). Head length 11–17–27% ML, HW 14–21–26% ML. Eyes sessile, set within cephalic cartilage; ED 7–14–19% ML. Fourteen circular photophores on eyes (Fig. 3.2a): eight along ventral surface, four ventral to lens, smaller two dorsal to lens. Funnel length 5–9–15% ML, narrowing sharply to aperture (FA 16–27–33% FB).

Buccal crown with webbing, minimal between tentacles and Arms IV; low trabeculated membrane along each side of oral surface, aboral keel on all arms. Arm formula III>IV>II>I: Arm I 5–12–21% ML, Arm II 15–18–25% ML, Arm III 19–28–34% ML, Arm IV 14–21–26% ML. Longest arm with up to 58 suckers on unmodified arm; suckers subequal on Arms I and IV, increasing slightly midarm on Arm II and tripling in size (from base to mid-arm) on Arm III; suckers densely set proximally. Sucker dentition absent (Fig. 3.4b). Mature females with brachial end organs on arm pair III (Fig. 3.5a); mature males with modifications on Arms III and IV (developing ~90 mm ML). Arm III with four series of small suckers along distal half; Arm IV (variably left or right) with enlarged suckers with small apertures, dorsal series ending proximal to tip, ventral series continuing along dorsal margin; modification curving slightly dorsally (Fig. 3.6). Tentacles 32–60–76% ML; 16–20 suckers on stalk, suckers and pads in pairs spaced widely along stalk length. Club length 8–12–15% ML (14–20–28% TnL); ~86 suckers on club in four series; suckers subequal in size, inner manus suckers slightly larger. Large suckers with 15–21 short pointed teeth around entire margin (Fig. 3.5c).

**Juvenile** (ML ~15–65 mm; Fig. 3.7b)—Mantle oblong, tapering slightly at posterior end, MW 30–45–60% ML. Ventral cartilaginous strips nearly equal in length; ~12 tubercles on ventral strips, 20–50 dorsal tubercles. Fins circular, FL 9–18–30% ML, FW 17–31–40% ML. Head length 2–10–14% ML, HW 21–26–29% ML. Eyes sessile, ED 9–11–14% ML, photophores developing (~10 photophores by 15 mm ML). Funnel base < 40% MW with wide aperture (30–42–60% FB). Arms proportionally shorter, arm formula III>IV>II>I: Arm I 3–4–8% ML, Arm II 4–8–14% ML, Arm III 9–16–25% ML, Arm IV 8–11–15% ML. Tentacles 38–52–61% ML, CL 7–11–17% ML, clubs with 80–90 suckers.

**Paralarva** (ML <15mm; Fig. 3.7a)—Mantle round or oblong, MW 44–49–58% ML. Ventral cartilaginous strips nearly equal in length; 7–12 tubercles on ventral strips, ~20 dorsal tubercles. Fins circular, FL 9–14–21% ML, FW 17–29–40% ML. Head length 7–11–14% ML, HW 22–25–29% ML. Eyes sessile, ED 9–11–13% ML, larger photophores developing. Funnel base < 40% MW with wide aperture (30–42–60% FB). Arms short, nearly subequal, arm formula III>IV=II=I: Arm I ~5% ML, Arm II ~7% ML, Arm III 6–10–14% ML, Arm IV ~6% ML. Tentacles 38–59–92% ML, CL 8–11–17% ML. Tentacle clubs with ~50 suckers.

**Known distribution:** Indo-Pacific species, from Japanese waters to Tasman Sea, some material found in Central Pacific, around Hawaiian Islands (Fig. 3.1). Present material collected from surface to 1450 meters (Fig. 3.2); elsewhere reported between 0–200 meters (Young, 1978).

**Remarks:** The characters used to differentiate the juvenile ontogenetic stage were the development of photophores and the lack of sexual modifications on arm tips. Male sexual modifications on Arms III and IV develop between 70 and 90 mm ML. These modifications appear as an abrupt mid-arm transition from two series of suckers to four series of suckers on the distal third of Arm pair III, and the expansion of the distal tip of Arm IV (this was either the left or right arm, but never both). *Liocranchia reinhardti* has a distinct BIN (BOLD: ACA9595) from the other sequenced species of *Liocranchia* (assumed to be *L. valdiviae*); however, the parent *L. reinhardti* specimens were from the Atlantic Ocean.

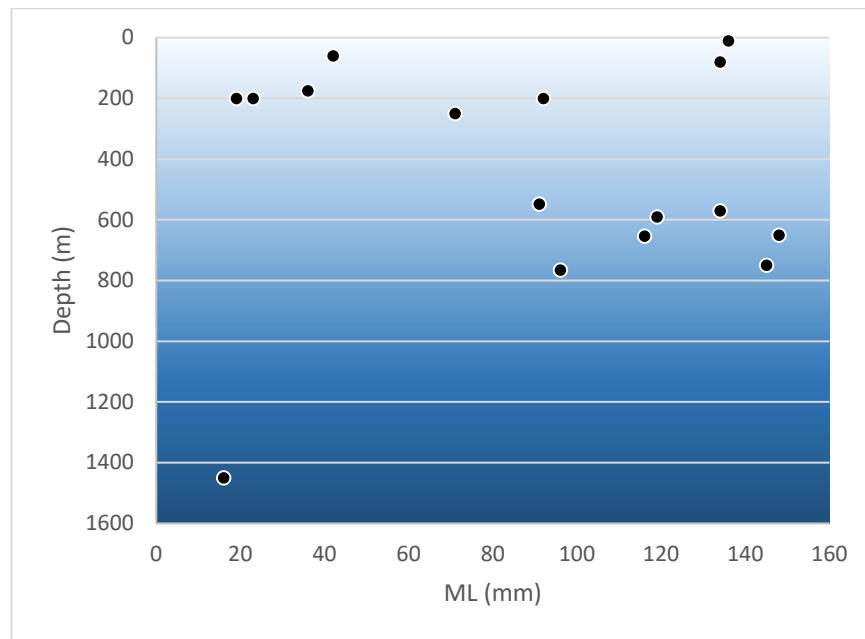


Fig. 3.2—Vertical distribution of *L. reinhardtii* material examined herein.

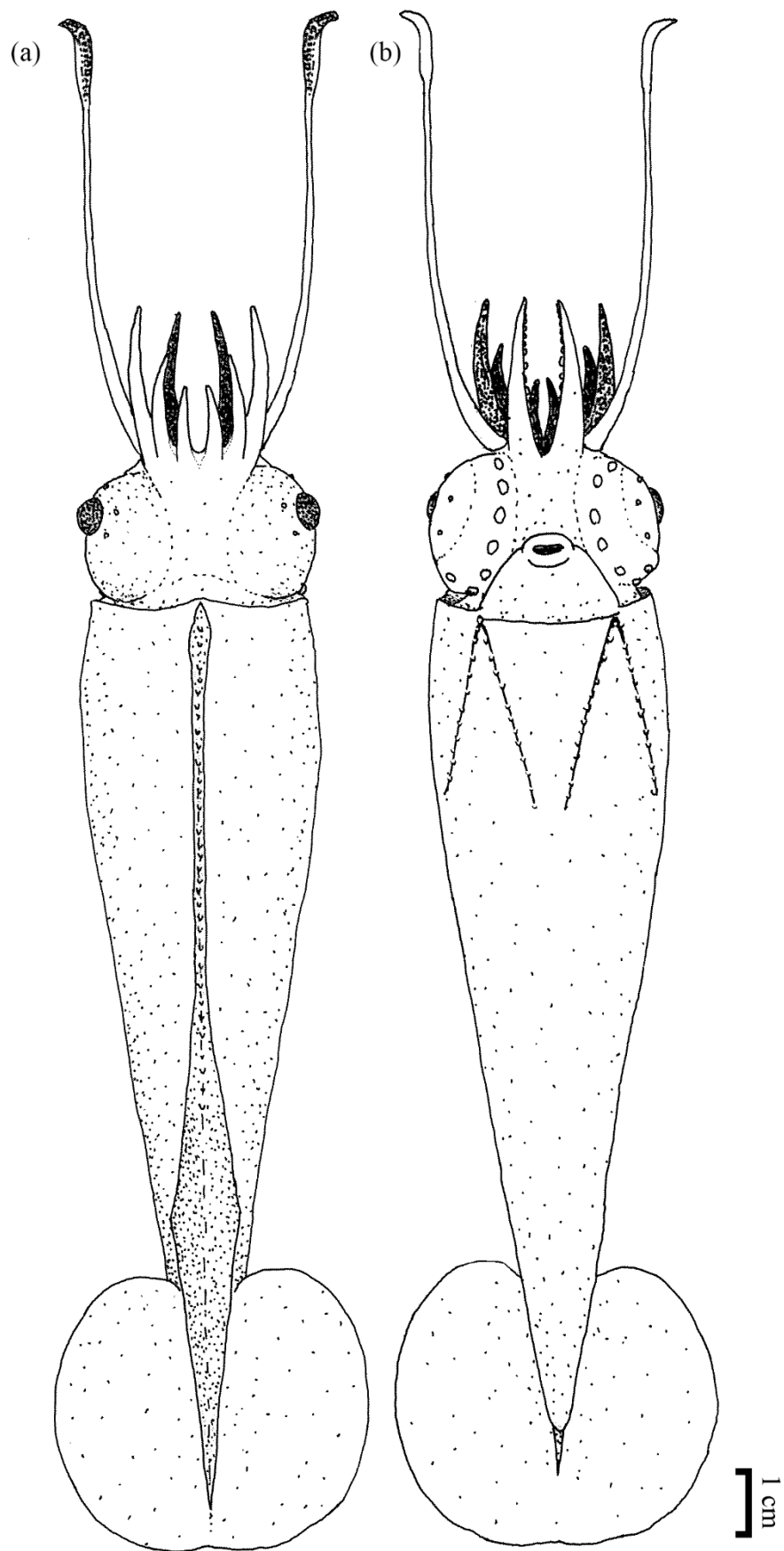


Fig. 3.3—Adult *Liocranchia reinhardti* (a) dorsal view (b) ventral view (NSMT Mo.85459, ML 145 mm).

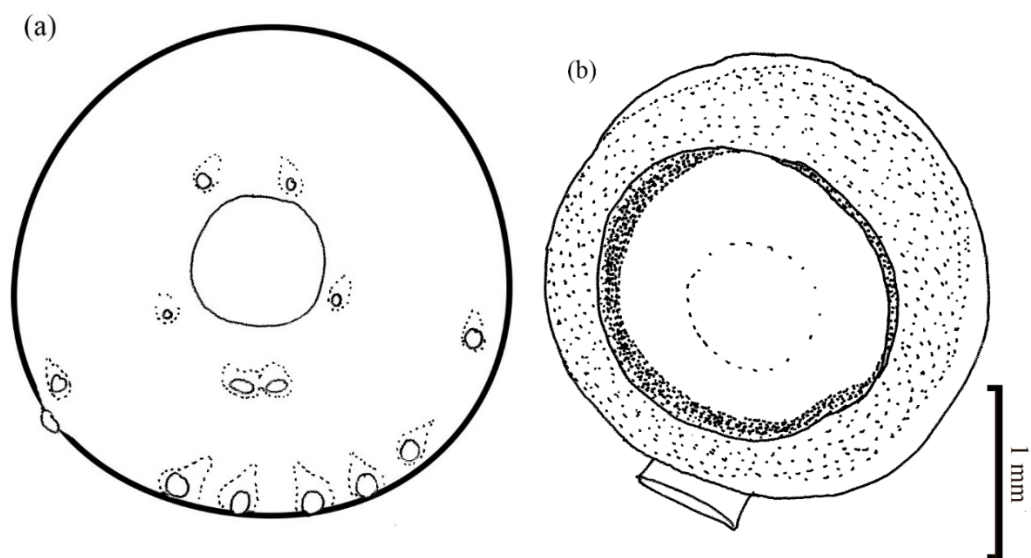


Fig. 3.4—(a) right eye schematic showing 14 photophores (b) largest sucker from Arm III (NMV F163702, ML 136 mm).

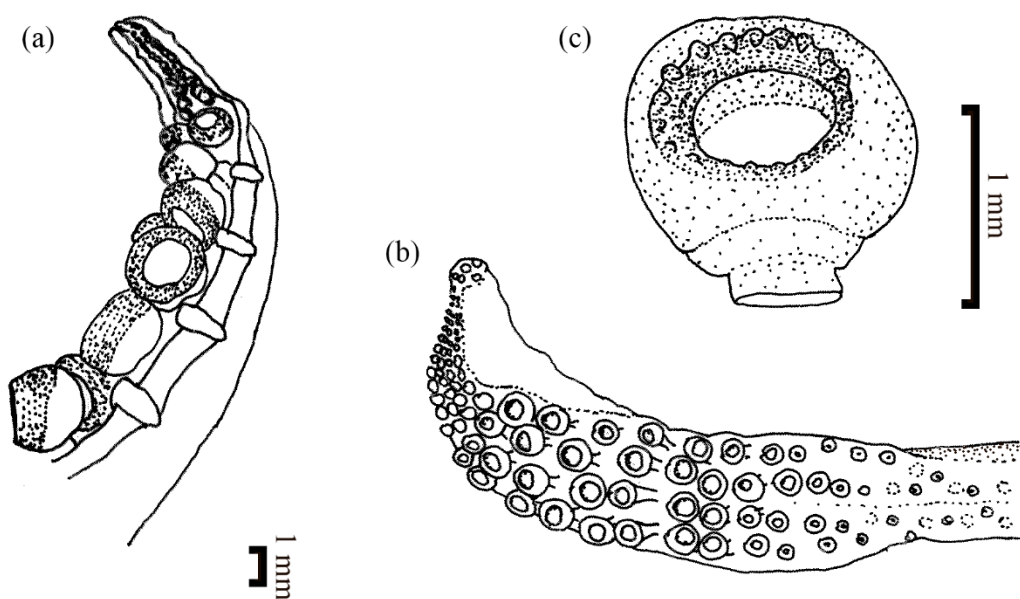


Fig. 3.5—*Liocranchia reinhardti* appendages and armature: (a) female brachial organ, (b) right tentacle club, (c) manus sucker (NMV F163702, ML 136 mm).



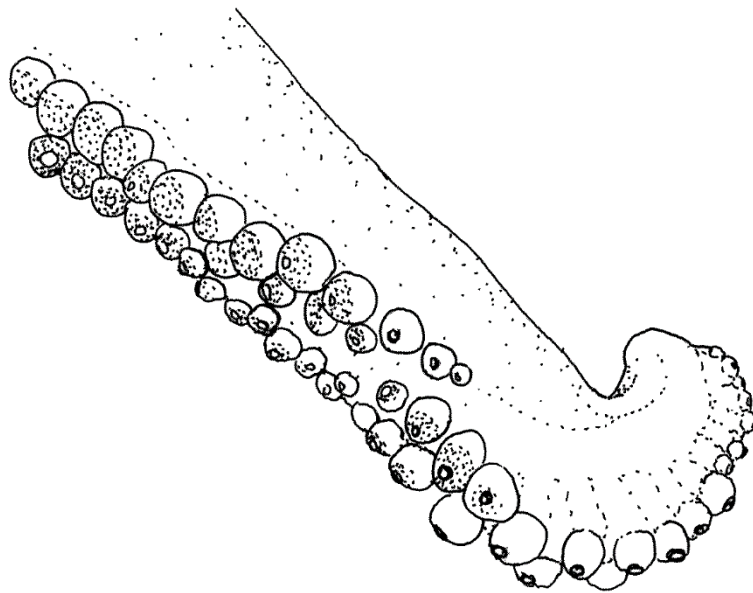


Fig. 3.6—*Liocranchia reinhardtii* male arm modification, left Arm IV (NSMT Mo:71607; 148 mm ML).

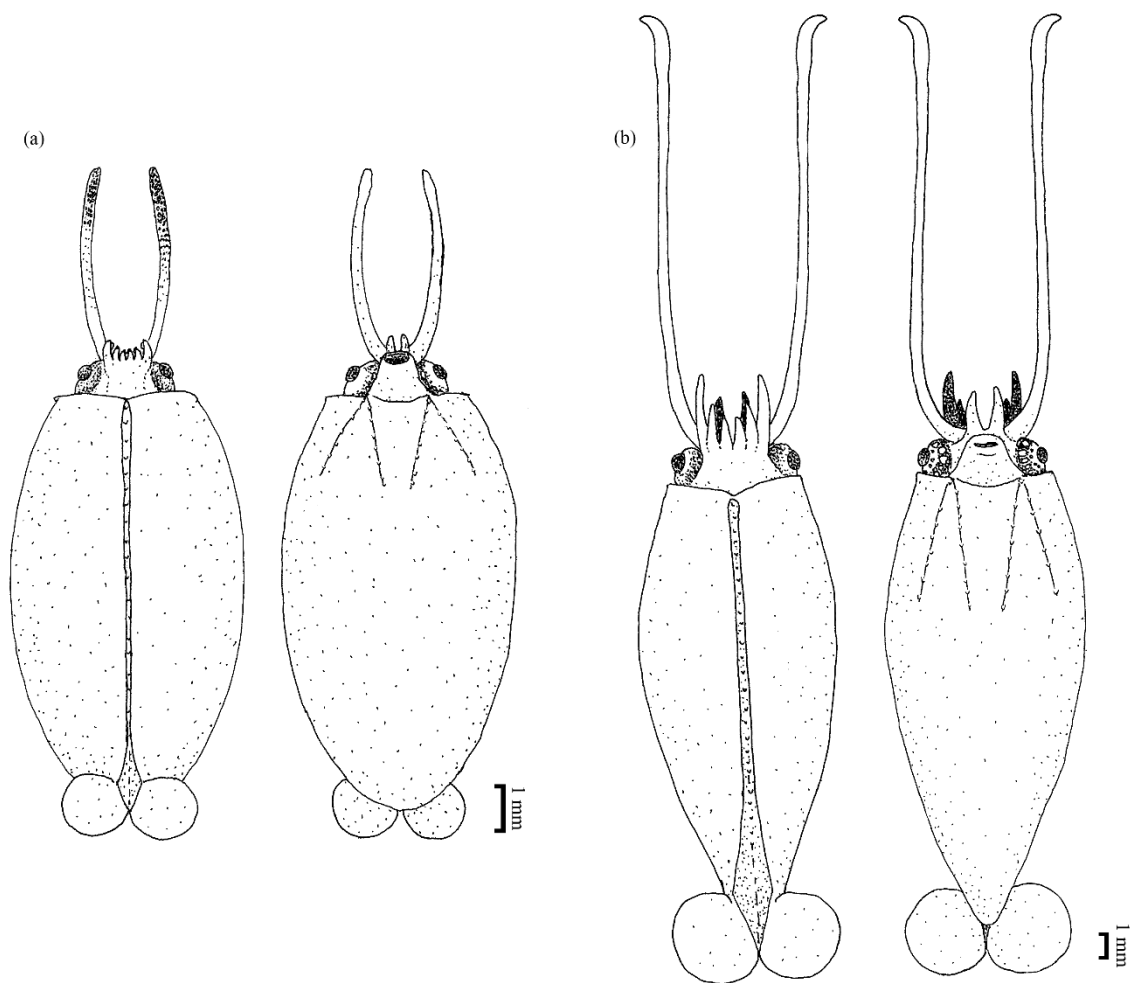


Fig. 3.7—*L. reinhardtii* ontogenetic stages: (a) paralarva (NSMT Mo.85214, ML 8 mm) and (b) juvenile (NSMT Mo.85216, ML 19 mm).

***Liocranchia valdiviae* Chun, 1910** (Figs 3.8–3.11, Table B6)

*Liocranchia valdiviae* Chun, 1910: 264–268, Pl. XLVIII fig. 3–4, Pl. LI fig. 1–4, 8–14, Pl. LX fig. 7–11; Pfeffer, 1912: 675–678; Voss, Stephen, & Dong, 1992: 189; Reid, 2016: 87–88.

**Diagnosis:** Lacks cartilaginous tubercles along dorsal midline. Adult eye with four round photophores along ventral surface. Arms suckers with 7–10 pointed teeth along distal margin.

**Type material:** (examined) *Liocranchia valdiviae* **ZMB Lectotype 110038a** [*fide* Glaubrecht and Salcedo-Vargas (2000:279)]. Type locality 4°45'S, 48°58'E (Indian Ocean).

**Material examined (5 specimens):** **SBMNH 460921**, ML 26 mm, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, Leeward Coast, FIDO XV two 63, 01/01/1980; **SBMNH 461173**, ML 34 mm, sex indet., 8.25°N, 86.26°W, Costa Rica, Velero 19002, 1000 m, 23/05/1973; **NMV F163698**, ML 13 mm, sex indet., 28.38°S, 154.93°E, Coral Sea, CSIRO, SP8/82/36, 29/08/1982; **NMNZ M.172990**, ML 82mm, sex indet., 29.53°S, 167.63°E, Norfolk Ridge, S of Norfolk Island, 200–1200 m, RV *Tangaroa*, NORFANZ Stn.23, 15/5/2003; **NMV F163709**, ML 63 mm, 42.38°S, 147.08°E, ACC No. 82/8; NMNZ M.172978, ML 73 mm, sex indet., 29.69°S, 168.02°E, Norfolk Ridge, S of Norfolk Island, 337 m, RV *Tangaroa*, Stn. 2003022, 14/05/2003.

**Description:**

(ML 13–82 mm; Fig. 3.8, 3.11)—Mantle spindle shaped, narrowing to point, MW 32–37–42% ML in larger individuals (up to 70% ML in smaller). Cartilaginous strips 20–38% ML, each with 12–17 tubercles; tubercles often single point. Fins together circular, FL 12–17–24% ML; FW 23–29–33% ML (FW≥FL). Head length 10–13–18% ML, HW 22–25–29% ML; eyes sessile, ED 8–10–12% ML; four circular photophores on ventral ocular surface. Funnel length 8–12–15% ML, narrowing sharply to aperture (FA 18–26–30% FB).

Buccal crown with webbing, minimal between tentacle and Arm IV; low trabeculate membrane along both sides of oral face and aboral keel on all arms. Arm formula III>IV≥II>I: Arm I 6–8–11% ML, Arm II 11–12–16% ML, Arm III 19–23–33% ML, Arm IV 12–14–15% ML. Longest unmodified arm with up to 48 suckers; arm sucker rings lacking dentition in smaller specimens; on largest specimens, basal arm suckers with ~5 blunt teeth on distal margin, switching to pointed teeth mid-arm, distal half of arm with 5–9 pointed teeth on distal third of sucker margin (Fig. 3.9). Tentacles 42–58–85% ML; ~10 suckers on stalk. Club length 8–11–15% ML (18–21% TnL); 65–72–84 suckers on club in four series (Fig. 3.10); suckers subequal in size, inner manus suckers slightly larger; largest suckers with ~11 pointed teeth. Clubs with reduced dorsal membrane. No sexual modifications seen on arms.

**Remarks:** Material available for *L. valdiviae* was limited and this description spans several growth stages. The few smaller specimens (e.g. Fig. 3.11) examined seemed to generally follow a similar developmental pattern as *L. reinhardti* (Fig. 3.7); however, delineating specific growth stages will require additional material and further investigation. *Liocranchia valdiviae* could be confused with *L. reinhardti* as there is considerable overlap in gross morphology between the two species (*L. valdiviae* lacks

tubercles along the dorsal midline), and can occasionally be confused with smaller *Sandalops melancholicus*, as the fin shape is very similar; however, *L. valdiviae* can be distinguished from both taxa by the number of ventral ocular photophores present (four circular photophores, compared with 14 in *L. reinhardti* and two in *Sandalops*). Material examined herein was not yet mature, and therefore lacked the secondary sexual modifications described by Voss (1980) as generic characters.

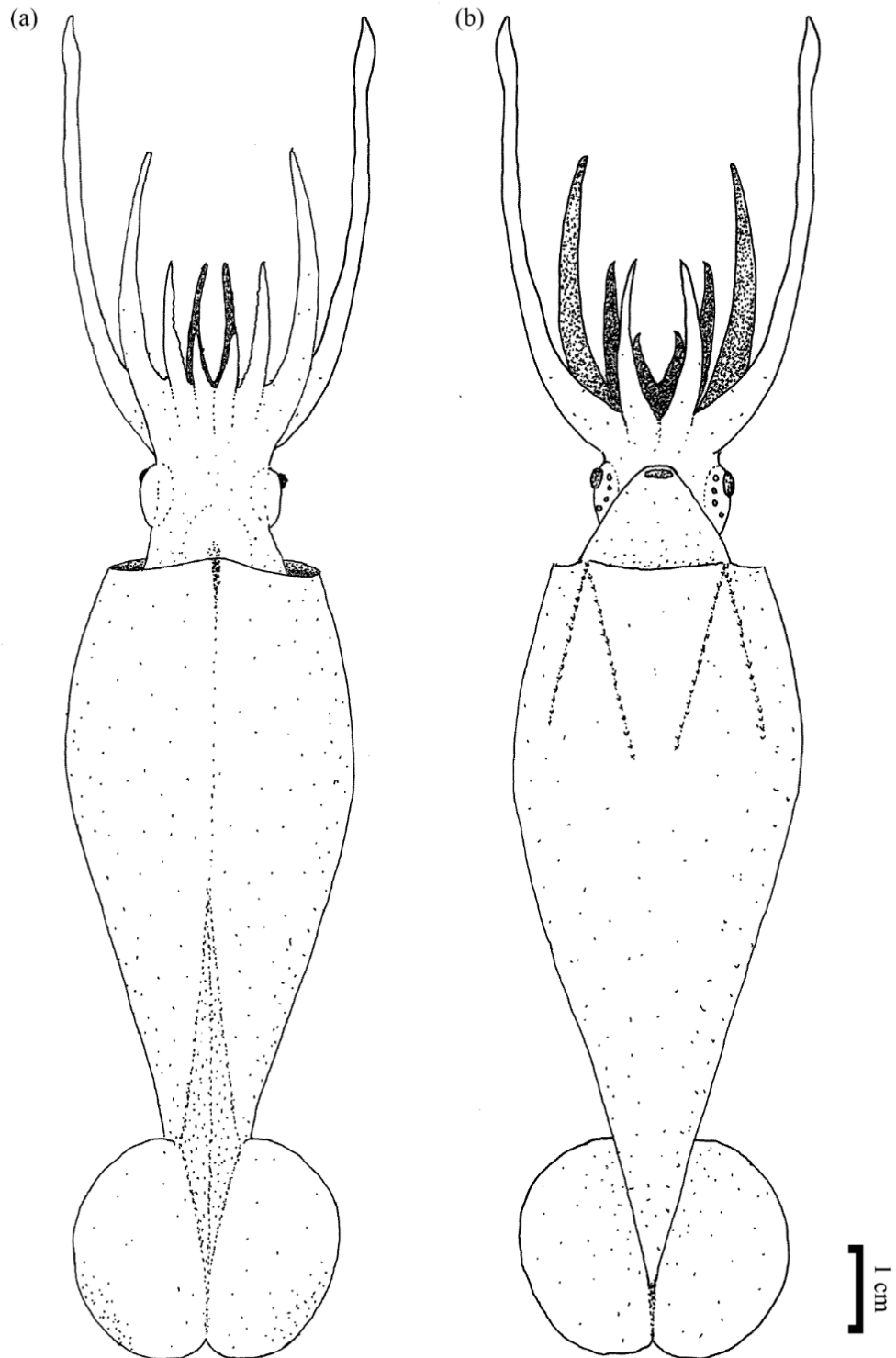


Fig. 3.8—Adult *Liocranchia valdiviae* (a) dorsal view and (b) ventral view (NMNZ M.172978, ML 73 mm).

## Discussion

Unlike some other cranchiid genera, species of *Liocranchia* appear to undergo minimal change throughout ontogenetic development. The mantle of older specimens becomes more elongated and the length of the more medial cartilaginous strips increases relative to the more lateral strips; however, many of the features seen in adults are already present in paralarval and juvenile size ranges. This makes delineation of these life stages more difficult. However, even small individuals of *Liocranchia* can be readily identified as it is one of the few genera that lacks stalked eyes (the other being *Cranchia scabra*), and tubercles are present from small sizes (ML 8 mm). In the absence of the mantle, arm sucker dentition can be used to distinguish between the two species of *Liocranchia*. *Liocranchia reinhardtii* lacks sucker dentition while *L. valdiviae* has ~5 blunt teeth on the distal ring margin. If the eyes are intact, the photophore patterns can also be used as a distinguishing feature, as *L. valdiviae* has four ventral photophores and *L. reinhardtii* has 14 on the ventral, dorsal and lateral eye surfaces.

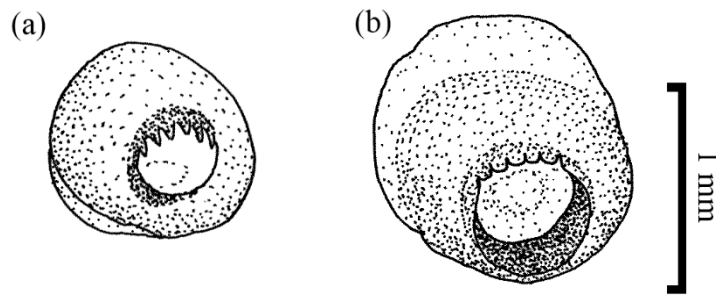


Fig. 3.9—Arm suckers from *Liocranchia valdiviae* (a) distal arm sucker and (b) mid-arm sucker (NMNZ M.172990, ML 88 mm).

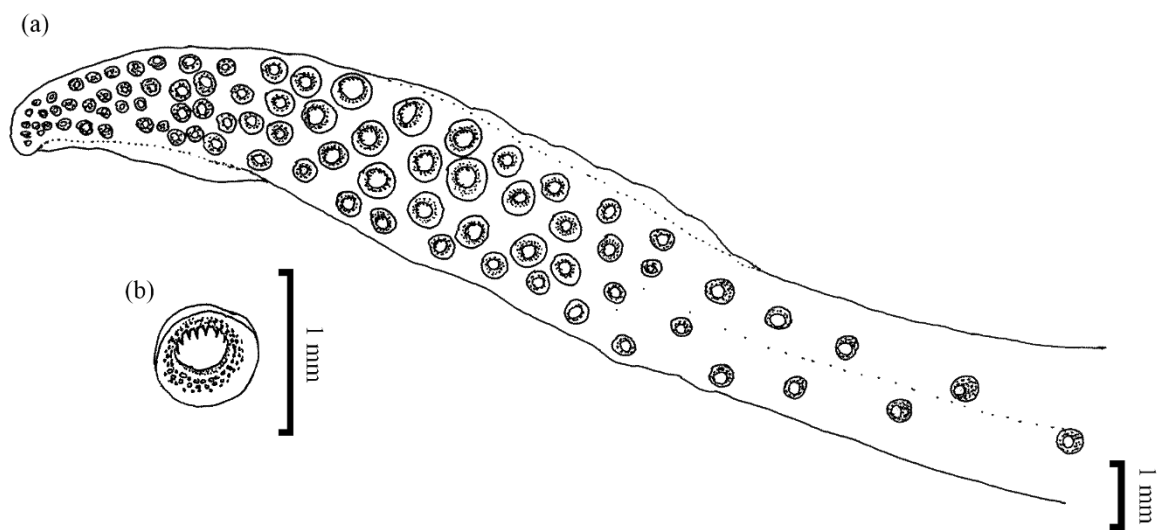


Fig. 3.10—(a) Left tentacular club and (b) manus sucker (NMNZ M.172990, ML 88 mm).

In general, most specimens of *Liocranchia* in natural history collections had been correctly identified as such; however, there can occasionally be some confusion between the genera *Liocranchia* and *Sandalops*, particularly when specimens are damaged or at smaller sizes. Key differences for distinguishing these two genera when examining paralarvae are found on the eyes. Although photophores may have yet to develop on younger individuals, *Liocranchia* will have sessile eyes that do not protrude from the head, whereas small *Sandalops* have laterally flattened eyes (often tear shaped) that are on thin stalks. At larger sizes, the universal presence of the cartilaginous ‘V’s on the ventral mantle surface is a unique and clearly visible feature of *Liocranchia*.

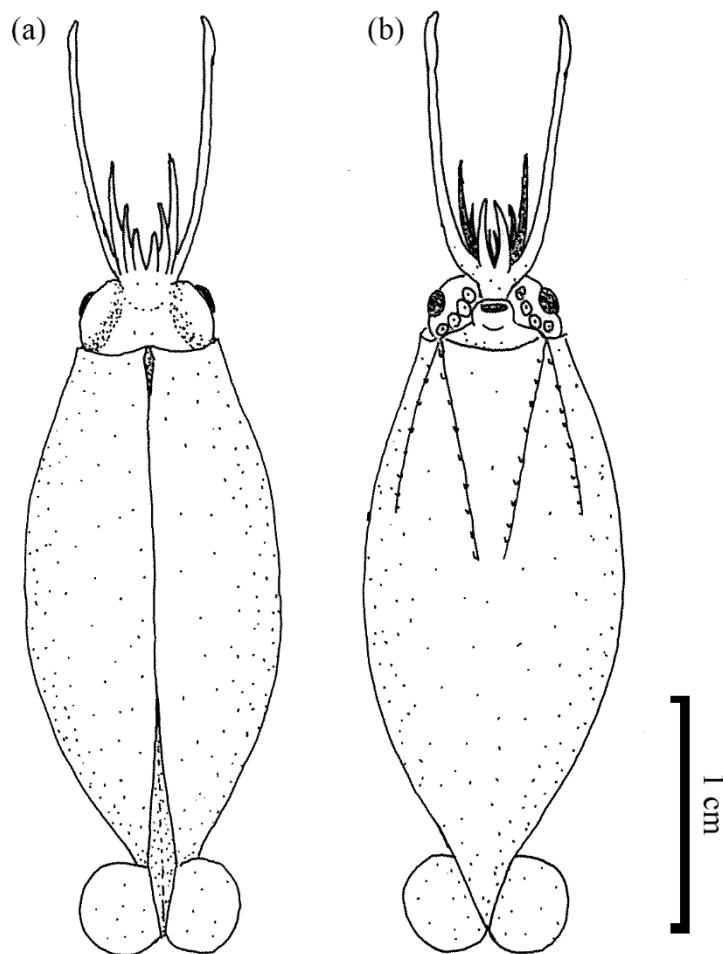


Fig. 3.11—Juvenile *L. valdiviae* (a) dorsal view and (b) ventral view (SBMNH 460921, ML 26 mm).

## Taoniinae Pfeffer, 1912

The morphological division between the taoniin and cranchiian sub-families was first recognised by Pfeffer (1912) who differentiated the Taoniinae as having two (or occasionally one) crescent shaped photophores on the ventral surface of the eye and lacking the ventral cartilaginous strips characteristic of the Cranchiinae. Pfeffer also noted that all but one genus, ‘*Crystalloteuthis*’ (= *Galiteuthis*) lacked branched tubercles on the mantle (another character associated with the Cranchiinae).

Pfeffer (1912) grouped the Taoniinae into three tribes: those which appeared similar to *Taonius* (*Taonius*, *Galiteuthis*, *Desmoteuthis*, *Megalocranchia*, *Phasmatopsis*, *Phasmatoteuthion*, *Toxeuma*, *Crystalloteuthis*, *Corynomma*, and *Taonidium*), those that appeared similar to *Teuthowenia* (only *Teuthowenia*), and those that appeared similar to *Bathothauma* (only *Bathothauma*). Since some of these genera were known only from early ontogenetic stages, many later became junior synonyms of the thirteen genera accepted today (Voss, 1980). Taoniinae is currently considered to comprise ten genera: *Bathothauma*, *Egea*, *Galiteuthis*, *Helicocranchia*, *Liguriella*, *Megalocranchia*, *Mesonychoteuthis*, *Sandalops*, *Taonius*, and *Teuthowenia* (Table 6). These genera remain united (and are distinguished from the Cranchiinae) by the arrangement of photophores on the ventral orbital surface, funnel–mantle fusion cartilage not extending into a strip, and the absence of a hectocotylus in mature males (Voss & Voss, 1983). Several of the genera can be generally grouped together based on shared morphological characters, such as the ‘hooked’ taxa: *Taonius*, *Mesonychoteuthis*, and *Galiteuthis* (Voss, 1988); however, overall the sub-family shows remarkable diversity in morphology and distribution, with several genera (*Sandalops*, *Bathothauma*, and *Liguriella*) believed to be monotypic circumglobal taxa.

Table 6—Morphological distinctions among taoniin genera.

Genus	Fins	Hooks/ Enlarged teeth	Paralarval Eyes	Eye Photophores
<i>Bathothauma</i>	individually circular	absent	Long, slender stalks	1
<i>Egea</i>	lanceolate	absent	unknown	2
<i>Galiteuthis</i>	lanceolate	present	Short, stout stalks	2
<i>Helicocranchia</i>	paddle-shaped	absent	Short, stout stalks	1
<i>Liguriella</i>	ovate	absent	Long, slender stalks	2
<i>Megalocranchia</i>	lanceolate	absent	Stout stalks	2
<i>Mesonychoteuthis</i>	together circular	present	Short, stout stalks	2
<i>Sandalops</i>	semi-circular	absent	tubular	2
<i>Taonius</i>	lanceolate	present	tubular	2
<i>Teuthowenia</i>	lanceolate	absent	Short, stout stalks	3

## *Bathothauma* Chun, 1906

### Historical Review

*Bathothauma lyromma* Chun, 1906 was initially described as ‘saccular with rounded fins’, from a single specimen caught in the Atlantic Ocean at 3000 meters depth (Chun, 1906). The most diagnostic characters mentioned in this description were that the posterior end of the gladius was a ‘crossbar’ shape and that the eyes were on long, bent eye stalks. Pfeffer (1912) described these features in greater detail and noted the presence of a single light organ on the ventral surface of the eye. Several smaller specimens, caught in surface waters off the Australian coast, were subsequently described by Allan (1940, 1945), although Aldred (1974), who described a large ontogenetic series of *B. lyromma* material, queried Allan’s identifications based on the illustrations of Allan’s material. The illustrations in question do appear to depict small *Bathothauma*, and also illustrated a uniquely ‘hooded’ funnel on some specimens, with an extended section of tissue on the dorsal surface of the funnel (see remarks for *B. lyromma*).

Grimpe (1922) considered *Bathothauma* to be a unique family, Bathothaumatidae, which contained two genera (*Bathothauma* and *Parateuthis* Thiele, 1920 [= *Alluroteuthis*, *fide* Odhner, 1923]); however, this systematic revision was largely ignored by other researchers of the day and was not maintained in further revisions of the family. *Bathothauma* did not appear in the literature for several decades until examined by Voss (1960), who noted that *B. lyromma* undergoes a considerable ontogenetic shift in relative body proportions. He observed that the eyes and head remained relatively small while the mantle grew rapidly (to ML ~100mm); the arms also underwent rapid growth at ML 30–60mm (gaining proportional as well as absolute length), but remained constant in proportions outside this size class.

Young (1970) made the next observations on ontogenetic development in *Bathothauma*, examining four immature specimens (ML 12–25 mm) and reporting the eye development in juveniles in greater detail; variation in tentacle stalk length and extension of the buccal crown in smaller individuals were also discussed. In observing the eyes, Young (1970) noted the large ventral patch of reflective tissue and inferred the presence of a light organ (although it could not be conclusively distinguished), which he hypothesised might assist in feeding at greater depths. He also discussed the shape of the eye, and specifically compared the ventral extension of the rostrum on three specimens with similar features seen on other small cranchiids such as *Sandalops* and *Liguriella*.

Aldred (1974) examined a large collection of 87 individuals, ML 4–205 mm, from the North Atlantic, and was able to describe nearly all ontogenetic stages of *B. lyromma*. This study provided considerable insight into ontogenetic changes in cranchiid morphology, a notorious source of historic confusion. Aldred highlighted that, in addition to the eye shape changing dramatically, the ventral eye photophore only became visible as the animal neared maturity, and that arm sucker dentition also varied ontogenetically. Aldred noted that immature specimens had pointed sucker dentition while mature adults had smooth sucker rings — an important note as sucker dentition can be used as a distinguishing feature in other cranchiid genera. Aldred (1974) also

discovered that maturity in *Bathothauma* is attained across a large size range, and that sexual differentiation within the species can only be determined after the dorsal mantle length reaches 80 mm ML, either by gonad development or secondary sexual modifications on the arms of males.

Okutani (1975) described two large specimens (ML 120–160 mm), but questioned their maturity, as he felt that they still retained many paralarval features (small fins and a blunt tail). Okutani found that the arm suckers had smooth sucker rings, or at most, undulations of the ring margins, which agreed with the findings of Aldred (1974). A mature female was subsequently described (Voight, 2008) which lacked terminal arm modifications, a feature that had been described in females of several other cranchiid genera. At ML 93 mm, this specimen had swollen nidamental glands and over 1500 eggs, subequal in size (Voight, 2008).

Voss (1980) provided a more comprehensive description of the genus, with details regarding tentacle armature, internal anatomy, and arm modifications. Little attention was paid to the genus *Bathothauma* by Nesis (1987); considering it a well-understood monotypic genus, he characterised it as a tropical cosmopolitan taxon, with a single ventral eye photophore and paralarvae with long eye stalks. Voss, Stephen, and Dong (1992) later speculated that *Bathothauma* may actually consist of four morphologically similar species, with sympatric distributions; however, no further taxonomic resolution has been achieved to date.

## Systematics

*Bathothauma* Chun, 1906

*Bathothauma* Chun, 1906: 86; Voss, 1980: 384–386, fig. 5; Nesis, 1987: 266, 270, fig. 72U–W.

*Leucocranchia* Joubin, 1912: 396.

**Diagnosis:** Taoniin with truncated mantle, tail blunt posteriorly; gladius with unique posterior ‘T-shape’ formed by broad lateral ‘lobes’ projecting at right angles from conus (Fig. 4.2); fins circular or lobed; tubercles absent at funnel–mantle fusions. Eyes on long stalks through ML 100 mm; adults with spherical, sessile eyes bearing single crescent-shaped photophore. Arm sucker rings with rounded or angular teeth. Club length proportionally large (20–30% ML).

***Bathothauma lyromma* Chun, 1906** (Figs 4.3–4.9, Table B7).

*Bathothauma lyromma* Chun, 1906: 86; Chun, 1910: 303–304, Pl. LVI fig. 9, Pl. LVII fig. 1–2, Pl. LVIII fig. 6–7; Pfeffer, 1912: 753–755; Voss, 1960: 438–439; Young, 1970: 437–446; Aldred, 1974: 995–1005; Imber, 1978: 468–469, fig. 1R, 6B; Voss, Stephen, & Dong, 1992: 193, fig. 223; Reid, 2016: 88–89.

*Leucocranchia pfefferi* Joubin, 1912: 396.



**Diagnosis:** *Bathothauma* species with mean Arm length 32–44% ML and 40–70 suckers on longest arms; suckers with 8–28 variably rounded or angular teeth; mature males with four series of small elongated suckers on distal half of Arms I.

**Type:** *Bathothauma lyromma* **ZMB Holotype Moll-110019** [fide Glaubrecht and Salcedo-Vargas (2000:276)]. Type locality: West of Cape Verde Islands (17°28'N, 29°42'W).

**Material examined (29 specimens):** **SBMNH 461081**, ML 85 mm, ♂, 21.38°N 158.30°W, Hawaii; Oahu; Leeward coast; **SBMNH 460903**, ML 47 mm, sex indet., 21.38°N 158.30°W, Hawaii; Oahu; Leeward coast, 1500–2500 m, 1980; **SBMNH 460946**, ML 46 mm, sex indet., 21.38°N 158.30°W, Hawaii; Oahu; Leeward coast, 1500–2500 m, 01/1983; **NSMT-Mo. 85212**, ML 45mm, sex indet., 14.20°N, 142.86°E, West of the Island of Guam, 520 m, *Hakuho-maru*, 1995/09/22; **MNHN 3256**, ML 100 mm, sex indet., 00.13°N, 140.57°W, 680 m, Stn. 65, 26/09/1968; **MNHN 3257**, ML 89 mm, sex indet., 00.01°N, 144.05°W, 680 m, Stn. 65, 28/09/1968; **NMV F163825**, ML 29 mm, sex indet., 06.30°S, 151.58°E–06.57°S, 151.26°E, Solomon Sea, 10 m, RV *Lady Basten*, 19/05/1981; **NMV F163813**, ML 29 mm, sex indet., 09.68°S, 151.43°E–09.90°S, 151.51°E, Solomon Sea, 10 m, RV *Lady Basten*, 14/05/1981; **NMV F71707**, ML 78 mm, ♂, 14.47°S, 147.23°E–14.67°S 147.10°E, 800 m over 1820 m, RV *Lady Basten*, Stn.1050, 04/07/1981; **NMVF163799**, ML 46 mm, ♂, 15.95°S, 146.87°E–15.88°S, 146.73°E, Pacific Ocean, 850 m, RV *Lady Basten*, 05/12/1981; **NMNZ M.074318**, ML 112 mm, sex indet., 25.80°S, 176.67°W, 755 m over 1280 m, RV *James Cook*, Stn.J17/38/76, 06/12/1976; **NMNZ M.074325**, ML 65 mm, sex indet., 28.15°S, 177.37°W, New Zealand, 93 m over 2000 m, RV *James Cook*, MWT, Stn.J17/30/76, 06/12/1976; **NMNZ M.074349**, ML 24 mm, sex indet., 30.92°S, 178.62°W, New Zealand, RV *James Cook*, 0 m, Stn.J09/13/76, 14/06/1976; **NMNZ M.172937**, ML 144 mm, sex indet., 32.19°S, 160.86°E, Lord Howe Rise SE of Lord Howe Island, 1342–1361 m, RV *Tangaroa*, Stn.2003072, 24/05/2003; **NMNZ M.172954**, ML 98 m, ♂, 32.69°S, 162.56°E, Lord Howe Plateau, 855–874 m, RV *Tangaroa*, 25/05/2003, Stn.2003079; **NMV F163818**, ML 94 mm, ♂, 32.82°S 154.17°E–35.80°S 155.14°E, 20–425 m, CSIRO RV *Soela*, 28/11/1983; **NMNZ M.172945**, ML 107, sex indet., 34.27°S, 168.40°E, West Norfolk Ridge west of Cape Reinga, 1246–1249 m, RV *Tangaroa*, Stn.2003142, 02/06/2003; **NMNZ M.172948**, ML 95 mm, sex indet., 34.30°S 168.39°E, West Norfolk Ridge west of Cape Reinga, 809–857 m, RV *Tangaroa*, Stn.2003147, 03/06/2003; **NMV F163819**, ML 46 mm, ♂, 34.59°S, 155.14°E, 425 m, CSIRO RV *Soela*, Stn: 04/81/66, 09/10/1981; **NMV F163800**, ML 30, 28 mm, sex indet., 34.95°S 151.25°E–34.90°S 151.26°E, Australia, NSW 56 km ESE of Nowra, RV *Franklin*, Stn.Slope 50, 20/10/1988; **NIWA 90017**, ML 110 mm, ♂, 34.98°S, 179.02°E–34.98°S, 179.03°E, 1350–1500m, Station X606, 07/02/1996; **NMV F71702**, ML 42 mm, sex indet., 35.01°S, 151.28°E–35.45°S, 151.25°E, 1706–1675 m, FRS/86, 16/07/1986; **NMA C108566**, 102 mm, 35.62°S, 150.93°E, 0–650 m, 27/10/1977; **NIWA 95913**, ML 75 mm, sex indet., 35.98°S 173.17°E, 701 m, station: E884, 23/03/1968; **NMV F163814**, ML 76 mm, sex indet., 36.42°S, 150.37°E, New South Wales, CSIRO RV *Soela*, 01/03/1981; **NIWA 90016**, ML 17 mm, sex indet., 38.43°S, 47.34°E, 25 m, 28/06/1983; **NIWA 90016**, specimen damaged, sex indet., 38.43°S, 47.34°E, 25 m, 28/06/1983; **NIWA 90028**, ML 9.4 mm, 40.49°S, 171.54°E, 352 m, station: Z10297, 08/08/2000.

**Non-localised material examined (2 specimens):** **NMV F163796**, ML 7 mm, sex indet., SP7/80/8; **NMV F163803**, ML 4 mm, sex indet., SP7/80/15, 02/03/1981.

## Description:

**Adult** (ML 75–150 mm; Fig. 4.3) — Mantle truncated, often cylindrical, MW 29–44–64% ML, becoming proportionally more slender with age; widest point at anterior margin (although MW changes very little from anterior to posterior margin). Fins lobe-shaped, separated by ‘T-shaped’ gladius, FL 10–16–20% ML, FW 29–43–59% ML becoming proportionally smaller with age. Ventral fusions broad; no tubercles or cartilaginous windows at fusions. Head length 10–22–34% ML; HW 16–33–45% ML; ED 8–19–40% ML, with single crescent photophore (Fig. 4.4) (some eyes becoming sessile by 75 mm ML; however, most around 100 mm ML).

Arms thin, formula  $III > II \geq IV > I$ : Arm I 12–32–59% ML, Arm II 15–39–67% ML, Arm III 18–44–73% ML, Arm IV 16–37–58% ML; chromatophores in several series along length. Arms each with 20–35 sucker pairs, sucker counts increasing ontogenetically; largest suckers with 8–28 larger variably rounded to angular teeth on ring margin (Fig. 4.5a). Male Arms I modified, with four sucker series on distal half (Fig. 4.6); smallest observed specimen with modifications at ML 48 mm. Tentacles long, slender, TnL 75–121–200% ML, stalk with sucker pairs along entire length, set more densely on distal 60%; clubs proportionally large, CL 21–35–46% ML (13–25–31% TnL); low membrane on dorsal and ventral surface; 80–124 round suckers (mid-manus suckers enlarged slightly). Club suckers on slender peduncles, 5–10 long, pointed teeth around distal half of sucker ring margin (Fig. 4.5b,c).

**Juvenile** (ML 30–75 mm) — Mantle stout, MW 35–60–100% ML (dependant on specimen preservation), relative width generally decreasing with size. Fins lobe shaped; FL 13–18–37% ML, FW 21–47–62% ML (dependant on mantle contraction at

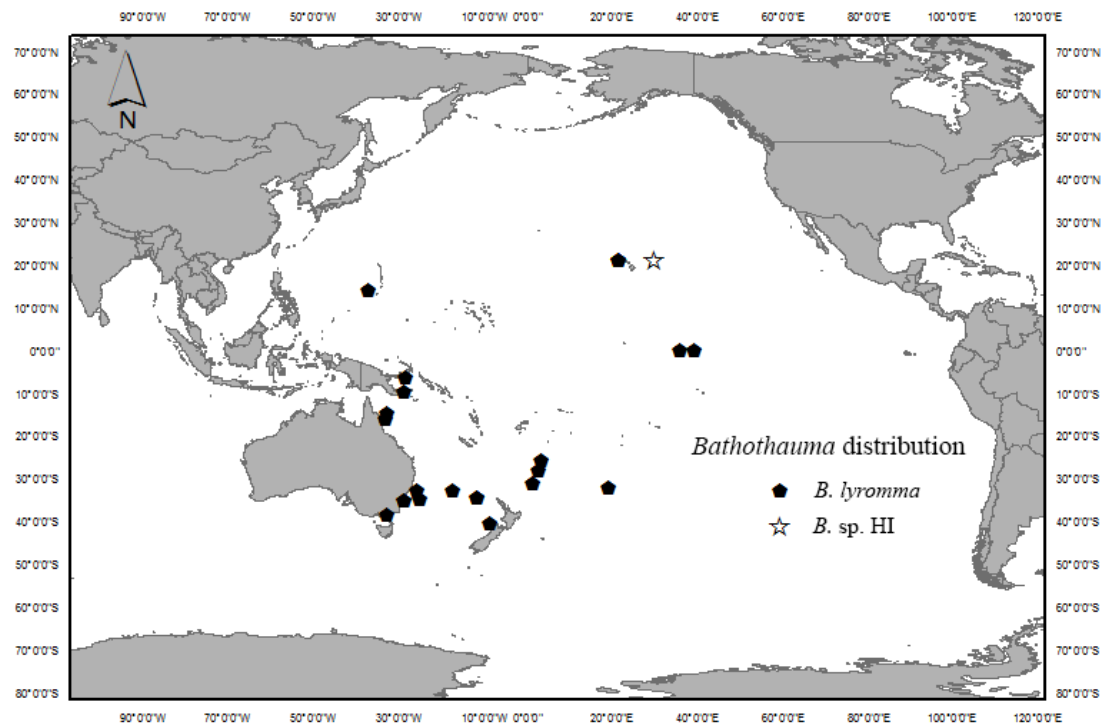


Fig. 4.1— Distribution of examined *Bathothauma* material in the Pacific Ocean.

preservation). Head and eyes transitioning between paralarval and adult features, considerable variation among specimens, HL 13–31–70% ML; HW 45–64–85% ML. Eye diameter 6–16–41% ML, spherical or slightly compressed antero-posteriorly, single photophore developed or developing. Ventral margin of funnel aperture produced into flap, with leading edge variably entire or notched into deep V (Fig. 4.9).

Arm lengths vary greatly among individuals. General arm formula III>II>IV>I; Arm I 3–21–67% ML, Arm II 4–32–96% ML, Arm III 4–35–98% ML, Arm IV 4–30–93% ML. Arms with 16–40 small suckers, subequal in size across all arms; sucker rings with 4–10 blunt to rounded teeth. Male modifications present or developing in animals above 48 mm ML. Tentacles greatly variable in length, but always longer than mantle, 130–186–333% ML; CL 25–44–104% ML (18–23–30% TnL). Tentacular stalk with 44–124 suckers, set in pairs along entire length; club armature not clearly differentiated; 66–112 suckers on club.

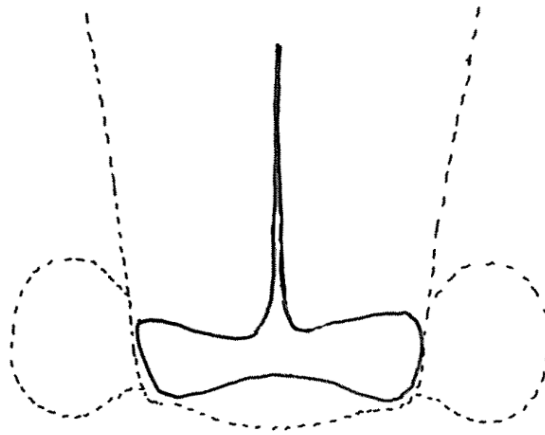


Fig. 4.2—Schematic of posterior glacial terminus (conus) in *Bathothauma*.

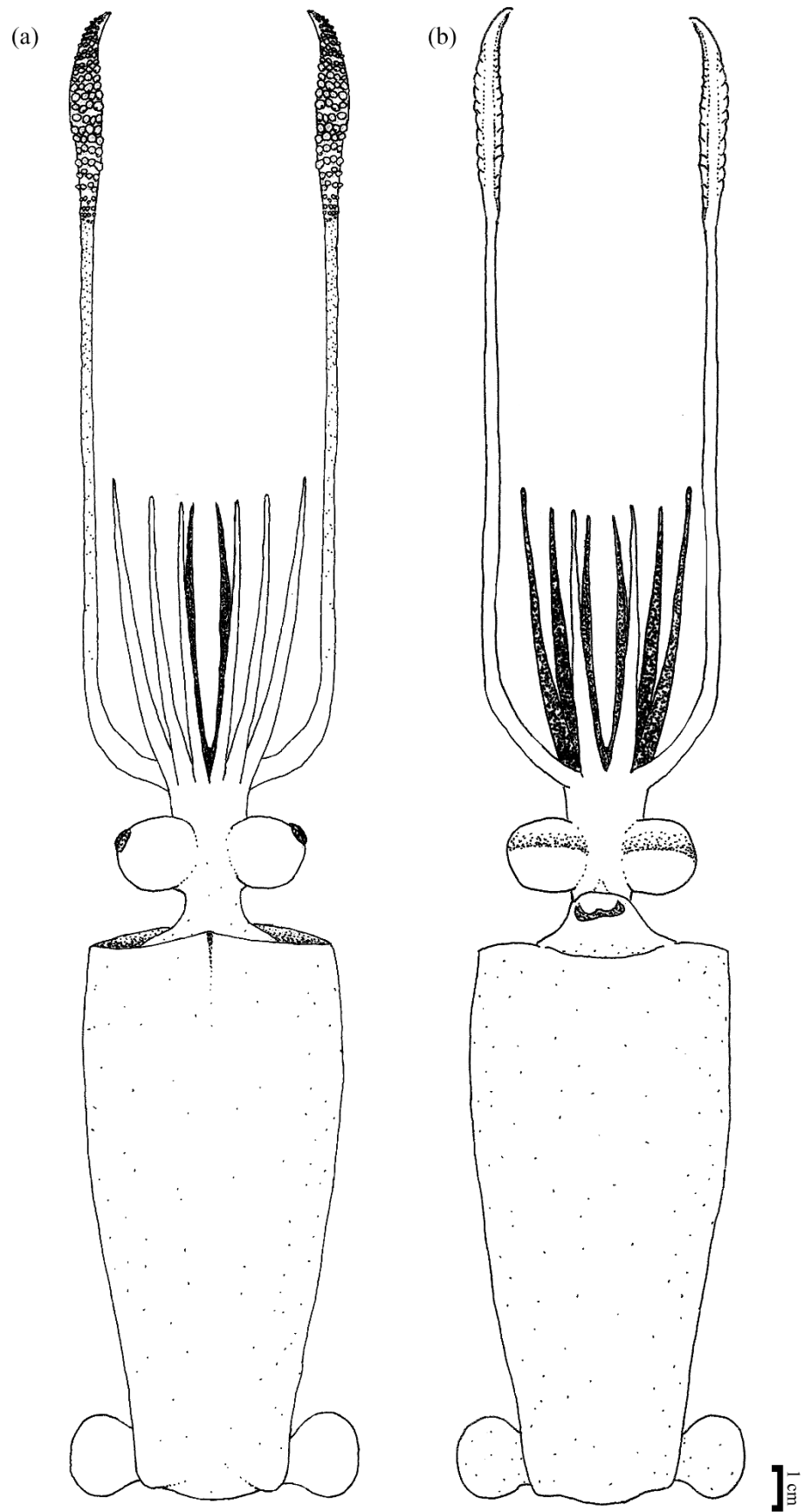


Fig. 4.3—Adult *Bathothauma lyromma* (a) dorsal view (b) ventral view (NIWA 90017, ML 110 mm)

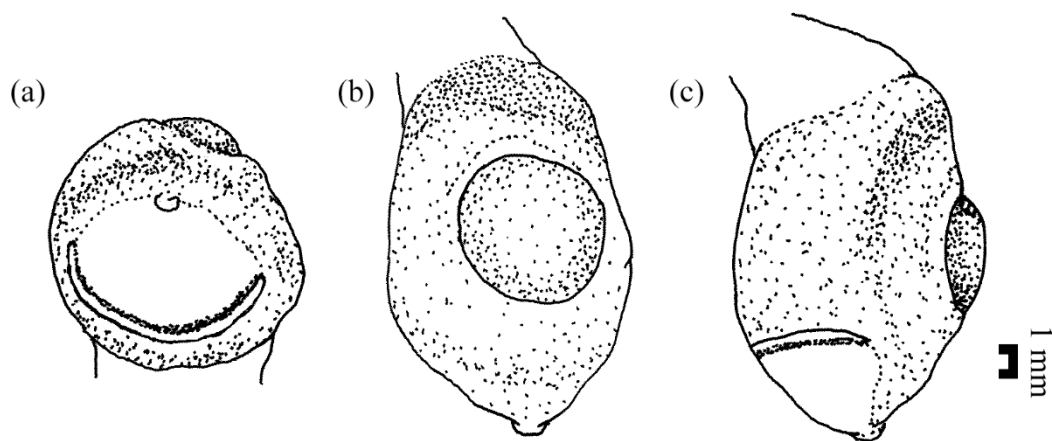


Fig. 4.4—Juvenile *B. lyromma* left eye (a) ventral, (b) lateral, (c) anterior view (NIWA 95913; 75 mm ML).

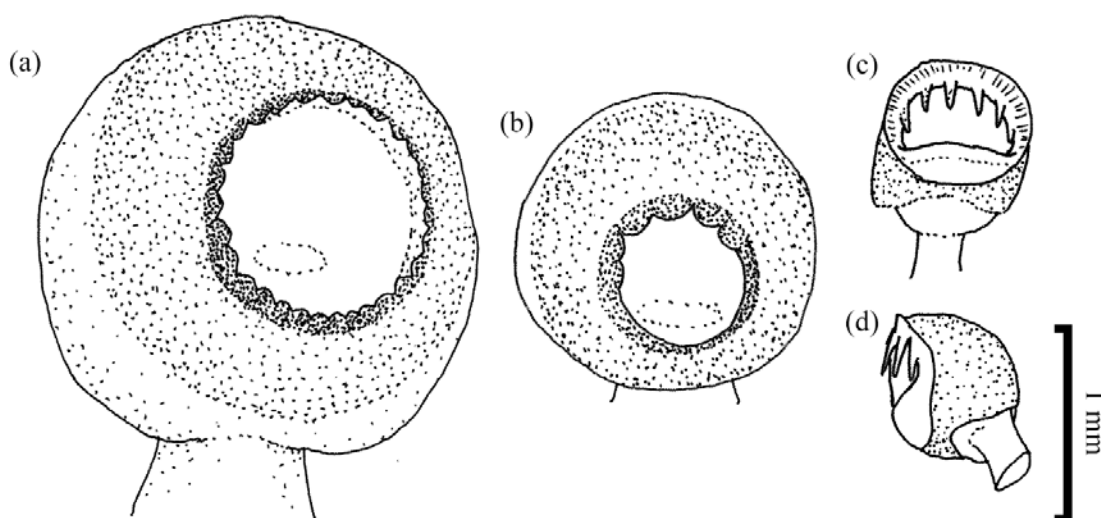


Fig. 4.5—Suckers from male *B. lyromma* (a) adult medial Arm III sucker (NIWA 90017; 110 mm ML), (b) juvenile medial Arm III sucker, (c,d) club manus sucker (NMNZ M.074325, ML 65 mm).

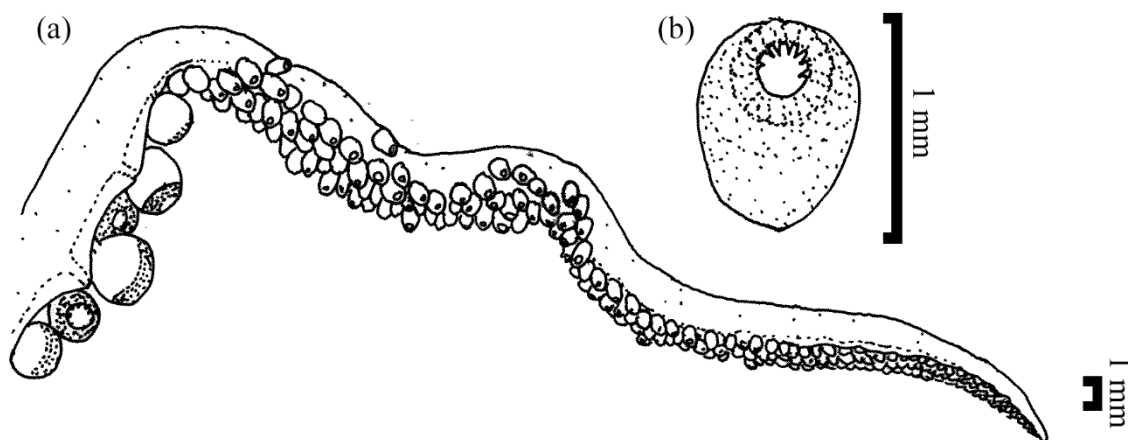


Fig. 4.6—Male arm modification (a), Arm I of *B. lyromma* showing sucker arrangement, (b) enlargement of modified sucker (NIWA 90017, ML 110 mm ML).

**Paralarva** (ML <30 mm; Fig. 4.8) — Mantle stout, MW 52–73–100% ML; fins lobe-shaped; FL 13–23–50% ML, FW 55–67–88% ML (varies according to preservation). Head narrow, with eyes on long slender stalks, HL 33–51–100% ML; HW 41–90–150% ML. Eye diameter 5–10–25% ML, tear-shaped or round, single photophore not yet evident. Funnel aperture approximately 50% basal width.

Arms short, often subequal; Arm I 5–10–25% ML, Arm II 6–12–25% ML, Arm III 7–13–25% ML, Arm IV 6–11–25% ML. Suckers small, 4–10 suckers per arm, sucker rings small, dentition not distinguishable even at high magnification. Tentacle length 86–156–262% ML; CL 21–53–75% ML (25–38–46% TnL). Tentacular stalk with 40–80 suckers, arranged in pairs along entire length; club not well defined; ~80 suckers on club.

**Known distribution:** Tropical to sub-tropical species from Hawaiian Islands to northern New Zealand (Fig. 4.1), elsewhere reported from the Northern Atlantic (Voss, *et al.*, 1992). Present material collected from 0–3799 meters (Fig. 4.7), elsewhere reported from 200–1200 meters depth (Young, 1978).

**Remarks:** *Bathothauma lyromma* Chun, 1906 has long been regarded as a single cosmopolitan species; however, Voss, Stephen, and Dong (1992) hypothesised that up to four closely related species may exist. The Pacific material examined herein is morphologically consistent with previous accounts of *B. lyromma*, and many of the defining characters used to distinguish among cranchiid squid are damaged on the holotype (ZMB Moll-110019). Given that the type locality of *B. lyromma* is the Cape Verde Islands, off the west coast of Africa, the Pacific material examined may well prove to represent an undescribed taxon; tissue samples from *B. lyromma* (*sensu stricto*) from the type locality should be sequenced and compared with the present material (BOLD ADH6205) when possible. Among sympatric cranchiids, this taxon most closely resembles *Bathothauma* sp. HI, and presently only mature males can be reliably distinguished, based on hectocotylus morphology.

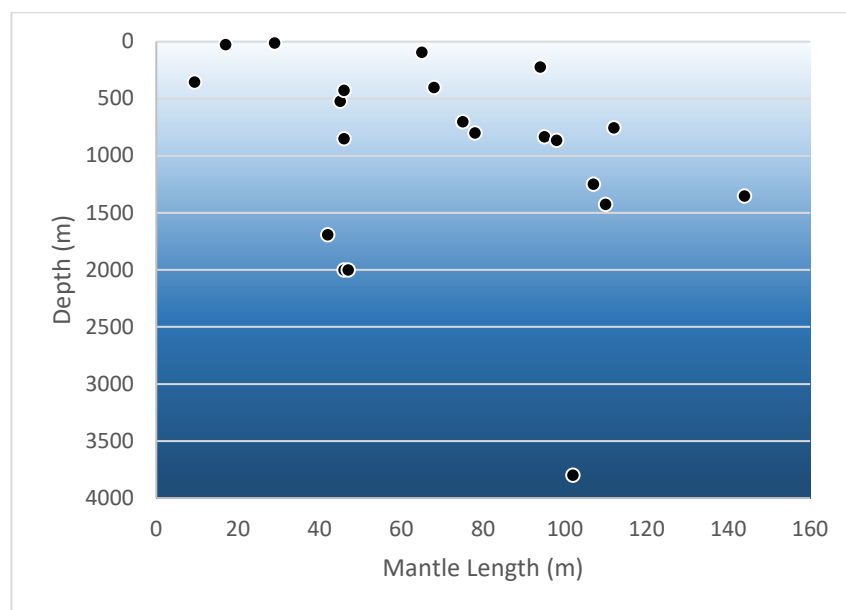


Fig. 4.7—Collection depths of *B. lyromma* material examined in this study.

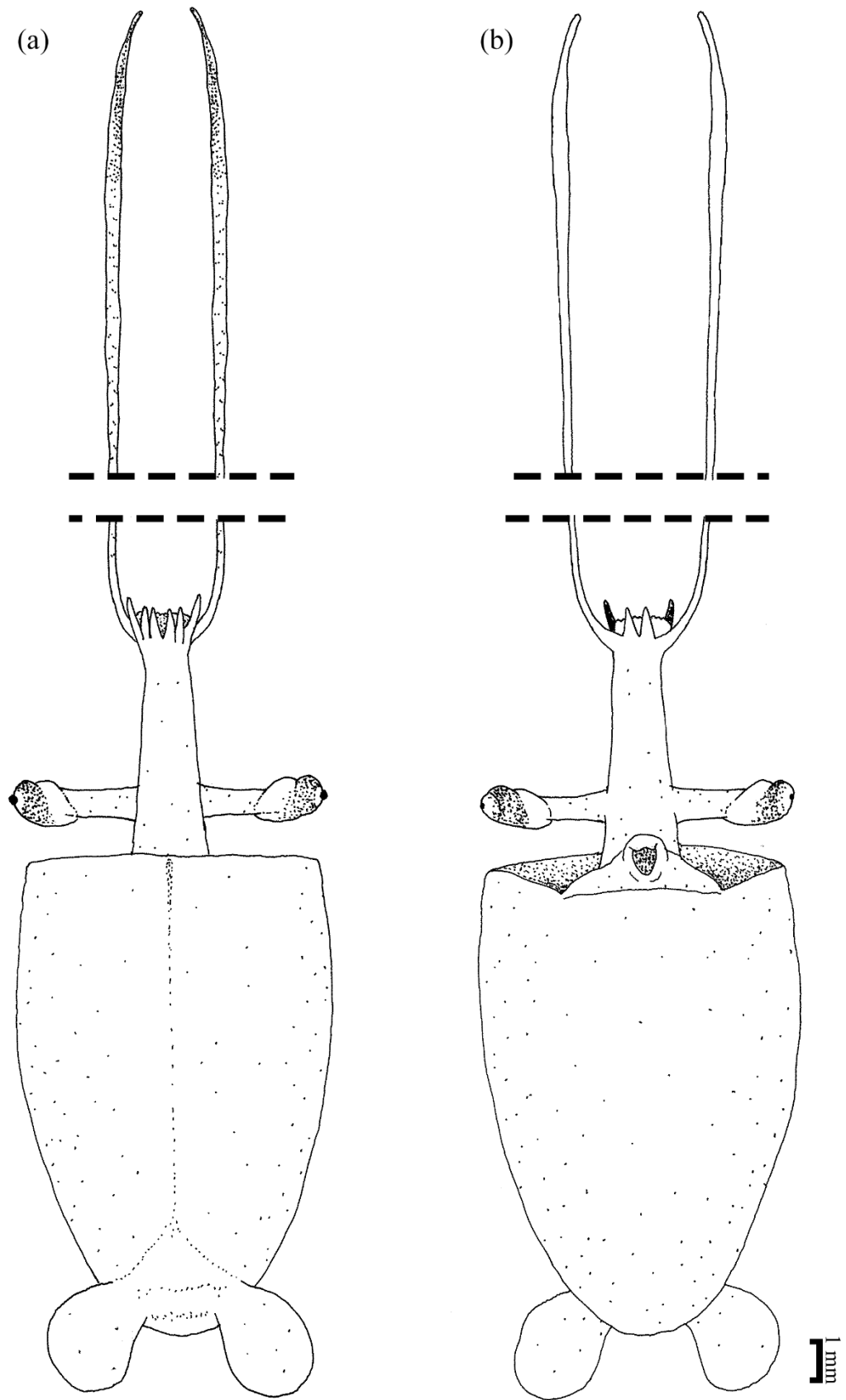


Fig. 4.8—*B. lyromma* paralarva (a) dorsal view and, (b) ventral view (NIWA 90016, ML 17 mm; TnL 24 mm).

***Bathothauma* sp. HL.** (Figs 4.10–4.11)

*Bathothauma* sp. Voss, 1977.

**Diagnosis:** Mature males with secondary sexual modifications on Arms I, spanning 95% of arm length. Arm suckers with 3–6 blunt teeth in both sexes. Eye photophore with minimal surrounding reflective tissue, not encircling entire ventral hemisphere of eye.

**Material examined (1 specimen):** NMNH 814113, ML 68 mm, ♀, 21.20°N 150.20°W, 0–800 m, Stn. 137, Tucker trawl, 23/05/1972.

**Non Localised Material examined (1 specimen):** MPE 608091, ML 104 mm, ♂, Scripps survey (S10).

**Description:**

**Adult** (ML 68–104 mm)—Mantle stout, MW 30–45% ML, cartilaginous windows at ventral funnel–mantle fusions appear as short curved lines. Fins lobe shaped, FL 15% ML, FW 34–41% ML. Head length 10–16% ML in adults; HW 30–45% ML (percentage affected by stalked eyes in smaller specimen); eyes oblong, with one small ventral crescent-shaped photophore, reflective patch minimal. Arm formula variable: I>III>II=IV in mature male individual and III>IV=II>I in the smaller female; arm lengths for the female (former) and male (latter) were 21% and 66% ML for Arm I, 37% and 34% for Arm II and IV, and 46% and 40% ML for Arm III. Arms with 18–26 sucker pairs, apertures small; largest suckers with 3–6 blunt, square teeth. Neither specimen with intact tentacles. Both Arms I in mature male specimen with modification along 95% of arm, several unmodified sucker pairs at arm base, suckers in four series proximally becoming biserial mid-way along arm; wide atrabeculate protective membrane starting at this point. Modified suckers slightly elongate with swollen or puckered apertures (Fig. 4.10).

**Known distribution:** All known material from Hawaiian Islands (Fig. 4.1).

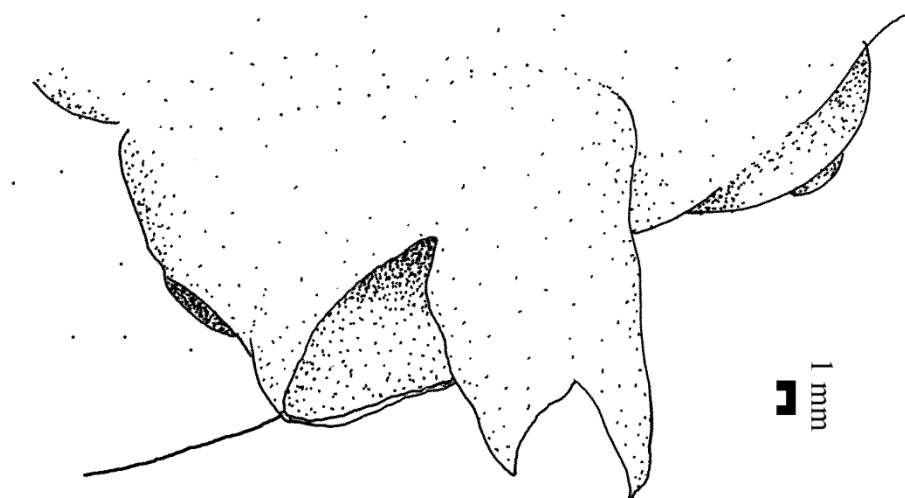


Fig. 4.9—*B. lyromma* funnel with notched ventral flap (NMNZ M.172937; ML 144 mm).



**Remarks:** As only two specimens from Hawaii have currently been examined, these measurements are unlikely to capture the full range of morphology of the species; tentacle morphology also remains unknown at present. Based on these two individuals, the arm proportions may prove useful in distinguishing Pacific *Bathothauma* species:



Fig. 4.10—*Bathothauma* sp. HI, male Arms I (MPE 68091; ML 104 mm)

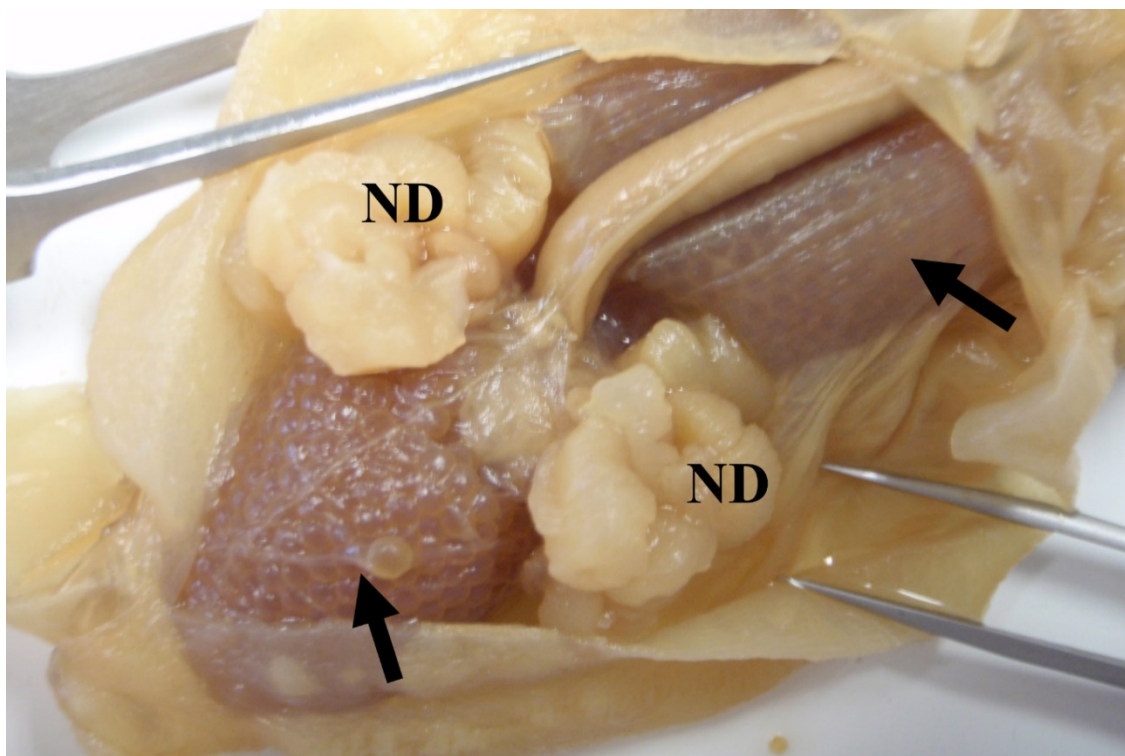


Fig. 4.11—Eggs *in situ* in presumed (*sensu* Voss) female *Bathothauma* sp. HI. Arrows indicate egg masses, ND, nidamental glands (NMNH 814113; ML 68 mm).

while the modified male Arms I (65% ML) were dramatically longer in *B. sp. HI*. than was observed in *B. lyromma* (~30% ML), the remaining arms were proportionally shorter (36% ML, compared with ~50% in *B. lyromma*). The arms of the female specimen followed the same general arm formula as the male.

This material was collected in Hawaiian waters; only a single male specimen of *B. lyromma* (with the arm modifications believed to characterise that species; see Fig. 4.6) was also examined from this region. It is possible that the unique Arm I morphology attributed herein to *B. sp. HI* represents intraspecific variation, but, if it not, then these taxa occur sympatrically. However, several of the specimens from Hawaiian waters also had arm suckers lacking dentition, so it is possible that there are additional undescribed species from that region.

The female examined, ML 68 mm, had what appeared to be two separate batches of eggs developed: one at the posterior end of mantle, at the conus, and the other at the anterior end, posterior to the gills. However, this could simply be a single egg mass, constricted in the middle due to crowding by the remaining viscera. The nidamental glands were large and swollen. Eggs in both masses were similar in size, and proportionally large (several millimetres in diameter) and appeared unattached to the specimen apart from containment within the membrane. The dorsal surface of the mantle had several implanted spermatangia, appearing as short, white transverse lines, several millimetres long.

## Discussion

*Bathothauma* is one of the most distinctive cranchiids, making generic identification relatively straightforward. However, within its relatively consistent overall appearance, considerable variation is seen in bodily proportions and degree of ontogenetic development, even among specimens from similar size classes. Due to the elasticity of the cranchiid mantle, some variation in mantle width occurs in most genera, but specimens of *Bathothauma* also showed variation in general mantle shape. Some specimens have mantles that are approximately cylindrical (such as in Fig. 4.3), while others have a slightly more conical shape overall. This variation is primarily due to the unique glacial shape seen in all *Bathothauma* (Fig. 4.2) and the specimens' treatment and preservation history. The characteristic T-shape at the posterior end of the gladius gives intact specimens their distinctive non-attenuate mantle appearance; breakage of the gladius thus alters the mantle shape more in this genus than in others and can lead to a seemingly more attenuate tail and more conical mantle overall.

*Bathothauma lyromma* appears to be the cranchiid taxon that retains its paralarval morphology to the greatest size, occasionally to nearly 100 mm ML (Aldred, 1974), a size at which most other genera have reached maturity or are nearly mature. The transition between paralarval and mature morphology is often characterised by proportional lengthening of the arms, the eye increasing in size, and the resorption of eye stalks (when present). In other cranchiids, such as *Teuthowenia*, the morphological transition of these features is linked and shows clear ontogenetic stages of development (Evans & Bolstad, 2014). The material of *Bathothauma* examined herein shows greater variability in the size at maturation, and eye stalk resorption and arm length do not appear to be inversely linked. One specimen (SBMNH 460903; ML 47 mm) has

proportionally short arms (4% ML) and has stalked eyes (despite smaller specimens already showing signs of maturation) while another of similar size (NMV F163819; ML 46 mm) has nearly sessile eyes and arm lengths nearly equal to the mantle length (up to 98% ML). Inconsistencies such as this may support the hypothesis that there are several morphologically similar species of *Bathothauma* in the Pacific (Voss, Stephen, & Dong, 1992), and that these species may start maturation at different sizes. Alternatively, this apparent developmental plasticity may be a reflection of the external conditions experienced during growth; for example, prey type and availability or water temperature could be external factors that might influence ontogenetic development. The results of this study are also inconsistent with Aldred (1974), whose examined material did not show signs of maturation (as determined by the eyes becoming sessile) until ML 80 mm. A sharp proportional increase in eye stalk length is known to occur in paralarvae up to ML 40 mm, reaching a plateau that is retained to ML ~80 mm, after which stalk length again decreases or the eyes were found to be sessile (Aldred, 1974). Material between ML 40 and 60 mm was unavailable to Aldred, and it is possible that specimens from a greater range of sizes may have shown signs of maturation at sizes less than 80 mm ML.

Historically, *Bathothauma* has been considered monotypic, with a single cosmopolitan species easily recognised by its distinctive morphology. However, recent studies have shown that some oegopsid ‘species’ historically considered widespread — similarly identified by distinctive morphology, without the need for detailed character examination — in fact represent groups of closely related species, often with more restricted distributions (e.g., *Onychoteuthis ‘banksii’*, Bolstad 2008, 2010; *Taningia danae*, Kelly in prep.; *Idioteuthis cordiformis*, Braid *et al.* 2017; *Histioteuthis bonnellii*, Braid *et al.* in prep). Given its unique morphology, it would be easy to see a specimen of *Bathothauma* and automatically attribute it to the known species. Voss, Stephen, and Dong (1992) suggested that there may be up to four congeners with overlapping geographic distributions; however, no further work has yet addressed this hypothesis. Aldred (1974) reported that some features, such as arm sucker dentition, showed variation and changed dramatically with growth; however, this variation seen among younger individuals may also be indicative of morphologically similar species (in fact, Voss *et al.*, [1992] suggested that Aldred’s specimens from the Indian Ocean are indeed a separate species). Aldred (1974) reported that smaller specimens could have between four and 24 teeth on the sucker rings; however, specimens examined herein had a maximum of ten blunt teeth on ring margins. All of the material Aldred examined was from western Australian waters, which could support the existence of multiple species in the genus, or regional morphological variation within a single more widely distributed species. Aldred also mentioned that larger specimens of *Bathothauma* lack sucker dentition entirely, suggesting that dentition varies with age (with a possible ontogenetic trend toward reduced dentition). This trend was not observed in the Pacific material examined in this study, although the largest available specimen (ML 144 mm) was smaller than some of Aldred’s largest material (ML 205 mm). The low number of teeth observed on Hawaiian material (usually three to six at ML 100 mm) initially appeared to be a potentially useful character for differentiating these from Australian specimens, but subsequent re-examination of southern material revealed some overlap; some Australian specimens also lack true teeth, possessing only low crenulations around the ring margin.

Voss *et al.* (1992) mentioned that sub-adult and adult males of two of their hypothesised species could be distinguished; however, they did not detail the characters they had used for this differentiation, or how the other hypothesised species were distinguished. The Arm I morphology in males was the most obvious differentiating feature in this study. In most submature to mature male *B. lyromma* specimens examined, modifications appear on the first arm pair, can be seen in specimens from 40 mm ML, and take up approximately 45–50% of the length of the arm (Fig. 4.6). The structure of these modified arms appears similar to male modifications seen other Taoniinae, such as *Teuthowenia* (Evans, 2013), in which the suckers on Arms I are biserial and spherical basally, and tetraserial, tightly packed and oblong further toward the distal end of the arm. In *Bathothauma* sp. HI, the first pair of arms have two series of suckers distally, with the sucker aperture appearing swollen or puckered (Fig. 4.10); however, the proximal suckers appear to be in four series. The modification itself takes up almost the entire length of the first arm pair; however, there are several pairs of unmodified suckers at the arm base. Arms I are proportionally longer than the other arm pairs in *B. sp. HI*, while Arms I in *B. lyromma* are usually the shortest pairs of arms, even when modified. Okutani (1975) also illustrated a male specimen (which he believed to be *B. lyromma*) that had proportionally longer Arms I, with most of the arm showing male modification; however, in Okutani's description this modification had four series of smaller elongated suckers rather than the two series seen distally herein. The modified arms of *B. sp. HI* are also more gelatinous (compared to the other arm pairs) and a wide lateral membrane is present on the oral margin on each side of the arm. The morphology of this modification has not been described by previous authors and appears unique among known cranchiids.

Little is known about the mating and spawning behaviours of squid from the family Cranchiidae (and deep-sea squid in general). Evans and Bolstad (2014) estimated that female *Teuthowenia pellucida* can produce approximately 18,000 eggs — more than double the previous fecundity estimate. In *Teuthowenia*, and several other Taoniinae, females produce large egg clutches, where eggs are small and often clustered together and connected via filaments (which appear similar to stems or branches) (Evans & Bolstad, 2014). In *Bathothauma*, the gravid females examined had fewer (but larger) eggs, which appeared to all be contained within a membranous casing, allowing the eggs free movement within this enclosure. In one specimen, (NMNH 814113) there were two such masses in a single female: one at the posterior end of the mantle and a second near the digestive gland, or more likely the nidamental glands, which were quite swollen (Fig. 4.11). It is possible that this indicates an iteroparous style of spawning, although the eggs in both masses were of similar sizes and appeared to represent similar stages of development.

Another morphological characteristic of *Bathothauma* that requires further investigation is the morphology of the funnel aperture, as two specimens (NMNZ M.172937 and NMV F163818) had an unusual indentation along the aperture margin. On the ventral margin of the funnel aperture there is an extended flap of tissue with what appears to be a triangular notch, as if someone had folded the funnel at the midline and snipped off a corner (Fig. 4.9). This was initially attributed to tissue sampling for genetic work; however, this feature was also observed in an Australian specimen. This appears to be similar to the hooded funnel illustrated by Allan (1945). In most cases, the indentation is clearly defined, but lacks the raw leading edge that would indicate

human dissection, and often the angular notch has a slight curve towards the lowest point. Although this feature has only been observed in a few specimens, it would be interesting to see whether this feature is present in other specimens, or is indeed simply a case of repetitive tissue sampling across multiple collections.

Although extensive research has been done on the ontogenetic development of *Bathothauma lyromma* (with particular emphasis on the morphology of the eyes and photophores), treated as a supposedly monotypic genus, little systematic work has been deemed necessary. However, there appears to be at least one more species within the genus, with the possibility that several others exist in other geographic localities. The present description of *Bathothauma* sp. HI is limited primarily to males that have reached maturity; therefore, further research into this species should investigate what characters can be used to delineate species at smaller sizes and confidently identify females. A global review of specimens is needed to determine whether the Atlantic and Indian Oceans and/or Mediterranean Sea contain further new species. In addition, previous research on ontogenetic development should be reevaluated in the light of evidence that more than one species likely occurs in this genus.

## *Galiteuthis* Joubin, 1898

### Historical Review

*Galiteuthis* species were initially reported over a decade before the genus itself was formalised. Specimens were first attributed to the genus *Taonius*, as was the case for the paralarval stage of '*T.* *suhmi*' (Hoyle, 1886; =*G. suhmi*, *fide* Nesis, 1987). Similarly, Joubin (1895) described *T. richardi* (= *Galiteuthis* sp., *fide* Voss, 1980) noting many features now associated with *Galiteuthis*, including elongated hooks on the tentacle clubs, and musing that the specimen probably did not belong in *Taonius*; however, due to damage of the specimen, Joubin was unable to determine its proper systematic placement. Several years later, Joubin (1898) erected a new genus, which he named *Galiteuthis*, as part of his new family Cranchionychiae (Joubin, 1898). This grouping was an intermediate family between cranchiid and onychoteuthid squid, having both the fused mantle and head of Cranchiidae and the elongated hooks on the tentacle clubs, thought at that time to be unique to Onychoteuthidae (Joubin, as cited in Voss, 1980). Joubin's original type specimen for this new family, *G. armata* Joubin, was described from the Mediterranean, and is now known to occur all over the Atlantic Ocean (Joubin, 1898; Bolstad *et al.*, 2015).

In 1900, Pfeffer erected a new genus for *T. suhmi*, which he named *Taonidium* (= *Galiteuthis*, *fide* Chun, 1910). Representatives of this genus differed from *Taonius* in having small, heart-shaped fins, small arms lacking webbing, and long stalked eyes. *Taonidium suhmi* (Pfeffer, 1900; =*G. suhmi*) was the only species assigned to this genus until the description of *T. pfefferi* (Russell, 1909; =*G. armata*, *fide* Nesis, 1987) nine years later. Characters that distinguished *T. pfefferi* from *T. suhmi* included its geographic locality, mantle shape, arm length formula, and chromatophore patterns; however, the specimen itself was small and many of these features were still developing.

Chun (1906) noted that as species of *Taonidium* developed, the suckers on their tentacle clubs elongated forming hooks and he indicated that this later life-stage was actually *Galiteuthis* (this observation, meaning, in effect that *Taonidium* is a synonym of *Galiteuthis*); however, Chun did not formally revise the systematic classification at that time. Instead, he introduced a new genus and species from the Antarctic, *Crystalloteuthis glacialis* (Chun, 1906; =*G. glacialis* *fide* Nesis 1987), which was distinguished by having 'antler-like' tubercles at the ventral fusion points (Chun, 1906). Four years later, Chun (1910) further revised the family and gave full recognition to *Galiteuthis* as a valid genus while also synonymising *Taonidium* with it. In a further explanation of his brief generic description for *Crystalloteuthis*, Chun described the physical structure of the branched ventral tubercles, also noting a single blunt tubercle on either side of the nuchal fusion. These features were determined to be the most distinguishable features for identifying *Crystalloteuthis*. However, in the same revision, Chun identified and described his new species, *Teuthowenia antarctica*, also from the Antarctic. He did not make note of any tubercles on the dorsal or ventral portions of the body in his original description of this species. Largely as a result of the subsequent recognition of these characters, *T. antarctica* was eventually synonymised with *G. glacialis* by Nesis (1987).

During exploration off the western coast of North America, Berry (1911) described a new species, *Galiteuthis phyllura*, which he considered to be morphologically similar to the previously described *G. armata* Joubin, 1898 from the Mediterranean. Unfortunately, aside from geographic separation, Berry never explained how these two animals were morphologically distinct. Unlike many previously described species, Berry's examined specimen had reached maturity. He described the tentacle clubs as having 12 elongated hooks (as well as a few small suckers on the dactylus) and the tentacle stalk having alternating pairs of suckers and pads (Berry, 1911). A year later, in a second description of cephalopods from western North America, Berry amended his previous systematics and erected a new sub-family in the Cranchiidae, which he named Galiteuthinae (Berry, 1912). Berry supported this decision by referring back to Joubin's attempt to try to explain morphological similarities between *Galiteuthis* and members of the family Onychoteuthidae; however, this sub-family does not appear in later revisions of the family.

Despite Chun making *Taonidium* a junior synonym of *Galiteuthis* two years prior, Pfeffer (1912) retained it as a genus when he divided the Cranchiidae into 'tribes'. In a 'tribe' which he named *Taonius*-like cranchiids, Pfeffer amalgamated a large number of other genera: *Taonius*, *Galiteuthis*, *Desmoteuthis*, *Megalocranchia*, *Phasmatopsis*, *Toxeuma*, *Crystalloteuthis*, *Corynomma*, and *Phasmatoteuthion* (a new genus described by Pfeffer [= *Galiteuthis*, *fide* Voss, 1980]). Although many of these genera persisted well into the 20<sup>th</sup> century, the large tribal groupings used in this revision of the family were not maintained in most literature.

Several new species were described over the next few decades; however, many of these were based on juvenile material. For instance, *Crystalloteuthis beringii* Sasaki 1920 was differentiated from the previously described *C. glacialis* by having pedunculated eyes, bifid tubercles at both ventral funnel-mantle fusion points and a broader 'shield-shaped' fin. This species was later identified as an early life stage of *G. phyllura* by Nesis (1987). Similarly, Robson (1948) identified a species he named *Taonidium pacificum* from the Indian Ocean, and discussed how, according to Pfeffer's taxonomic key, the species should be *T. chuni* Pfeffer, 1912. Robson found that the morphological ratios differed slightly from Pfeffer's previously described species and stated that *T. chuni* was "obviously a juvenile form"; however, Robson failed to consider that his own new species also had many paralarval features as well. The systematic status of this species remains unclear; however, it has been attributed to the genus *Galiteuthis* (Voss, 1980).

In a review of oceanic squid, Clarke (1966) decided that all described adult specimens from the genus *Galiteuthis* were referable to *G. armata* Joubin, and seemed doubtful about Hoyle's description of *G. suhmi* in 1885 (despite Pfeffer [1912] validating it as a distinct species). Clarke also synonymised *G. phyllura* with *G. armata*; however, he neglected to also combine *G. glacialis* as it was still considered to be a member of the genus *Crystalloteuthis*, which Clarke consequently grouped with the Cranchiinae (presumably due to the presence of tubercles on the skin). Based on this synonymy, Filippova (1972) described what she considered to be the second species of *Galiteuthis*, which she named *G. aspera* (= *G. glacialis*, *fide* Nesis, 1987). This taxon was differentiated from *G. armata* due to it being located in the Southern Ocean (not a taxonomic trait), and by the presence of tubercles on the mantle surface. However, a year prior, McSweeney (1971) had already identified *Crystalloteuthis glacialis* as a

species of *Galiteuthis*, and had provided a detailed description of its morphology and geographic distribution. Nesis (1987) re-instated several of the previously described *Galiteuthis* species that had been synonymised by Clarke in 1966, naming five species within the genus: *armata*, *phyllura*, *suhmi*, *glacialis*, and *pacifica* (the previously described *T. pacificum* Robson).

Due to its abundance in Antarctic waters and an increased focus on polar research at the turn of the century, *G. glacialis* became a common focus for pelagic cephalopod research. The species was used in examining Southern Ocean trophic systems (Croxall & Prince, 1994), early-life distribution and lipid analysis (Piatkowski & Hagen, 1994), and female reproductive descriptions and spawning methods (Nesis, Nigmatullin, & Nikitina, 1998). Thus, since 1990, our understanding of this particular species has increased dramatically; however, the other four accepted species within this genus have received considerably less focus, and many aspects of their ecology still remain unknown.

## Systematics

*Galiteuthis* Joubin, 1898 (Table 7)

*Galiteuthis* Joubin, 1898: 279; Voss, 1980: 392–394, fig. 9; Reid, 2016: 90–91.

*Taonidium* Pfeffer, 1900: 192; Russell, 1909: 451; Pfeffer, 1912: 719–720;  
Robson, 1948: 129.

*Crystalloteuthis* Chun, 1906: 85; Chun, 1910: 290; Pfeffer, 1912: 726.

*Phasmatoteuthion* Pfeffer, 1912: 729.

**Diagnosis:** Mantle goblet shaped, abruptly tapering to fine point at conus; tubercles variably present at funnel–mantle fusion points; paralarval individuals >50 mm ML with two or three tubercles on either side of nuchal fusion, absent by 50 mm ML. Fins lanceolate; fin width often subequal to MW. Eyes spherical, with two photophores: one large crescent outlines ventral hemisphere of eye and one smaller photophore slightly ventral to lens. Arms robust basally, slender at distal tips; trabeculate protective membrane on all arms. Tentacle clubs with low protective membrane along dorsal surface; manus with 8–12 elongated hooks.

Table 7— Characters used to distinguish Pacific *Galiteuthis* species in this study.

Species	Inner eye photophore shape	Ventral tubercles	Arm dentition
<i>G. glacialis</i>	Crescent	Tricuspid on either side of fusion	12–14 blunt teeth
<i>G. pacifica</i>	Square	Absent	Absent
<i>G. phyllura</i>	Linear	Complex (4–5 point) tubercle	Absent
<i>G. suhmi</i>	Crescent	Complex (3–5 point) tubercle	14–20 rounded teeth



***Galiteuthis glacialis* (Chun, 1906)** (Figs 5.2–5.7, Table B8).

*Crystalloteuthis glacialis* Chun, 1906: 85; Chun, 1910: 290–293, Pl. LIII figs 2–9, Pl. LIV fig. 18.

*Teuthowenia antarctica* Chun, 1910: 293–295, Pl. 56 figs 1–5, Pl. 57 figs 3–7; Pfeffer, 1912: 745–746.

*Crystalloteuthis gracilis* Pfeffer, 1912: 726–728.

*Galiteuthis aspera* Filippova, 1972: 400–403, fig. 7.

*Galiteuthis glacialis* (Chun, 1906): Nesis, 1987: 275, fig. 71P–S; Voss, 1980: fig. 9; Sweeney *et al.*, 1992: 200–202, fig. 227; Voss, Stephen, & Dong, 1992: 200–202, fig. 227; Reid, 2016: 91–93.

**Diagnosis:** Adults with small, round, tubercles scattered randomly on mantle. Ventral eye photophores crescent shaped. Medial arm suckers with 12–14 round teeth on distal ring margin. Juveniles and paralarval specimens with pointed tubercles at nuchal and funnel fusion points.

**Type material:** (examined) *Crystalloteuthis glacialis* **ZMB Holotype Moll-110013** [*fide* Glaubrecht and Salcedo-Vargas (2000, 275)]. Type locality: 59°16'S, 40°13'E.

**Material examined (15 specimens):** NMNZ M.286166, ML 131 mm, 43.51°S, 167.13°E, New Zealand, 170–250 m over 1250 m, RV *James Cook*, Stn. J15/52/87, MWT, 16/12/1987; **SBMNH 464506**, ML 67 mm, sex indet., 55.82°S, 24.80°W, Antarctica, South Georgia and the South Sandwich Islands, 1922 m, 01/03/1963; **MV F66301**, ML 299 mm, sex indet., 64.99°S, 69.03°E–64.98°S, 68.97°E, Prydz Bay, Antarctica, 800 m over 2882 m, RSV *Aurora Australis*, Stn. 61B, 10/02/1991;

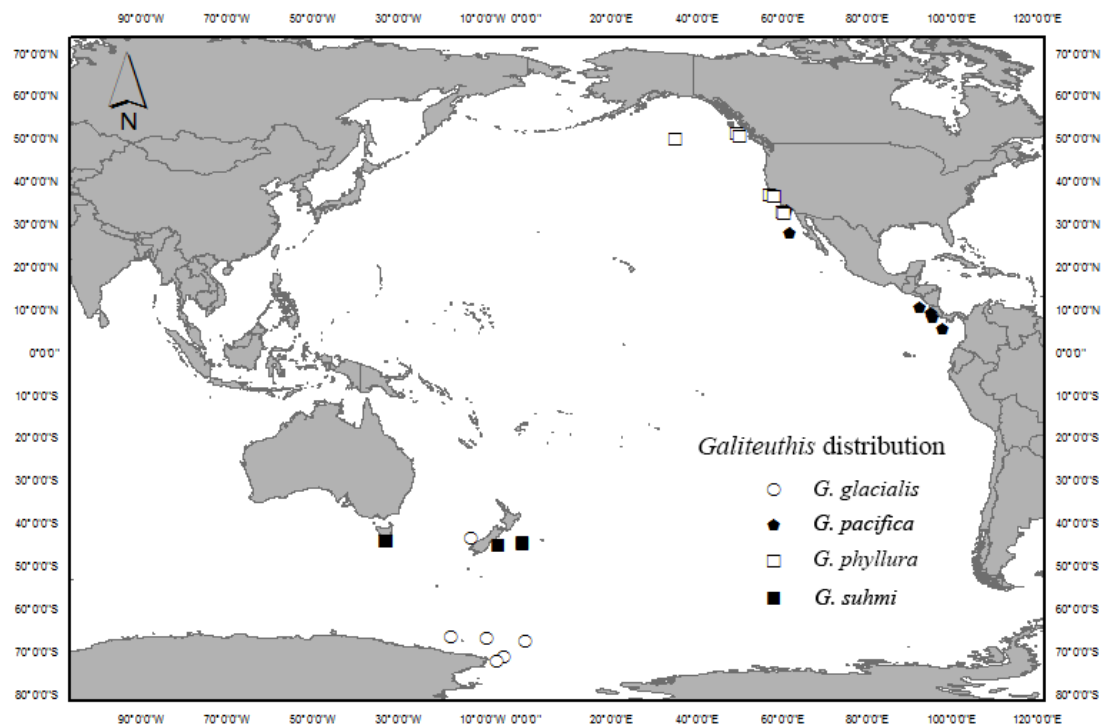


Fig. 5.1— Distribution of examined *Galiteuthis* material in the Pacific Ocean.

**MV F66641**, ML 175 mm, sex indet., 66.02°S, 68.99°E–65.99°S, 68.97°E, Prydz Bay, Antarctica, 800 m over 2243 m, RSV *Aurora Australis*, Stn. 63B, 11/02/1991; **MV F66638**, ML 166 mm, sex indet., 66.51°S, 78.00°E–66.50°S, 78.00°E, Prydz Bay, Antarctica, 5–200 m over 1844 m, RSV *Aurora Australis*, Stn. 49, 5/02/1991; **MV F66311**, ML 206 mm, sex indet., 66.51°S, 72.01°E–66.54°S, 72.07°E, Prydz Bay, Antarctica, 800 m over 1280–1157 m, RSV *Aurora Australis*, Stn. 15B, 22/01/1991; **MV F66633**, ML 171, 76 mm, sex indet., 66.52°S, 69.10°E–66.53°S, 69.17°E, Prydz Bay, Antarctica, 800 m over 1783–1762 m, RSV *Aurora Australis*, 11/02/1991; **NIWA 70997**, ML 8.7 mm, 66.51°S, 162.36°E–66.51°S, 162.36°E, 0–350 m, Stn. Tan1002/5; **NIWA 44344**, ML 104 mm, 67.01°S, 170.70°E–66.94°S, 170.73°E, 1078–100 m, Stn. TAN0802.312, 14/03/2008; **NIWA 44588**, ML 52, 46, 45 mm, sex indet., 67.39°S, 179.85°W–67.37°S, 179.84°W, 740–50 m, Stn. TAN0802/240, 07/03/2008; **NIWA 44345**, ML 41 mm, 71.34°S 174.64°E–71.45°S, 174.95°E, 10–2000 m, Stn. TAN0802/170, 26/02/2008; **NIWA 44332**, ML 10 mm, 72.08°S, 173.05°E–72.08°S, 172.93°E, 10–450 m, Stn. TAN0802/158, 24/02/2008.

**Non-localised material examined:** **NMNZ M.277830**, ML 225 mm, New Zealand, Stn. 2184/53, 14/01/2006; **NMNZ M.277836**, ML 374 mm, New Zealand, Stn. 2332/106.

### Description:

**Adult** (ML >75 mm; Fig. 5.2–5.5) Mantle with small round tubercles from ~160 mm ML, randomly distributed, MW 15–19–27% ML; chromatophores small brown dots. Fins lanceolate, lacking dermal structures, FL 30–43–50% ML, FW 11–18–25% ML. Gladius long and narrow, conus 45% GL; rachis terminus with opaque circle on either side, rachis funnel-shaped. Tubercles with two or three points on either side of each ventral funnel–mantle fusion point; cartilaginous ridge extends onto funnel. Head length 8–11–15% ML, HW 9–14–20% ML. Eyes spherical, bulbous, ED 8–10–12% ML; inner ventral photophore >50% eye diameter (Fig. 5.3). Olfactory papillae on aboral surface of eye, funnel-shaped. Funnel base 20–44–60% MW, aperture 20–37–60% FB.

Arms sub-equal, with heavily trabeculate membrane over 75% of arm; general arm formula  $IV \geq III \geq II > I$ : Arm I 13–22–30% ML, Arm II 18–26–31% ML, Arm III 22–28–35% ML, Arm IV length 20–29–37% ML. Longest arms with 50–73–98 small, biserial suckers, sub-equal in size; basal suckers with smooth ring margin, 12–14 blunt teeth medially, 3–5 pointed teeth distally (Fig. 5.4), no transitional suckers between mid and distal dentition patterns. Tentacles 47–64–77% ML, with 15–20 pairs of tiny suckers on stalk; suckers interspersed with fleshy pads towards distal end. Club ~10% ML (9–14–20% TnL); 60–80 suckers (Fig. 5.5); carpus with 8–12 suckers interspersed with fleshy pads; manus with 8–12 elongated hooks, dactylus with 40–52 suckers, three or four blunt teeth on inner sucker margin.

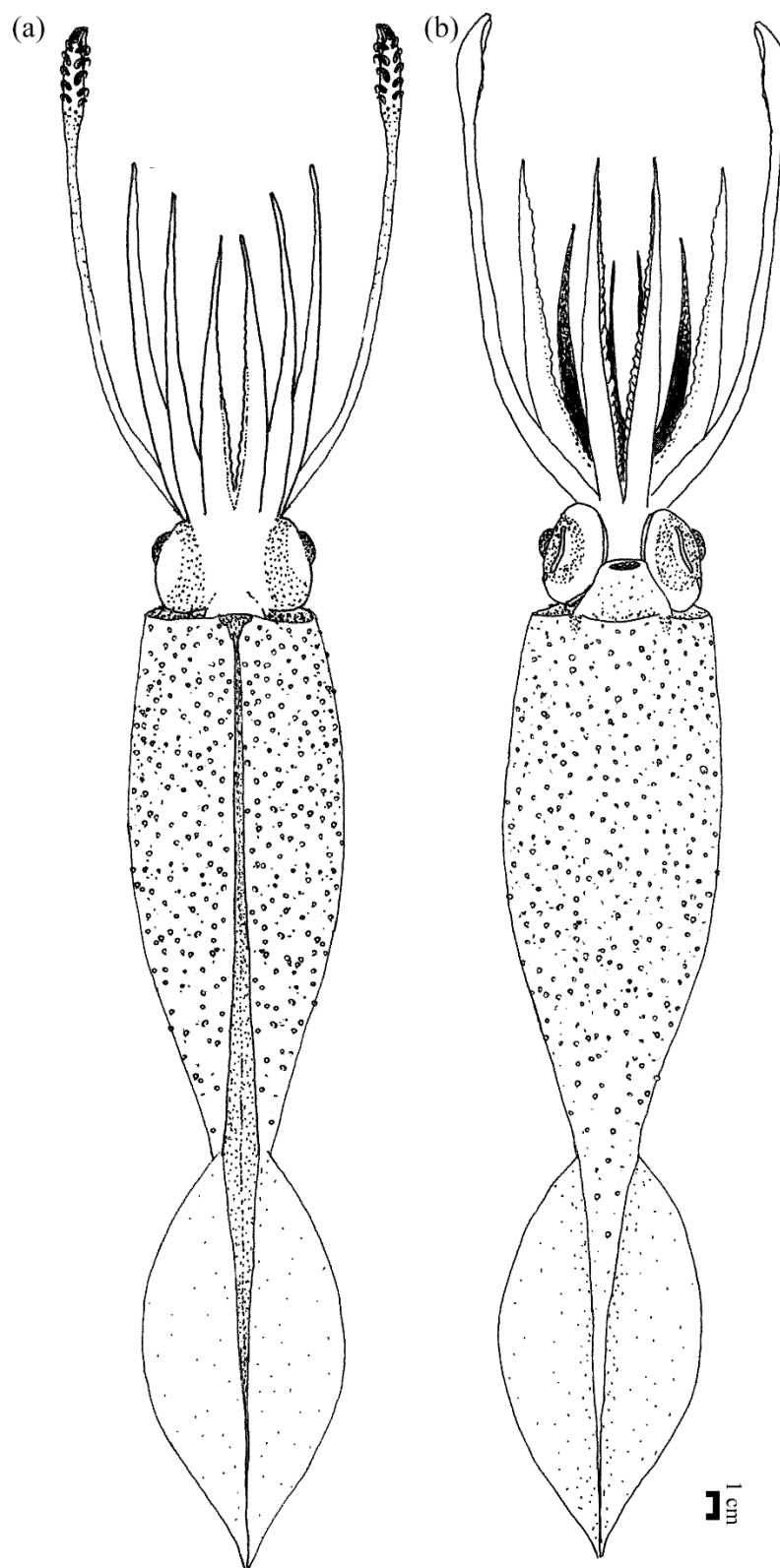


Fig. 5.2—Adult *G. glacialis* (a) dorsal view and (b) ventral view (NMNZ M.277836; ML 374 mm).

**Juvenile** (ML 40–75 mm; Fig. 5.6)—Mantle lacking dermal structures; MW 17–28–32% ML; chromatophores small brown dots. Fins lanceolate, lacking dermal structures, FL 24–31–39% ML, FW 11–12–15% ML. Gladius narrow, conus 45% GL; rachis broader at anterior margin. Tubercles with two or three points on each side of nuchal and each ventral funnel–mantle fusion point. Head length 6–9–11% ML, HW 15–18–22% ML. Eyes spherical, on stout stalks, ED 5–7–10% ML; inner ventral photophore >50% eye diameter. Funnel base 27–42–54% MW, aperture narrowing gradually to 20–28–44% FB.

Arms sub-equal, with heavily trabeculate membrane over 75% of arm; general arm formula  $IV \geq III \geq II > I$ : Arm I 8–11–14% ML, Arm II 11–15–20% ML, Arm III 13–18–24% ML, Arm IV length 15–19–26% ML. Arms with 24–44 small, subequal suckers (Arms IV with highest count). Tentacles 52–64–80% ML, 15–20 pairs of tiny suckers along stalk; club 7–9–15% ML (9–14–21% TnL); each club with 60–70 suckers; some specimens lacking developed hooks; some with several elongated hooks (developing ~60 mm ML), dactylus with 40–57 suckers, three or four blunt teeth on inner sucker ring margin.

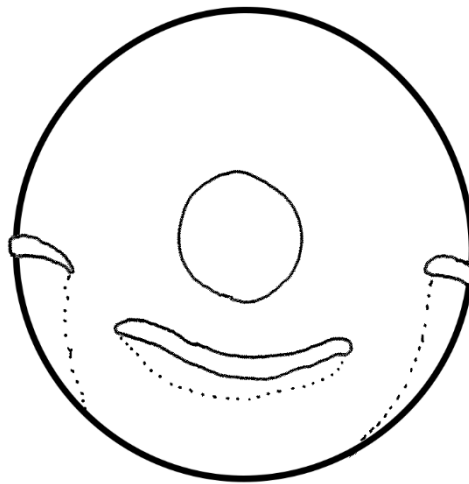


Fig. 5.3—Left eye schematic for *G. glacialis*

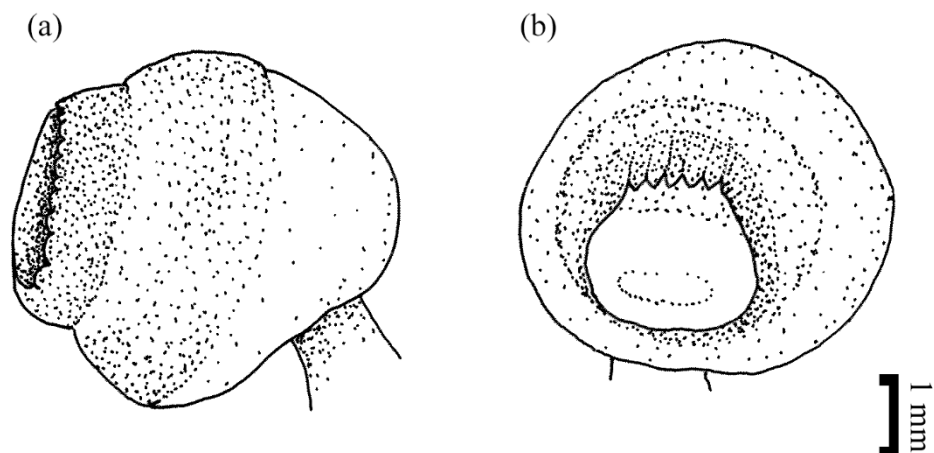


Fig. 5.4—Arm suckers of *G. glacialis* (a) mid arm sucker (lateral view) and (b) distal arm sucker (M.277836; ML 374 mm).

**Known distribution:** Predominantly Southern Ocean; Tasman Sea, west of New Zealand, to the Ross Sea, Antarctica (Fig. 5.1), elsewhere reported from Antarctic waters circumglobally (Sweeney *et al.*, 1992). Present material collected from 102–1922 meters (Fig. 5.7), elsewhere reported to depths of 2000 meters (juveniles) and >2500 meters (mature adults) (Sweeney *et al.*, 1992).

**Remarks:** Few Southern Ocean squid species have dermal sculpture, so adult *G. glacialis* should be easily identifiable; however, younger specimens that have not yet developed dermal sculpture could be confused with *G. suhmi*, as their geographic range may have some overlap, or *Teuthowenia pellucida* for a similar reason. Paralarval specimens of *G. glacialis* strongly resemble paralarvae of *Mesonychoteuthis hamiltoni*. These species can be distinguished by tubercles found at the three fusion points: *G. glacialis* have one simple tubercle on either side of the nuchal fusion and a two or three pointed tubercles (cusps often arranged linearly) on either side of each ventral funnel–mantle fusion while *M. hamiltoni* lacks a nuchal tubercle (or only has one on the dorsal midline) and has a small complex tubercle at each fusion point (Rodhouse & Clarke, 1985; Sweeney *et al.*, 1992).

The ‘juvenile’ description above encompasses several size classes; some ontogenetic differences were noted (e.g., two relatively large individuals in this group had minimally stalked eyes and developing tentacle club hooks), but due to the limited material available for study, detailed observations on discrete stages are not possible at this time.

There is strong support (BS 100) for *G. glacialis* as a distinct species, and all material sequenced fell into a single BIN (BOLD:AAB8549). Two additional undescribed *Galiteuthis* species were closely related to *G. glacialis*, and appear to form a clade. It is unclear how these two species morphologically compare to *G. glacialis* and *G. suhmi*; therefore, additional morphological analysis is required to further stabilise this genus.

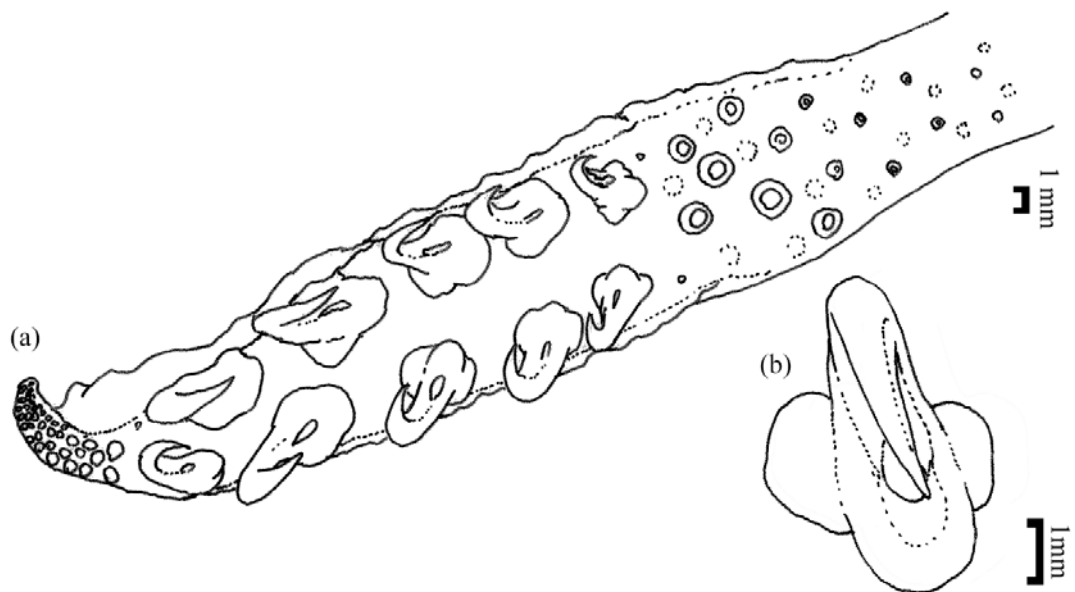


Fig. 5.5—(a) Right tentacle club of adult *G. glacialis*, (b) enlargement of hook (M.277836; ML 374 mm).

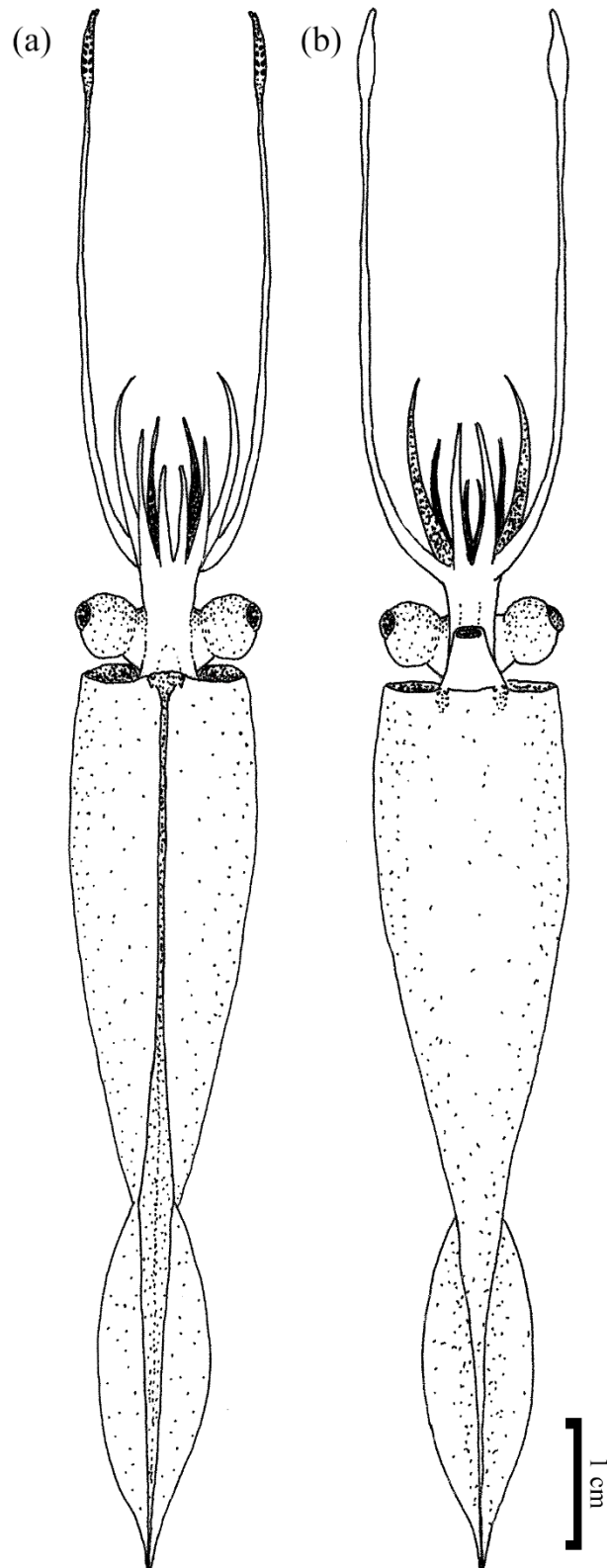


Fig. 5.6—Juvenile *G. glacialis* (a) dorsal view and (b) ventral view (NMV F66633; ML 171 mm).

***Galiteuthis pacifica* (Robson, 1948)** (Figs 5.8–5.12, Table B9)

*Taonidium pacificum* Robson, 1948: 130, fig. 14.

*Galiteuthis pacifica* (Robson, 1948): Nesis, 1987: 275, fig. 71T; Young, 1972: 86–87; Voss, Stephen, & Dong, 1992: 202.

**Diagnosis:** Mantle smooth, lacking tubercles at funnel–mantle fusion points. Inner eye photophore short, square or rectangular in shape. Arms suckers lacking dentition.

**Type material:** (examined) *Taonidium pacificum* **BMNH Syntypes (2) 1947.7.7.8.1-2** [*fide* Nesis, 1987: 275]. Type locality: north of Cocos Island.

**Material examined (8 specimens):** **SBMNH 464473**, ML 78 mm, sex indet., 33.39°N, 118.77°W, United States, California, Los Angeles County, Channel Islands, Santa Catalina Island, 24/06/1971; **SBMNH 464475**, ML 135 mm, sex ♀, 33.07°N, 119.11°W, USA, California, Ventura County, Channel Islands, San Nicolas Island, 1719 m, 18/11/1951; **SBMNH 464476**, ML 91 mm, sex indet., 27.83°N 118.18°W, Mexico, Baja California Sur, Isla Guadalupe, 3566 m, 18/06/1969; **SBMNH 49343**, ML 40 mm, sex indet., 10.37°N, 86.47°, Costa Rica, Guanacaste, 3657 m, 5/05/1973; **SBMNH 51341**, ML 62 mm, sex indet., 10.29°N, 87.76°W, Costa Rica, Guanacaste, 3236 m, 11/05/1973; **SBMNH 51342**, ML 244 mm, ♀, 9.16°N, 85.05°W, Costa Rica, Puntarenas, 18/05/1973; **SBMNH 49647**, ML 24 mm, sex indet., 8.33°N, 84.62°W, Costa Rica, Puntarenas, 25/05/1973; **SBMNH 49324**, ML 120 mm, sex indet., 5.40°N, 82.50°W, Panama, 18/06/1973.

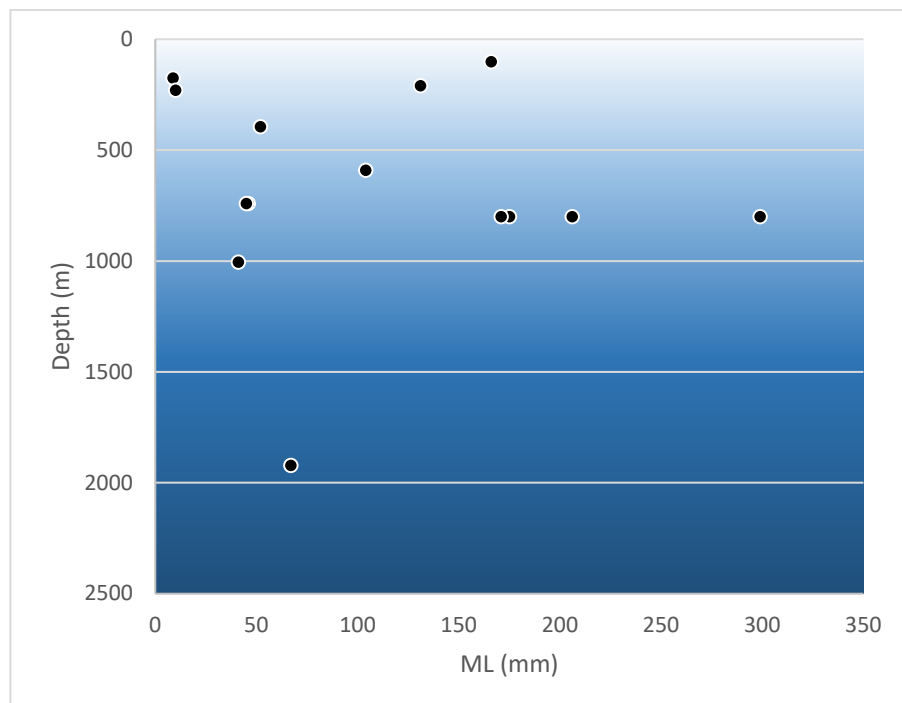


Fig. 5.7—Collection depths of *G. glacialis* material examined in this study.

**Description:**

**Sub-adult/Adult** (ML 60–244 mm; Fig. 5.8–5.12)—Mantle smooth, tapered to a point, MW 13–26–31% ML. Fins lanceolate, FL 34–41–45% ML, FW 14–18–20% ML. Gladial conus ~60% GL, rachis terminus appears flask-shaped. Tubercles absent at funnel–mantle fusion (Fig. 5.10a), ventral cartilaginous window triangular. Head length 6–8–9% ML; HW 16–18–20% ML; ED 9% ML; smaller ventral photophore square or rectangular in shape (Fig. 5.9). Olfactory papilla on posterior-ventral surface of eye, cylindrical in shape, transparent, often quite long (~20% ED). Funnel base 21–40–61% MW, narrowing to aperture 30–35–40% FB.

Arms proportionally short, with low trabeculate membrane along proximal 50% of arm; arm formula  $IV \geq III > II > I$ : Arm I 10–12–15% ML, Arm II 14–16–20% ML, Arm III 17–20–21% ML, Arm IV 17–21–23% ML. Arms with 20–40 adentate suckers (Fig. 5.10b) (Arms III with a greater number of suckers than remaining arms), subequal in size. Female sexual modifications not present; mature males not examined.

Tentacles 53–56–81% ML (Fig. 5.11), usually with 12–28 pairs of tiny suckers along length; suckers interspersed with fleshy pads at distal end. Club 8% ML (8–14–17% TnL), carpus with 8–10 suckers interspersed with fleshy pads, manus with 10–12 elongated hooks (present by 40 mm ML), dactylus with up to ~25 suckers, with three or four pointed teeth.

**Known distribution:** Eastern Pacific from California to Panama (Fig. 5.1), but also reported in the Hawaiian Islands (Young, 1978).

**Remarks:** Every specimen examined lacked dentition on the arm suckers; however, two gravid females had encysted suckers on the inner wall of the anterior end of the mantle. Microscopic examination revealed that they had approximately 30 very small pointed teeth around the sucker margin. It might be possible that the suckers on a modified arm of a male might have dentition; however, with no mature males available, these suckers' potential origin with a conspecific male this cannot be confirmed at present. *Galiteuthis pacifica* most closely resembles *G. phyllura* as both taxa lack dentition on the arms suckers; however, *G. pacifica* can be distinguished by having a noticeably short (nearly square) inner eye photophore.



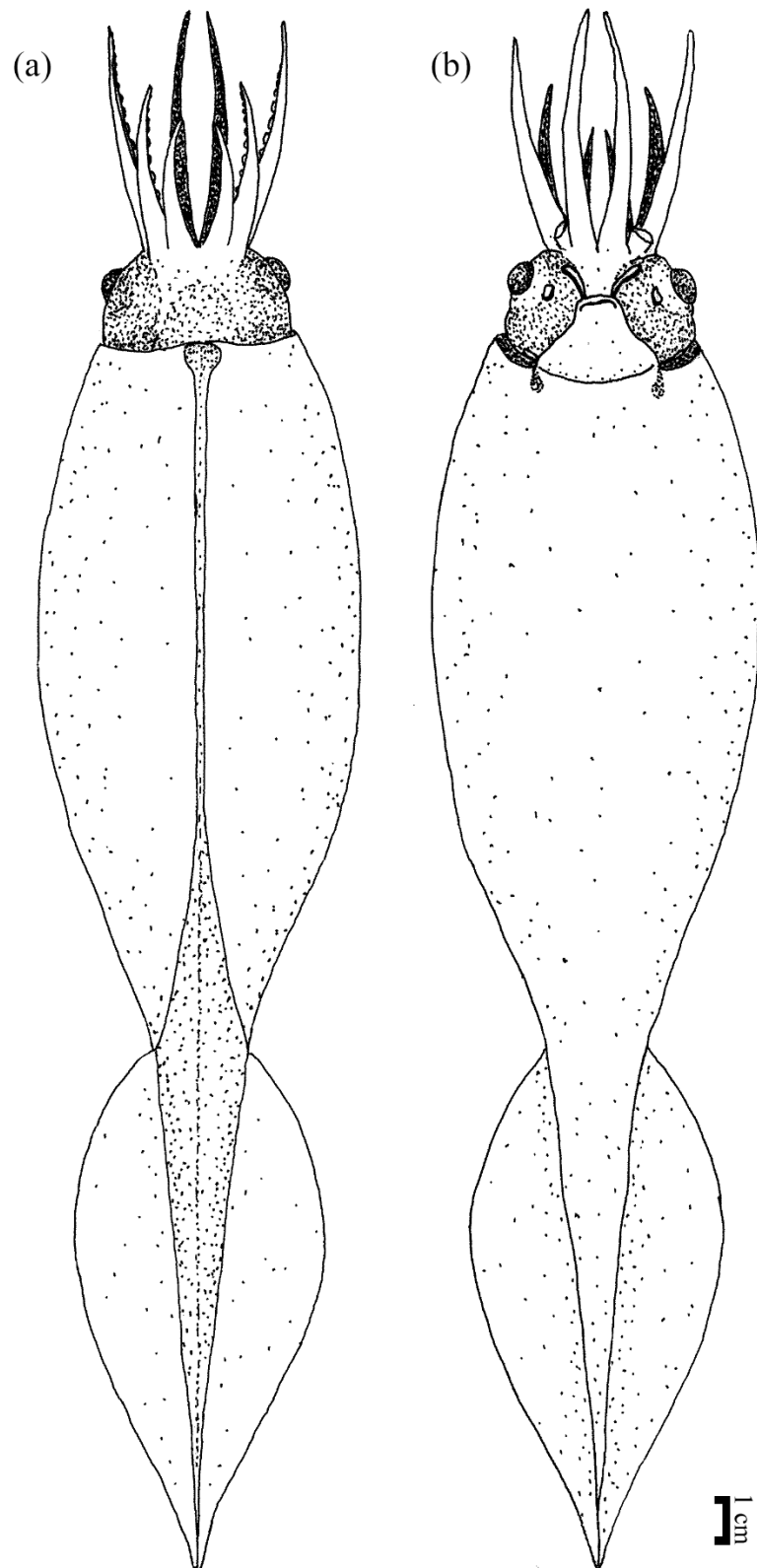


Fig. 5.8—Adult *G. pacifica* (a) dorsal view and (b) ventral view (SBMNH 51342; ML 244 mm, female).

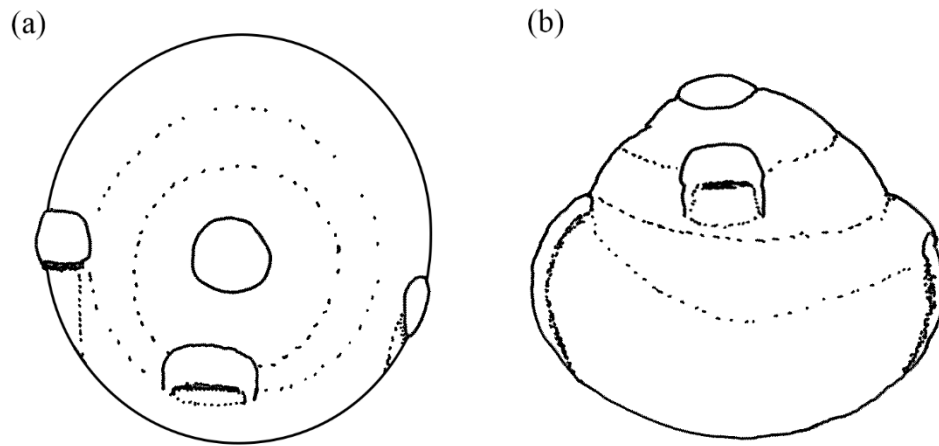


Fig. 5.9—Left eye schematic for *G. pacifica*: (a) lateral view, (b) ventral view (SBMNH 49324; 120 mm ML).

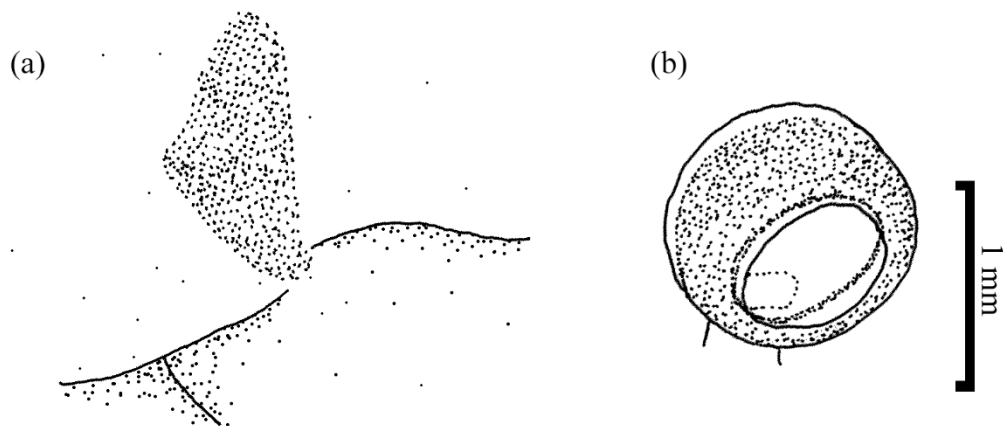


Fig. 5.10—(a) Left ventral funnel-mantle fusion cartilage and (b) Arm III medial sucker (SBMNH 49324; 120 mm ML).

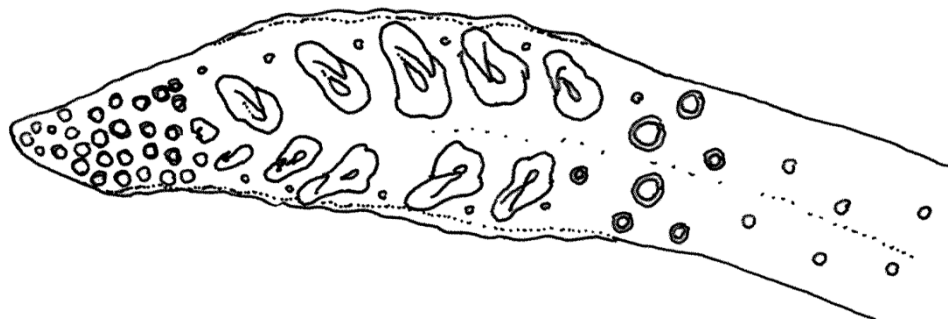


Fig. 5.11—Right tentacle club schematic for *G. pacifica* (SBMNH 49324 [some reconstruction necessary; clubs damaged]; 120 mm ML).

***Galiteuthis phyllura* Berry, 1911** (Figs 5.13–5.17, Table B10)

*Galiteuthis phyllura* Berry, 1911: 592; Young, 1972: 84–86; Nesis, 1987: 274, fig. 71M–O; Voss, Stephen, & Dong, 1992: 202.

*Crystalloteuthis beringiana* Sasaki, 1920: 202, Pl. 26 fig. 4.

*Galiteuthis armata* (not Joubin, 1898) Sasaki, 1920: 200–20.

**Diagnosis:** Mantle smooth, with cluster of four or five pointed tubercles at each ventral funnel–mantle fusion point. Inner eye photophore linear. Arm suckers lacking dentition.

**Type material:** (not examined) *Galiteuthis phyllura* **NMNH Holotype 214325** [*vide* Sweeney *et al.* (1988: 16)]. Type locality: Monterey Bay, California.

**Material examined (14 specimens):** **RBCM 010-0 0295-002**, ML 295 mm, sex indet., 51.43°N, 130.79°W–51.43°N, 130.78°W, Queen Charlotte Sound, midway between Cape Scott (Vancouver Island) and Cape St. James (Haida Gwaii), 2000 m, 15/10/2006; **RBCM 010-00454-002**, ML 258 mm, sex indet., 50.59°N, 130.09°W–50.60°N, 130.07°W, West off of north end of Vancouver Island, 2125–2150 m, 08/10/2006; **RBCM 979-11242-2**, ML 157 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 23/08/1979; **RBCM 979-11244-5**, ML 140 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 24/08/1979; **RBCM 979-11245-3**, ML 35, 33 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 26/08/1979; **RBCM 979-11233-4**, ML 7.5 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 15/08/1979; **CAS 030342**, ML 11 mm, sex indet., 37.09°N, 122.91°W, USA, California, SW of Pigeon Point, top of Guide Seamount, surface, USS *Mulberry*, Stn. 46, 15/02/1950; **CAS 002306**, ML 90 mm, sex indet., 36.79°N, 121.91°W–36.78°N, 121.95°W, USA, California, Monterey Bay, 417–466 m, Sta. A44, 12/03/1975; **CAS 002301**, ML 48 mm, sex indet., 36.78°N, 121.94°W–36.77°N, 121.98°W, USA, California, Monterey Bay, 453–518 m, Stn. 63, 14/10/1975; **CAS 002328**, ML 61 mm, sex indet., 36.78°N, 121.94°W–36.76°N, 121.97°W, USA, California, Monterey Bay, 403–504 m, Stn. V78, 23/01/1976; **CAS 030994**, ML 80 mm, sex indet., 36.77°N, 122.03°W, USA, California, Monterey Bay, 570 m, 15/03/1974; **CAS 002452**, ML 35 mm, sex indet., 36.76°N, 122.04°W–36.74°N, 122.00°W, USA, California, Monterey Bay, Stn. Hb20, tow 20, 7/10/1974;

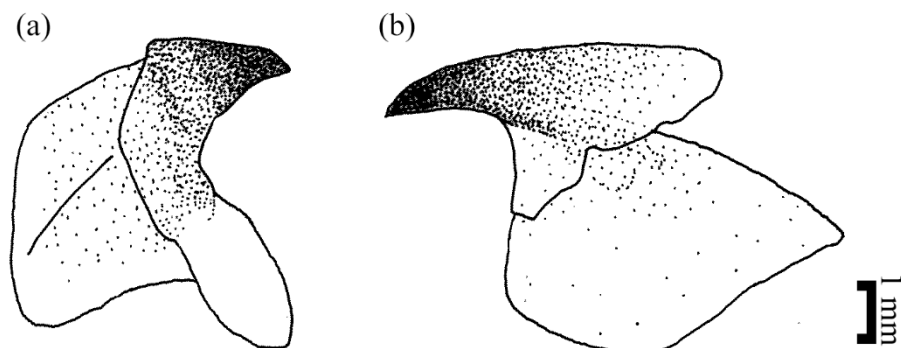


Fig. 5.12—Beak of *G. pacifica* (a) lower beak and (b) upper beak (SBMNH 49324; ML 120 mm).

**CAS 034278**, ML 45 mm, sex indet., 32.82°N, 119.95°W–32.93°N, 118.85°W, USA, California, Channel Islands, SW of San Nicolas Island, 1463 m, Stn. 45, *Zeca*, 19/09/1938; **SBMNH 464477**, ML 275 mm, sex indet., 32.66°N, 119.46°W, USA, California, Los Angeles County, Cortes Bank, 914 m, 13/08/1969.

**Non-localised material examined (2 specimens): NSMT-Mo.62630**, ML 275 mm, sex indet., 1000 m, *Tenyo-maru*, Stn. 89, 04/08/1954; **CAS 095792**, ML 29 mm, sex indet., Gulf of the Farallones; SW of the Farallon Islands, Stn. 3030, 20/03/1979.

### **Description:**

**Adult** (ML 100–295 mm; Fig. 5.13, 5.14)—Mantle smooth, tapered to a point, MW 10–16–20% ML. Fins lanceolate, FL 45–49–55% ML, FW 12–15–18% ML. Gladius narrow, rachis terminus expanded; tubercles at ventral fusion points with four or five cusps (Fig. 5.13), fusion extends into raised cartilaginous ridge on funnel surface. Head length 6–7–9% ML, HW 11–14–17% ML; eyes spherical, ED 5–10% ML (ED 80–103–120% HL), inner photophore linear, outer photophore often double thickness of inner. Olfactory papilla present on ventro-lateral surface of eye, cylindrical in shape, transparent, often quite long (~20% ED). Funnel 28–42–57% MW, narrowing gently to aperture 25–36–50% FB.

Arms sub-equal in length, with low trabeculate membrane over proximal half of arms; general arm formula IV>III>II>I: Arm I 10–14–16% ML, Arm II 14–17–20% ML, Arm III 15–20–25% ML, Arm IV 20–22–25% ML. Arms with 20–56 spherical, subequal suckers (greatest number on Arms IV); sucker rings smooth. Arms IV robust, stouter than tentacle stalk, with wide keel on aboral surface. No secondary sexual modifications apparent on material examined (maximum ML 295 mm).

Tentacle length 37–44–60% ML, usually with 15–20 pairs of tiny suckers set along stalk; sucker pairs alternate with pads distally. Club proportionally longer than in other species, 5–8–11% ML (14–17–20% TnL). Approximately 40–50 suckers on clubs, carpus with 8–10 suckers interspersed with fleshy pads, manus with 8–14 hooks (rudimentary hooks present by 30 mm ML); cusp of largest hook at nearly right angle to club, distally; dactylus with 22–28 suckers.

**Juvenile** (ML 35 mm–100 mm; Fig. 5.15)—As for adult with following exceptions: MW 20–26–40% ML; FL 22–40–50% ML, FW 9–14–21% ML. Two tubercles at ventral funnel–mantle fusion points; HL 6–10–20% ML, HW 9–19–31% ML; eyes on stout stalks, ED 5–7–9% ML (ED 50–85–150% HL), both photophores rudimentary, papilla present on eye stalk.

Arms sub-equal in length, with low trabeculate membrane along ~50% of arms; general arm formula IV>III>II>I: Arm I 6–9–12% ML, Arm II 9–12–16% ML, Arm III 11–16–20% ML, Arm IV 14–18–23% ML. Arms with 20–52 adentate, subequal suckers (greatest number on Arms IV). Tentacle length 47–62–80% ML, usually with 10–18 pairs of suckers set along stalk. Club (Fig. 5.16c) length 8–12–17% ML (17–19–26% TnL). Approximately 40–50 suckers on clubs, carpus with 8–10 suckers with interspersed pads, manus with 2–6 hooks, other rudimentary hooks present (Fig. 5.16a); dactylus with 18–28 suckers, with three or four sharp teeth.

**Known distribution:** North-western Pacific Ocean, from Bering Sea to northern California (Fig. 5.1) and reported in Japanese waters (Nesis, 1987). Present material collected from 403–2150 meters (Fig. 5.17).

**Remarks:** This species appears most similar to *G. pacifica*, with which it occurs sympatrically in Californian coastal waters; these species can be distinguished by examining the inner eye photophore, which is noticeably shorter in *G. pacifica* (often shorter than the lens diameter) than in *G. phyllura* (which has a photophore longer than the lens diameter). However, *G. phyllura* is more likely to be confused with *Taonius borealis*, as the two co-occur throughout much of their range. These species can be distinguished by the tentacle club armature (large, individual hooks in *G. phyllura* compared to multi-cusp manus suckers in *T. borealis*), the dentate arm suckers in *Taonius*, and the presence of ventral fusion tubercles in *Galiteuthis*. All available sequences from the north-western Pacific Ocean form a single BIN (BOLD:ACQ6814) and are attributed to *G. phyllura*. Additional material from *G. pacifica* is needed to compare the phylogenetic relationship between these two species.

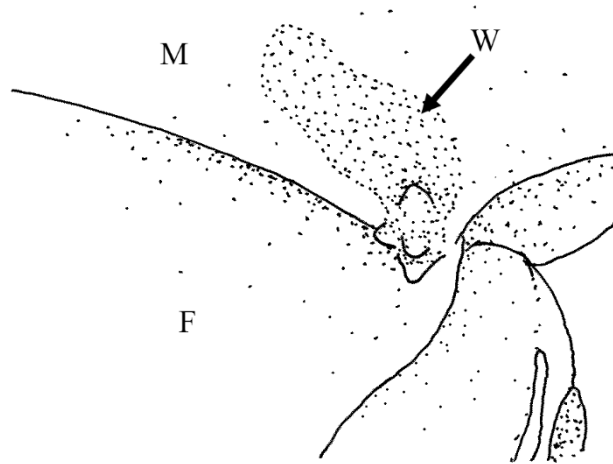


Fig. 5.13—Right ventral funnel–mantle fusion of *G. phyllura* showing tubercle cluster (F = funnel, M = mantle, W = ventral cartilaginous window).

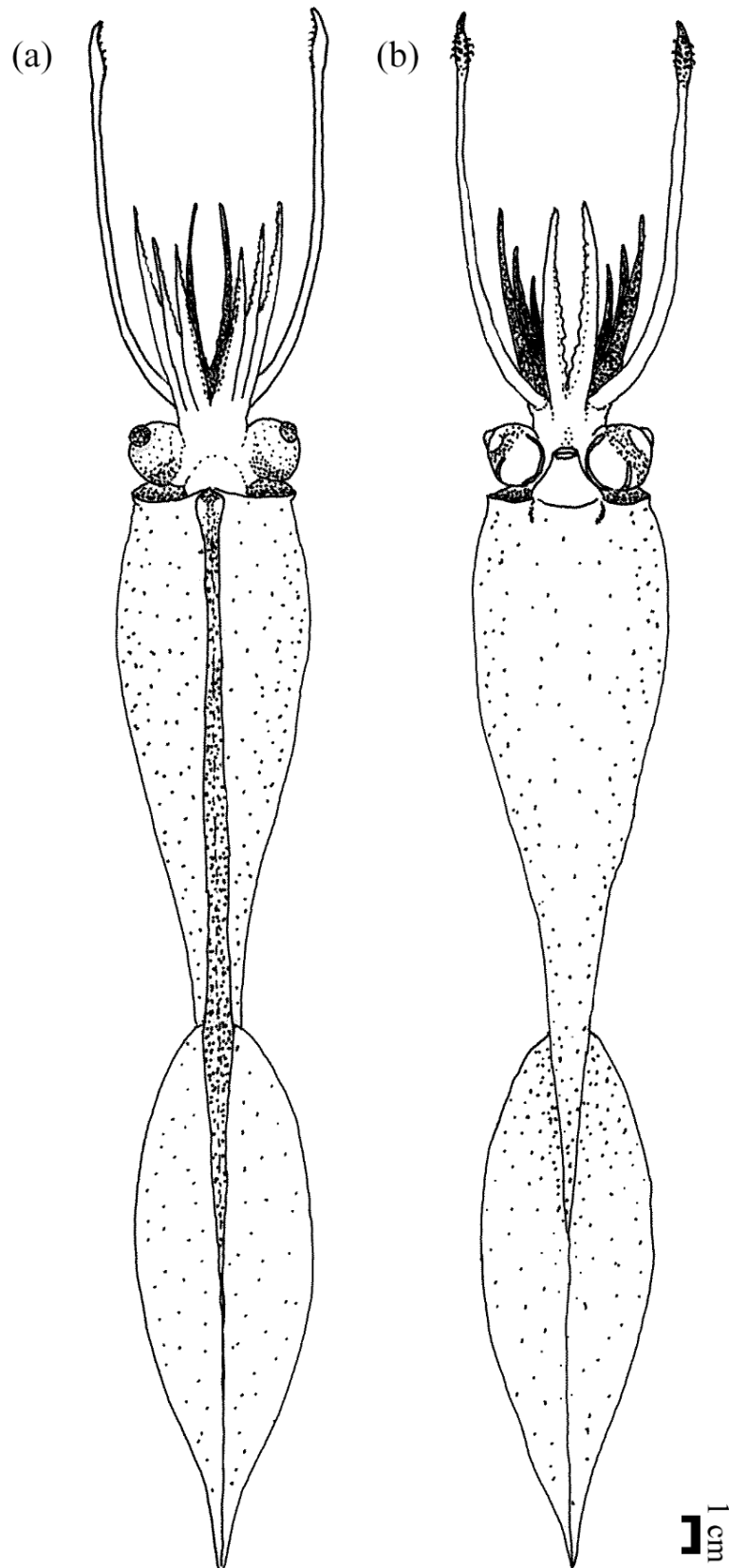


Fig. 5.14—Adult *G. phyllura* (a) dorsal view and (b) ventral view (NSMT Mo:62630; ML 275 mm).

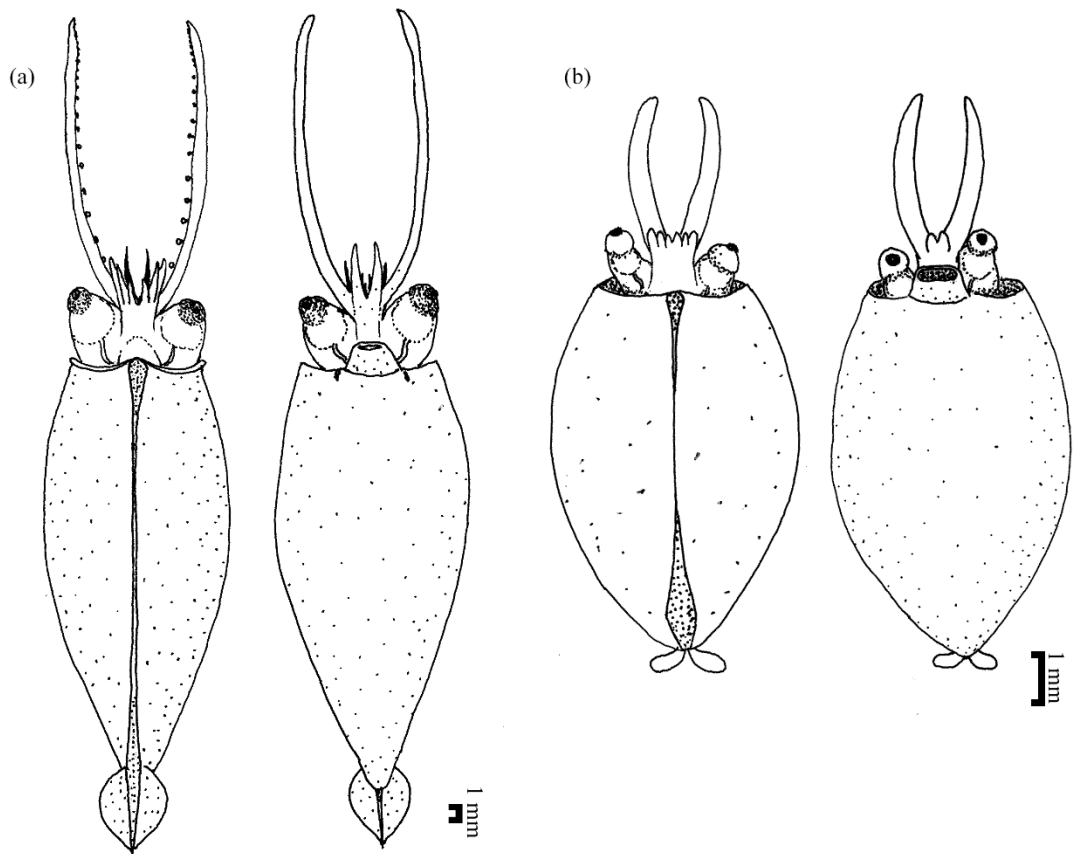


Fig. 5.15—Ontogenetic stages of *G. phyllura*: dorsal and ventral view of (a) juvenile stage (RBCM 979-11252-5; ML 36 mm) and (b) paralarval stage (RBCM 979-11233-4; ML 7.5 mm).

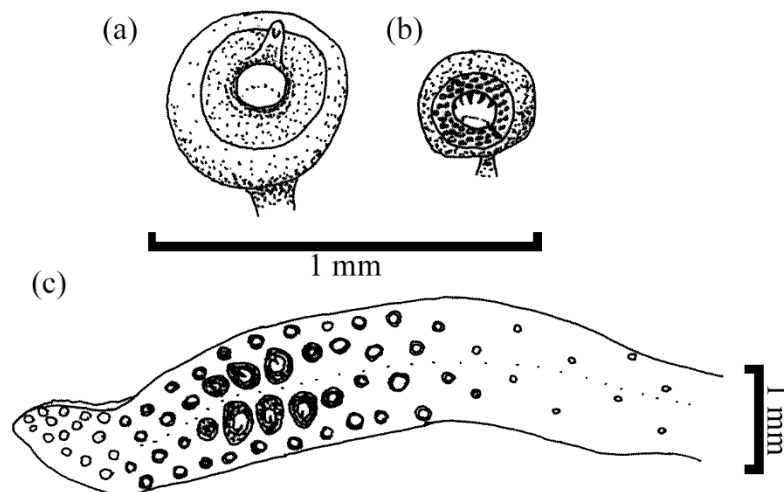


Fig. 5.16—Suckers and club of juvenile *G. phyllura* showing (a) rudimentary hook, (b) dactylus sucker, and (c) the right club of a juvenile specimen (CAS 34278; ML 45 mm).

***Galiteuthis suhmi* (Hoyle 1886)** (Figs 5.18–5.23, Table B11)

*Taonius suhmi* Hoyle, 1886: 192–198, Pl. XXXII 5–11.

*Galiteuthis* (*Taonidium*) *suhmii* (Hoyle, 1886): Chun 1910: 297–302, Pl. LIX.

*Taonidium suhmii* (Hoyle, 1886): Pfeffer, 1900: 192; Pfeffer, 1912: 721–722.

*Galiteuthis armata* (not Joubin) Imber, 1978: 461–463, fig. 1M, 5E.

*Galiteuthis suhmi* (Hoyle, 1886): Nesis, 1987: 274; Reid, 2016: 93.

**Diagnosis:** Mantle lacking dermal sculpture apart from three to five tubercles present at each ventral fusion point; arm sucker rings with ~16 teeth on largest suckers.

**Type material:** (not examined) *Taonius suhmi* **Type repository unresolved;** (examined) **BMNH syntype 90.1.24.19** [*fide* Lipinski et al. (2000:109)]. Type locality 47°25'S, 130°22'E (Southern Ocean) [*fide* Hoyle (1886:192)].

**Material examined (8 specimens):** NMV 78309, ML 62 mm, sex indet., 44.21°S, 147.01°E–44.21°S, 147.22°E, 200–300 m over 1127 m, RV *Southern Surveyor*, Stn. 5505/93/12, 16/07/1993; NMV 78129, ML 25 mm, sex indet., 44.24°S, 147.153°E–44.30°S, 147.31°E, 0–100m over 1257 m, RV *Southern Surveyor*, Stn. 5501/92/20, 17/02/1992; NIWA 92491, ML 410 mm, ♂, 44.53°S, 179.01°W, 1108 m, Stn. TAN 1401/76, 15/01/2014; NIWA 90029, ML 212 mm, sex indet., 44.80°S, 179.11°W–44.81°S, 179.15°W, 1417–1438 m, Stn. TAN9511/57, 14/10/1995; NIWA 89452, ML 211 mm, 44.84°S, 173.17°E, 953–971 m, 13/04/1997, Stn. Z8791; NIWA 90019 (2 specimens), ML 214, 184 mm, 44.84°S, 173.37°E–44.70°S, 175.38°E, 1000–983 m, Station Z8795, 16/04/1997; NMNZ 091735, ML 267, sex indet., 44.93°S, 173.27°E, New Zealand, South Island, south of Banks Peninsula, 1150–1220 m, RV *James Cook*, BT, Stn. J15/31/83, 29/11/1983.

**Non-localised material examined (1 specimen):** NIWA 90030, Station TAN9511/008.

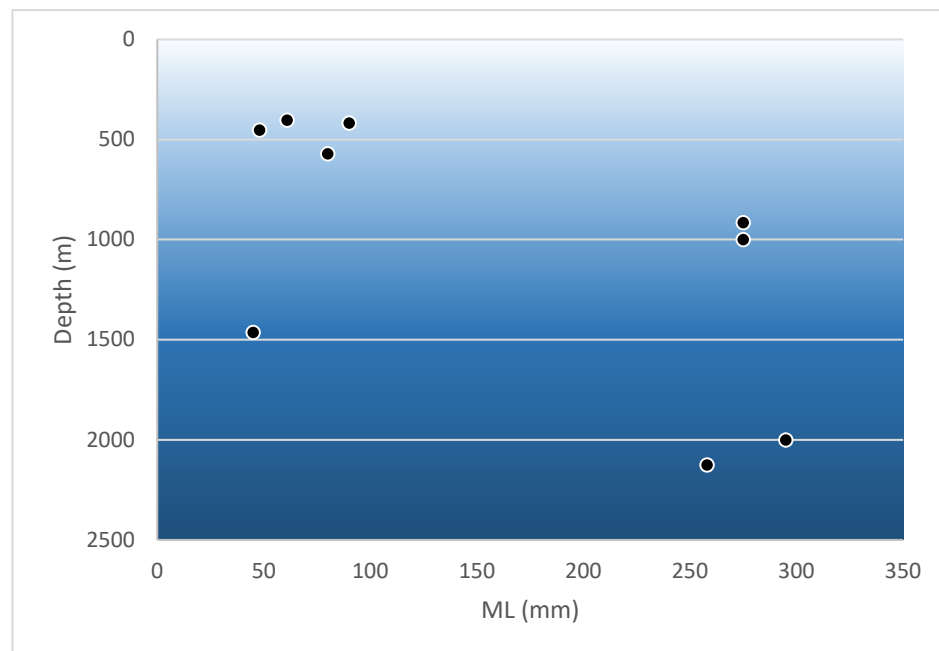


Fig. 5.17—Collection depths of *G. phyllura* material examined in this study.



**Description:**

(ML 62–410 mm; Fig. 5.18–5.22)—Mantle smooth, goblet-shaped, MW 14–21–32% ML. Fins lanceolate, FL 32–43–50% ML, FW 16–20–22% ML; FL–FW ratio decreases with size. Gladius narrow, conus 50% GL, anterior rachis terminus appears expanded with rounded lobes on either side of fusion point. Funnel-mantle fusion with cluster of three to five pointed tubercles, contiguous with short raised cartilaginous ridge on funnel surface (Fig. 5.19a); ventral fusion window kidney-shaped. HL 10–13–16% ML, HW 8–13–20% ML (HW less than MW). Eye diameter ~8% ML; eyes bulbous, sessile at ~50 mm ML. Photophores thin crescents; exact configuration unknown due to damage on all specimens examined. Olfactory papilla present on aboral surface of eye, funnel-shaped. Funnel base width 25–34–50% MW, narrowing to aperture 30–45–60% FB.

Arms nearly sub-equal in length, exact formula variable, generally:  $IV \geq III \geq II > I$ ; Arm I 19–21–25% ML, Arm II 24–27–29% ML, Arm III 25–28–30% ML, Arm IV 26–29–31% ML. Low trabeculate protective membrane along proximal half. Arms with 24–62 suckers (greatest number on Arm III or IV), suckers large, decreasing in size distally; medial arm sucker rings with 14–20 rounded teeth (5.19b). Secondary sexual modification on Arms I and II in males (Fig. 5.20): suckers modified into two series of large flattened papillae on distal third (modification only seen on single specimen, NIWA 92491; ML 410 mm); females lacking secondary sexual modification.

Tentacles 45–58–76% ML, club ~8% ML (10–13–17% TnL). Tentacle stalks with 15–20 pairs of small suckers along length; sucker pairs alternate with pads on distal half. Clubs with 50–60 suckers (Fig. 5.21); carpus with 6–8 suckers and interspersed pads, carpal suckers adentate, sucker ring margins wide with rough texture; manus with 8–12 hooks, largest hooks at distal 2/3 of manus, hooks curve away from club at ~100°, with expansion of inner side of hook base; dactylus with 4–40 suckers, sucker ring wide and papillated.

**Known distribution:** Southern Pacific species, material from New Zealand and eastern Australia (Fig. 5.1). Present material collected from 50–1438 meters (Fig. 5.23).

**Remarks:** The largest specimen examined had minimal armature on the dactylus (three or four small suckers at distal end of the club, appearing as though the entire club was composed of curved hooks). Arm sucker dentition varies among specimens and can variably appear as crenulations or short angular teeth. The suckers of *G. suhmi* were described as lacking dentition by Nesis (1987) but when magnified it is clear that the suckers are dentate.

**Discussion**

Species of *Galiteuthis* share relatively similar morphological features and can be a challenge to distinguish. The taxa known from the north Pacific (*G. phyllura* and *G. pacifica*) lack dentition on their arm sucker rings while those known from the Southern Hemisphere (*G. suhmi* and *G. glacialis*) appear to have some dentition at some point during their ontogenetic development. Hook morphology on the tentacle clubs often differs only slightly, and fin ratios are proportionally similar in all species. Eye photophores can be used to differentiate species to some degree; however, as with all cranchiid squid, the eyes can be easily damaged during capture, so it is not always possible to examine the photophore arrangement. At present, despite a very incomplete

understanding of these animals' zoogeography, the collection locality of specimens can be useful in narrowing possible taxa.

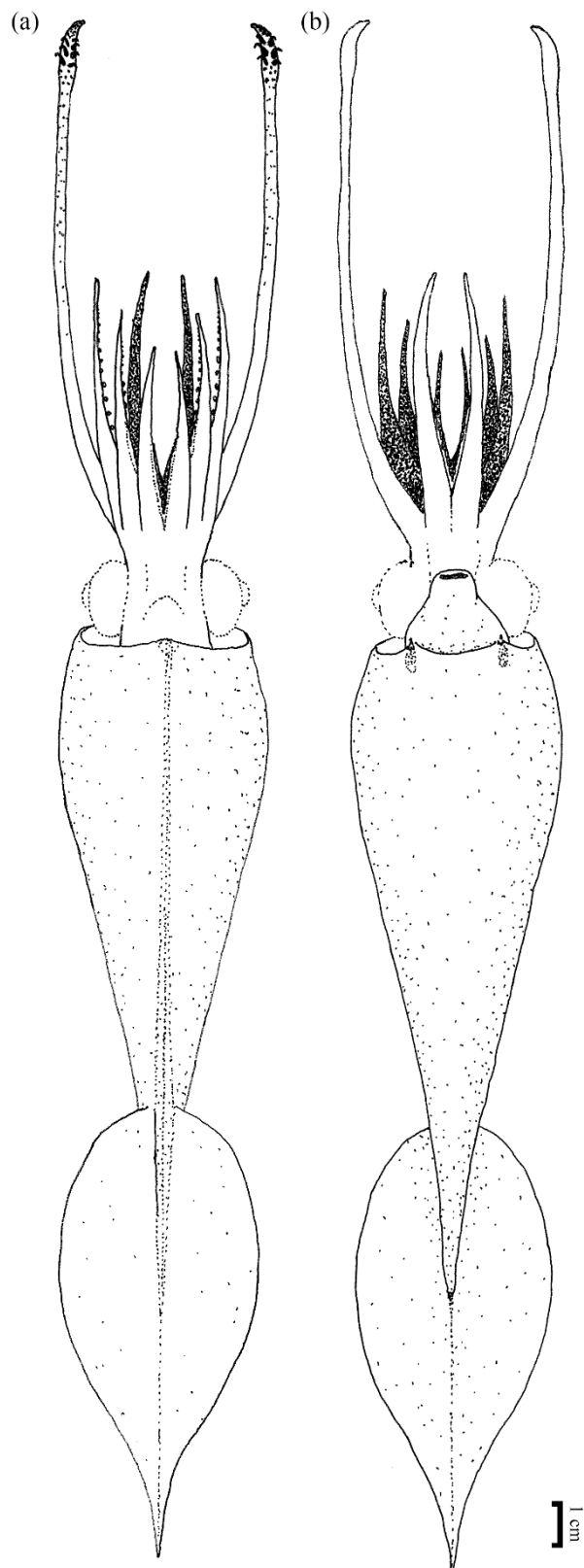


Fig. 5.18—*Galiteuthis suhmi* (a) dorsal and (b) ventral view (NIWA 90029; ML 212 mm).

Southern Ocean *Galiteuthis* specimens are largely referable to *G. glacialis*. This can be easily confirmed if the specimen is also of mature size; above ML 150 mm, individuals of this species possess a covering of dermal tubercles that is unique within the genus. Although many junior synonyms have been described (based on the identification of different life stages), there is little doubt of the validity of *G. glacialis*. Material for this taxon showed variation in sucker counts, ranging from 40 to 98. The maximum sucker count was found on Arms III of the largest specimen (ML 374 mm); the mean count for smaller individuals (74) was also higher than the mean for other Pacific *Galiteuthis* species (*G. pacifica* = 42, *G. phyllura* = 42, *G. suhmi* = 52). This character may be useful in distinguishing large *G. glacialis* from other taxa in this genus; however, its utility decreases in smaller individuals (50–75 suckers in specimens ML < 200 mm).

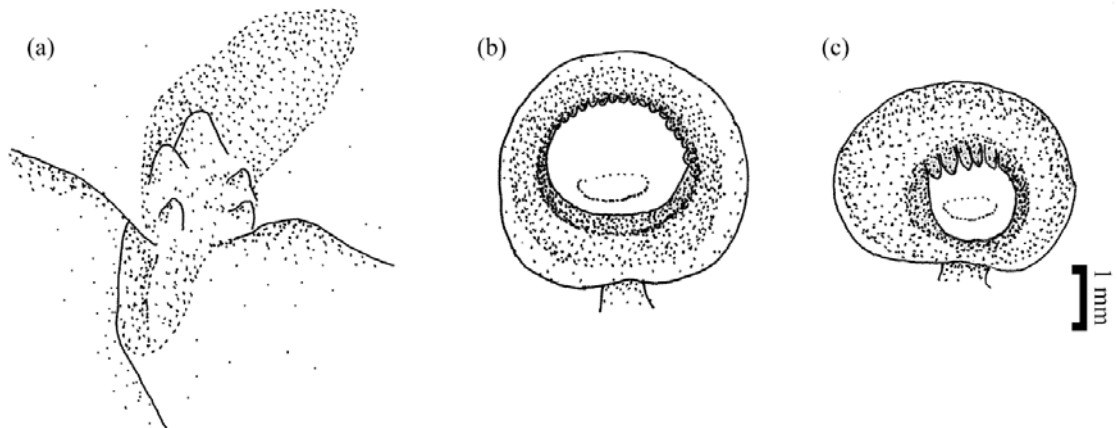


Fig. 5.19—(a) Left funnel–mantle fusion tubercles, (b) medial sucker and (c) distal arm sucker (NIWA 90019, ML 184 mm).

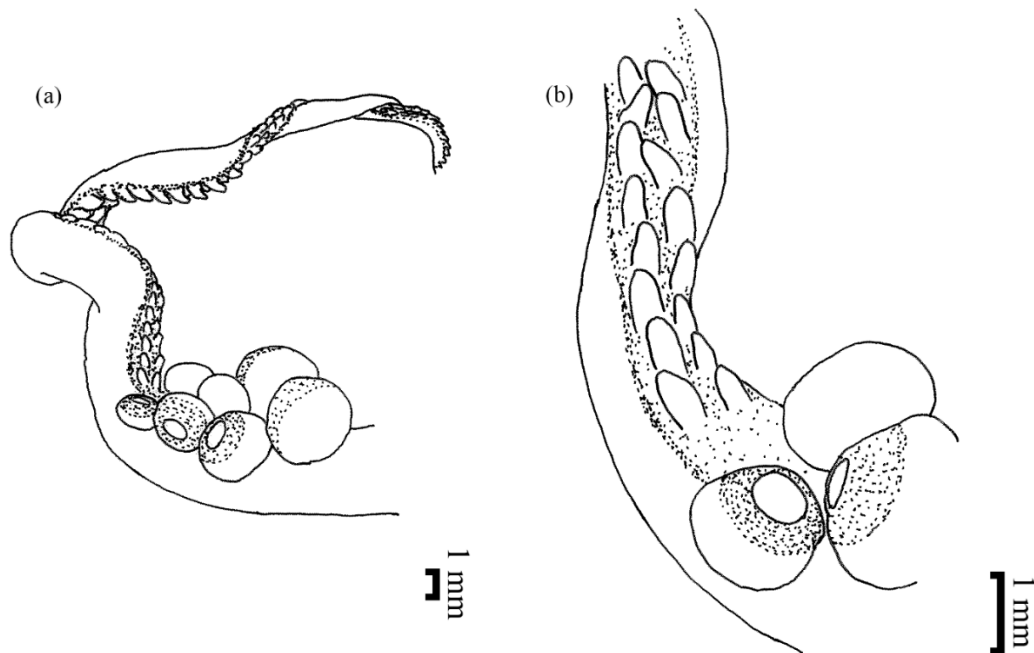


Fig. 5.20—(a) Male modification on Arms I and II, (b) enlarged portion of Arm I showing transition from basal suckers to papillae distally (NIWA 92491; ML 410 mm).

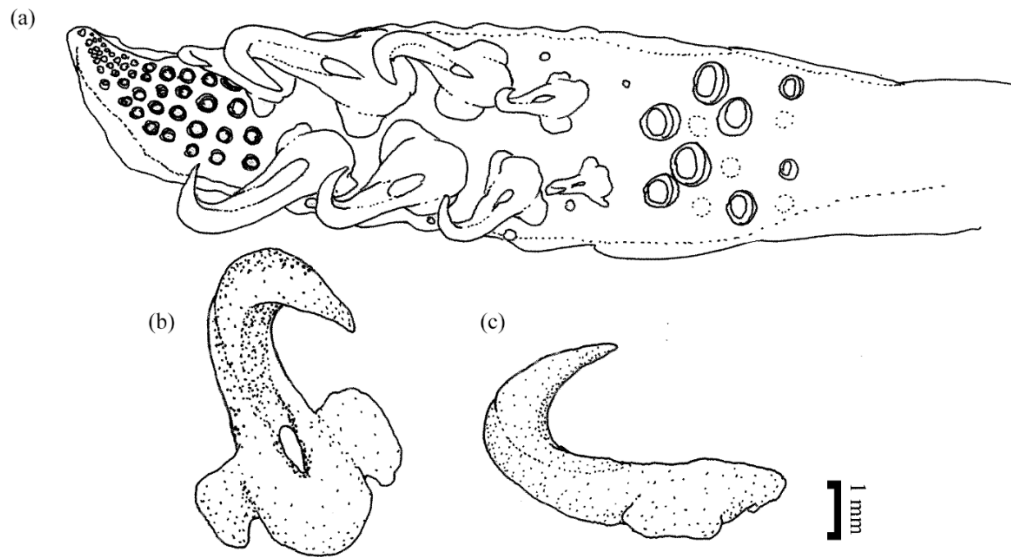


Fig. 5.21—Right tentacle club of *G. suhmi* (a) with (b) enlargement of largest manus hook and (c) lateral view of hook shown in (b) (NIWA 89452; ML 211 mm).

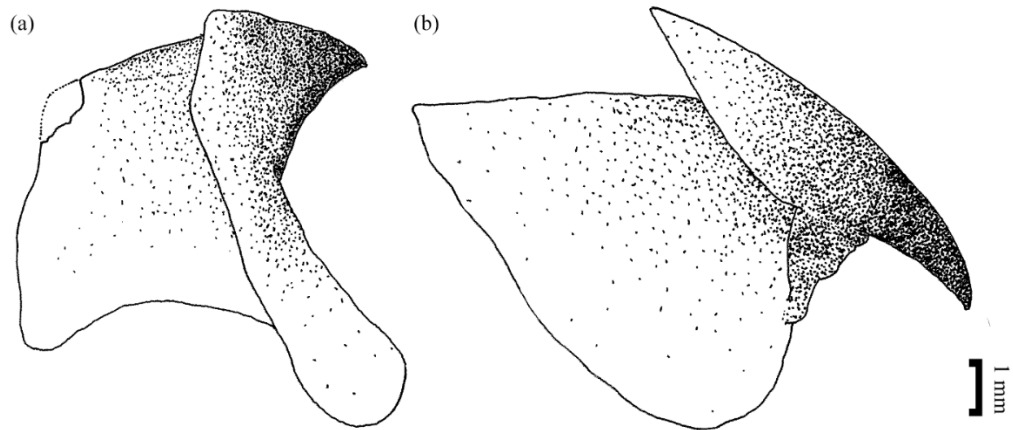


Fig. 5.22—Beak of *G. suhmi* (a) lower beak, (b) upper beak (NIWA 89452; ML 211 mm).

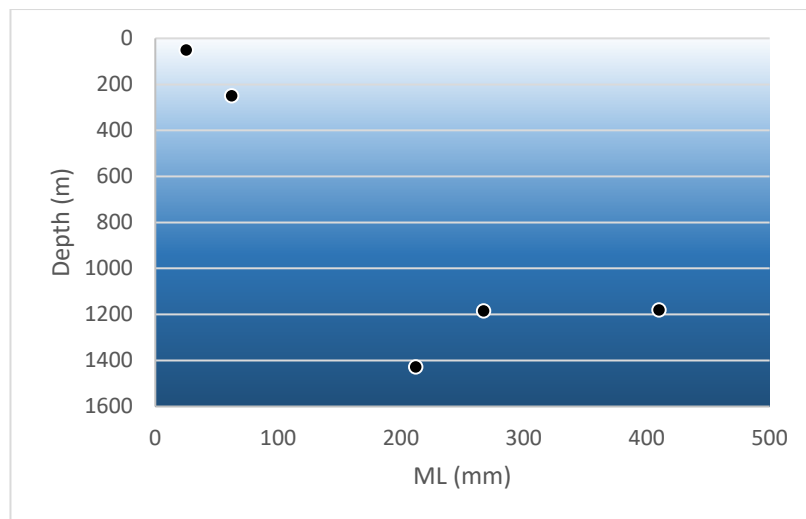


Fig. 5.23—Collection depths of *G. suhmi* material examined in this study.

At present, two species are recognised in the north Pacific. The more northern species, *G. phyllura*, is found off the western coast of North America, from the Bering Sea to California. This species can grow quite large (possibly over 300 mm ML [Nesis, 1987]), and is one of two cranchiids commonly found in this region (the other being *Taonius borealis*). The second species of *Galiteuthis*, *G. pacifica*, has some overlap with *G. phyllura*, being distributed from southern California to equatorial waters. Both these species lack dentition on their arm suckers, but have slightly different eye photophore morphology, should the eyes be intact. The inner photophore of *G. pacifica* is quite short and stout, in some specimens appearing completely square, while *G. phyllura* has a more linear photophore, spanning approximately half of the diameter of the eye. In terms of gross morphology, *G. phyllura* has a more slender mantle (MW 16% ML) and the gladius does not expand significantly at the conus. *Galiteuthis pacifica* is stouter in mantle width (MW 29% ML) and has a wider conus that sharply decreases to a narrow glacial vane.

The final known species of *Galiteuthis* found in the Pacific Ocean is *G. suhmi*. Historically, descriptions of this species have lacked detail, and its validity has been questioned (Imber, 1978). It is possible that *G. suhmi* will prove synonymous with *G. armata* Joubin, 1898 (type locality: Atlantic Ocean), in which case the known distribution of *G. suhmi* (the senior name) will be substantially expanded to include the Atlantic. The original species description of *G. armata* (Lankester, 1884) depicted paralarval specimens with unclear illustrations, making subsequent re-identification a challenge, and Hoyle's (1886) placement of this species in the genus *Taonius* further complicated the systematics. Of the three specimens Hoyle examined, only two had suckers. Despite the largest specimen having a mantle length of 42 mm, there is no mention of hooks on the tentacular club; by this size, those should have begun to develop. Nesis (1987) maintained *G. armata* as a valid species, and considered it a southern circumglobal taxon; however, Chun (1910) and Pfeffer (1912) questioned the systematic position of *G. armata*, noting the lack of clarity in the taxon's original description. Both authors suspected that the genus *Taonidium* was a junior synonym for *Galiteuthis* and that '*T.* *suhmi*' was a junior synonym for *G. armata* (despite '*suhmi*' being the senior name). It is impossible to confirm whether the originally described specimen of *Taonidium suhmi* is indeed the taxon referred to presently as *G. suhmi*, as the type repository is unresolved; however, the geographic area from historical observations is similar to that of the present day known distribution for *Galiteuthis suhmi*; therefore, the most conservative action is to retain this name for the southern Pacific *Galiteuthis* species, pending further evidence such as molecular data.

## *Helicocranchia* Massy, 1907

### Historical Review

*Helicocranchia* was first described by Massy (1907) from the North Atlantic Ocean (off the south-west coast of Ireland), and was distinguished from known taxa because the type specimen, *H. pfefferi*, had an ‘extremely large’ siphon. Despite the size of the type specimen being comparatively small (ML 39 mm), Massy still described arm suckers as being in multiple series on the distal third of the arms, and biserial proximally, a character that is now recognised to indicate a nearly mature (or mature) male. It is thought that a specimen earlier described by Pfeffer (1900) as *Hensenioteuthis joubini* may have been affiliated with *Helicocranchia* (Nesis, 1987); this squid was distinguished from other cranchiids by suckers ‘only being present on the tentacle clubs’; however, this species is now considered a *nomen dubium* (Voss, 1980).

Grimpe (1922) considered *Helicocranchia pfefferi* and *Hensenioteuthis joubini* to be best aligned with *Teuthowenia* and reassigned them to this genus; however, this systematic revision appears not to have been upheld by subsequent authors, as Robson (1948) described a new species of *Helicocranchia*, *H. beebei* (= *H. pfefferi*, *fide* Nesis, 1987), because the fin shape and funnel organ morphology differed from *H. pfefferi*. These features are unfortunately very delicate in *Helicocranchia*, and it is difficult to determine whether the observed differences resulted from damage to the specimen.

Voss (1960) described *Megalocranchia papillata* (= *Helicocranchia papillata* *fide*, Nesis, 1987) in his paper on Bermudan cephalopods, easily distinguishing it from other known locally occurring cranchiids by the presence of small, sharp papillae on the surface of the mantle and funnel. As in *H. pfefferi* and *H. beebei*, the funnel of ‘*M.*’ *papillata* was extremely large, extending past the eyes and the arm crown itself. In his discussion of this new species, Voss explained that he was dubious of the systematic position of this taxon, but that the species closely resembled *Helicocranchia pfefferi*. However, due to the systematic instability of several cranchiid genera during that time, *Helicocranchia* was believed to be a junior synonym of *Megalocranchia*, resulting in *H. papillata* being initially placed into the wrong genus. Voss (1962) then erected a new genus, *Ascocranchia*, for his new north Atlantic species *A. joubini* (= *H. joubini*, *fide* Voss, 1980). This specimen had two or three round photophores on the eyes and three series of suckers on the distal portion of the arms yet was missing the ventral cartilaginous strips seen in other members of the Cranchiinae (Voss, 1962). Voss discussed the difficulty of discerning the correct systematic position as the morphological characters of ‘*A.*’ *joubini* species appeared intermediary between the Cranchiinae and Taoniinae; however, Roper, Young, and Voss (1969) found morphological similarities in the funnel shape of *Ascocranchia* and *Helicocranchia* and determined that both should be part of the sub-family Taoniinae. Voss (1980) went further, considering *Ascocranchia* to be a junior synonym of *Helicocranchia*, noting that the three series of suckers described from the holotype were simply preservation artefacts (or possibly a mature male arm modification); however, Voss did not mention the circular eye photophores of this species, a character that would be unusual in the Taoniinae. There is general agreement that much taxonomic uncertainty remains in *Helicocranchia*, and Voss *et al.* (1992) postulated that there may be up to 14 distinct taxa, although currently only three are described.

## Systematics

*Helicocranchia* Massy, 1907

*Helicocranchia* Massy, 1907: 382–383; Voss, 1980: 382–384, fig. 4.

*Ascocranchia* Voss, 1962: 1–6.

**Diagnosis:** Small squid (max ML often <100 mm), with proportionally large funnel. Fins proportionally small, paddle-shaped. No tubercles present at fusion point (in Pacific material). Eyes with single ventral photophore. Arm and tentacle club suckers small, often subequal in size.

***Helicocranchia pfefferi* Massy, 1907** (Figs 6.2–6.5, Table B12)

*Helicocranchia pfefferi* Massy, 1907: 382, 383; Voss, 1980: 383, fig. 4e.

*Helicocranchia beebei* Robson, 1948: 130–132, fig. 14–18; Imber, 1978: 469–470.

**Diagnosis:** Small squid with at least three distinct bands of pigment (formed by transverse rows of single chromatophores) on the ventral mantle surface, with additional distinct chromatophore patches on the lateral mantle surfaces.

**Type material:** (examined) *Helicocranchia pfefferi* **BMNH Holotype 1890.1.24.10** [fide Freeman] **1909.11.27.10** [fide Voss (1980:382) and Lipinski *et al.* (2000:108)]]]. Type locality: 51°54'N, 11°57'W, southwest coast of Ireland.

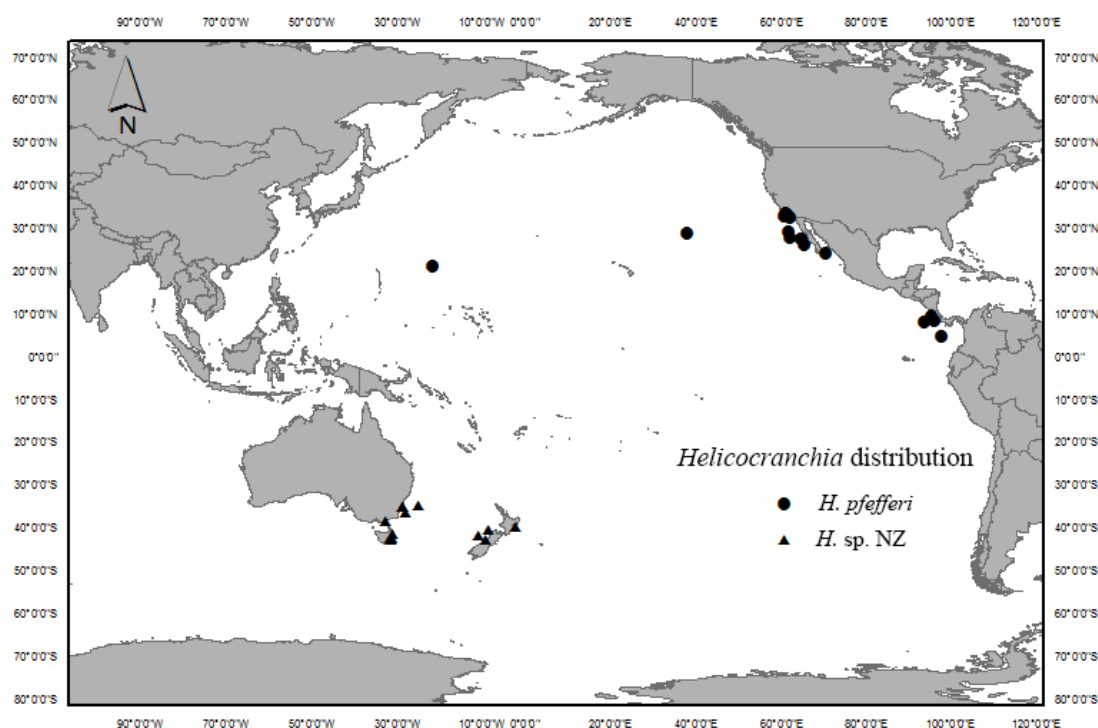


Fig. 6.1— Distribution of examined *Helicocranchia* material in the Pacific Ocean.

**Material examined (18 specimens):** **SBMNH 463049**, ML 32, 20 mm, sex indet., 33.47°N 118.88°W, USA, California, Santa Catalina Island, 1152 m, 30/03/1965; **SBMNH 464203**, ML 66 mm, ♂, 33.21°N 118.54°W, USA, California, Santa Catalina Island, 1302 m, 24/06/1964; **SBMNH 45741**, ML 27 mm, sex indet., 33.14°N 118.35°W, USA, California, Santa Catalina Island, 1216 m, 24/01/1964; **SBMNH 464220**, ML 74 mm, sex indet., 33.02°N, 119.34°W, USA, California, San Nicolas Island, 1371 m, 13/08/1969; **SBMNH 461011**, ML 69 mm, sex indet., 32.45°N 117.95°W, USA, California, San Clemente Basin, 0–900 m, Tucker Trawl, 7/09/1996; **SBMNH: 464210**, ML 61 mm, sex indet., 29.42°N 118.31°W, Mexico, Baja California, Isla Guadalupe, 3109 m, 28/08/1965; **SBMNH 47541**, ML 4.4 mm, sex indet., 28.80°N, 141.98°W, USA, Hawaii, Stn. 19B, 12/04/1966; **SBMNH 42209**, ML 63 mm, sex indet., 28.00°N 118.00°W, Mexico, Baja California, Isla Guadalupe, 1200 m, 12/09/1978; **SBMNH 464233**, ML 41 mm, sex indet., 27.57°N 115.25°W, Mexico, Baja California Sur, 2377 m, 15/06/1967; **SBMNH 463042**, ML 42 mm, sex indet., 27.43°N 115.35°W, Mexico, Baja California Sur, 2560 m, 16/06/1967; **SBMNH 464239**, ML 64 mm, sex indet., 26.40°N 114.42°W, Mexico, Baja California Sur, 3474 m, 23/06/1968; **SBMNH 460703**, ML 56 mm, ♂, 24.23°N 109.67°W, Mexico, Baja California Sur, Isla Cerralvo, MBARI Tiburon Dive 547, 972 m, 31/03/2003; **SBMNH 460894**, ML 44 mm, sex indet., 21.38°N 158.30°W, Hawaii, Oahu Leeward coast, 2500 m, 1980; **SBMNH 49437**, ML 39 mm, sex indet., 9.39°N, 84.88°W, Costa Rica, Puntarenas, 17/05/1973; **SBMNH 49454**, ML 28 mm, sex indet., 8.30°N, 86.40°W, Costa Rica, Puntarenas, 22/05/1973; **SBMNH 49502**, ML 16 mm, sex indet., 8.59°N, 84.23°W, Costa Rica, Puntarenas Isla del Cano, 26/05/1973; **SBMNH 51282**, ML 15 mm, sex indet., 8.51°N, 84.40°W, Costa Rica, Puntarenas, 26/05/1973; **SBMNH 51288**, ML 18 mm, sex indet., 4.83°N, 82.56°W, Panama, 20/06/1973.

### **Description:**

**Adult** (ML >50 mm; Fig. 6.2–6.5)—Mantle roundly conical, MW 33–41–48% ML, gladius only partially visible through dorsal mantle; chromatophores in distinct transverse bands along ventral surface (Fig. 6.2b) and irregular patches on lateral mantle surface. Fins paddleshaped, FL 5–8–13% ML, FW 15–21–27% ML, often more than twice as wide as long. Head short, ~5% ML, sometimes with transparent area on dorsal surface; HW 18–21–23% ML. Eyes small, ~6% ML, with single crescent photophore on ventral surface. Funnel wide, length 12–14–16% ML, funnel base subequal to anterior mantle width, funnel aperture 27–35–40% basal width; tubercles absent at fusion points.

Arms slender; formula III>II>I>IV: Arm I 12–18–25% ML, Arm II 18–23–31% ML, Arm III 23–26–30% ML, Arm IV 13–15–17% ML. Arms with 40–60 suckers (greatest number on Arms III), suckers subequal; in mature males, distal 40% of Arms I and II modified, biserial basally, tetraserial distally, distal suckers elongate. Tentacles often long, slender, TnL 42–64–80% ML; 14–17 small sucker pairs along stalk; clubs small, CL ~9% ML (10–15–19% TnL), ~60 subequal circular suckers on club, without distinct regions based on sucker type; suckers with ~7–13 pointed teeth (Fig. 6.3).

**Juvenile** (ML <50 mm)—As in adult, with following exceptions: MW 32–48–63% ML; FL 6–10–16% ML, FW 17–26–38% ML, fin width 2–4x greater than length. Head short, 2–5–9% ML, often with transparent area on dorsal surface; HW 21–26–31% ML. Eyes small, stalked, often tear-drop shaped, ED 5–7–9% ML, photophore variably



visible. Funnel wide, length 13–19–24% ML, funnel aperture 22–34–57% BW; ventral fusion windows not visible.

Arm formula III>II>I>IV: Arm I 6–13–22% ML, Arm II 13–21–34% ML, Arm III 17–26–44% ML, Arm IV 8–15–25% ML. Arms with 22–62 suckers, Arms III with most, suckers subequal; male sexual modifications developing on Arms I and II by ML 60 mm. Tentacles long, slender, TnL 70–105–140% ML, with 14–17 small sucker pairs along stalk; clubs small, CL ~11% ML (7–12–15% TnL), 38–64 subequal circular suckers on club.

**Known distribution:** Northern sub-tropical Pacific, from Californian coast to Hawaiian Islands (Fig. 6.1). Present material collected from 0–3474 meters (Fig. 6.4), elsewhere recorded between 400–600 meters (Young & Mangold, 2018).

**Remarks:** *Helicocranchia pfefferi* was originally described from the North Atlantic. The animals examined here, largely from the northern Pacific Ocean, could not morphologically be distinguished from the Atlantic type specimens, or the descriptions of the Atlantic species. It would be valuable to compare representatives of a number of populations from the Atlantic and Pacific Oceans using molecular tools to further test what appears to be conspecificity over a wide area. It may be that more than a single species is present, but this is not obvious from morphological comparison.

The most readily visible distinguishing feature of *H. pfefferi* is the pattern of chromatophores on the ventral mantle. These are set in transverse rows of large, oval, red-brown chromatophores medially, and patches of smaller chromatophores along the lateral mantle margins (Fig. 6.2b). Although chromatophore patterns are not always a reliable diagnostic trait, this pattern was evident in almost all examined material, even in smaller sizes. In most instances of male arm modification, mature specimens displayed the usual secondary sexual morphology (with suckers biserial basally, tetraserial distally on Arms I and II); however, one specimen (SBMNH 460703) had unusual sucker morphology on these two arm pairs. While showing the same biserial to tetraserial arrangement, from the base to the distal part of the arm, the more distal suckers were flattened (Arms I) or swollen (Arms II), as seen in Fig. 6.5. The arm lengths also proportionally increased, as Arm I was 48% ML and Arm II was 60% ML, noticeably longer than the other two arm pairs, and proportionally longer than males with the ‘typical’ style of arm modification. Male modification can often have systematic value in the differentiation of cephalopods, so this unique feature could be indicative of a separate species; however, as this specimen is in all other respects similar to *H. pfefferi*, it is included with this taxon.

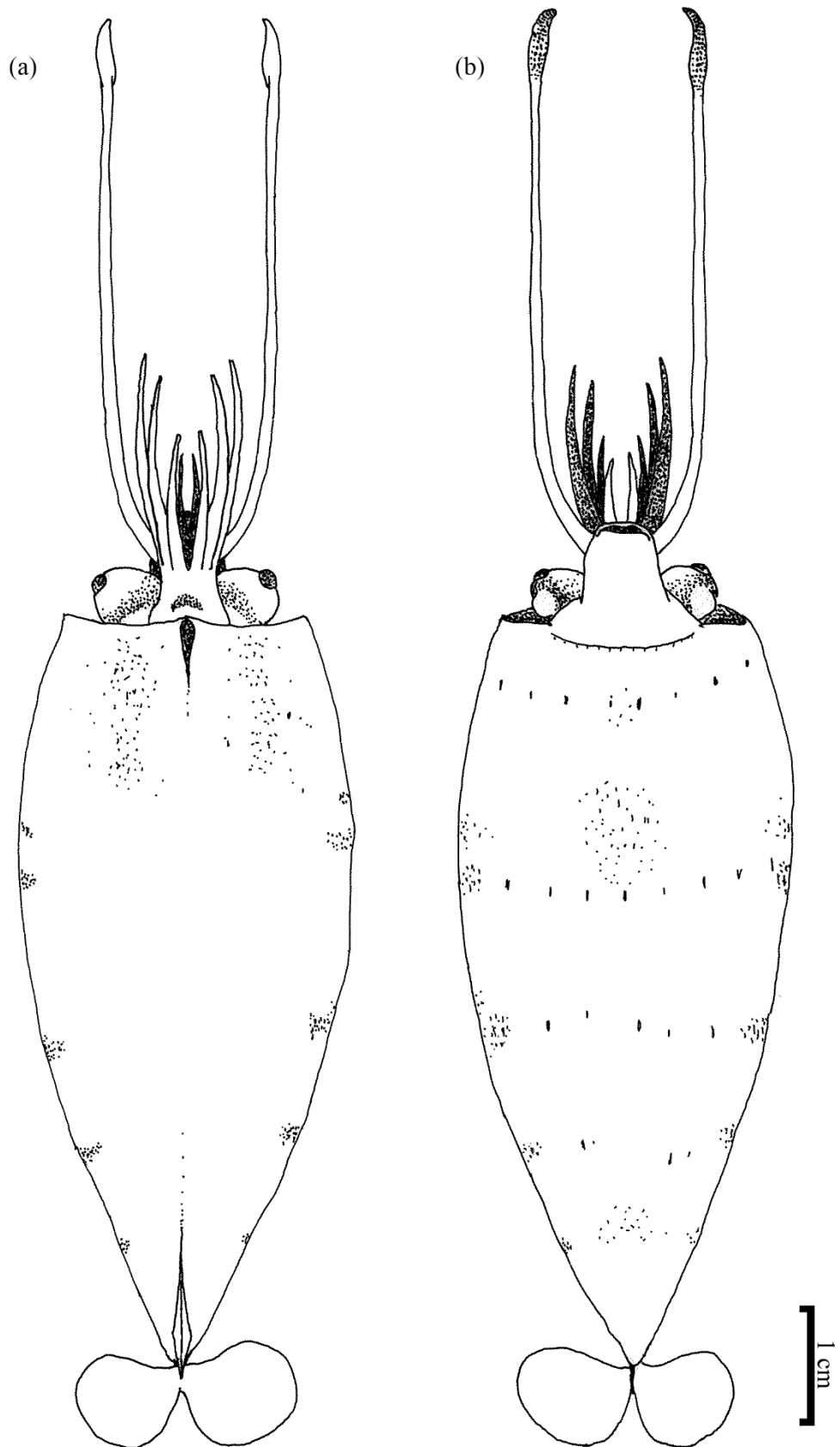


Fig. 6.2—*Helicocranchia pfefferi* (a) dorsal view and (b) ventral view (SBMNH 42209; ML 63 mm).

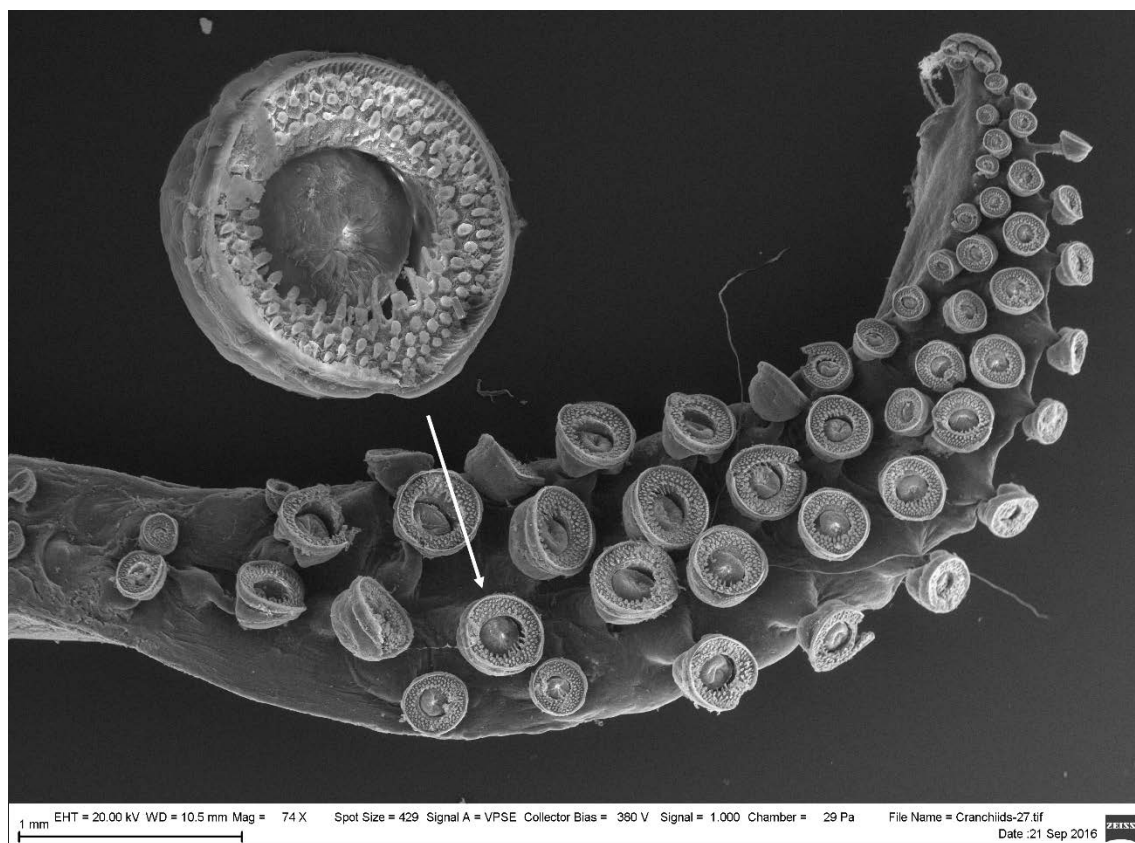


Fig. 6.3—Right tentacle club of *H. pfefferi* with enlarged manus sucker (SBMNH 464203; ML 66 mm).

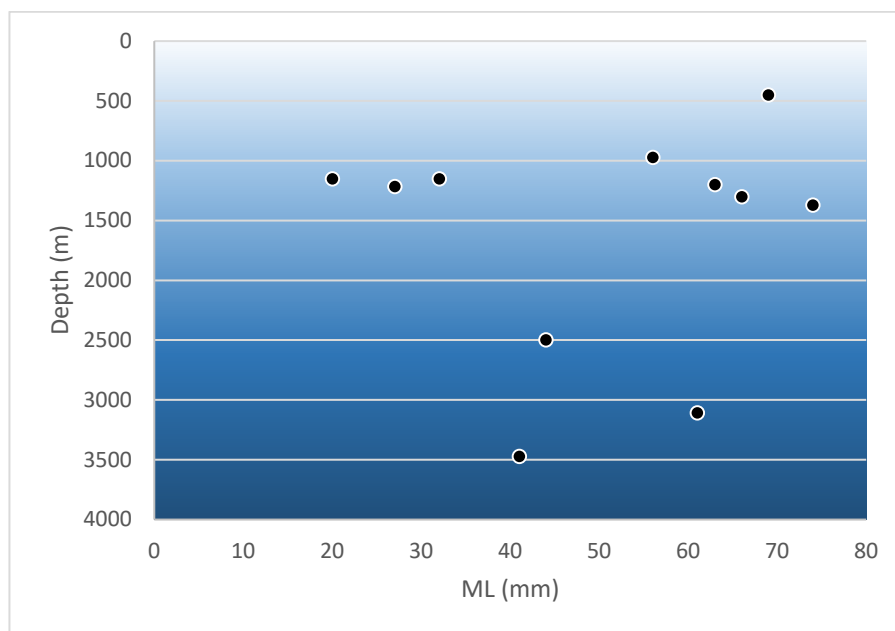


Fig. 6.4—Collection depths of *H. pfefferi* material examined in this study.

***Helicocranchia* sp. NZ** (Figs 6.6–6.8, Table B13)

*Helicocranchia beebei* (not Robson, 1948): Imber, 1978: 469–470.

**Diagnosis:** Mantle variably stout, funnel large, arms proportionally long, becoming nearly subequal in adults; absence of obvious chromatophore pattern on mantle.

**Material examined (16 specimens):** NMV F163932, ML 63 mm, sex indet., 34.59°S, 155.14°E, CSIRO RV *Soela*, 425 m, 09/10/1981; NMV F163946, ML 49 mm, ♂, 34.93°S, 151.24°E–34.87°S, 151.27°E, New South Wales, 52 km ESE of Nowra, 3 m, CSIRO RV *Franklin*, 21/10/1988; NMV F163949, ML 45 mm, sex indet., 34.94°S, 151.24°E–34.90°S, 151.26°E, New South Wales, 53 km ESE of Nowra, MWT, 3 m, CSIRO RV *Franklin*, 20/10/1988; NMV F163807, ML 45 mm, 34.95°S, 151.34°E–34.72°S, 151.44°E, New South Wales, ESE of Nowra, 3 m, CSIRO RV *Franklin*, 21/10/1988; NMV F163821, ML 46 mm, ♂, 36.36°S, 151.87°E, New South Wales, off Sydney, RV *Courageous*, Q30/567, 01/01/1978; NMNZ M.091679, ML 39 mm, ♂, 39.86°S, 177.87°E, New Zealand, 200–470 m over 1217 m, RV *Kaiyo Maru*, MWT, Stn. KM/223C/85, 21/09/1985; NIWA 95897, ML 46, 37, 22 mm, sex indet., 38.43°S 47.35°E, 25 m, Stn. TAN9101/12, 28/06/1991; NIWA 95902, ML 18 mm, 40.49°S, 171.54°E, 352 m, Stn. Z10297, 08/08/2000; NMV F163944, ML 32 mm, sex indet., 41.24°S, 149.01°E, Tasmania, 1000 m, 28/07/1991; NIWA 95924, ML 29 mm, sex indet., 41.58°S 168.90°E, surface, Stn. TAN9101/28, 19/07/1991; NMV F163805, ML 17 mm, sex indet., 42.22°S, 148.77°E–42.13°S, 148.76°E, 0–1000 m, CSIRO RV *Franklin*, 27/07/1986; NMV F163937, ML 42 mm, sex indet., 42.50°S, 148.50°E–42.53°S, 148.47°E, Tasmania, 491 m, FV *Petuna Endeavour*, 01/12/1982; NIWA 95955, ML 24 mm, sex indet., 42.61°S, 170.61°E, 420 m, Stn. Z10302, 09/08/2000; NMV F51904, ML 54 mm, sex indet., 42.72°S, 148.47°E, Eastern Tasmania, 295–310 m, RV *Soela*, 22/06/1984.

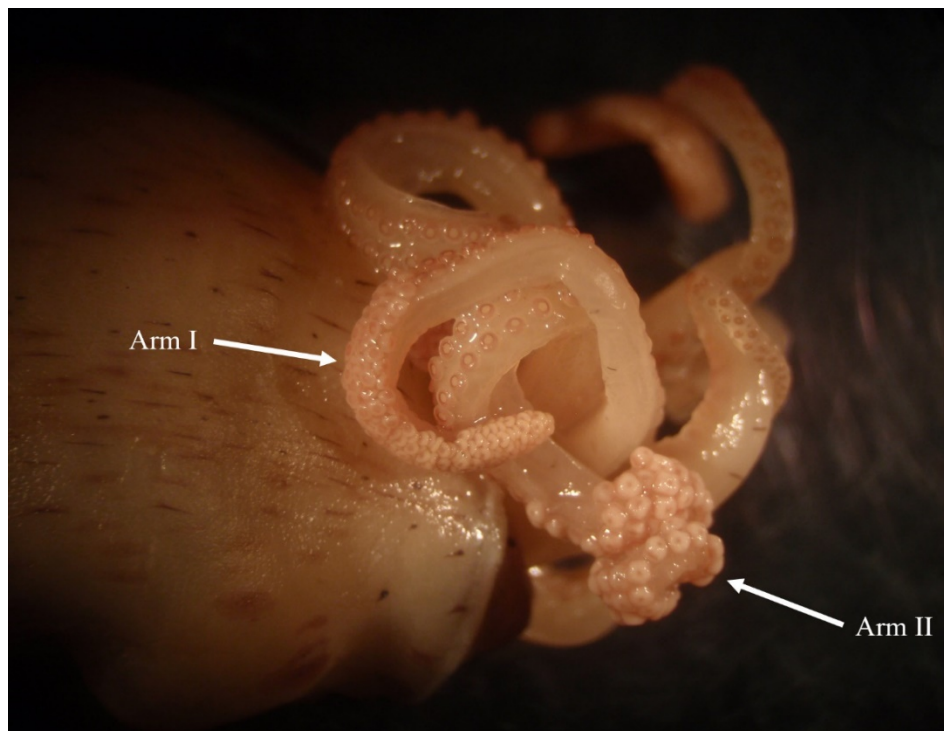


Fig. 6.5—Unusual secondary sexual modification morphology in male *H. pfefferi* (SBMNH 460703; ML 56 mm).

**Non-localised material examined (1 specimen):** NMV F163947, ML 11 mm, sex indet., Australia, RV *Sprightly*, PS8/82/33, 29/08/1982.

**Description:**

(ML >40 mm; Figs 6.6, 6.7)—Mantle stoutly ovate, MW 30–48–60% ML, chromatophores not visible or sparsely distributed with no obvious pattern. Fins paddle-shaped or oval, FL 6–10–15% ML, FW 13–25–48% ML, often more than twice as wide as they are long. Head small, 5–10–16% ML, sometimes with transparent area on dorsal surface; HW 17–25–36% ML. Eyes small, 5–8–12% ML, with single ventral photophore (Fig. 6.7). Funnel proportionally large (Fig. 6.6b), length 14–20–26% ML, base nearly subequal to anterior mantle width, funnel aperture 25–37–50% basal width; tubercles absent at fusion points.

Arms narrow, general arm formula III>II>I>IV: Arm I 20–29–46% ML, Arm II 19–32–48% ML, Arm III 24–36–52% ML, Arm IV 11–18–26% ML; Arms IV with low aboral keel. Arm suckers subequal in size, sucker rings with ~10–12 blunt teeth. In mature males, distal 40% of Arms I and II variably modified, changing from two to four series of small elongated suckers. Tentacle length exceeds mantle length (67–111–160% ML), ~9 small sucker pairs along stalk; clubs 10–15–20% ML, with 50–60 subequal suckers; sucker rings with ~6–12 small teeth along distal margin, small bumps along proximal margin.

(ML <40 mm; Fig. 6.8)—As above with following exceptions: Funnel length 14–21–32% ML, aperture 25–49–75% funnel base. Arm formula III>II>I=IV: Arm I 15–23–32% ML, Arm II 25–30–41% ML, Arm III 25–37–50% ML, Arm IV 18–23–30% ML. Tentacles 80–110–135% ML.

**Known distribution:** Southern Pacific: Australian and New Zealand waters (Fig. 6.1). Examined material collected between 3–491 meters depth.

**Remarks:** Morphologically distinguished from *H. pfefferi* by the proportionally longer arms in adults (arm lengths becoming more equal with size), and the stouter mantle shape. Unfortunately, as with other species of *Helicocranchia*, the arm sucker rings are very small, and discerning the dentition is a challenge on most specimens. The number of teeth on the arm sucker rings (~10–12) is based only on a single specimen and is approximate as these (as for other species in this genus) are difficult to discern, even under high magnification. It would be useful to compare sucker dentition among all species using SEM to determine whether this is a useful diagnostic trait.

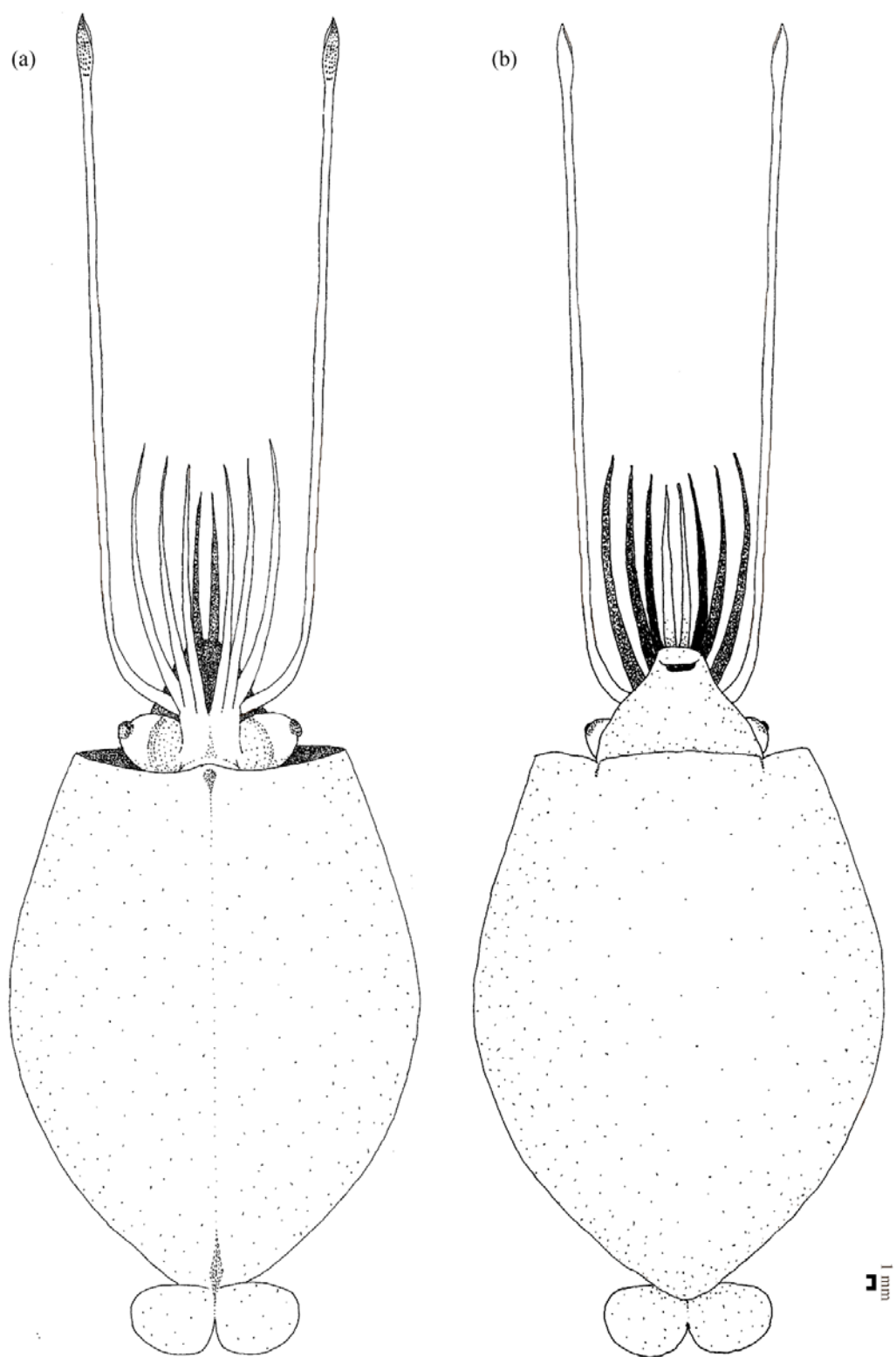


Fig. 6.6—*Helicocranchia* sp. NZ (a) dorsal and (b) ventral view (NIWA 95897; ML 46 mm).

## Discussion

The material attributed to *Helicocranchia pfefferi* examined herein was primarily from the north-eastern Pacific, and housed at the Santa Barbara Museum of Natural History. It was primarily attributed to *H. pfefferi* because of the distinctive chromatophore patterns on the mantle surface (Fig. 6.2b), which are also known to occur in Atlantic material attributed to this taxon. Although chromatophore patterns can be very useful in distinguishing taxa (particularly in paralarval specimens) they should not be used as the sole diagnostic character, as they are variably present depending on material preservation. That said, the patterns considered characteristic of *H. pfefferi* have been apparent in most examined specimens attributed to that taxon. In comparison, material from the Southern Hemisphere frequently lacked visible chromatophores entirely, possibly due to preservation methods. In general, material attributed to *H. pfefferi* also tended to be slightly more slender, and *Helicocranchia* sp. NZ had proportionally longer arms; however, both of these morphological characters showed variability and overlap between the two species.

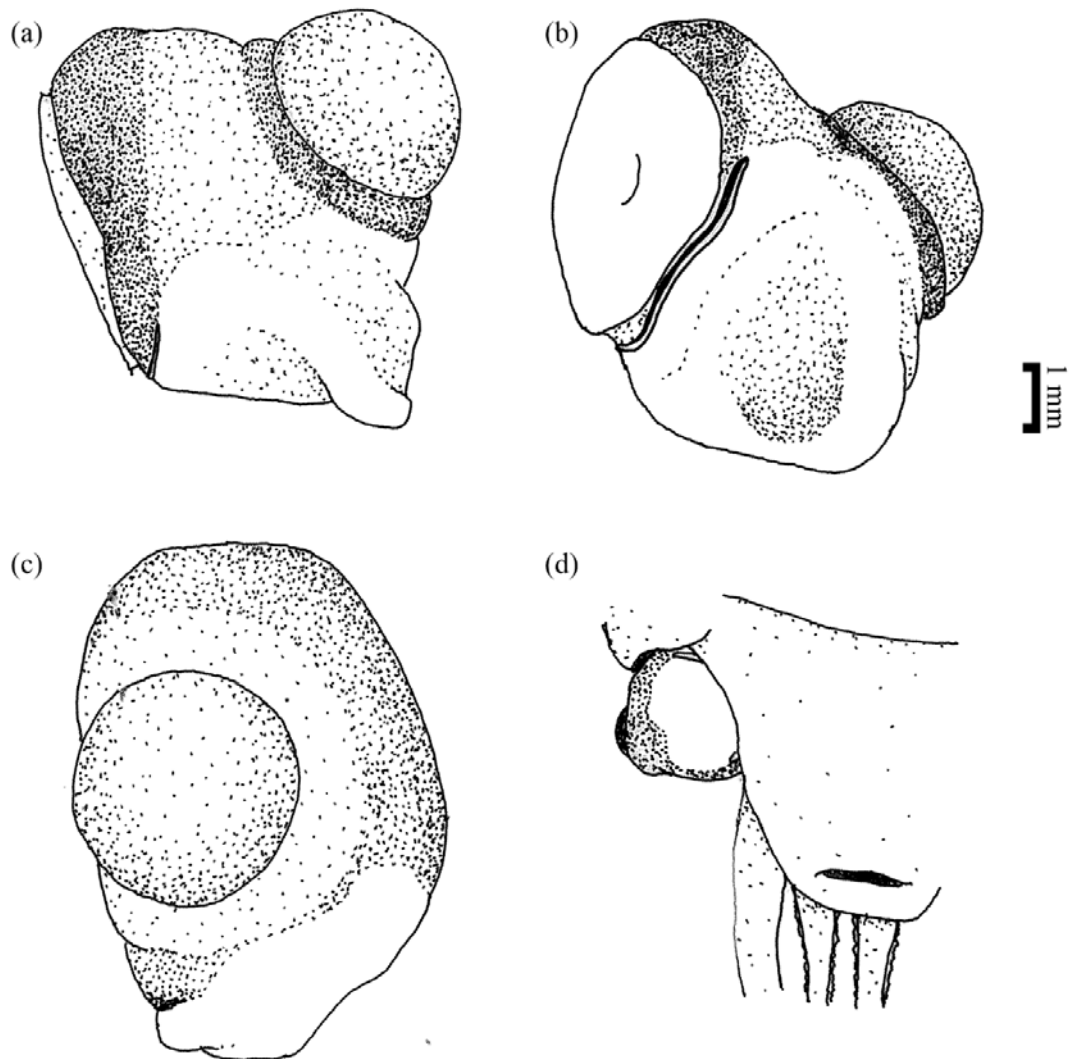


Fig. 6.7—Eye of *Helicocranchia* sp. NZ in (a) anterior, (b) ventral, (c) medial, and (d) ventral in-situ perspectives (NIWA 95897; ML 46 mm).

In many other cranchiid genera, sucker dentition can assist in distinguishing among taxa; however, due to the small size of *Helicocranchia* suckers, this is a challenging character to use without the assistance of SEM. Often the suckers on the tentacle club are large enough to distinguish individual distal teeth; however, even at high magnifications, obtaining consistent tooth counts is challenging. Hopefully, future descriptions will make use of SEM for a more accurate summary of sucker dentition. The values stated in these descriptions are simply an estimate.

Voss, Stephen, and Dong (1992) suggested that there could be up to 14 species of *Helicocranchia* globally but did not explain how they distinguished among these hypothesised species. The two taxa described above represent a small step towards resolving the systematics of this genus. At present, Pacific material from the Southern Hemisphere can be differentiated from specimens from the Northern Hemisphere, but it is probable that further taxon divisions may be eventually be recognised. As fresh material becomes available, a global integrative taxonomic revision of this genus would be invaluable.

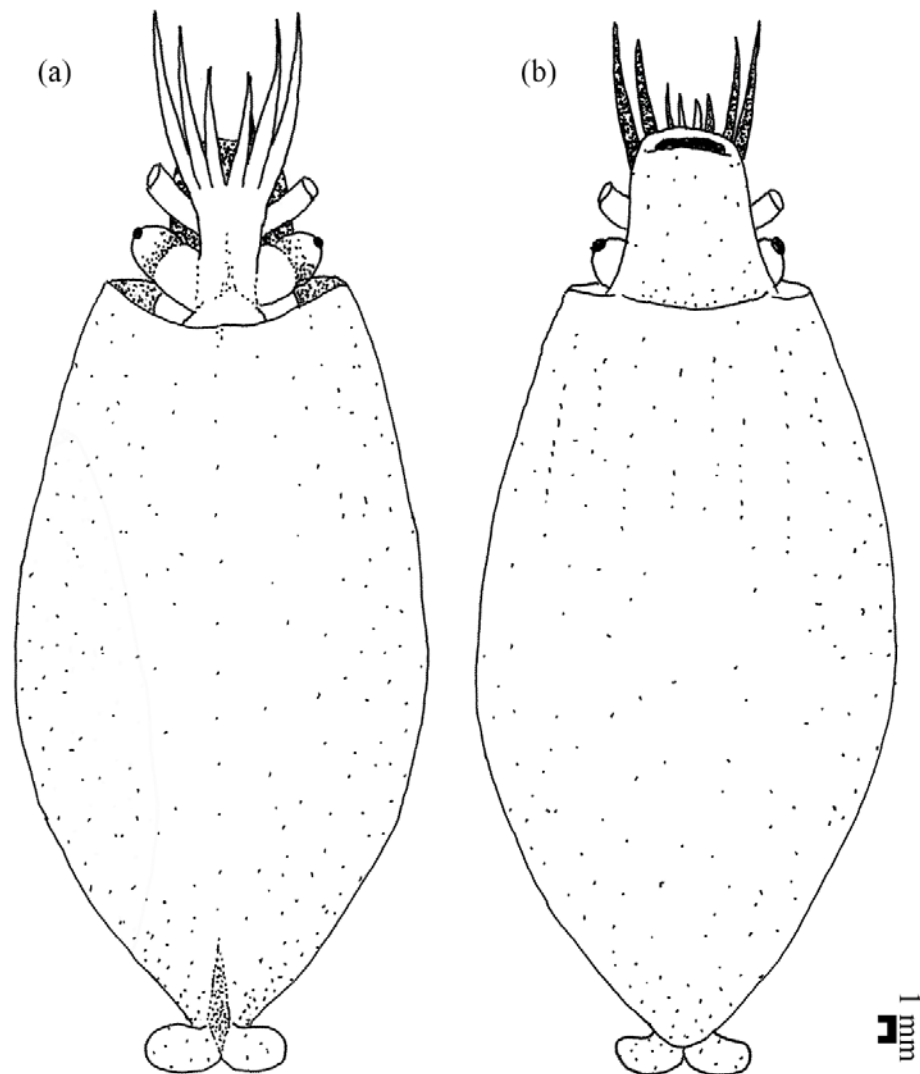


Fig. 6.8—Juvenile *Helicocranchia* sp. NZ (a) dorsal and (b) ventral view (NMNZ M.091679; ML 39 mm).



## *Liguriella* Issel, 1908

### Historical Review

*Liguriella* was originally described by Issel (1908) as having stalked eyes with two rows of hemispherical ‘tubercles’ on them. Issel believed that these ‘tubercles’ were light-producing organs, and also described the species as having a row of tubercles along the dorsal midline, differing from those previously described in genera like *Liocranchia* and *Zygaenopsis* as they had antero-dorsal ridges rather than conical protuberances. This feature caused some debate in following years; however, due to the presence of these dorsal tubercles, Issel attributed *Liguriella* to the subfamily Cranchiinae.

Chun (1910) named *Liguriella* as a junior synonym of his genus *Corynomma* Chun, 1906 (= *Megalocranchia*, *fide* Voss, 1980). Chun decided that the specimens of *Corynomma* that he examined looked identical to Issel’s *Liguriella* specimen, as they had the same mantle shape and the tentacle clubs had a similar sucker configuration. In response to Issel’s description of dorsal tubercles, Chun explained that the protuberances along the dorsal midline were simply a result of glacial damage when the mantle contracted during preservation (Chun, 1910). Pfeffer (1912) disagreed with Chun’s conclusion regarding the tubercles, stating that he believed the features could have been distinct and natural, but that he was unsure of what systematic position the taxon should hold. Pfeffer (1912) concluded that *Liguriella* should be retained as the fifth genus in Cranchiinae, a decision supported by Thiele (1934) who also retained *Liguriella* as part of Cranchiinae, and described how the genus had a line of sawtooth-shaped tubercles along the dorsal midline. Thiele did not mention the shape of the eye photophores, but noted that the eyes were stalked, indicating that the specimen would not yet have been mature.

In 1974, Nesis erected a new genus, *Vossoteuthis*, for the taxa *Desmoteuthis pellucida* (Chun, 1906; = *Teuthowenia pellucida*, *fide* Voss, 1985) and *Megalocranchia pardus* (Berry, 1916; = *Liguriella pardus*, *fide* Nesis, 1987). The identification of Nesis’ specimen of *Vossoteuthis pellucida* was later found by Voss (1980) to be erroneous. She re-examined them and concluded that the specimen examined was a member of *Liguriella*. In her revision of the family, Voss placed *Liguriella* in the same sub-family with other Taoniinae, as no tubercles were found on the dorsal mantle surface of more recently collected specimens, and the eyes had two crescentic photophores. Voss, Stephen, and Dong (1992) speculated that several species of *Liguriella* might exist, but never described additional species.

### Systematics

*Liguriella* Issel, 1908

*Megalocranchia* Berry, 1916: 61–64.

*Corynomma* Chun, 1906: 85; 1910: 286–290.

**Description:** Mantle conical; gladius visible along entire dorsal midline, rachis rounded or diamond-shaped at anterior margin; ventral fusion cartilaginous windows oval, one

or two tubercles at each ventral fusion. Fins ovate (or paddle shaped in smaller individuals); anterior fin margin connects to mantle tissue, not conus. Eyes spherical; eyes with two photophores, both crescentic; eyes stalked in paralarva.

Arms tapering quickly to spindly tips, with low membrane on all arms; formula  $\text{III} \geq \text{IV} \geq \text{II} > \text{I}$ . Sucker counts vary per arm pair, 25–80 suckers on arms; suckers generally expanded mid-arm; largest medial suckers with 8–36 teeth, suckers often dorso-ventrally compressed. Tentacles 60–180% ML, up to 40 small suckers on stalk; club often proportionally long and expanded from tentacular stalk, with 60–120 suckers; largest manus suckers with 5–10 pointed teeth.

***Liguriella podophthalma* Issel, 1908** (Figs 7.2–7.6, Table B14)

*Liguriella podophthalma* Issel, 1908: 233–234; Nesis, 1974: 27–29.

*Corynomma speculator* Chun, 1910: 286–290, Pl. LV, Pl. LX fig. 13–16.

**Diagnosis:** Mantle conical, fins lanceolate (but proportionally stout). Inner ocular photophore terminates close to outer photophore (sometimes appearing connected). Basal to medial arm suckers with many angular teeth, distal suckers with fewer, rounded teeth. Tentacle stalks with close-set pairs of suckers distally.

**Type material:** (not examined) *Liguriella podophthalma*; type repository unresolved. Type locality: Atlantic Ocean (28°38'S, 47°31'W).

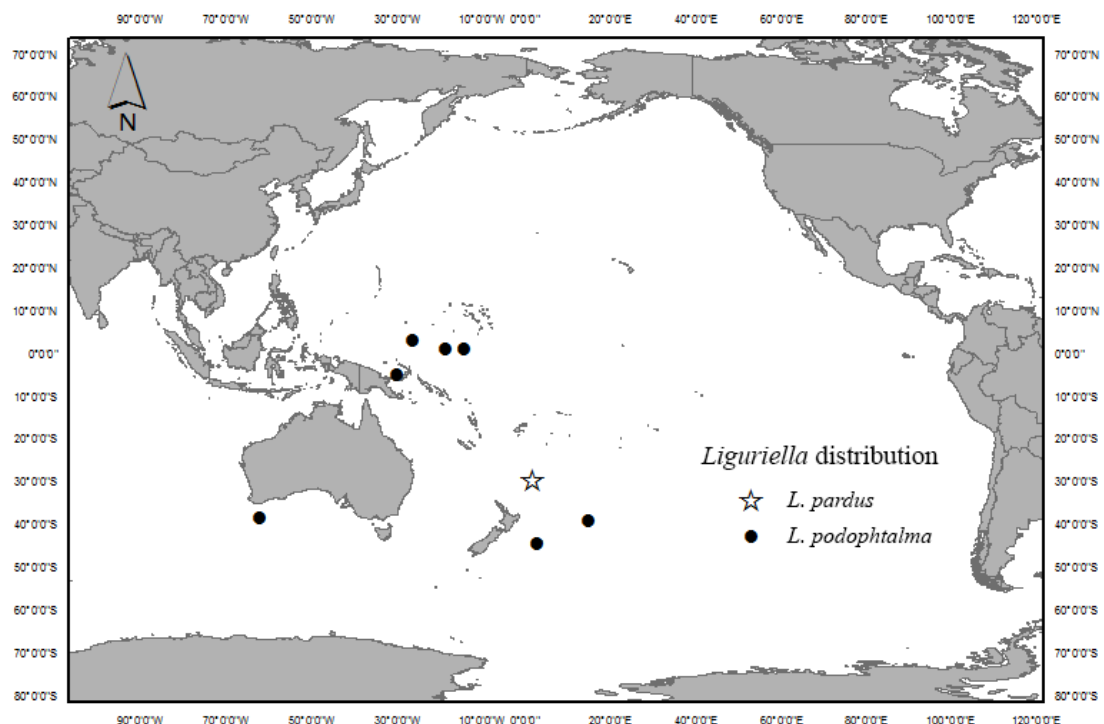


Fig. 7.1— Distribution of examined *Liguriella* material in the Pacific Ocean.

**Material examined (7 specimens):** **NSMT-Mo. 85252**, ML 20 mm, sex indet., 3.03°N, 153.62°E, north of Papua New Guinea, Central Pacific, 09/09/1995; **NSMT-Mo.85233**, ML 9 mm, sex indet., 1.16°N, 161.38°E, east of Papua New Guinea, Western Pacific, 0–188 m, 08/08/1995; **NSMT-Mo. 85232**, ML 34 mm, sex indet., 1.02°S, 156.82°E, northeast of Papua New Guinea, Pacific, 190 m; **NSMT-Mo.85229**, ML 20 mm, ♂, 4.76°S, 150.11°E, north of Papua New Guinea, central Pacific, 17/10/1992; **NIWA 95923**, ML 83 mm, sex indet., 38.25°S, 117.95°E, TAN9101/21, 07/09/1991; **NMNZ M.286168**, ML 123 mm, 38.98°S, 165.25°W, north of Valerie Guyot, Louisville Ridge, 20–95 m over 5000 m, RV *Tangaroa*, Stn.TAN9503/21, 22/03/1995; **NIWA 2257**, ML 68 mm, 44.56°S, 177.15°W–44.55°S, 177.14°W, 150–50 m, Stn. TAN9202/100, 24/02/1992.

**Non-localised material examined:** **NIWA 95893:** ML 29 mm, Stn. TAN 9802/126, 02/1998.

### **Description:**

(ML 9–123 mm, Figs 7.2–7.6)—Mantle conical, MW 26–43–69% ML; rachis rounded or diamond shaped at anterior margin; conus short, ~25–30% ML (Fig. 7.2); ventral fusion cartilaginous windows oval, commonly one or two simple tubercles at each ventral fusion (Fig. 7.5) (occasionally one of the tubercles is complex with several smaller cusps at base). Fins each ovate, FL 8–16–26% ML, FW 8–26–33% ML. HL 6–17–33% ML, eyes spherical, ED 4–10–18% ML; HW 24–31–42% ML). Eyes with two photophores, both crescentric, inner photophore appears to connect to outer photophore at posterior end (Fig. 7.3). Funnel narrows slightly, funnel length 5–11–17% ML, FA 29–53–75% FB.

Arms tapering abruptly to spindly tips, heavily trabeculated low membrane on all arms; formula  $III \geq IV = II > I$ : Arm I 6–14–35% ML, Arm II 10–20–43% ML Arm III 16–27–53% ML, and Arm IV 16–22–45% ML. Sucker counts and morphology vary per arm pair, some specimens with up to 80 suckers; suckers generally expanded mid-arm. Arm I with 22 pointed teeth on distal 60% of margin in basal suckers, medial suckers with 36 angular teeth around entire margin (Fig. 7.4b), dentition decreases suddenly towards the distal tip with seven to nine rounded teeth around margin. Arm II basal suckers with ~15 blunt teeth on distal 60% of margin (Fig. 7.4a), 40 blunt teeth on entire margin on medial suckers, distal suckers with 4–8 rounded teeth on entire margin (Fig. 7.4d); distal suckers compressed dorso-ventrally (Fig. 7.4e); Arms III and IV basal suckers with 18 pointed teeth on distal 60% of margin, medial suckers with 36 angular teeth on entire margin, distal suckers with five large rounded teeth. Tentacles 60–96–180% ML, up to 40 small suckers on stalk; CL 10–24–33% ML (~25% TnL) with 60–120 suckers (over 100 in larger specimens). Largest manus suckers with approximately five pointed teeth (Fig. 7.4c).

**Known distribution:** Western Pacific, off the coast of Papua New Guinea to southern Pacific around New Zealand (Fig. 7.1). Vertical distribution of examined material from 0–188 meters depth.

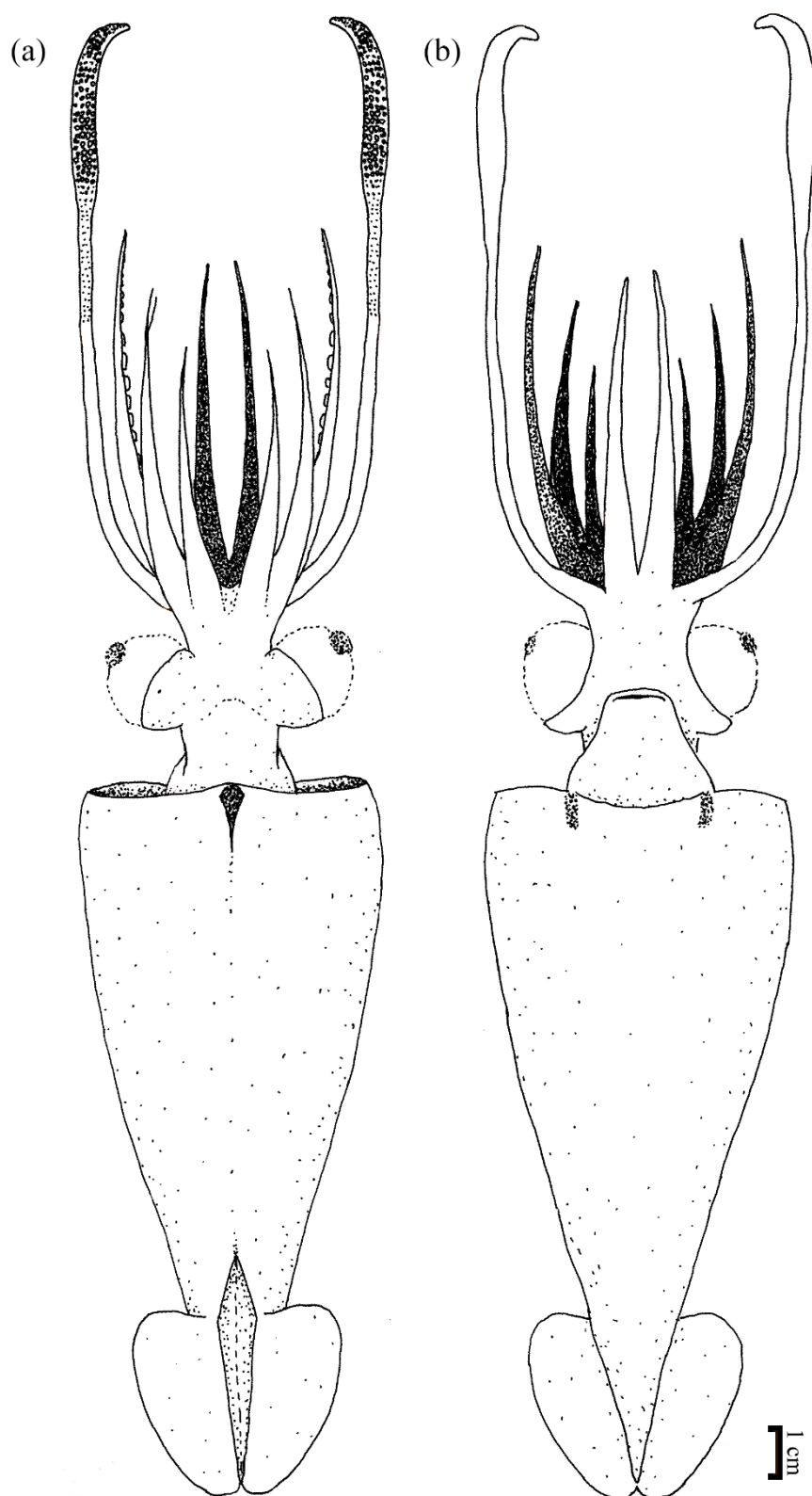


Fig. 7.2—Adult *Liguriella podophtalma* (a) dorsal view and (b) ventral view (NMNZ M.286166; ML 123 mm).

**Remarks:** *Liguriella* remains one of the most enigmatic cranchiids. Because there were so few specimens of *Liguriella* in collections, it was a challenge collect enough data to create a detailed morphological description. The description herein provides data for all stages of development (ML 9–123 mm) and as such does not provide a specific range of values divided into ontogenetic stages; however, illustrations have been included to assist in identification (Fig. 7.6). *Liguriella* appears most similar to species of *Megalocranchia*, and for certain life stages the quickest way to differentiate between the two genera is to determine whether an internal photophore (characteristic of *Megalocranchia*) is present. This photophore usually begins to develop around 30–40 mm ML, so smaller growth stages still appear very similar. When examining these ‘paralarval’ specimens, the arrangement of the suckers on the tentacle stalk can be

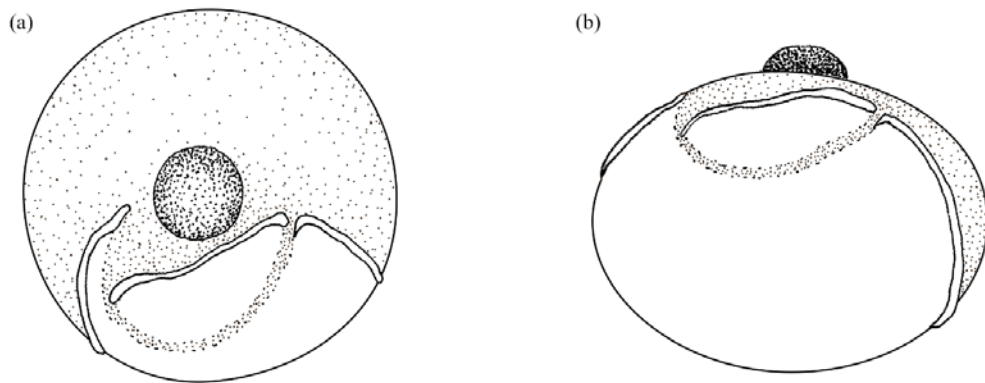


Fig. 7.3—Left eye schematic for *Liguriella podophtalma* (a) lateral view and (b) ventral view.

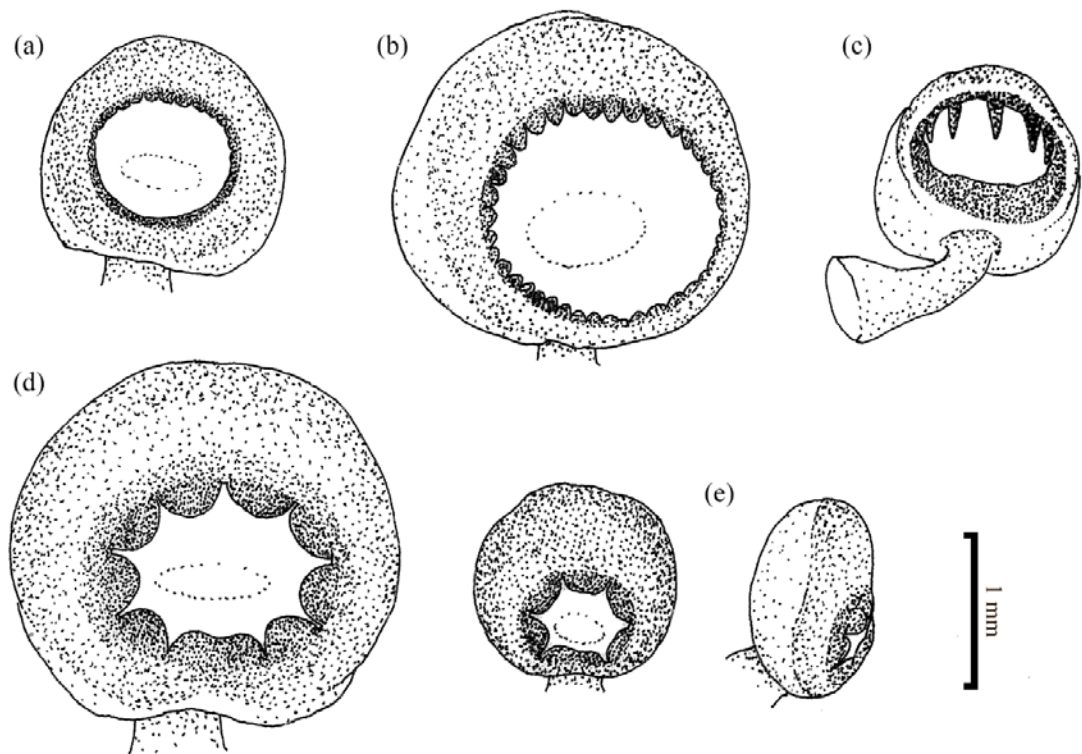


Fig. 7.4—Arm and club dentition of *L. podophtalma*: (a) basal Arm III, (b) medial Arm III (proximal), (c) manus sucker, (d) medial Arm III (distal), and (e) distal Arm III oral and lateral view (NMNZ M.286166, ML 123 mm).

useful, as the pairs of suckers on *Liguriella podophtalma* are spaced closely on the distal end and do not continue beyond the midpoint of the stalk, compared to *Megalocranchia*, where the suckers usually pairs are found along the tentacle stalk length. A non-diagnostic character that was frequently observed was the coloration of the arms, as in many specimens examined, arm coloration changed from pink basally to yellow distally, which was not observed on preserved material of any other genus.



Fig. 7.5—Right ventral funnel-mantle fusion of *Liguriella podophtalma*.

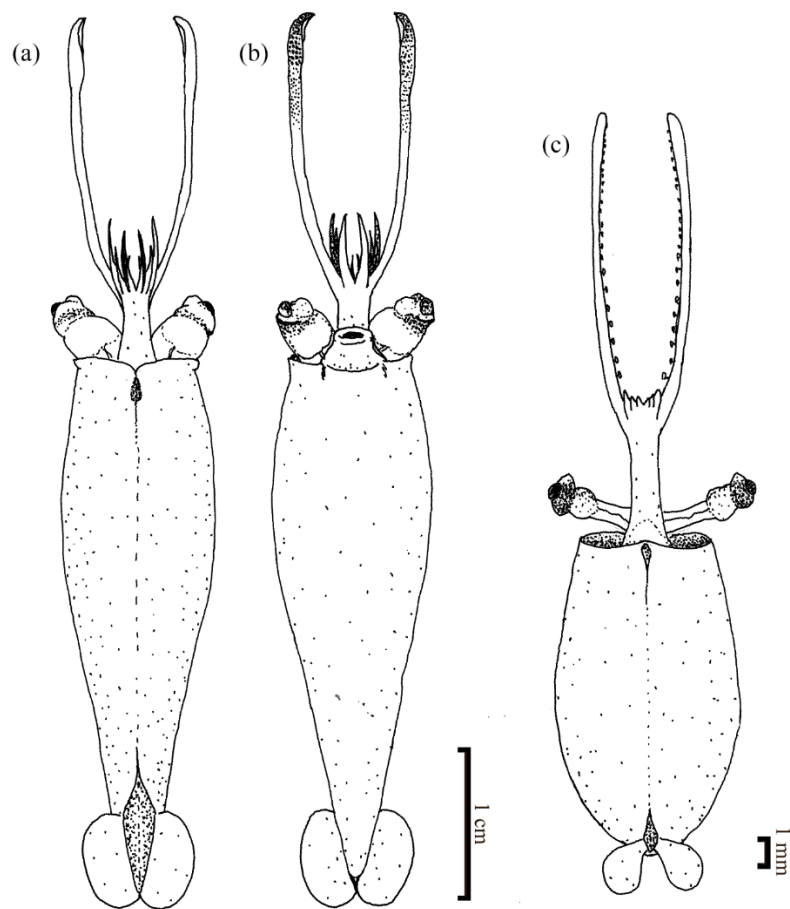


Fig. 7.6—Younger stages of *L. podophtalma* (a) dorsal and (b) ventral view of 'juvenile' (NSMT Mo:85232; ML 34 mm) and (c) dorsal view of 'paralarval' specimen (NSMT Mo:85233; ML 9 mm).

***Liguriella? pardus* (Berry, 1916) (Fig. 7.7)**

*Megalocranchia pardus* Berry, 1916: 61–64, Pl. IX, fig. 2.

*Vossoteuthis pardus* (Berry, 1916): Nesis, 1974: 19.

*Liguriella pardus* (Berry, 1916): Nesis, 1987: 274.

**Type material:** (examined) **NMNH Holotype 816465**, ML 51mm, sex indet., 29.83°S, 178.25°W, south Pacific Ocean, New Zealand, Kermadec Islands, Sunday Island, 0 m, 1910.

**Description:**

(ML 51 mm; Fig. 7.7)—Mantle stout, MW 47% ML, funnel–mantle fusions with single pointed tubercle; fins rounded, FL 22% ML, FW 20% ML. Head proportionally short, HL 6% ML, HW 29% ML; eyes slightly oblong, ED 10% ML, tissue surrounding lens with small sinus along oral midline; two crescent photophores visible (Fig. 7.7c). Funnel stout, FuL 8% ML, narrowing abruptly to aperture, FA 22% FB.

Arms short with robust protective membrane along length, arm tips robust, ending bluntly; formula III>IV>II>I: Arm I 12% ML, Arm II 16% ML Arm III 21% ML, and Arm IV 17% ML. Arms with 25–35 round suckers, slightly compressed dorso-ventrally. Arm suckers with ~8 small blunt teeth on distal margin of larger suckers; suckers increasing in size until distal third, then decreasing again; Arm II sucker series spaced widely apart. Tentacle proportionally short, 33% ML, with expanded club; CL 12% ML (35% TnL). Tentacle stalk with four series of small suckers along entire length, club with 90–100 suckers; manus suckers not significantly enlarged, 10–12 blunt/angular teeth.

**Known distribution:** Currently only known from the Kermadec Islands (Fig. 7.1).

**Remarks:** These results are based solely on the type specimen, caught in the Kermadec Islands. There are very few extant specimens of this taxon in collections, the holotype being the only one examined during this research. Although this specimen is in good condition, it does not fit neatly into any particular known genus (for which paralarval morphology is well understood). Nesis (1987) placed this species in *Liguriella*, a genus with which it does share some traits (such as fin shape and ventral tubercle arrangement). At the present time (and due to the lack of available material and evidence) the most conservative approach is to maintain it here; however, molecular analysis may place *L. pardus* in another known genus, or possibly indicate that it should be in a distinct genus. With only the paralarval type specimen available, it is challenging to determine what other taxon this species may resemble; initial examination raised the possibility of affinities with the genera *Megalocranchia* or *Teuthowenia*, as specimens of similar size from these genera have a similar body shape. However, further examination showed that *L. pardus* lacks a third photophore on the eyes (indicative of *Teuthowenia*) and lacks an internal photophore (indicative of *Megalocranchia*) which should have begun developing at this size; therefore it is most similar to *Liguriella*.

## Discussion

Due to the brief nature of the original description of *Liguriella* (Issel, 1908), it has been challenging to accurately determine what features could be used to characterise the genus. When analysing the original illustrations done by Issel, which showed ‘saw-like’ dorsal tubercles, I believe that the original description of these tubercles was actually damage to the gladius; this is in accordance with Chun’s (1910) conclusions. The mantle of many cranchiid specimens contracts significantly during the preservation process, often causing the gladius to fracture perpendicular to the midline. Should enough of these fractures occur, it can resemble natural ridges in the skin, as had been assumed by Pfeffer (1912). When examining Issel’s illustration of *Liguriella podophthalma* (image 45; Issel, 1908), the mantle is shown to be wrinkled in appearance. This is a common sign that the mantle of the specimen has undergone significant contraction during the preservation process.

The ‘tubercles’ on the eyes are more difficult to interpret without being able to examine the type specimen. Issel believed that these organs produced light, indicating they were photophores. However, comparing these structures to tubercles seems to indicate that they were small individualised structures, rather than the continuous crescentic photophores seen in Taoniinae. This explains how *Liguriella* was originally placed into the Cranchiinae, as damaged specimens of *Leachia*, for example, have small photophores that can appear like a tubercle or a protrusion from the surface of the eye. This brings into question the initial identity of the specimen that Issel described. Of the two images of the eye provided by Issel to accompany the genus description, one (image 46; Issel, 1908) appears to have an extended portion of tissue, which could simply be a damaged ventral surface of the eyeball. Protrusions such as this were seen

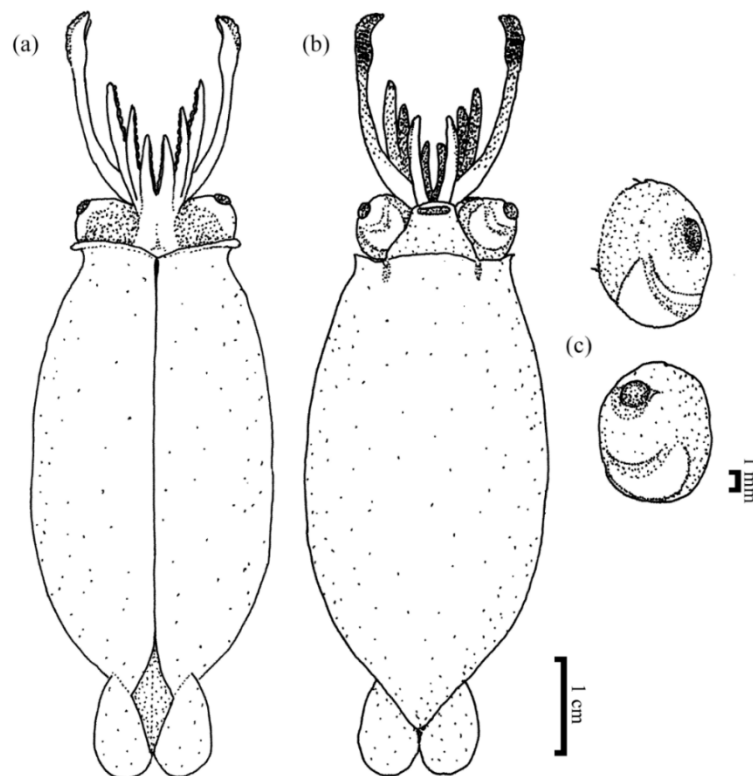


Fig. 7.7—*Liguriella? pardus* (a) dorsal view, (b) ventral view, and (c) right eye with two photophores (NMNH 816465; ML 51 mm).



in *Helicocranchia* (Fig. 6.7a) and *Sandalops* (Fig. 9.5d) as well. The second illustration of the eye (image 47; Issel, 1908), appears to show a series of circular ventral photophores in a curved line. This strongly resembles the photophore patterns of *Leachia pacifica* (named *Zygaenopsis pacifica* in Issel's text). Examination of the two illustrations of the two specimens (images 33 and 45) leads to doubt regarding the identity of that eye (image 47). In image 45, *Liguriella* was shown to have proportionally larger eyeballs with a stout stalk that quickly narrows to a smaller peduncle near the base of the head, much like the eyeball shown in image 46. In contrast, the illustration of *Z. pacifica* shows a specimen with a small eyeball and a long subequal eye stalk connecting to the head. This appears to be very similar to the eyeball shown in image 47. Based on this comparison, it is possible that there was simply an error in the text and that the eyeball showing multiple round photophores is not a species of *Liguriella*, but is actually a species of *Leachia*. This would clarify the confusion regarding the initial description of this genus.

One of the greatest limitations of this research was the lack of material examined for the genus *Liguriella*. This genus is not commonly caught as bycatch (in comparison to genera like *Teuthowenia* or *Leachia*, which were much more common in museum collections), and therefore few have been preserved. Often, *Liguriella* were identified as an unknown species of cranchiid squid or were occasionally misidentified as being a member of the genus *Megalocranchia*. The lack of available material precluded a detailed examination or report of morphometric ratios in this genus, but hopefully the images provided herein will allow further identification of specimens caught so that this genus can be more accurately described in the near future.

Due to the lack of specimens, the description of *Liguriella podophtalma* covers several morphological stages. There was not sufficient information to confidently describe the paralarval stage of this species; however, the illustration included (Fig. 7.6c; ML 9 mm) was believed to be a paralarval stage of this species. A majority of the specimens examined were between 20 and 50 mm ML, and appeared morphologically similar to Fig. 7.6a (ML 34 mm). These juvenile specimens were identified by the presence of an oval- or diamond-shaped rachis at the anterior of the mantle; the gladius was frequently not visible (or only partially visible) through the mantle integument. The conus of all specimens was proportionally shorter than most other Taoniinae (considering members of genera such as *Taonius* and *Galiteuthis* have conus that can extend over half the length of the mantle). When looking at the appendages, *L. podophtalma* has a very distinctive sucker arrangement on the tentacle stalk. Sucker pairs are spaced closely together, and unlike most other cranchiids remain arranged closely until they terminate 25–50% of the way along the tentacle stalk. A rather less technical character that may have some utility was the coloration of adult specimens. Although many specimens were damaged, the arm crowns were often in fairly good shape. The arms themselves were robust at the base and abruptly tapered to narrow tips. While the base of the arms were pink in colour (most likely due to the chromatophore covering on the arms), the distal tips appeared to fade to yellow. Given the transparent nature of these species when alive, it was unusual to find a consistent coloration in several specimens. This coloration is most likely due to preservation using formaldehyde; however, similar coloration was not witnessed in any genus within the Cranchiidae. This gradient should not be considered diagnostic, but any potential

character in this family is worth exploring, and establishing the reason for this pattern would be interesting. It may be more distinctive in fresh caught animals.

The systematic position of *Liguriella pardus* remains a conundrum. Several of this species' characteristics align well with morphological characters of *Liguriella*. For instance, the eye photophores of both species are similar. The inner photophore sits within the curvature of the outer photophore so that it appears that they are nearly connected to each other; however, the photophore of *L. podophtalma* does extend a bit closer to the lens on the oral side of the eyeball. The ventral funnel–mantle fusion points have a single pointed tubercle, a common characteristic of a *Liguriella* specimen of that size. The arms were similar in proportion to other *Liguriella* specimens, and the presence of protective membranes were also seen in other specimens (although to a lesser extent). There are some morphological differences that may indicate its validity as an independent genus; however, without finding additional material, there is no way of fully knowing. Features such as the small eye sinus indentation along the lens are unique to this species within *Liguriella* and among all other known cranchiids. Although *Liguriella* has proportionally long clubs, they are often quite narrow. The clubs of this specimen were expanded into a paddle shape, and it is unusual for *Liguriella* specimens to have pairs of suckers along the entire length of the tentacle stalk, as often sucker pairs begin at some point along the distal half. This information indicates that the taxon could potentially fit into the genus, but that it is most likely a distinct species from *L. podophtalma*. The systematic position of *L. pardus* will need to be clarified with additional material or molecular analysis. The preliminary molecular analysis herein (see Fig. 11.1) shows (what is thought to be) the first sequences for *Liguriella* (BIN BOLD:ADH4163), which have been given a unique BIN distinguishing this taxon from other cranchiids. The Australian *Liguriella* material that was sequenced appears morphologically similar to *L. podophtalma*, but the specimens were quite small, and given the lack of understanding of this genus could prove to be something else.

Ultimately, *Liguriella* is one of several cranchiid genera that are underrepresented in natural history collections and, in many instances, those present lacked identification beyond the family level. The general body type of *Liguriella* looks morphologically similar to juvenile *Teuthowenia* and *Megalocranchia* (both genera appear to attain a larger overall size as mature adults), making identification to the genus level complicated at smaller sizes. Therefore, given the variation seen in the small amount of material examined during this research, it is possible that Voss *et al.* (1992) were correct in hypothesising the existence of several species of *Liguriella*; however, these will unfortunately remain undescribed for the time being.

# *Megalocranchia* Pfeffer, 1884

## Historical Review

The genus *Megalocranchia* was first established by Pfeffer in 1884, for his new species *M. maxima*. This species was described as having a large, sac-like mantle, and being mainly colourless, with ovate fins. Pfeffer (1884) made note of the protective membranes on all arms, and described the tentacles as comparatively short and stout with suckers on the club with 10 pointed teeth. At this early stage of description, the characteristic internal photophores of *Megalocranchia* taxa had not yet been noted; however, the other characters described are consistent with the features used to identify this genus today. Goodrich's (1896) description of '*Taonius*' *abyssicola* (= *Megalocranchia abyssicola*, *fide* Voss, 1960) provided further detail regarding the genus, noting the large eye size, the funnel organ, and describing the arm suckers as having 14 blunt-square teeth; he was also the first to include several illustrations of these features.

In 1900, Pfeffer placed his genus *Megalocranchia* into synonymy with Verrill's (1881) previously described *Desmoteuthis* (= *Taonius*, *fide* Berry, 1912), for which he described a new north-Atlantic species, *D. hyperborea* (= *Teuthowenia megalops*, *fide* Voss, 1985). This species was characterised by having long ovular fins, large eyes, arm sucker rings with many small teeth around the entire margin, and tentacle clubs with enlarged manus suckers. Pfeffer (1900) distinguished *Desmoteuthis* from (what at that time he considered a sub-genus) *Megalocranchia*, due to the fins of *Desmoteuthis* being relatively shorter and the suckers on the arms having a definable number of blunt teeth. Pfeffer (1912) later re-instated *Megalocranchia* after further investigation, claiming the differences previously distinguishing *Megalocranchia* and *Desmoteuthis* to only be ontogenetic in nature. Thus, Pfeffer re-described *Megalocranchia*, this time attributing four species to it: his previously described *M. maxima* and *M. abyssicola*, as well as '*Desmoteuthis*' *pellucida* Chun, 1910 (= *Teuthowenia pellucida*, *fide* Voss, 1985) and *Helicocranchia fisheri* Berry, 1909; however, for the latter it seems that Pfeffer never examined Berry's specimen, and was grouping this species in the genus because the description sounded similar (Pfeffer, 1912). In the same year, Berry (1912) published a revision on cephalopod nomenclature in which he agreed that *H. fisheri* was indeed a species of *Megalocranchia* and placed *Desmoteuthis* into synonymy with *Taonius* Steenstrup, 1861.

The internal photophores, considered to be a derived characteristic of the genus *Megalocranchia* (Voss, 1988), were first mentioned by Chun (1906), who stated that the ink sac was positioned in between two luminous organs. However, according to Chun, this unique feature characterised members of his novel genus *Corynomma*, in which he placed his species *C. speculator* (= *M. abyssicola*, *fide* Voss, 1980). The internal photophores were later described in further detail as being a "prominent organ" that was symmetrical, with the ink sac bisecting the midline, and four spherical luminous organs deeply embedded into the tissue (Joubin, 1924). The discrepancy between these descriptions was most likely due to Chun's *C. speculator* being a paralarval specimen, in which two lobes can appear joined by connective tissue.

A fifth species was added to the genus *Megalocranchia* by Berry (1916) in his description of '*M.*' *pardus* (= *Liguriella pardus*, *fide* Nesis, 1987) from the Kermadec

Islands. In this description he noted the fins being semi-circular in shape, the eyes being on stout stalks, and the suckers on the arms being minutely dentate but with 'teeth' more precisely resembling crenulations in the sucker ring. Berry discussed the physical similarities between *M. pardus* and the existing four species, commenting that this new species had particularly strong physical similarities to *M. cf. fisheri*, but noting that this was the only other member of the genus he had examined. Dell (1959) later proposed another species from New Zealand waters, *M. richardsoni* (= *Teuthowenia pellucida*, *fide* Voss, 1985), which was described as having a wider body and have significantly larger eyes than *M. pardus*, even at similar sizes.

In the Atlantic Ocean, Voss (1960) described *Megalocranchia papillata*, a small cranchiid with subequal arms, a large funnel, and lacking a visceral photophore. Although conceding that the specimen was closely related to the two named species of *Helicocranchia*, Voss decided that, given the general confusion regarding cranchiid nomenclature, *Helicocranchia* was a junior synonym of *Megalocranchia*, but should be retained as a sub-genus. Voss also placed *M. abyssicola* (Joubin, 1924) into a new genus, *Carynoteuthis* (= *Megalocranchia*, *fide* Voss, 1980), as Voss felt that Joubin's *M. abyssicola* was significantly different from *M. abyssicola* Goodrich (1896); however, this decision was made with the concession that Goodrich's original type specimen was too badly damaged to examine (Voss, 1960). Taxa from the genus *Carynoteuthis* were described as being morphologically similar to *M. abyssicola*, but with the unusual presence of an internal photophore, which had not been part of Goodrich's original description.

Nesis (1974) undertook a general revision of four cranchiid genera that had historically suffered from imprecise description, aiming to avoid the 'catch-all' genus that previous authors had attempted to create. Nesis (1974) considered *Megalocranchia* and *Corynomma* to be synonymous, but considered the latter to be the valid genus name, as the holotype of the *Megalocranchia* type species (*M. maxima*) had not been preserved after description. In the genus *Corynomma*, Nesis placed two species: *C. oceanica* (from the Atlantic Ocean) and *C. abyssicola* (from the Indian and Pacific Ocean). He delineated these species by the fin shape, and the number of teeth on the arm and tentacular club suckers (Nesis, 1974). Nesis (1987) later reinstated *Megalocranchia* as the valid genus name and moved *Corynomma* into synonymy with it. In addition to the two previously mentioned species, Nesis added a third undescribed species (*Megalocranchia* sp. Nesis, 1987) from Japanese waters, but commented that without further data, there would be no way to prove its validity. Nesis also considered *M. maxima* a junior synonym of *M. abyssicola*, despite the former being the originally designated species. No explanation was provided for this systematic switch.

In Voss' (1980) familial revision of the Cranchiidae she noted that *Egea* and *Megalocranchia* are strongly allied. She grouped these two genera with *Teuthowenia* on the basis of elongated terminal lateral fins and noted that these three genera also belonged to a wider grouping of taoniin taxa with brachial end organs on the arms of mature females (Voss, 1988). Voss (1980) also illustrated a mature adult specimen of an unidentified species of *Megalocranchia*. She observed that the internal photophores begin to develop between 23 and 30 mm ML in this genus. Voss *et al.* (1992) mentioned that there was ongoing research regarding the genus and suggested that there may be about six species of *Megalocranchia* globally, and that most could only be

identified when mature; however, further information on these taxa was never published.

## Systematics

*Megalocranchia* Pfeffer, 1884 (Table 8)

*Megalocranchia* Pfeffer, 1884: 24; Imber, 1978: 459; Voss, 1980: 398–400, fig. 12; Reid, 2016: 96–97.

*Corynomma* Chun, 1906: 85.

*Carynoteuthis* Voss, 1960: 434 – 438, fig. 75.

**Diagnosis:** Mantle conical; widest point of mantle at anterior 1/3. Anterior rachis window often diamond or oval in shape, usually one or two mm from anterior mantle margin; ventral cartilaginous fusion window often wing-shaped (Fig. 8.4). Fins lanceolate, oval in smaller specimens. Eyes large and bulbous, each with two photophores, inner photophore often with several curves (non-linear) (Fig. 8.6). Four internal photophores that develop on the digestive gland (usually first appearing at 20–30 mm ML; Fig. 8.7a). Arms robust, with large trabeculate membrane along entire length of arm. Suckers increase in size mid-arm, largest suckers on Arms III; tentacle clubs often proportionally long, manus suckers not greatly enlarged, club suckers with pointed teeth.

Table 8—Distinguishing features of *Megalocranchia* taxa. \*, this study.

	Fin length	Arm sucker ring teeth (number, shape):	Manus sucker ring dentition
<i>M. abyssicola</i>	FL 50–60% ML	8–15, blunt	4–8 pointed teeth
<i>M. cf. fisheri</i>	FL ~40% ML	15–30, blunt	7–9 pointed teeth
<i>M. maxima</i>	FL 45–49–57% ML	30–40, rounded/angular	9–17 pointed teeth
<i>M. sp. NZ*</i>	FL 16–29–37% ML	12–18, blunt	5–10 pointed teeth

***Megalocranchia abyssicola* (Goodrich, 1896)** (Figs 8.2–8.3, Table B15)

*Taonius abyssicola* Goodrich, 1896: 17–18; Pl. V, fig. 72–80.

*Corynomma speculator* Chun, 1906: 85.

*Megalocranchia abyssicola* (Goodrich, 1896): Voss, 1960: 437; Nesis, 1987: 275.

**Diagnosis:** Fins (and conus) proportionally long (50–60% ML), arms proportionally short (mean length 16–27% ML) with very wide oral membranes on all arms; arm suckers with 8–15 blunt teeth on distal margin. Papillae present on aboral surface of arm suckers in larger individuals. Largest manus suckers with 4–8 pointed teeth. No secondary sexual modification observed.

**Type material:** (not examined) *Taonius abyssicola* **ZSI Holotype M309/1** [*fide* Ramakrishna and Mitra (2004:93)]; **ZSI Type M310/1** [*fide* Tripathy (2013:36)]. Type Locality: Laccadive Sea, Indian Ocean.

**Material examined** (3 specimens): **NSMT-Mo:67345**, ML 263 mm, sex indet., 35.65°N, 171.05°E, 530 m, RV *Kouei-Maru*; **NSMT-Mo:67203**, ML 189 mm, sex indet., 34.71°N, 172.57°E, 50 m, JAMARC, 15/05/1980; **NMNH 730789**, ML 92 mm, sex indet., 21.25°N 158.25°W, North Pacific, Hawaiian Islands, Oahu, 0–140 m, 16/06/1971.

**Non-localised material examined** (1 specimen): **MU 332928**, ML 57 mm, sex indet.

### Description:

(ML 57–263 mm; Figs 8.2, 8.3)—Mantle conical, tapering gradually to posterior end; MW ~38% ML in specimens <100 mm ML, MW <20% ML in larger specimens. Fins lanceolate, slightly rounded in smaller specimens; FL 25–31–35% ML in specimens under 100 mm, FL 50–60% ML in larger individuals. Fin width 20–25% ML in individuals ML <100 mm, FW <20% ML in larger individuals. Head length 9–10–13% ML, HW 18–25–43% ML, HW exceeding MW in mature specimens; eyes bulbous, ED 10–13–20% ML; two photophores, outer photophore large crescent, inner photophore with several curves. Funnel with medium base (37–44–52% MW), small aperture (27–33–36% FB).

Arms robust, with wide trabeculate membranes (noticeably wider than arm diameter) along oral surface, Arms IV also with wide aboral keel. Arm formula III>IV>II>I (lengths of III and IV decrease proportionally with age); Arm I 15–16–18% ML, Arm II 18–22–25% ML, Arm III 21–27–32% ML, Arm IV 19–24–28% ML. Arms with up to 84 suckers (Arms IV); suckers with 8–15 blunt teeth; medial posterior sucker surface with apical papilla in larger individuals (Fig. 8.3). Tentacle length 25–36–45% ML; with ~30 suckers on stalk, widely spaced and alternating proximally, becoming more densely set in pairs distally. Clubs 9–12–14% ML (24–32–37% TnL), with 100–120 suckers; sucker margin wide, flat, with 4–8 pointed teeth.

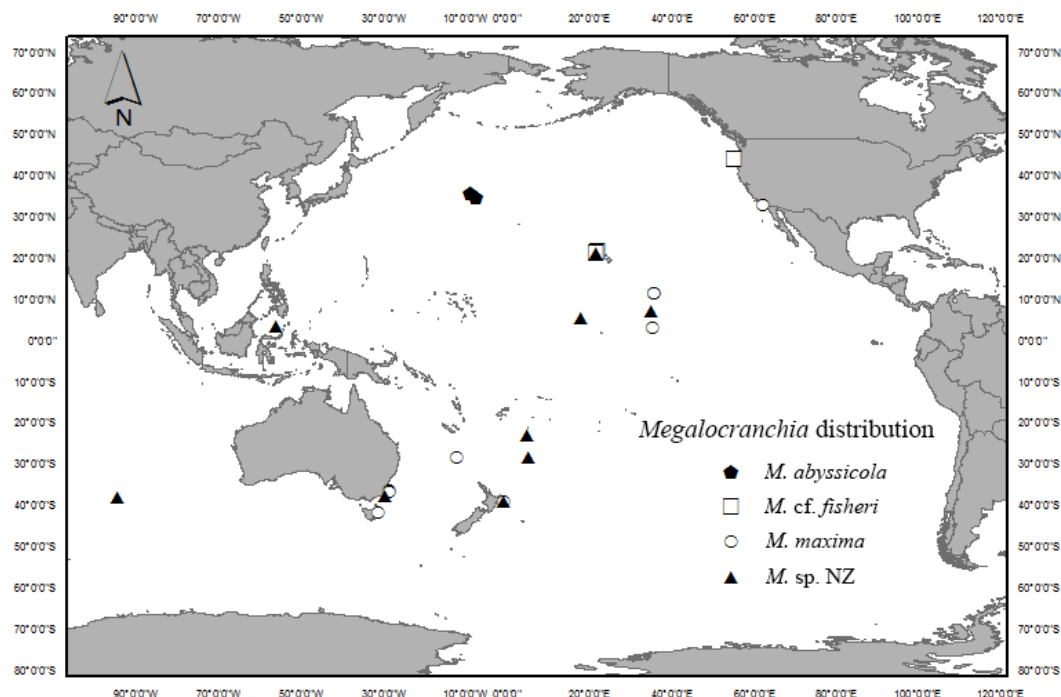


Fig. 8.1— Distribution of examined *Megalocranchia* material in the Pacific Ocean.

**Known distribution:** From north western Pacific Ocean, in Japanese waters (35.65°N), to Hawaiian Islands (Fig. 8.1). Believed to be an Indo-Pacific species (Nesis, 1987). Material examined found from 0–530 m; elsewhere reported to 1650 m (*vide* Goodrich, 1896).

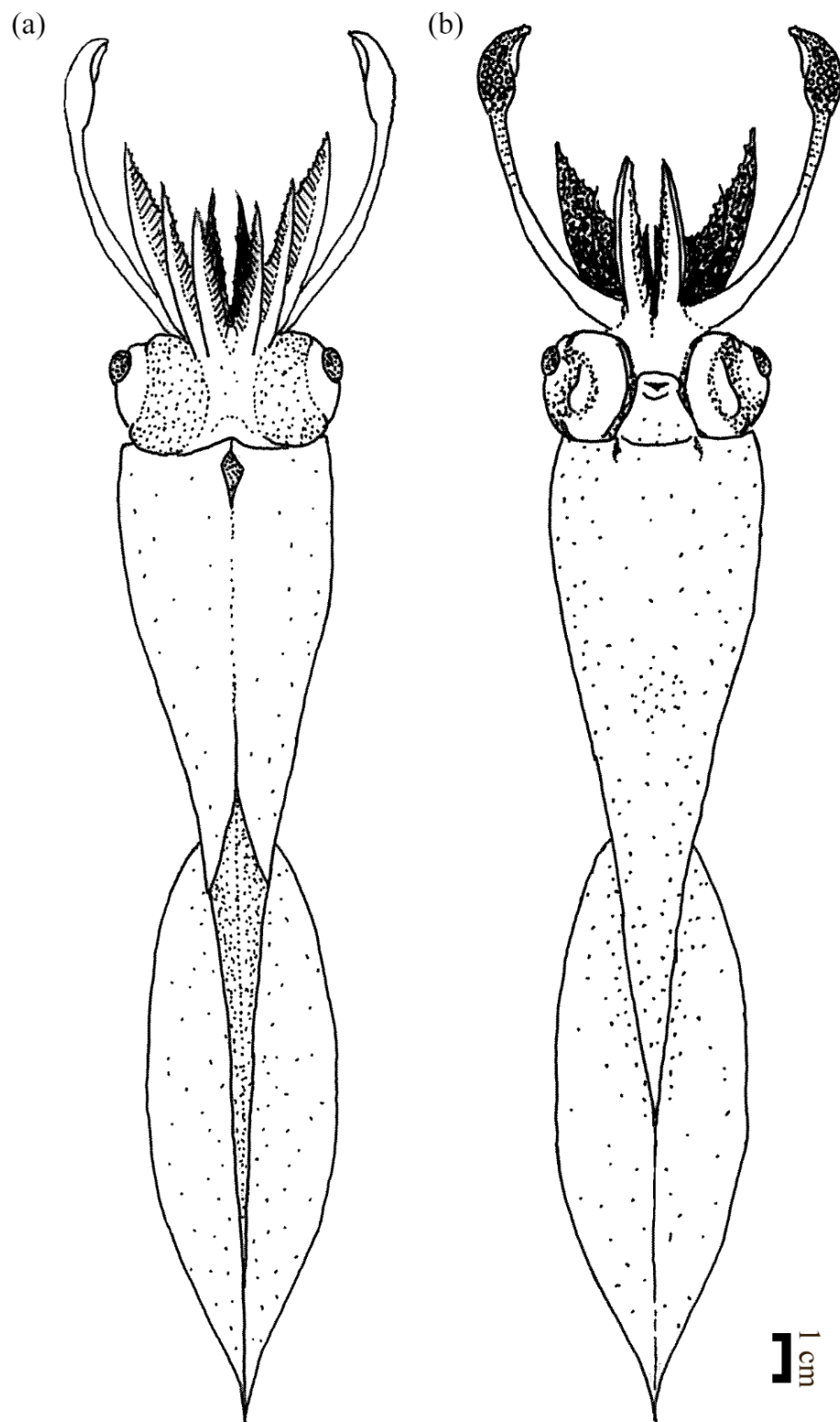


Fig. 8.2—Adult *M. abyssicola* (a) dorsal and (b) ventral view (NMST Mo:067345; ML 263 mm).

**Remarks:** *Megalocranchia abyssicola* is most easily recognised by the large trabeculate membrane flanking the suckers on the oral faces of all arm pairs. When compared with other *Megalocranchia* species, this membrane is noticeably broader; often the membrane is wider than the arm thickness. Although the relative size of the fins increases with ontogeny in all *Megalocranchia* species, the conus and fin length of this taxon appear to be proportionally longer in adult individuals (up to 60% ML) than in those of other taxa described in the genus (FL 16–40% ML, except in *M. maxima* where FL 45–57% ML). The apical papillae along the outer sucker surfaces are variably present; however, in the two largest individuals they are very distinctive. This character has not been reported in any other *Megalocranchia* species.

***Megalocranchia cf. fisheri* (Berry, 1909)** (Figs 8.4–8.8, Table B16)

*Helicocranchia fisheri* Berry, 1909: 417–418.

*Megalocranchia cf. fisheri* (Berry, 1909): Pfeffer, 1912: 718–719; Berry, 1914: 348–350; Pl. LIII 5–6, Pl. LV fig. 2.

**Diagnosis:** Fins proportionally short (~40 % ML). Inner eye photophore with slight curved angles. Arm suckers with 15–30 blunt teeth; largest manus suckers with 7–9 pointed teeth. Female secondary sexual modifications (brachial organs) not observed.

**Type material:** (not examined) *Helicocranchia cf. fisheri* **NMNH Holotype 214316** [*fide* Sweeney *et al.* (1988:13)]. Type locality: Pailolo Channel, Hawaiian Islands.

**Material examined (12 specimens):** **SBMNH 462283**, ML 20 mm, sex indet., 44.00°N 125.00°W, USA, Oregon, Lane County, 0–260 m, RV *Th. Wash*, OSU MT1879, 24/01/1980; **SBMNH 462261**, ML 24 mm, sex indet., 44.00°N 125.00°W, USA;



Fig. 8.3—Apical papilla on suckers of adult *M. abyssicola*; Arm III in foreground (NSMT Mo:67345; ML 263 mm).



Oregon, Lane County, 1000 mi N-NE of Oahu; 0–230 m, 26/01/1980; **SBMNH 464761**, ML 51 mm, sex indet., 21.50°N, 158.00°W, USA, Hawaii, Hawaiian Islands, 08/09/1970; **SBMNH 460755**, ML 60 mm, sex indet., 21.43°N 157.97°W, USA, Hawaii, Oahu, 08/07/1983; **SBMNH 460742**, ML 154 mm, sex indet., 21.43°N, 157.97°W, USA, Hawaii, Oahu, 1983; **SBMNH 464905**, ML 19 mm, sex indet., 21.38°N 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 01/01/1980; **SBMNH 460924**, ML 26 mm, sex indet., 21.38°N 158.30°W, USA, Hawaii, Oahu, Leeward coast, 01/01/1980; **SBMNH 460962**, ML 28 mm, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 1500–2500 m, 1980; **SBMNH 460904**, ML 29 mm, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 1500–2500 m, FIDO XVI tow 17, 19/03/1980; **SBMNH 460969**, ML 43 mm, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 1500–2500 m, 1980; **SBMNH 460892**, ML 54 mm, sex indet., 21.38°N 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 1500–2500 m, 1980; **NMNH 815097**, ML 124 mm, ♀, 21.33°N 158.33°W, North Pacific Ocean, Hawaii, 200 m, MWT, Stn. 70-9-18, 21/09/1970.

### Description:

**Adult** (>100 mm ML; Figs 8.5–8.7) Mantle tapers gradually to posterior end; MW 25% ML; widest point at anterior 1/3 of specimen. Fin length ~40% ML; FW 18%. Head length 12% ML, HW 27% ML; ED 20% ML; two curved photophores, outer photophore long, terminating just dorsally to lens (Fig. 8.6). Funnel base ~45% MW, narrowing towards aperture (40% FB). Ventral cartilaginous window ‘wing-shaped’ (Fig. 8.4).

Arms robust, with trabeculate membranes (width less than arm diameter) along length; Arms IV with thick aboral keel. Arm formula III>II≥IV>I: Arm I 22% ML, Arm II 26% ML, Arm III 32% ML, Arm IV 25% ML. Arms with up to 55–65 suckers (highest counts on Arm IV); sucker size decreases from base toward distal end of arm, enlarge medially on Arm III, then decreases again toward distal arm tip; sucker rings with 15–30 blunt teeth. Tentacle length ~45% ML; stalk with ~34 suckers, widely spaced and alternating proximally, pairs set more densely distally. Clubs (Fig. 8.7b) ~12% ML (26% TnL), with over 100 suckers; suckers with wide flat surface and 7–9 large pointed teeth (Fig. 8.7c).



Fig. 8.4—‘Wing shaped’ right funnel–mantle fusion window of *Megalocranchia* cf. *fisheri*.

**Sub-adult** (internal photophores present; ML 40–60[+?] mm)—Mantle width 35–44–60% ML. Fins rounded or oval, 16–20–27% ML; FW 18% ML. Head length 7–11–17% ML, eyes ovoid, on short, stout stalks, ED 7–10–13% ML, HW 22–27–32% ML. Funnel basally 15–29–40% MW, aperture variable, 25–45–74% FB.

Arms robust, with narrow trabeculate membrane down the entire lengths of Arms I–III. Arm formula III>IV>II>I: Arm I 10–13–18% ML, Arm II 14–16–20% ML, Arm III 22–24–30% ML, Arm IV 17–20–23% ML. Arms with up to 20–50 suckers (Arm IV with highest count); sucker rings with 15–30 blunt rounded teeth. Tentacle length 37–48–56% ML; stalk with 24–34 suckers, widely spaced and alternating proximally, becoming more densely set in pairs distally. Clubs 16–17–18% ML (30–50% TnL), with 80–100 suckers (Fig. 8.7b).

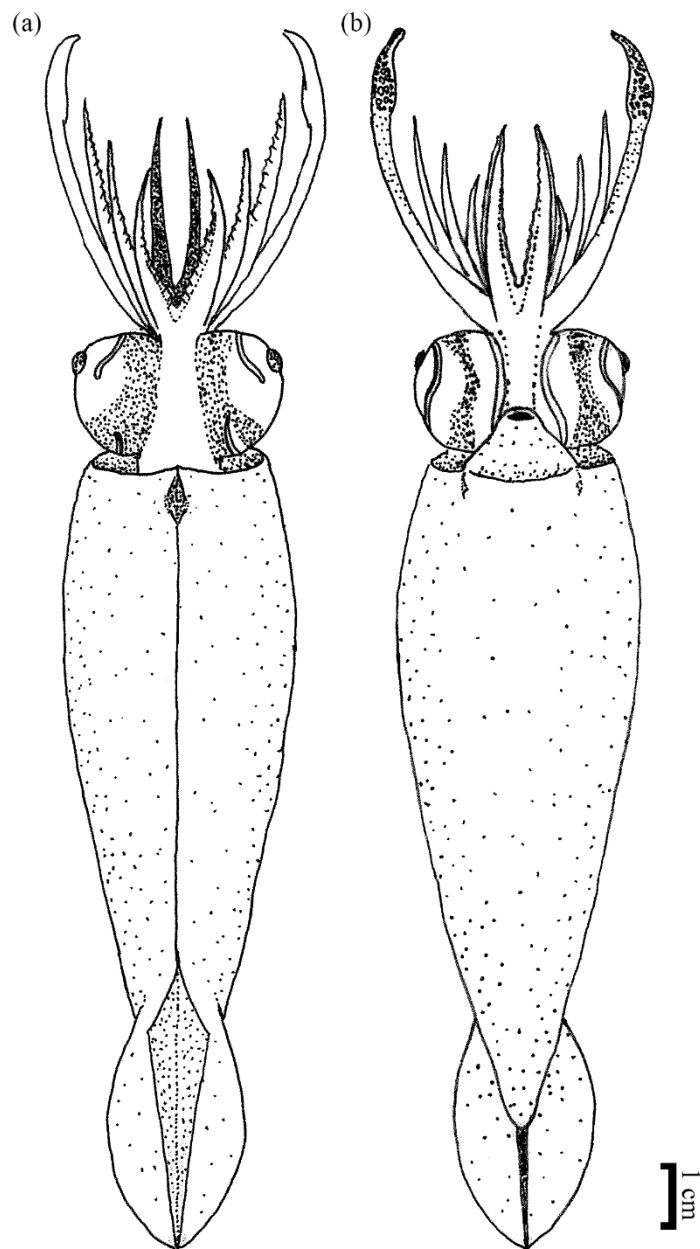


Fig. 8.5—Female *Megalocranchia* cf. *fisheri* in (a) dorsal and (b) ventral view (NMNH 815097; ML 124 mm).

**Juvenile** (internal photophore undeveloped; ML 20–40 mm; Fig. 8.8)—Mantle conical; MW 27–37–46% ML. Fins rounded, each nearly circular, 11–14–17% ML; FW 17–24–32%. Head length 6–10–17% ML, eyes ovoid with ventral protuberance, on stout stalks, ED 4–7–10% ML; HW 21–27–30% ML. Funnel base 34–43% MW, aperture varying, 30–55–90% FB.

Arms short, lacking membranes, arm formula III>IV>II>I: Arm I 4–7–10% ML, Arm II 6–10–15% ML, Arm III 7–15–26% ML, Arm IV 8–13–22% ML. Arms with up to 12–34 suckers (Arm IV with greatest count). Tentacle length 23–73–140% ML; with ~40 suckers on stalk. Clubs 11–16–23% ML (20–58% TnL), with 60–110 suckers.

**Known distribution:** Primarily known from Hawaiian Islands (around 21°N); however, distribution appears to extend further north, as one specimen was found off the coast of Oregon (Fig. 8.1). Known depth range 0–2500 m for material examined, previously recorded from 200–800 m depth during the day and around 200 m at night (Young, 1978).

**Remarks:** A single adult specimen was available for examination; unfortunately, damage to the eyes precluded detailed examination of the ventral eye photophore pattern. *Megalocranchia* cf. *fisheri* was originally described as lacking teeth on the arm sucker ring margins; however, in the specimens examined herein, teeth were visible on the sucker rings of specimens ML 40 mm and larger. The specimen originally examined by Berry (1909) was 46.5 mm ML, by which size the dentition (if present) should have been visible under magnification. Despite this difference, the material described conforms in other respects with previous descriptions of *M.* cf. *fisheri*. Until additional adult specimens are examined, the status of this species is uncertain; however, *M.* cf. *fisheri* specimens sequenced from the Hawaiian Islands do form a distinct BIN (BOLD:ADH7420).

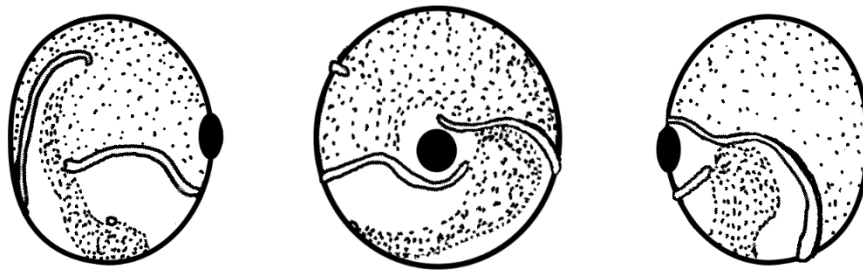


Fig. 8.6—Right eye schematic for *Megalocranchia* cf. *fisheri* (NMNH 815097; ML 124 mm).

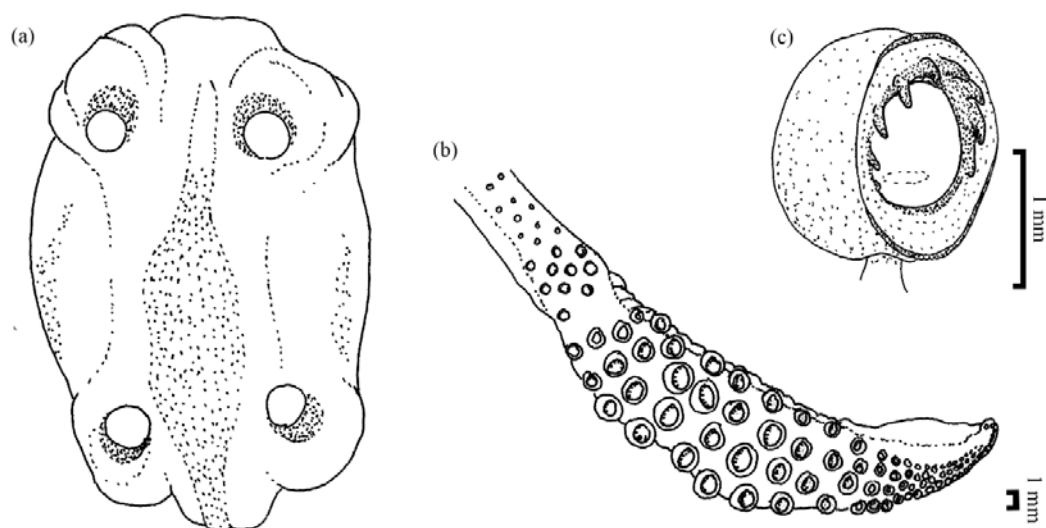


Fig. 8.7—*Megalocranchia* cf. *fisheri* (a) internal photophore (anterior end at top of image), (b) left tentacle club with (c) enlarged manus sucker (SBMNH 460742; ML 154 mm).

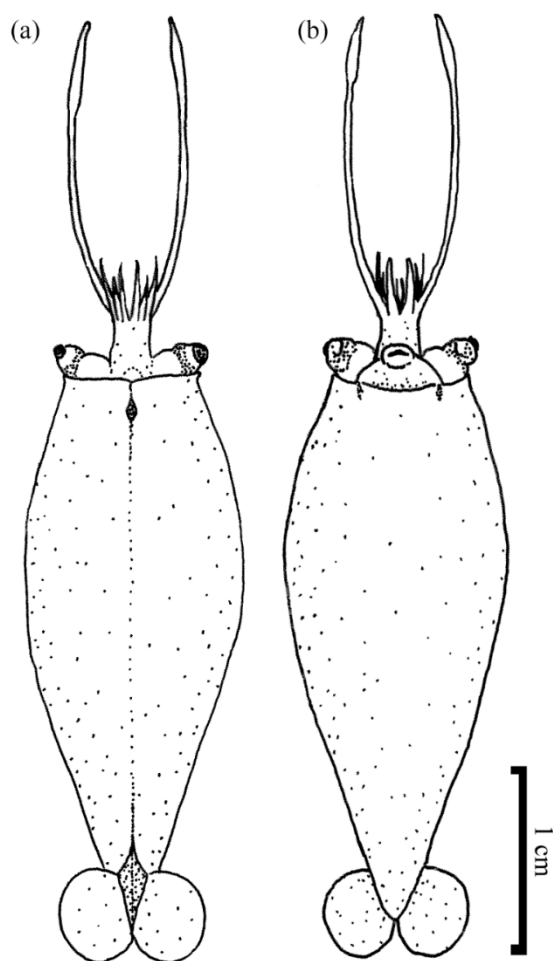


Fig. 8.8—Juvenile *M. cf. fisheri* (a) dorsal view and (b) ventral view (SBMNH 460904; ML 29 mm).

***Megalocranchia maxima* Pfeffer, 1884** (Fig. 8.9, Table B17)

*Megalocranchia maxima* Pfeffer, 1884: 24–25, fig. 32a; Pfeffer, 1912: 712–715, Pl. 48, fig. 1–4; Imber, 1978: 459–461.

**Diagnosis:** Fins 45–49–57% ML. Largest arm suckers with 30–40 angular teeth set around entire sucker ring margin, club manus suckers with (usually) 9+ pointed teeth (largest teeth along distal half); brachial end organs on all arms of mature females.

**Type material:** (not examined) *Megalocranchia maxima* **ZMH Holotype not extant** [fide Guerrero-Kommritz (2001:174)]. Type locality: Cape of Good Hope.

**Material examined (14 specimens):** **SBMNH 464902**, ML 87 mm, 33.00°N, 118.00°W, USA, California, Childress station 05-11; **NMNH 815197**, ML 180 mm, sex indet., 21.20°N 158.20°W, North Pacific Ocean; USA; Hawaii, 200 m, Stn. 70-9-18, 21/09/1970; **NMNH 815100**, ML 118 mm, sex indet., 11.53°N 144.48°W, North Pacific Ocean, 50 m, RV *Townsend Cromwell*, Stn. 46-17, 18/10/1969; **NMNH 815199**, ML 100 mm, sex indet., 11.53°N 144.49°W, North Pacific Ocean, 100 m, RV *Townsend Cromwell*, Stn. 44-18, 02/17/1969; **NMNH 815194**, ML 94, 123 mm, ♀, 11.47°N 144.46°W, North Pacific Ocean, 50 m, RV *Townsend Cromwell*, 31/03/1970; **NMNH 815194**, ML 94 mm, sex indet., 11.47°N 144.46°W, North Pacific Ocean, 50 m, RV *Townsend Cromwell*, Stn. 48-11, 31/03/1970; **NMNH 815193**, ML 128 mm, sex indet., 3.17°N, 144.58°W, North Pacific Ocean, 50 m, RV *Townsend Cromwell*, Stn. 48-42, 13/04/1970; **NMNZ M.172973**, ML 130 mm, sex indet., 28.49°S, 167.79°E, Norfolk Ridge, N of Norfolk Island, 1056–1116 m, RV *Tangaroa*, Stn. 2003033, 16/05/2003; **NMV F163958**, ML 128 mm, sex indet., 36.48°S, 151.40°E–36.50°S, 151.43°E, New South Wales, 95 km east of Narooma, 0–15 m, CSIRO RV *Courageous*, 01/12/1978; **NMV F71717**, ML 300, 420 mm, ♀, 36.55°S, 151.45°E, 40–60 m, RV *Courageous*, 09/11/1978; **NMNZ M.067228**, ML 410 mm, ♀, 39.13°S, 178.95°E, 18/01/1980; **NMV F163948**, ML 666 mm, ♂, 41.77°S, 148.69°E–41.75°S, 148.69°E, Tasmania, E of Bicheno, 1110–1115 m, RV *Soela*, 20/04/1989.

**Description:**

**Adult** (ML 300–666 mm)—Mantle elongate, tapering sharply to posterior end; MW 13–17–20% ML, fins lanceolate, slightly rounded in smaller specimens; FL 45–49–57% ML; FW 17–21–24 ML. Head length 10–14–20% ML, eyes round, ED 8–10–12% ML (ratio decreasing with size), HW 10–27–43% ML (75–120% MW). Funnel base (40–57–73% MW), aperture small (32–44–47% FB).

Arms robust, narrow trabeculate membranes along arm length, membrane barely extending past largest suckers; arm formula III>II>IV>I: Arm I 27–31–36% ML, Arm II 29–34–41% ML, Arm III 33–35–38% ML, Arm IV 28–32–35% ML. Arms with 48–96 suckers (Arm pair IV); sucker rings with 30–40 low teeth around entire margin, teeth variably rounded or angular (Fig. 8.9a). Mature females with secondary modifications on all arms; brachial organ proportionally small (~4% arm length), darkly pigmented. Tentacle length 49–53–60% ML; tentacles with 30–36 suckers on stalk, widely spaced and alternating proximally, becoming more densely set in pairs distally. Clubs 11–13–14% ML (23–24–26% TnL) with 100–120 suckers; carpus with ~12 suckers, manus with 60–80, dactylus with 18–28; manus suckers with 9–17 pointed teeth distally, small stubs on proximal margin (Fig. 8.9b).

**Juvenile** (ML 94–200 mm)—Mantle conical, MW 31–38–45% ML. Fins lanceolate, slightly rounded in smaller specimens; FL 29–31–34% ML; FW 20–24–27 ML. Head length 10–17–22% ML, eyes spherical, ED 16–18–22% ML (ratio decreasing with size), HW 25–34–40% ML (65–120% MW). Funnel base (38–49–70% MW), aperture small (24–31–35% FB).

Arms robust, formula III>IV>II>I: Arm I 24–28–40% ML, Arm II 31–37–47% ML, Arm III 37–44–50% ML, Arm IV 29–36–46% ML. Arms with 48–70 suckers (Arm pair IV); modifications developing on Arms III only. Tentacle length 57–73–90% ML; tentacles with 30–48 suckers on stalk, widely spaced and alternating proximally, becoming more densely set in pairs distally. Clubs 17–20–23% ML (24–27–30% TnL) with 97–125 suckers.

**Known distribution:** From the north eastern sub-tropical Pacific (33.00°N) to south western sub-tropical Pacific (42.00°S); off Tasmania.

**Remarks:** The original illustration of this species by Pfeffer (1884) lacked specific detail, and it was challenging to interpret key features such as sucker dentition or eye photophore arrangement. The description above was based on a limited selection of material. The key characters used to distinguish this taxon are the presence of 36–40 rounded or angular teeth around most of the arm sucker margin. This character appears to be shared with *M. oceanica* Voss (1960), from the Atlantic Ocean. Large mature individuals (from the Southern Hemisphere) had brachial end organs on all arms and smaller individuals (from the Northern Hemisphere) only had these secondary sexual modifications on Arms III. Future examination of more material of different sizes and stages of maturity is needed to determine whether these differences are related to maturity, geographic variation, or intraspecific differences.

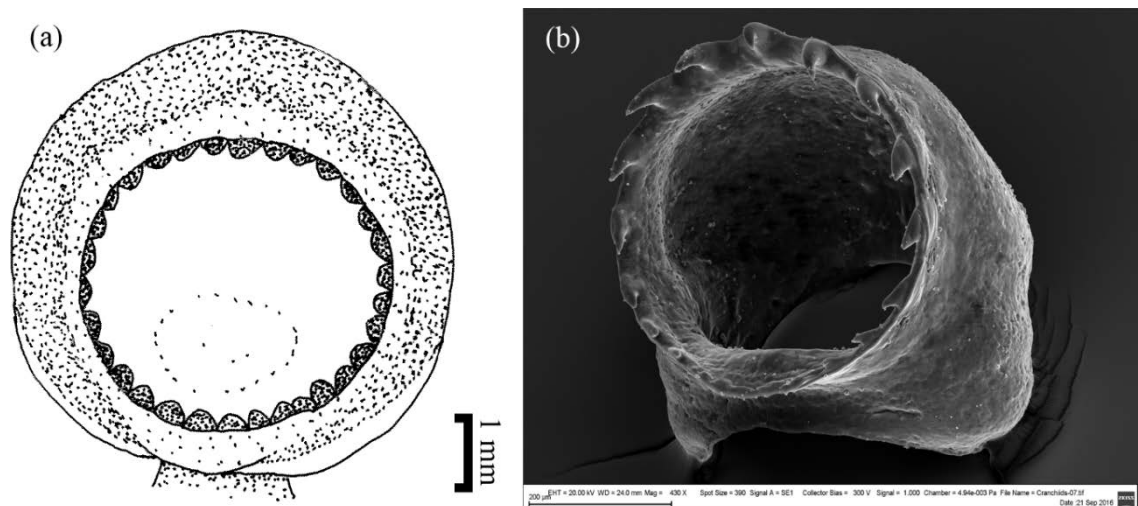


Fig. 8.9—(a) Largest Arm III sucker (NMNZ M.067228; ML 410 mm), (b) largest manus sucker (SBMNH 464902; ML 87 mm) from *Megalocranchia maxima*.

***Megalocranchia* sp. NZ** (Figs 8.10, 8.11, Table B18)

*Megalocranchia maxima* (not Pfeffer, 1884) Imber, 1978: 459–461.

**Diagnosis:** Fins proportionally short (16–29–37% ML). Outer eye photophore terminates on dorsal surface of eye, often just above lens. Arm suckers with 12–18 blunt teeth on distal half of ring margin; club manus suckers with up to 10 pointed teeth. Mature females with secondary sexual modification on Arms III only.

**Material examined:** **SBMNH 460939**, ML 71 mm, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, Leeward Coast, 01/01/1980; **NMNH 815569**, ML 83 mm, sex indet., 5.48°N, 162.07°W, North Pacific Ocean, Kiribati, Line Islands, 70–110 m, Stn. 89-34, 22/02/1966; **MU**, ML 61 mm, sex indet., 3.33°N, 123.83°E, 2000 m, MWT, Stn. 3739 IX, 02/07/1929; **NMNZ M.074320**, ML 82 mm, 22.83°S, 175.33°W, New Zealand, 377 m over 4000 m, RV *James Cook*, MWT, Stn. J17/60/76, 12/12/1976; **NMNZ M.074305**, ML 225 mm, ♀, 28.30°S, 174.93°W, New Zealand, Kermadec Islands, NE of Raoul Island, 94 m, RV *James Cook*, MWT, Stn. J17/71/76, 14/12/1976; **NMV F51377**, ML 131 mm, sex female, 37.55°S, 150.37°E, 50–600 m, CSIRO 501/82 Stn. 21, 20/01/1982; **NIWA 95951**, ML 61, sex indet., 37.93°S, 85.20°E, 30 m, Stn. TAN9101/17, 04/07/1991; **NMNZ M.286201**, ML 60 mm, 39.16°S, 179.17°E, New Zealand, off Mahia Peninsula, 150 m over 1700 m, RV *James Cook*, MWT, Stn. J09/65/81, 04/06/1981.

**Description:**

(ML 60–225 mm; Figs 8.10, 8.11)—Mantle conical, MW 25–33–40% ML (ML 60–120 mm), MW ~20% ML (at ML 225 mm). Fins lanceolate, slightly rounded in smaller specimens; FL 16–29–37% ML (ML 60–120) FL ~45% ML (at ML 225 mm); FW 20–22–27 ML. Head length 10–16–22% ML, eyes spherical, ED 13–16–22% ML, HW 23–26–30% ML (67–100% MW). Funnel base 38–50% MW, aperture small (33–38–47% FB).

Arms robust; width of each arm membrane roughly equal to arm diameter; arm formula III>IV>II>I: Arm I 10–19–28% ML, Arm II 15–23–35% ML, Arm III 25–33–43% ML, Arm IV 20–28–40% ML. Arms with 40–80 suckers (Arms IV with highest count); arm suckers with 12–18 blunt teeth on distal half of sucker ring, distal suckers with 4–7 angular teeth (Fig. 8.11a,b); female modifications developing on Arms III only by ML 180 mm. Tentacle length 38–47–77% ML; tentacles with 30–48 suckers on stalk, widely spaced and alternating proximally, becoming more densely set in pairs distally. Clubs 10–13–20% ML (24–29–34% TnL) with 80–110 suckers; largest manus suckers with 5–10 pointed teeth (Fig. 8.11c).

**Known distribution:** New Zealand and Australian waters, extending into North Pacific (Hawaiian Islands). Known depth range from 50–600 meters.

**Remarks:** This species appears morphologically similar to *M. maxima*; however, the dentition of both the arm and manus suckers differs slightly. In *M. sp. NZ*, the teeth are blunt, and only found on the distal half of the sucker ring, while in *M. maxima* sucker ring teeth are angular (or rounded) and are distributed around the entire ring margin. On the largest manus suckers *M. sp. NZ* has 10 or fewer pointed teeth while *M. maxima* has 10 or more pointed teeth.

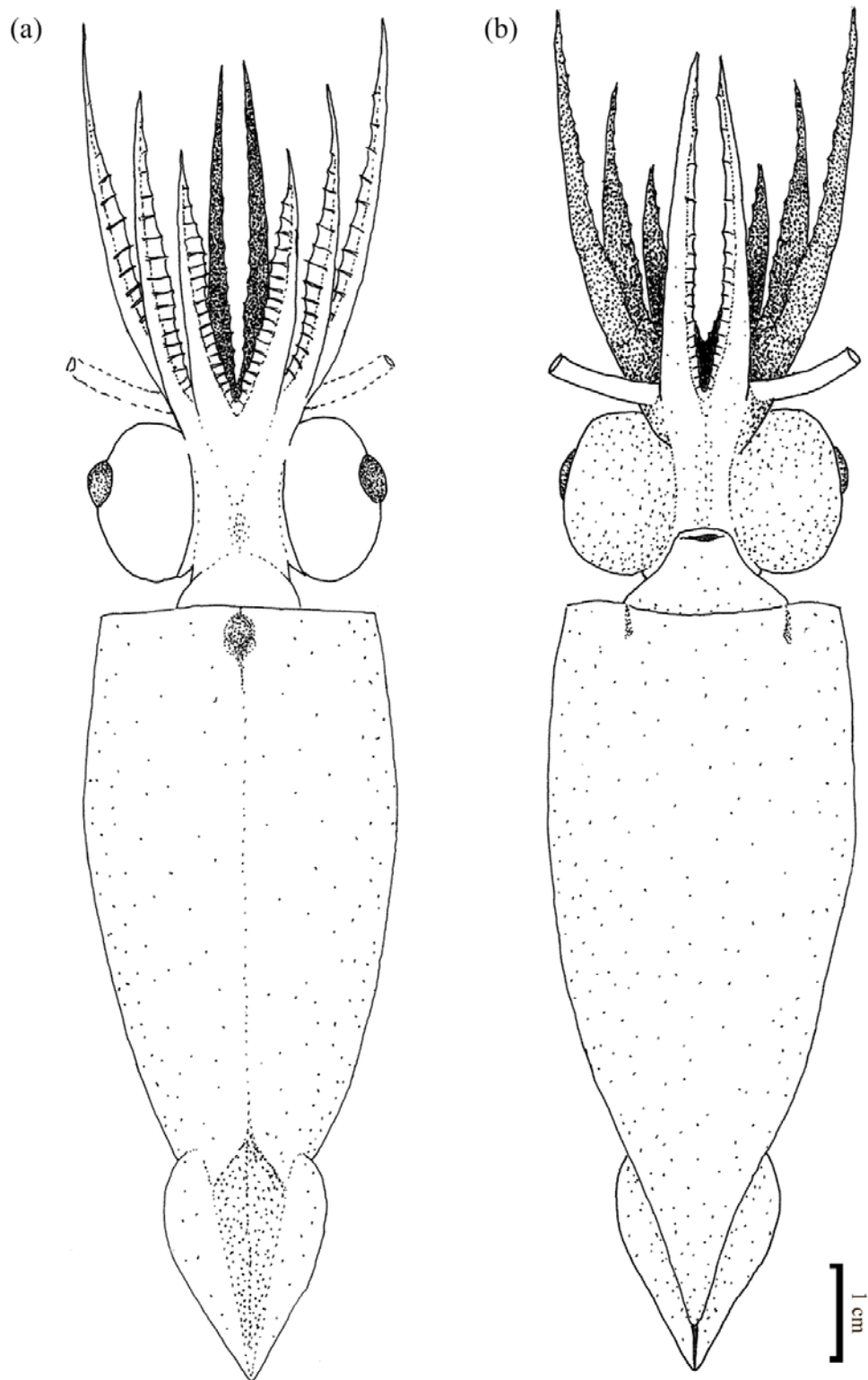


Fig. 8.10—Full body of *Megalocranchia* sp. NZ (a) dorsal and (b) ventral view (NMNZ M.074320; ML 82 mm).



## Discussion

Of the cranchiid genera treated in this study, *Megalocranchia* has been one of the most challenging. As has been stated several times throughout the systematic results, the resolution of many Pacific cranchiid species is hindered by a severe lack of material, particularly across the full ontogenetic, and therefore, developmental range of each species. While a relatively large number of specimens in this genus were examined, this material was often degraded or damaged, and both early and late life stages were underrepresented. In addition, many *Megalocranchia* species were encountered in collections that had been preliminarily attributed to other genera (often *Liguriella*, *Teuthowenia*, *Sandalops*, and *Liocranchia*). It is safe to say that a full revision of *Megalocranchia* is needed (including a worldwide review of all available material), but will be no small feat.

Many of the *Megalocranchia* specimens that had been attributed to other genera shared similar characteristics and represented early ontogenetic stages. They often had circular or oval fins and eyes that were transitioning from stalked to sessile eyes. One of the most useful characters for recognising *Megalocranchia* in these stages appears to be the shape of the ventral cartilaginous windows at the funnel–mantle fusion (pers. obs.). In all species, these windows have a distinctive shape created by two inward curves that begin at the fusion point and extend posteriorly. The outer curve is often longer than the inner, creating a shape reminiscent of a stylised wing (Fig. 8.4). This particular shape is not seen in other genera (which frequently have a triangular or oval-shaped cartilaginous window). Following examination of the fusion-point windows, the generic identification can be confirmed by establishing the presence of the unique internal photophores, which may still be developing but is usually visible by ML 20–30 mm. Often these photophores are quite small, but the visceral photophores still appear to be a complete, albeit a smaller version of the adult visceral photophores, as shown in Figure 8.7a.

In contrast to some other cranchiid genera (such as *Leachia* or *Galiteuthis*) reliable species-level morphological characters in the *Megalocranchia* taxa examined herein remain relatively few, and often show variability and sometimes overlap in character traits (e.g. counts of sucker teeth) among species. The ventral eye photophore

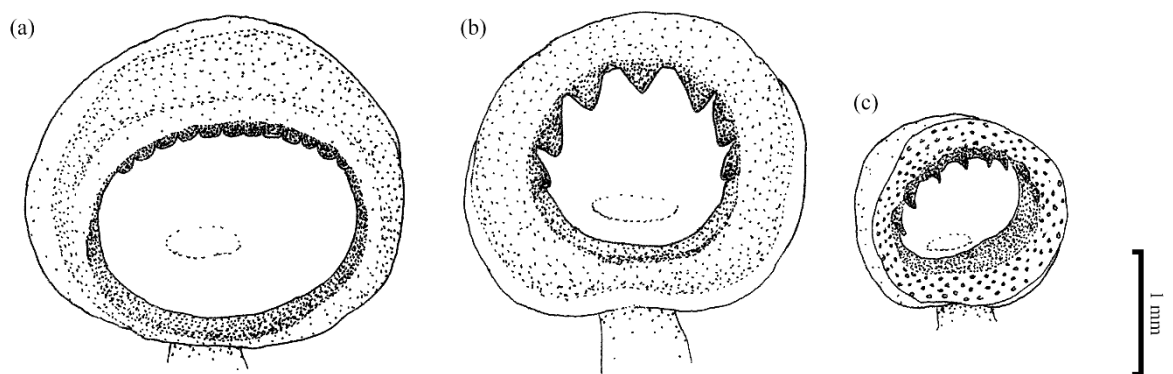


Fig. 8.11—*Megalocranchia* sp. NZ armature showing (a) largest mid-Arm III sucker, (b) distal Arm III sucker, (c) largest manus sucker (NMNZ M.074305; ML 225 mm).

arrangement has been used commonly as a source of information enabling specific identification; however, *Megalocranchia* taxa display both surprising similarities (across hypothesised taxa) and variation (within purported taxa), essentially blurring species boundaries. Specimens from the same location with many other identical characters appeared to have differing eye photophores; conversely some specimens caught at opposite ends of the Pacific Ocean had similar eye photophore patterns and minor variation in other characters. Identifying consistent patterns in other characters such as arm and manus sucker dentition, fin shape, and oral arm membrane size proved similarly difficult.

In many specimens examined, certain characters were well preserved while other were damaged, in some cases preventing species-level identification. Several of these specimens had eye photophores in excellent condition; however, a lack of published descriptions of *Megalocranchia* photophore morphology made evaluating the utility of this feature at a species-level challenging (particularly given the apparent intraspecific variation described above). Many of the inner photophores appeared to have two distinct 90-degree angles (or curves) in them. This general shape was commonly seen for the inner photophore of *Megalocranchia*; however, some specimens showed very sharp distinct angles while others had a smoother curve. It is not yet clear whether this could be a useful character for species determination, or whether it is simply natural intraspecific variation among specimens.

Of all *Megalocranchia* species encountered in this study, *M. abyssicola* appears the most straightforward to identify, with its very long trabeculate protective membranes on all arms (a feature illustrated in Goodrich, 1896) and proportionally long fins. The arms themselves were proportionally shorter (mean values = 16–27% ML) than in the other species described herein. On some of the suckers of larger individuals there was an apical papilla (Fig. 8.3), projecting from the medial posterior margin; these papillae were most easily seen on the largest suckers of the third arm, but were present on all suckers. Often, in these larger specimens, the mantle was reticulated in a mesh-like way, possibly indicating that the specimen was spent when it was caught. Nesis (1987) did not provide much detail when describing *M. abyssicola*, only mentioning that the club manus suckers had 10–12 teeth and that the arms had closely spaced turret-shaped teeth (Nesis did not mention the number or location of the arm sucker dentition). Goodrich (1896) reported and illustrated arm sucker rings with ~14 blunt teeth, and manus sucker rings with ~10. This seems to fit with the description from Nesis (1987) and correlates with the morphology of the suckers examined herein.

Material attributed to *M. maxima* was collected throughout the Pacific Ocean and was identified based on the dentition of both the arms and tentacle clubs. In general, species of *Megalocranchia* appear to continue developing arm sucker dentition throughout ontogeny, which is common in most cranchiid squid; however, even at smaller sizes, *M. maxima* specimens had between 30 and 40 (variably) angular or rounded teeth around the entire sucker ring margin, while the other two taxa identified herein only had teeth around part of the ring margin. Imber (1978) reported that *M. 'maxima'* (= *M. sp. NZ*) gained arm sucker dentition as it developed, with specimens over 50 mm ML having dentition around the entire sucker ring margin. The results of the material for *M. maxima* examined herein support Imber's description, as the specimens examined were larger than 90 mm ML (however, Imber underestimated the maximum size of this species, estimating that it reached maximum size at about 200

mm ML). Imber (1978) also found that his largest specimens had arm dentition solely on the distal portion of the ring. The largest specimen examined herein was over 600 mm ML, and that even at this larger size, the sucker rings still had teeth around the entire ring margin, rather than only distally as described by Imber (1978). Although it cannot be unambiguously confirmed that the material attributed to *M. maxima* herein represents the same taxon as Imber's (1978) *M. maxima*, some collection localities were similar (New Zealand waters), and there is overall agreement in character traits, so it seems probable that the same taxon is represented. This research indicates that there are two species of *Megalocranchia* found in New Zealand waters, as specimens of both *M. maxima* and *M. sp. NZ* are recognised.

One of the least certain taxon identifications within Pacific *Megalocranchia* is the material attributed to *M. cf. fisheri*. Most of the specimens examined were immature animals, collected from near the *M. cf. fisheri* type locality (near the Hawaiian Islands). Few useful details can be gleaned from the type description of *M. cf. fisheri* (Berry, 1909), which does not mention the internal photophore, although it should have been developing at the size of specimens available to Berry. Perhaps they may have been overlooked. He reported dentition to be lacking on the arm sucker rings, and did not mention the club sucker ring dentition. In similarly sized material (ML ~45 mm) attributed here to *M. cf. fisheri* the sucker rings often do have minimal dentition or low crenulations, which appeared more pronounced in larger individuals. The squid Berry described morphologically resembles a small *Megalocranchia*; however, due to these specific differences that this taxon has been designated *M. cf. fisheri*.

Nesis mentioned another species ('*Megalocranchia* sp.') from the Pacific Ocean, off the coast of Japan (Nesis, 1987). This species was described as having 15–18 teeth around the entire manus sucker ring margin, with the distal-most teeth spaced widely apart; however, Nesis was not able to confidently attribute this specimen to any known species. Although none of the examined material from Japanese collections matched that brief description, two other morphologically unique specimens are worth mentioning. The first (NSMT Mo.85220) appeared to lack eye photophores entirely (although they could have just been damaged) and had unique club suckers with approximately 10 straight pointed teeth along the distal margin and a single large square tooth along the proximal ring margin. The sucker rings did not appear to be damaged and every sucker from both clubs had this distinctive dentition. The second noteworthy specimen was NSMT Mo.85223, which had very similar morphology to other smaller *Megalocranchia* specimens (ML 49 mm) except for appearing to have three crescent photophores on the ventral surface of the eye. It may be that the 'third photophore' was an illusion caused by wrinkled reflective tissue, but without histological analysis its status cannot be resolved.

As has been mentioned several times (this cannot be stressed enough) distinguishing among species of *Megalocranchia* is challenging and will most likely require a global taxonomic revision—ideally taking an integrative approach, incorporating molecular characters as fresh material becomes available for sampling and study. The present revision improves the state of knowledge on Pacific *Megalocranchia* taxa somewhat, but is in no way a completion of work on this genus. Given the apparent morphological variability of taxa such as *M. maxima* and *M. sp. NZ*, it is extremely likely that additional (perhaps allopatric) taxa will be recognised. More work is also required on material from the western Pacific, given that several apparently

unique specimens were encountered that could not yet be confidently attributed to known taxa.

## *Sandalops* Chun, 1906

### Historical Review

The genus *Sandalops* was originally described by Chun (1906), deriving its name from the strangely shaped eyes which are reminiscent of Crackowes (an elongated sandal popular in the 15<sup>th</sup> century). However, Chun's descriptions of *S. melancholicus* in 1906, and later in 1910, lacked sufficient detail, simply identifying the shoe-shaped eyes, sub-equal arms, wide gladius, and thickened eye stalks. Pfeffer (1912) subsequently described the genus in significantly more detail, giving credit to Chun for his excellent illustrations. This description included information on the shape of the fins and eye stalks, both of which were indicative of a very young specimen, but provided little detail regarding the arms aside from reiterating that they were subequal in length (Pfeffer, 1912).

Two new species, *S. ecthambus* Berry and *S. pathopsis* Berry (systematic status undetermined), were added to the genus due to the presence of a keel along the tentacular club (Berry, 1920); however, Berry admitted that both species were most likely early ontogenetic stages of *S. melancholicus*, but decided that separation was the safest course of action at that time. Other morphological differences defining these two 'new species' included longer eye-stalks, larger fins, and odd spindle-shaped eyes; however, no exact measurements were supplied so these could have been within typical morphological variation for *S. melancholicus*. Several years later, Grimpe (1922) grouped *Sandalops* with *Teuthowenia* and *Helicocranchia* into his new sub-family Teuthoweniinae; however, this classification was not upheld in subsequent taxonomic works.

Robson (1924) recognised a new taxon, *Anomalocranchia impennis* (= *Teuthowenia pellucida*, *fide* Voss, 1980), which had a shape reminiscent of *Megalocranchia*, but had a larger funnel and no fins. This was later considered to be a junior synonym of *Sandalops* by Nesis in 1974, despite the type-specimen being extensively damaged and Nesis believing there to be significant morphological variation between it and *S. melancholicus*. It was more recently moved into synonymy with *Teuthowenia* (Voss, 1980). Nesis (1974) also confirmed Berry's suspicions that his two new species described in 1920 were simply early ontogenetic stages of *Sandalops melancholicus*. Another 'new genus', *Uranoteuthis*, was described by Lu and Clarke in 1974 and the holotype, *U. bilucifer*, was described as having large bulbous eyes facing antero-dorsally and no keel on Arms I–III but strongly keeled Arms IV. The name was derived from the upward orientation of the eyes. This genus was synonymised with *Sandalops* in a later revision of the family (Voss, 1980).

Young (1975) undertook an in-depth examination of the ontogenetic changes in the eyes of *Sandalops* and *Taonius*, both of which have a transitional tubular eye during their development. Young found that in early developmental stages, the stalked eyes of *Sandalops* were laterally compressed; even internally, the retina of these younger specimens was compressed into a strip. During ontogenetic descent (to about 450 meters depth) the stalked eyes rapidly transition to dorsally directed tubular eyes (Young, 1975). Young (1975) speculated that while in this state, the eyes would cast less shadow, but that the lens and the retina appeared to be far too closely spaced for the

animal to properly focus. During its continuing descent to inhabit greater depths with maturity, the eyes of *Sandalops* gradually become larger and hemispherical.

Herring, Dilly, and Cope (2002) examined the photophore structure among members of the family and found that, although similar in shape to other taoniins, the photophore ultrastructure of *Sandalops* showed distinct similarity to cranchiins due to their structural simplicity and lack of crystalloid bodies. Their study was intended to help solidify generic groupings of morphologically similar cranchiids; however, these results further confounded the attempt.

## Systematics

*Sandalops* Chun, 1906

*Sandalops* Chun, 1906: 86; Voss, 1980: 386–388; fig. 6; Reid, 2016: 99–100.

*Uranoteuthis* Lu & Clarke, 1974: 985–991.

**Diagnosis:** Stout taoniin with individually circular fins and two photophores on ventral surface of eye: small circular photophore set within concavity of much larger bean-shaped photophore. Arms often subequal in length, tentacles frequently absent in larger specimens. Tubercles absent at all three head–mantle fusion points.

***Sandalops melancholicus* Chun, 1906** (Figs 9.1–9.6, Table B19)

*Sandalops melancholicus* Chun, 1906: 86; Chun, 1910: 295, Pl. LVI 6–8; Pfeffer, 1912: 749–750; Voss, et al., 1992: 198, fig. 224b, c; Reid, 2016: 100–101.

*Sandalops ecthambus* Berry, 1920: 297–298, Pl. 16, fig. 2.

*Sandalops pathopsis* Berry, 1920: 297, Pl. 16, fig. 1.

*Uranoteuthis bilucifer* Lu & Clarke, 1974: 85–991, figs 1–2.

**Diagnosis:** As for genus.

**Type material:** (not extant) *Sandalops melancholicus* **BMNH Holotype** [*fide* Voss (1980:386)]; not found [*fide* Lipinski *et al.* (2000:114)]. Type Locality: 17°28'N, 24°50'W (Atlantic Ocean).

**Material examined (18 specimens):** NSMT-Mo. 85140, ML 38 mm, sex indet., 25.94°N, 141.99°E, West of Chichi-jima, Ogasawara, 2007/10/10; **SBMNH 461082**: ML 10 mm, 21.38°N, 158.30°W, USA, Hawaii, Oahu; **SBMNH 460893**, ML 51 mm, sex indet., 21.38°N 158.30°W, USA, Hawaii, Oahu; FIDO XVI tow 64, 20/03/1983; **NMNZ M.074565**, ML 79 mm, sex indet., 28.22°S, 174.93°E, New Zealand, 1064–5000 m, RV *James Cook*, Stn. J17/70/76, 14/12/1976; **NMNZ M.172990**, ML 59 mm, sex indet., 29.53°S, 167.63°E, Norfolk Ridge, S of Norfolk Island, 200–1200 m, RV *Tangaroa*, NORFANZ Stn. 23, 15/05/2003; **NMNZ M.074316**, ML 47 mm, sex indet., 30.53°S, 178.36°W, New Zealand, 971 m over 1100 m, RV *James Cook*, MWT, Stn. J17/19/76, 05/12/1976; **NMNZ M.074322**, ML 59 mm, sex indet., 32.87°S, 175.06°E, New Zealand, 277 m over 5000 m, RV *James Cook*, MWT, Stn. J17/88/76, 17/12/1976;

**MV F163739**, ML 48 mm, sex indet., 32.98°S, 124.52°E–33.02°S, 124.50°E, Western Australia, Great Australian Bight, 59 m, CSIRO RV *Soela*, 28/10/1981; **NSMT-Mo.66705**, ML 71 mm, ♂, 32.42°N, 142.06°E, KH88-4 Stn. 2, 23/09/1988; **NMNZ M.074324**, ML 51, 61 mm, sex indet., 33.23°S, 179.23°W, New Zealand, 695 m over 3000 m, RV *James Cook*, MWT, Stn.J17/09/76, 04/12/1976; **NMA C133442**, ML 72 mm, sex indet., 33.33°S, 153.06°E–33.20°S, 153.22°E, SE of Newcastle, 0–640 m over 4755 m, FRV *Kapala*, Stn: K79/19/05, 28/11/1979; **NMV F163723**, ML 42 mm, sex indet., 34.59°S, 155.14°E, New South Wales, 425 m, CSIRO RV *Soela*, 09/10/1981; **NIWA 95896**, ML 86 mm, sex indet., 34.80°S, 171.67°E, 934 m, Stn. Z9817, 19/06/1999; **NMNZ M.074330**, ML 64 mm, sex indet., 37.36°S, 178.76°E, New Zealand, 1380 m, RV *James Cook*, 0 m, PT, Stn. J16/73/76, 20/11/1976; **NMNZ M.287268**, ML 43 mm, ♂, 41.18°S, 176.64°E, New Zealand, off Castle point, 1148–1170 m, RV *James Cook*, Stn.J12/57/88, 24/10/1988; **NIWA 95960**, ML 48 mm, sex indet., 42.88°S, 177.46°E–42.88°S, 177.44°E, 500 m, Stn. TAN0701/36, 02/01/2007; **MV F78244**, ML 78 mm, sex indet., 44.23°S, 147.31°E–44.22°S, 147.03°E, 650–775 over 1394 m, Sta. 5503/93/20, CSIRO RV *Southern Surveyor*, 12/04/1993.

### Description:

**Adult** (ML > 75 mm; Figs 9.2, 9.3)—Mantle stout and saccular, MW 53–57–59% ML; rachis window oval, gladius not visible along most of dorsal midline (Fig. 9.2a), conus tip extends slightly past fins; no tubercles at fusions. Fins rounded, joined to mantle anterior to widest part of conus; FL 10–12–14% ML; FW 19–23–24% ML. Head length 5–14–23% ML; HW 29–33–37% ML. Eyes large (ED 13–14–17%), oriented anterio-dorsally; each with two photophores: one small circular photophore set within concavity of larger bean-shaped photophore. Funnel 15–19–24% ML, base of funnel 43–45–48% MW, funnel narrows to aperture 25–27–30% FB.

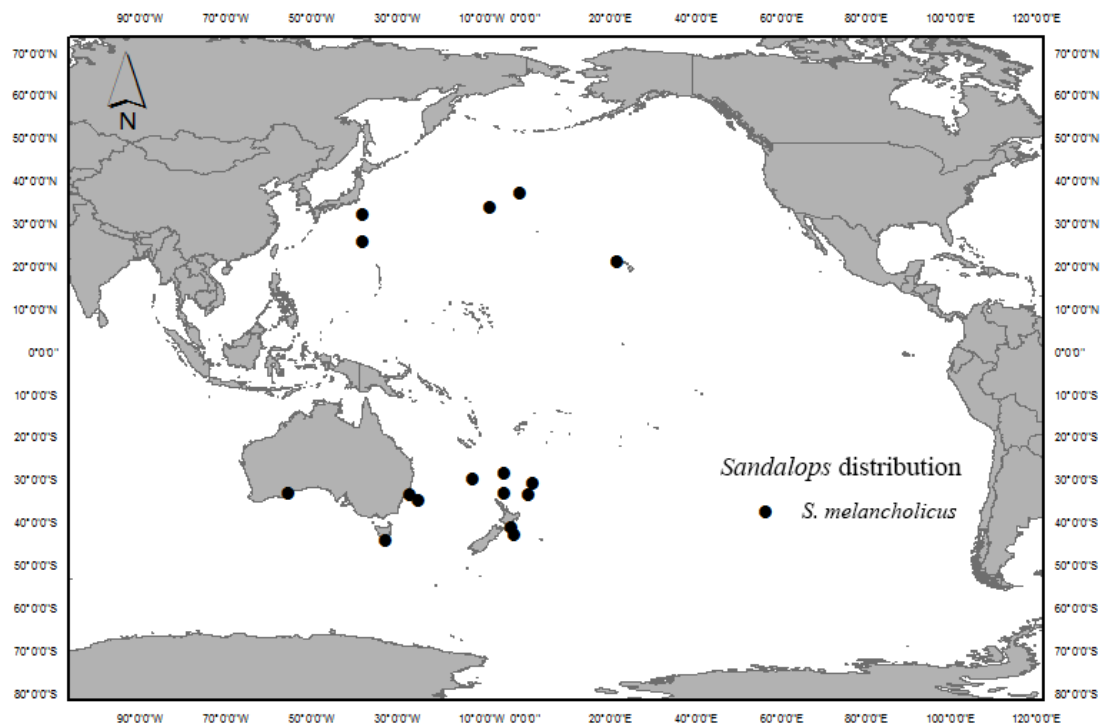


Fig. 9.1— Distribution of examined *Sandalops melancholicus* material in the Pacific Ocean.

Arm formula variable, commonly  $\text{III} > \text{II} > \text{IV} = \text{I}$  (occasionally  $\text{IV} > \text{III} > \text{II} > \text{I}$ , or arms subequal): Arm I 15–19–23% ML, Arm II 19–21–25% ML, Arm III 19–22–28% ML, Arm IV 15–21–28% ML; basal 20% of Arms I–III joined with thick webbing. Arm IV with highest sucker count (36–58), other arms with up to 50 suckers; sucker rings lacking dentition (Fig. 9.3). Tentacles often absent, TL ~100% ML, 4–16 suckers on tentacular stalk, CL ~15% ML, club with approximately 80 suckers.

**Juvenile** (ML 40–75 mm, Figs 9.4, 9.5)—Mantle shape varies with preservation, often elongated oval (Fig. 9.5), MW 30–52–75% ML; rachis window oval, gladius not visible along most of dorsal midline; conus tip extends slightly posterior to fins; no tubercles at fusions. Fins rounded, connecting to mantle at widest point of conus; FL 10–14–20% ML; FW 18–24–36% ML. Head length 2–14–20% ML; HW 20–27–40% ML; ED 8–11–18%, eyes tubular or cylindrical (Fig. 9.5c). Eye with two photophores: one smaller circular photophore encircled by larger bean-shaped photophore on flattened ventral surface. Funnel 7–16–25% ML, base of funnel 33–40–45% MW, funnel narrows to aperture 25–47–70% FB.

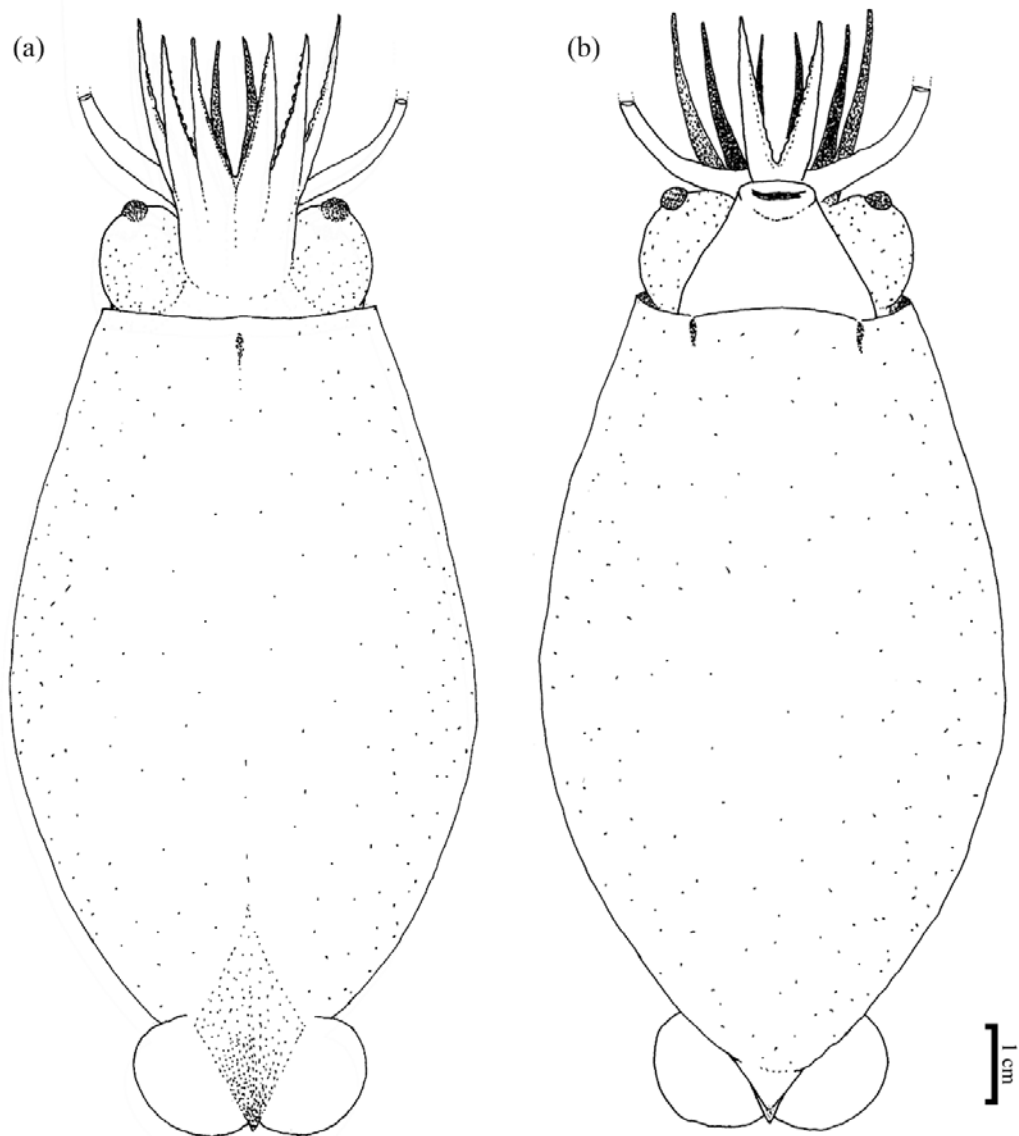


Fig. 9.2—Adult *S. melancholicus* (a) dorsal view and (b) ventral view (NIWA 95896; ML 87 mm).



Arms with low webbing, arm formula variable, commonly  $\text{III} > \text{II} > \text{IV} = \text{I}$  (occasionally  $\text{IV} > \text{III} > \text{II} > \text{I}$ , or arms subequal); Arm I 10–15–24% ML, Arm II 11–16–29% ML, Arm III 12–17–33% ML, Arm IV 10–16–22% ML. Arm IV with highest sucker count (36–58), other arms with up to 50 suckers; sucker rings lack dentition. Tentacles often absent, TnL 47–69–88% ML, 4–16 suckers on tentacular stalk, CL 14–16–17% ML, club with 68–76 suckers.

Beak (Fig. 9.4): Lower rostral length (LRL) 1.7 mm. At ML 64 mm, wings and lateral wall not fully darkened, 1.2 mm of clear margin remaining on wings, 0.8 mm on lateral wall. In lateral profile, crest-to-base ratio 0.8; baseline length less than height. Rostral tip curved, ending in broad point. Jaw and wing angles obtuse; rostral edge a continuous curve. Small rounded wing-fold covers jaw angle; wing-to-edge ratio 0.55. Wings broad, narrowing slightly at jaw angle. Hood slightly curved; hood-to-edge ratio 1.0; hood extends just above crest. Crest narrow, not thickened, straight edge.

**Known distribution:** *S. melancholicus* is found throughout the Pacific Ocean, from 26°N to 45°S (Fig. 9.1), elsewhere reported as a tropical or subtropical cosmopolitan species (Voss, 1980; Sweeney *et al.*, 1992). Material from this study was most commonly caught between 0–1200 m (Fig. 9.6), the depth range at which most trawls are commonly undertaken; however, the species could be found as deep as 5000 m (the deepest trawl depth).

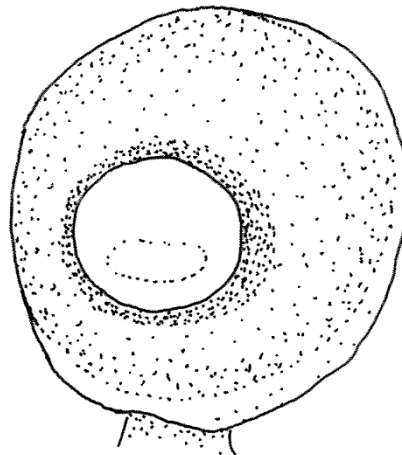


Fig. 9.3—Arm sucker of *S. melancholicus* (NMNZ M.074565; ML 79 mm).

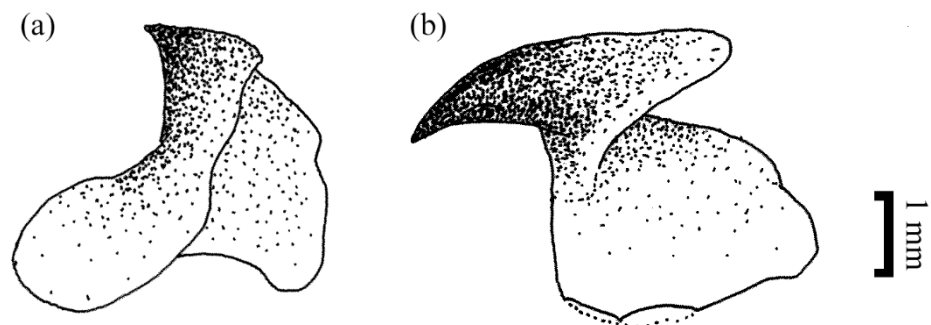


Fig. 9.4—Juvenile *S. melancholicus* beak (a) lower beak and (b) upper beak (NMNZ M.074330; ML 64 mm).

**Remarks:** Little morphological variation was observed in Pacific *Sandalops* material, and all specimens appeared to represent a single species, as material from both the across the Pacific form a single BIN (BOLD:ADH6536, see Fig 11.1); however, *S. melancholicus* can still be confused with other members of the family. Its rounded fins are reminiscent of small *Liocranchia* and *Cranchia*; however, both these taxa lack stalked eyes at early ontogenetic stages. The large funnel of *Sandalops* appears similar in proportion to that of *Helicocranchia*, and at small sizes, both genera have paddle-shaped fins. Species from both genera also have stalked eyes during their respective paralarval stages, but stalks of *Helicocranchia* tend to be short and stout, supporting spherical eyes, whereas *Sandalops* has longer stalks with narrow eyeballs with an extended ventral protrusion (Fig. 9.5e). In all instances, the eye photophore shape and the presence of sub-equal arms should distinguish it from other cranchiid genera that may appear morphologically similar.

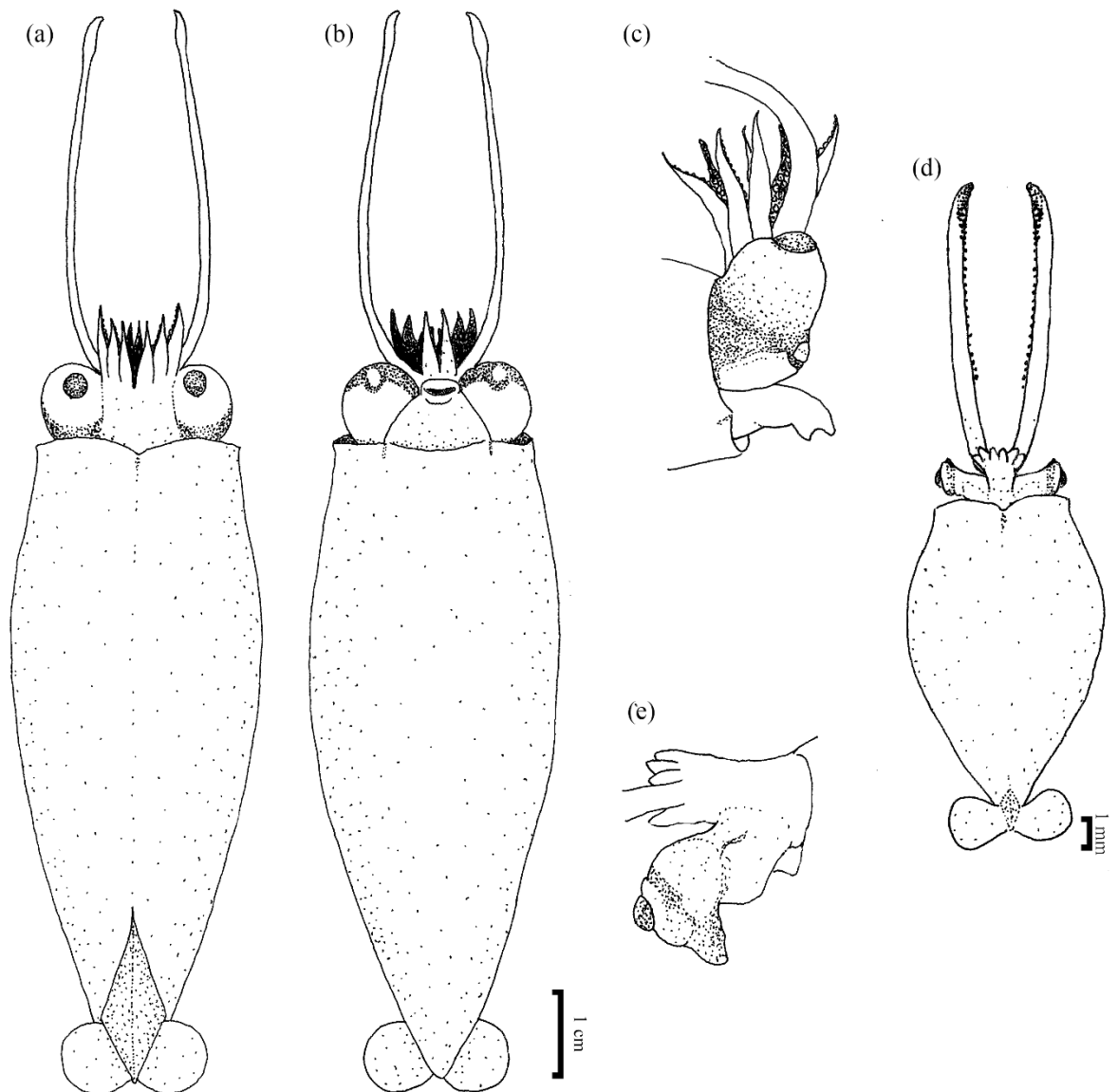


Fig. 9.5—Juvenile *S. melancholicus* (a) dorsal view, (b) ventral view, and (c) lateral view showing tubular eye (NSMT Mo:66705; ML 71 mm), paralarval *S. melancholicus*? (d) dorsal view (e) enlarged paralarval eye (SBMNH 461082; ML 10 mm).

## Discussion

The genus *Sandalops* has remained stable since its original description, with very little controversy over its systematic placement. Its sole known species, *S. melancholicus*, was first recognised from the Atlantic Ocean, and the type could not be examined as part of the present study. The morphology of Pacific material agrees with descriptions of Atlantic specimens, supporting our present understanding of *Sandalops* as a cosmopolitan monotypic genus. However, molecular comparisons could be made when fresh material becomes available, to further test the hypothesis of conspecificity of specimens found in these two oceans.

The most distinctive feature of *S. melancholicus* is the ventral eye photophore pattern. Unlike other members of the Taoniinae, which have a slender, crescent-shaped photophore combined with a large reflective patch of tissue, *Sandalops* appears to have broad, thickened photophores and no reflective tissues. The inner photophore is circular and is partially surrounded by the outer photophore, which appears bean-shaped (Fig. 9.5b). These photophores develop with the eyeball, but were already fully formed in the earliest examined juvenile stages (ML 40 mm), where the eyes are tubular and oriented dorsally. Strangely, unlike the photophores of other cranchiids, which develop under the outer integument, the photophores of *Sandalops* seem to develop on the outer surface of the epidermis. When examining material of *Sandalops* with tubular eyes, the photophores were occasionally partially detached from the eye, despite the outer layer of tissue surrounding the rest of the eyeball. Larger specimens with fully sessile eyes appeared to have the photophores under the outer layer of integument, so this photophore detachment in some specimens may be due to damage or prior dissection of the specimen.

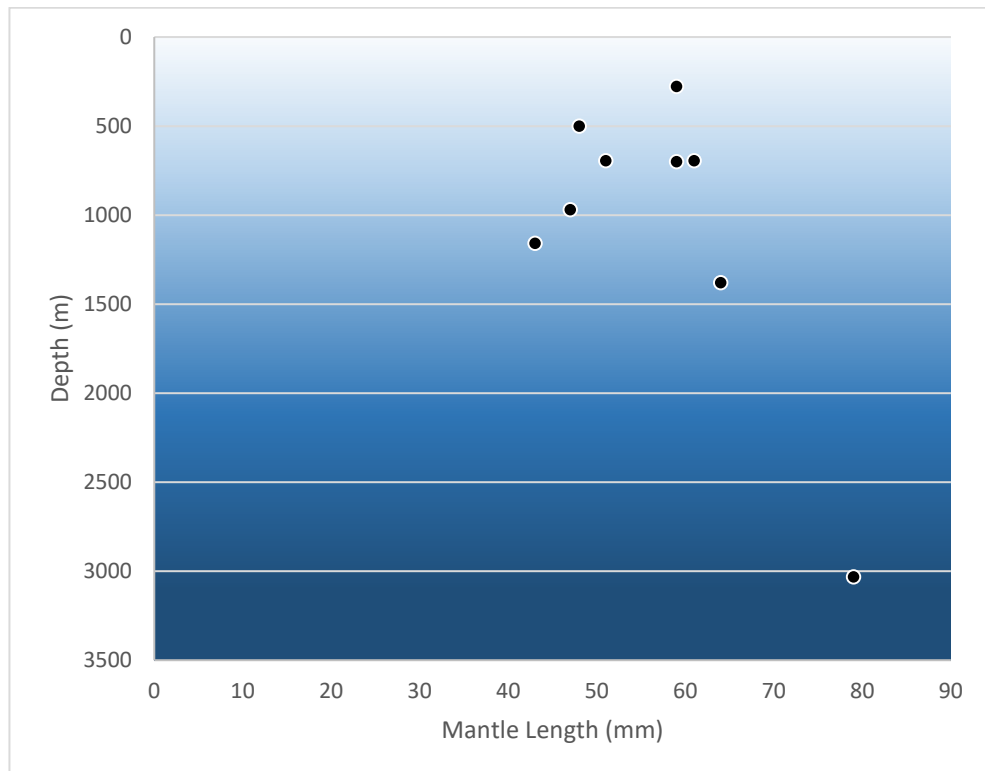


Fig. 9.6— Collection depth of *S. melancholicus* specimens examined.

Many of the larger individuals examined lacked tentacles, making it challenging to quantify the tentacle proportions and counts. In general, *Sandalops* appears to have a proportionally small club, lacking significantly modified armature. The reason for missing tentacles is unknown, although it appeared from the damaged stalks that most were detached naturally, rather than cut off. Often, the distal portion of the remaining stalk would be stretched and have an uneven surface, rather than a clean cut as would be expected if the appendage had been removed using a blade, as was seen occasionally for some specimens of 'hooked cranchiids'. In a few cases, the entire tentacle was missing, and the only remains were short stubs at the arm crown. In these instances, the lateral surface was often rounded or puckered, appearing to have healed over past damages. It is possible that this is due to predator interaction prior to the specimen being caught, or that this species autotomises its tentacles near to reproductive maturity. Little is known about the ecology and behaviour of cranchiid squid such as *Sandalops melancholicus*, and *in situ* observation would be required to better understand its natural interactions.

## *Taonius* Steenstrup, 1861

### Historical Review

The genus *Taonius* has suffered from systematic instability since its formation by Steenstrup (1861). Representatives of *Taonius* has been described in both the Atlantic and Pacific Oceans; however, the systematics of this genus has been notoriously unstable, and it is important to accurately understand the geographic distributions of these species as *Taonius* plays an important role in deep-sea ecosystems. For example, many cetaceans have been shown to feed on cranchiids, and *Taonius* can constitute up to 35% of an individual's diet (MacLeod, Santos & Pierce, 2003). Many ecological surveys identify *Taonius* only to the generic level, an indication of how challenging it can be to identify members of this genus. The ramifications of this history are still evident in current research.

Before the formation of the Cranchiidae by Prosch in 1849, species of this family were placed into the genus *Loligo* Lamarck, along with several other genera. The first described species (of what would later be called *Taonius*) was *Loligo pavo* (= *Taonius pavo*) Lesueur, 1821. Although the description for this animal was not brief, Lesueur failed to mention a fusion between the head and the mantle, which would have been considered an unusual feature for the squid known at that time. Instead, the description focused on the elongation of both the mantle and fins, as well as the large eyes protruding from a small head, a feature that was reiterated by future authors. Unfortunately, Lesueur was not able to comment on the tentacular clubs and the ends of the appendages, as all had been removed by the fishermen from whom his examined material was obtained. The original specimen was a mature female, and Lesueur described its tissue as being a mottled rusty brown colour, illustrating it with a large egg mass protruding from the siphon (Lesueur, 1821).

In 1845, d'Orbigny erected a new genus of squid that he called *Loligopsis*, into which '*Loligo*' *pavo* was placed. '*Loligopsis*' *pavo* was then moved again by Steenstrup (1861) who made it part of the genus *Leachia*, which he believed to be the oldest available generic name for any squid with fusions at the head and mantle; the designation *Taonius* was used as a sub-genus. Over the next few decades, new genera and species were erected to attempt to provide some stability in the family Cranchiidae. Unfortunately, this amassing of new species had the opposite effect, since many of these proposed 'species' ultimately proved to represent different growth stages of previously described taxa. Some of these nominal species were attributed to *Taonius*, and have since been synonymised with known species or moved to other cranchiid genera.

Chun (1906) described a new species and erected the genus *Toxeuma* to contain it. *Toxeuma belone* (Chun, 1906; = *Taonius belone*, *fide* Voss 1980) was described as being a slender squid with moderate stalked eyes that were elongated, which Chun felt differentiated it from *Taonius* because all known specimens of that genus, at that time, had large, sessile eyes (Chun 1910). Chun's description of *T. belone* lacked detail regarding the armature, which was used in subsequent descriptions to distinguish it from geographically similar species. Another 'new' genus, *Belonella*, was erected by Lane (1957), and replaced *Toxeuma* in the literature, as *Toxeuma* was an invalid junior homonym for a genus of insects. Nesis added two Pacific species to *Belonella*: *B. borealis* and *B. pacifica* (Nesis, 1972); the former is still considered a valid species, the

latter was later synonymised with *Taonius belone* by Nesis in 1987. *Taonius borealis* was (and is still considered to be) distributed throughout the northern Pacific, throughout the waters of Japan, the Bering Sea, and the west coast of Canada. *Taonius belone* is thought to be distributed throughout the central eastern Pacific as well as throughout Indonesia and in the Indian Ocean; however, the geographic distribution of this species is less well understood than that of *T. borealis*.

Lu and Clarke (1974) were the next to contribute to *Taonius* taxonomy (albeit inadvertently); they described what they believed to be a new species as '*Galiteuthis triluminosa*' (= *T. belone*, *fide* Imber 1978; Nesis, 1987). The specimen was quite long and slender, and possessed unusual eye morphology: slightly stalked eyes, with three luminous organs on the ventral surface, and on overall odd eye shape caused in part by their oblique upward orientation (Lu & Clarke, 1974). Shortly thereafter, Young (1975) reported that *Taonius* species develop telescopic eyes as a transitional stage between paralarval and adult morphology, which enabled Imber's (1978) recognition of '*G. triluminosa*' as a junior synonym of the known *T. belone*.

Taxonomic debate has continued through to the most recent studies. Voss's (1980) revision of the Cranchiidae placed *Belonella* into synonymy with *Taonius*, while Nesis' (1987) summary of the family retained *Belonella* as a valid genus. Nesis validated this choice by suggesting that the autotomisation of the tentacles was a distinguishing characteristic of *Taonius*, and due to this, the presence of the tentacle club armature was not discussed. Although today *Taonius* is largely believed to be the correct generic designation, there is still some debate regarding the validity of *Belonella* (Nesis, 1987) leading to this latter generic name being used in ecological reports (Watanabe *et al.*, 2006; Kubodera, Watanabe, & Ichii, 2007; Ormseth, 2017).

## Systematics

*Taonius* Steenstrup, 1861 (Table 9)

*Taonius* Steenstrup 1861: 37–38; Voss, 1980: 390–392, fig. 8.

*Toxeuma* Chun, 1906: 86; Pfeffer, 1912: 699–700.

*Belonella* Lane, 1957: 287; Nesis, 1987: 274, fig. 71 F–J.

**Diagnosis:** Mantle commonly long and narrow, tapering gradually to point, glacial conus long (50% ML), fins attach to conus at widest point; fins narrow, lanceolate. Tubercles absent at all head–mantle fusion points. Eyes large in adults, with two ventral photophores, one large and crescent shaped, the other a smaller crescent or linear. Arms robust, relative lengths differing minimally, arm sucker teeth blunt or rounded. Tentacles shorter than ML, medial manus club suckers with enlarged hook-like teeth (in most species), cusps varying from two to eight depending on species.

Table 9 — Summary of characters for known Pacific *Taonius* species. \*, this study.

Species	Mantle	Mean fin length	Relative arm lengths	Maximum arm sucker count	Arm sucker dentition (no. teeth)	Manus sucker dentition (no. teeth)
<i>T. belone</i>	Slender (MW 15–20% ML)	20–40% ML	III>II>IV>I	30–52	20+, rounded	2 primary
<i>T. borealis</i>	Stout (MW 15–40% ML)	~35% ML	III>II>IV>I	90	16–22, rounded	2 primary, 3–6 secondary
<i>T. exopolitus</i> * sp. nov.	Slender (MW 12–19% ML)	~28% ML	III>II≈IV>I	54	adentate	5–11 teeth (no primary)
<i>T. notalia</i> * sp. nov.	Slender (MW 11–17% ML)	~35% ML	III≈II>IV>I	36–48	5–7, blunt	1 primary, 6 secondary
<i>T. robisoni</i> * sp. nov.	Slender (MW 10–25% ML)	~50% ML	III≥II≥IV>I	28–48	3–4, blunt	2 primary, 2–4 secondary
<i>T. tanuki</i> * sp. nov.	Slender (MW 13–28% ML)	~35% ML	III>II>IV>I	50	12–18, blunt	2 primary, 0–2 secondary

***Taonius belone* (Chun, 1906)** (Fig. 10.2, Table B20)

*Toxeuma belone* Chun, 1906: 86; Chun, 1910: 296–297, Pl. LVI fig. 10, Pl. LVIII fig. 1–5; Pfeffer, 1912: 700–702.

*Taonius pavo* (not Lesueur, 1821): Sasaki, 1920: 201.

*Belonella pacifica pacifica* Nesis, 1972: 80–82, fig. 1.

*Galiteuthis triluminosa* Lu & Clarke, 1974: 991–994, fig. 3–4.

*Taonius belone* (Chun, 1906): Imber, 1978: 458–459, 1H, 3, 4, 5C.

**Diagnosis:** Mantle slender (mean MW 20% ML); 20–30 blunt teeth around entire arm sucker margin (Voss, 1963). Club mid-manus suckers with two enlarged primary cusps, secondary cusps absent.

**Type material:** (not examined) *Toxeuma belone* **Type repository unresolved** [species not traced Glaubrecht and Salcedo-Vargas (2000)]. Type locality: 10°08'S, 97°14'E (Indian Ocean) [*fide* Chun (1910: 380)].

**Material examined** (2 specimens): **NSMT-Mo.85452**, ML 250 mm, sex indet., 41.57°N, 143.48°E, off Enmo-misaki, Hokkaido, 850 m, *Tansei-maru*, 28/05/2010; **NSMT-Mo.75441**, ML 270 mm, sex indet., 29.68°N, 130.66°E, off Okinawa, 1000 m, *Tansei-Marui*, 23/10/2004.

**Non-localised material examined** (2 specimens): **NSMT-Mo.67349**, ML 121, 116 mm, sex indet., 480 m, 04/08/1986.

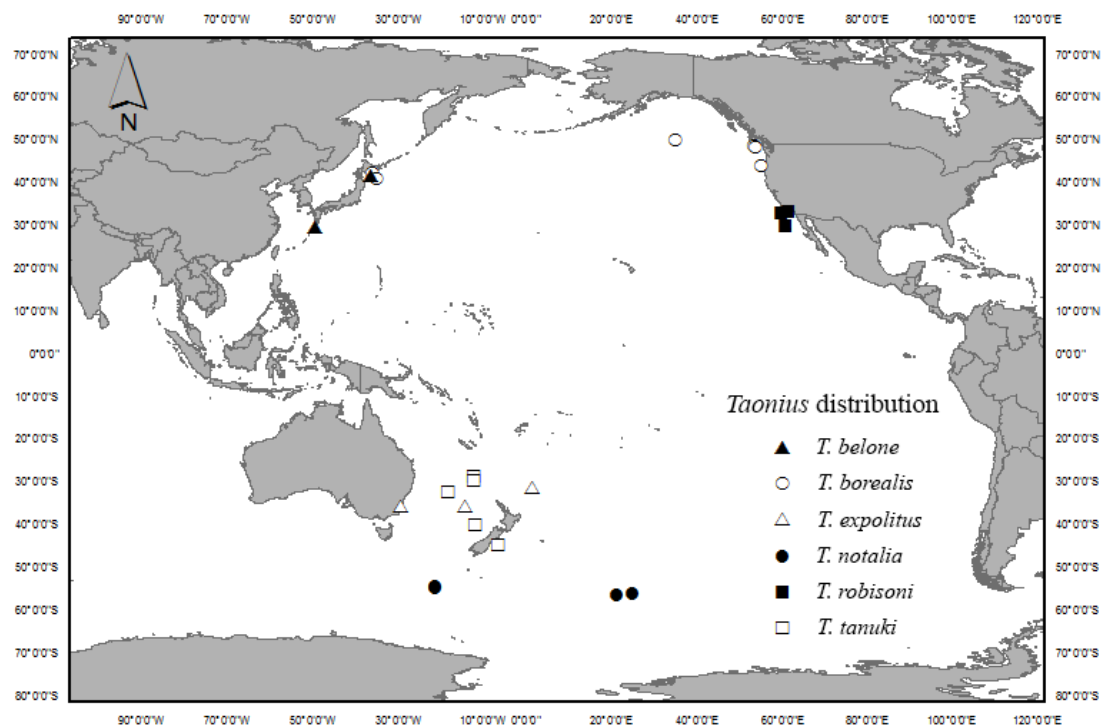


Fig. 10.1— Distribution of examined *Taonius* material in the Pacific Ocean.



**Description:**

(ML 113–270 mm; Fig. 10.2)—Mantle elongate, slender (MW 15–20–27% ML); fins lanceolate (FL ~40% ML in specimens ML ~120 mm, ~20% at ML ~250 mm), FW ~14% ML. HL ~9% ML, eyes proportionally small, ED ~9% ML, HW ~18% ML). Eyes with two crescentic photophores; outer photophore large crescent, inner photophore linear or slightly curved, ~50% ED. Funnel narrows to small aperture, FA 33–37–44% FB; ventral fusion cartilaginous windows appear slightly wider than in other species.

Arm formula III>II>IV>I: Arm I 10–13–16% ML, Arm II 15–17–26% ML, Arm III 17–20–26% ML, Arm IV 13–17–23% ML; minimal webbing between arms, Arm IV with aboral keel. Arms with 30–52 small subequal suckers, largest arm sucker with more than 22 blunt teeth. Tentacles 20–35–45% ML, stalks with ~14 suckers. Clubs ~9% ML (16–25–32% TnL) with up to 90 suckers. Largest manus suckers with two enlarged primary cusps and no small secondary cusps.

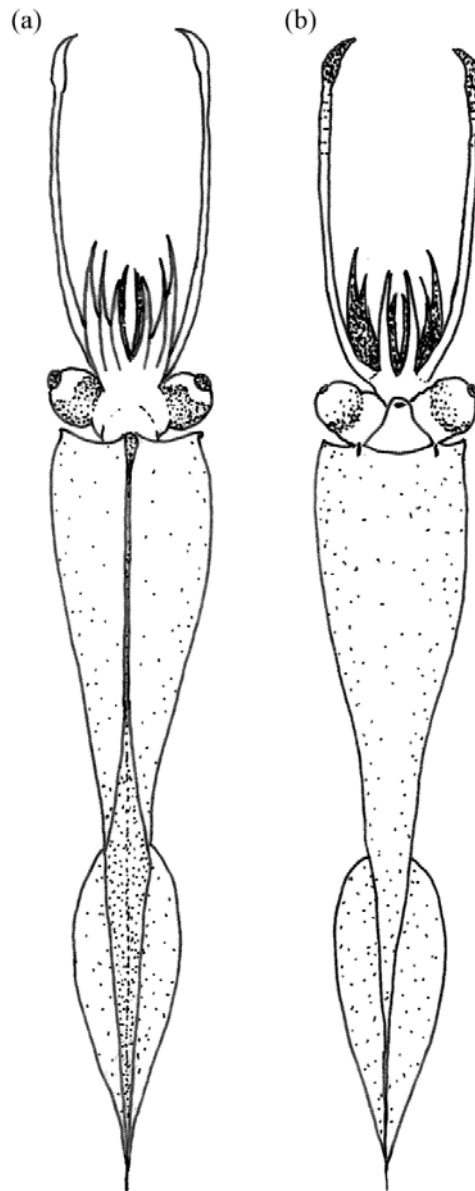


Fig. 10.2—*Taonius belone* (a) dorsal view and (b) ventral view (NMST Mo.75114; ML 113 mm).

**Known distribution:** Generally thought to be an Indo-Pacific species (as reported by Nesis, 1987). All material examined herein was from Japanese waters.

**Remarks:** Unfortunately, only four specimens of *T. belone* were available for examination, none of which appeared to be mature. *Taonius belone* appears most similar to *T. tanuki*, sp. nov. To differentiate between these species, the eye photophores, arm sucker dentition and manus dentition can be used. *Taonius belone* has noticeably more teeth on the arm suckers (>22 teeth, compared to 12–18 teeth in *T. tanuki*), and only two large cusps on the largest manus sucker, whereas *T. tanuki* has additional smaller cusps along the lateral sucker margins.

Lu and Clarke (1974) diagnosed their novel *Galiteuthis triluminosa* (= *T. belone*, *fide* Nesis, 1987) by the presence of three distinct photophores on the ventral surface of stalked, tubular eyes. The presence of tubular eyes is now understood to be an ontogenetic stage of the genus *Galiteuthis*, but as all known species of both *Galiteuthis* and *Taonius* only have two eye photophores, the presence of three would be unusual for either genus. Although Nesis (1987) placed *G. triluminosa* into synonymy with *T. belone*, it is possible that further examination of this genus may prove *G. triluminosa* is a junior synonym of a different taxon of *Taonius*, as the type specimen was from the northern Atlantic Ocean, while *T. belone* presently appears restricted to Indo-Pacific waters (Young, 2014b).

***Taonius borealis* (Nesis, 1972)** (Fig. 10.3–10.7, Table B21)

*Belonella pacifica borealis* Nesis, 1972: 82–86, fig. 2; Arkhipkin, 1996b: 123–132, fig. 1, 2, 4.

*Taonius borealis* (Nesis, 1972): Voss *et al.*, 1992: 198–200.

**Diagnosis:** Mantle stout (MW up to 40% ML); arm suckers with 16–22 rounded teeth along entire ring margin; club manus suckers with two enlarged primary cusps and three to six smaller cusps.

**Type material:** (not examined) *Belonella pacifica borealis* **ZIN Holotype** [*fide* Nesis (1987:274)]. Type locality: 44°07.8'N, 150°26.7'E (North Pacific Ocean).

**Material examined (14 specimens):** **RBCM 979-11242-1**, ML 185 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 23/08/1979; **RBCM 979-11252-4**, ML 154 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 31/08/1979; **RBCM 979-11230-2**, ML 145 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 04/08/1979; **RBCM 979-11252-4**, ML 58 mm, sex indet., 50.00°N, 145.00°W, Ocean Stn. Papa, 31/08/1979; **RBCM 010-00251-008**, ML 118 mm, sex indet., 48.71°N, 126.52°W–48.71°N 126.49°W, Pacific Ocean, Father Charles Canyon, offshore of Vancouver Island, 561–563 m, 30/08/2001; **RBCM 010-00264-001**, ML 245 mm, sex indet., 48.52°N, 126.47°W–48.52°N, 126.45°W, Pacific Ocean, offshore to SW of Ulcuelet, Vancouver Island, 1268–1270 m, 04/09/2001; **RBCM 010-00247-015**, ML 133 mm, sex indet., 48.37°N, 126.46°W–48.38°N, 126.47°W, Pacific Ocean, Loudoun Canyon, 1416–1433 m, 13/04/2011; **SBMNH 464441**, ML 144 mm, sex indet., 44.00°N, 125.00°W, USA, Oregon, OSU MT 2340; **NSMT-Mo: 71705**, ML 450 mm, sex indet., 42.30°N, 144.02°E, off Kushiro, Japan, NW Pacific Ocean, 867 m, *Wakataka-Maru*,

23/07/1999; **NSMT-Mo.76413**, ML 160 mm, sex indet., 41.03°N, 144.84°E, off Sanriku, Japan, Western North Pacific, 650 m, *Marusada-maru*, 06/07/1996.

**Non-localised material examined:** **RBCM 988-00212-003**, ML 141 mm, sex indet., Pacific Ocean, off Clayquot Canyon, 29/02/1998; **RBCM 987-00076-001**, ML 46, 57, 54 mm, sex indet., 0–500 m, Stn. 1, 03/03/1969.

### **Description:**

**Adult** (ML 118–450; Figs 10.3–10.5)—Mantle stout, MW 17–27–38% ML; skin reticulate in adults. Fin length 31–39–43% ML, FW 9–12–16% ML (55–80% MW). HL 10–13–17% ML; eyes large, often exceeding HL (ED 9–12–16% ML, ED 80–96–133% HL, HW 75–94–140% MW). Eyes sessile from ~60 mm ML, with two crescentric photophores (Fig. 10.4). Funnel narrows to narrow aperture, FL 6–9–12% ML, FA 32–36–42% FB, cartilaginous fusion windows rounded.

Arms robust basally, slender distally; low protective membrane present along arm length; formula III>II>IV>I (although relative lengths vary only slightly): Arm I 9–21–28% ML, Arm II 17–26–35% ML, Arm III 17–28–39% ML, Arm IV 15–22–29% ML. Longest arms with 40–52–90 suckers, subequal in proximal  $\frac{3}{4}$  of arm then rapidly decreasing in size distally; largest arm suckers with 16–22 rounded teeth (Fig. 10.5a), dentition decreasing on distal arm suckers. No sexual arm modifications observed on material examined (to ML 450 mm). Tentacles 33–56–74% ML, with ~20 suckers on tentacular stalk. Clubs (Fig. 10.5) 6–12–17% ML (12–25% TnL); wide trabeculate membrane on dorsal and ventral margins; total of 80–100 suckers: three or four pairs on carpal locking apparatus, 24–36 manus suckers, largest mid-manus suckers with two enlarged primary cusps and 3–6 small secondary cusps along sucker margin (Fig. 10.5c); 50–60 dactylus suckers, largest with ~8 long pointed teeth on distal margin and several smaller teeth on opposite margin.

**Known distribution:** Northern Pacific Ocean (north of 40°N) from Japanese waters to Bering Sea and northern Vancouver Island (Fig. 10.1). Present material collected from 250–1425 meters (Fig. 10.7); previously recorded from 400–700 meters depth (Watanabe, Kubodera, Moku, & Kawaguchi, 2006) and reported not to perform diel vertical migrations.

**Remarks:** *Taonius borealis* is the most morphologically distinctive member of the genus, as it is often proportionally stouter than other species (maximum MW 40% ML), whereas other taxa have mantles that are slender (maximum MW ~20–25% ML). Specimens of *T. borealis* form a distinct BIN (BOLD:ACD9245, see Fig. 11.1). This species is most likely to be confused with the sympatric *Galiteuthis phyllura*; however, *Galiteuthis* taxa have elongated hooks on their tentacle clubs which begin to develop by 40 mm ML. It is possible that *T. borealis* may be confused with *T. robisoni*, sp. nov. as there appears to be some geographic overlap between the two species in northern Californian waters. These species can be distinguished by examining mantle width (as mentioned previously), or by arm and sucker dentition. *Taonius borealis* has 16–22 rounded teeth on the arm sucker margin and three to six smaller cusps along the sides of the manus suckers, whereas *T. robisoni* has around four teeth on the distal margin of the arm sucker and fewer secondary cusps on the manus suckers.

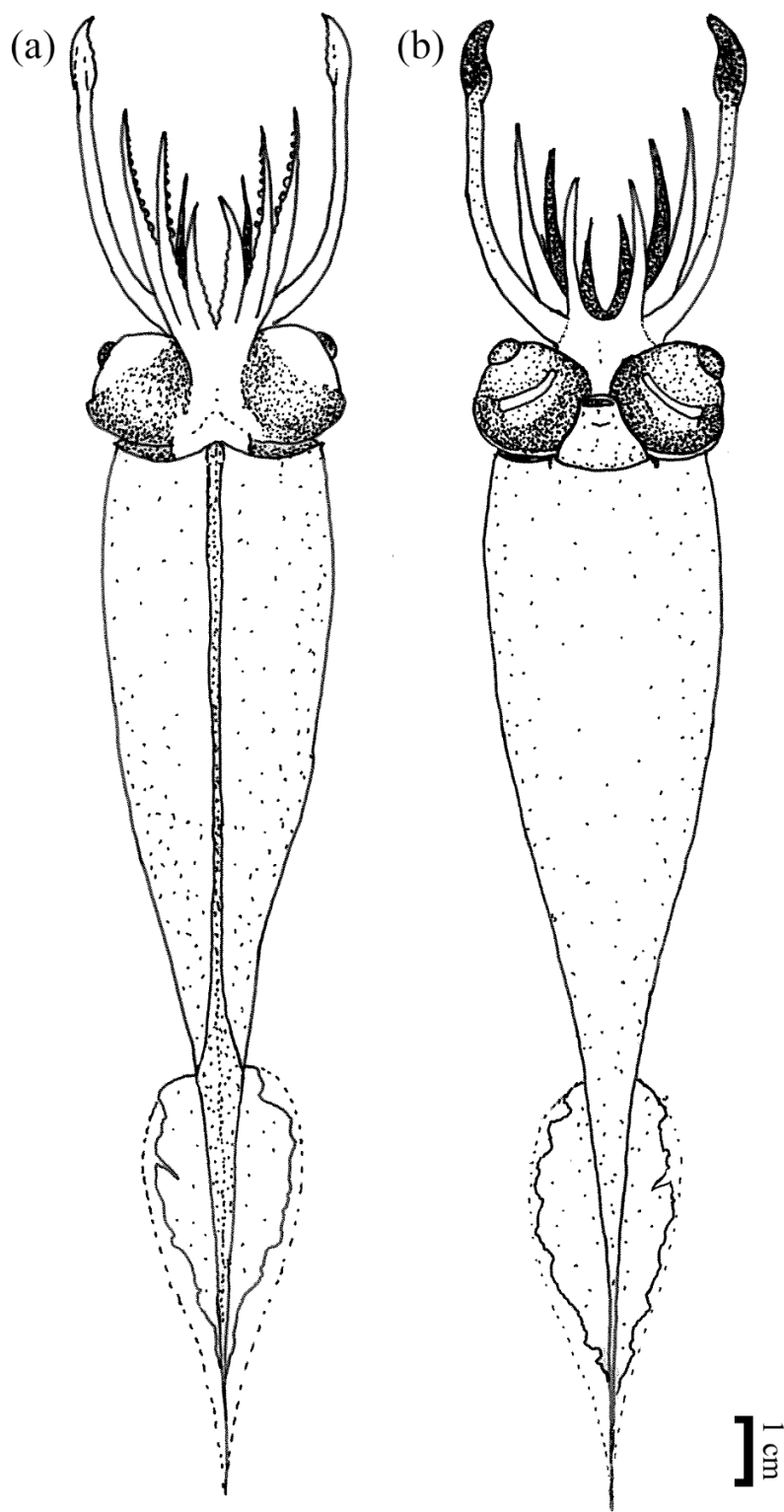


Fig. 10.3—Adult *Taonius borealis* (a) dorsal, and (b) ventral views (RBCM 988-00212-003, ML 141 mm).

When describing *Taonius borealis*, Nesis (1972) stated that his smallest specimens were 40 mm ML, and that the eyes were sessile and ocular photophores had developed by that size. The smallest specimens examined in this study were of similar size (ML 46–57) and had telescopic eyes in transitional states of development (Fig. 10.6). As these specimens are slightly larger than those examined by Nesis (1972), this could indicate that the development of mature features can occur over a fairly wide ontogenetic range in this particular species.

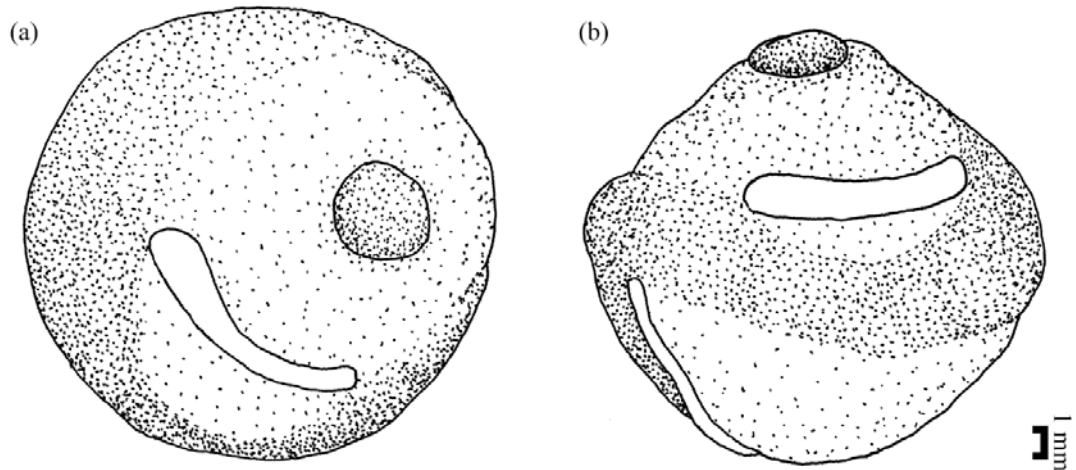


Fig. 10.4—Right eye schematic for *T. borealis* (a) lateral view, (b) ventral view (RBCM 988-00212-003; ML 141 mm).

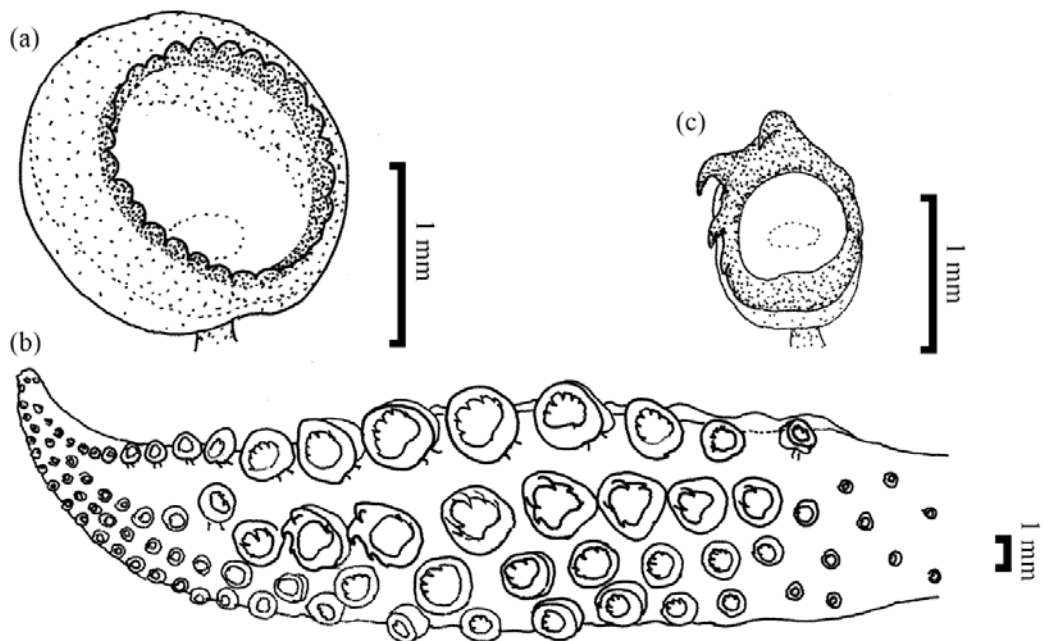


Fig. 10.5—(a) Mid-Arm III sucker, (b) right tentacle club with (c) largest manus sucker (RBCM 988-00212-003; ML 141 mm).

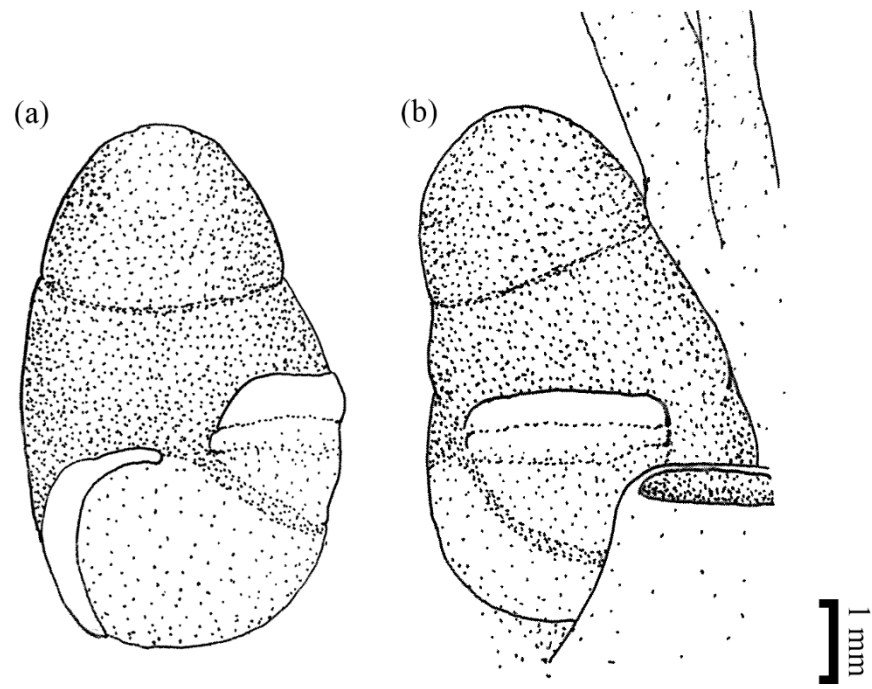


Fig. 10.6—Juvenile tubular right eye of *T. borealis* (a) lateral view and (b) ventral view (RBCM 987-00076-001; ML 57 mm).

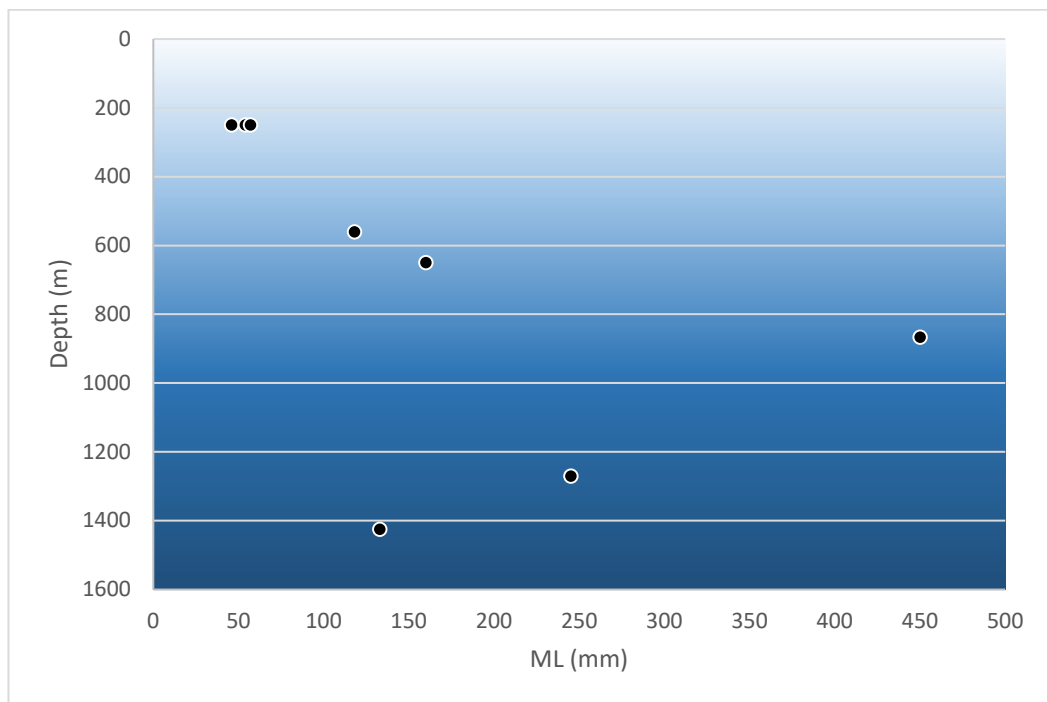


Fig. 10.2—Collection depths of *Taonius borealis* material examined in this study.

***Taonius expolitus*, sp. nov.** (Figs 10.8–10.10, Table B22)

*Taonius pavo* (not Lesueur, 1821): Imber, 1978: 453–455, fig. 3, 4.

**Diagnosis:** Mantle slender (mean MW 17% ML); largest arm suckers adentate; tentacular suckers with 5–8 long pointed teeth, lacks enlarged distal cusps. Male arm modification believed to lack suckers.

**Type material:** [Holotype] **NIWA 95946**, ML 285 mm, ♂. Type locality: North-west of New Zealand (35.87°S, 165.65°E), depth 1071 m; [Paratypes] **NIWA 119227**, 31.38°S, 178.63°W–31.35°S, 178.62°W, Kermadec Islands, 1000–110m, 03/11/2016.

**Material examined (4 specimens):** **AMS C.9070** (4 specimens): ML 223–282 mm, ♂/♀, NSW off Batemans Bay, 35.70°S 150.70°E, 940–975 m, FRV *Kapala*, Stn.K87-25-08, 17/12/1987.

**Description:**

**Adult** (ML 223–285 mm; Fig. 10.8)—Mantle conical (MW 12–17–19% ML); fins narrow, lanceolate, FL 23–28–33% ML, FW <9% ML (fins damaged in all known specimens). HL 10–12–14% ML, eyes damaged on all known specimens, estimated ED 6–9–13% ML; HW 10–12–13% ML. Funnel narrows markedly anteriorly, FA 18–42–73% FB; cartilaginous window at funnel–mantle fusion expands posteriorly, curving slightly towards ventral midline.

Arm formula III>II≈IV>I: Arm I 13–16–22% ML, Arm II 15–19–25% ML, Arm III 18–22–28% ML, Arm IV 17–19–22% ML. Arms with up to 54 suckers, increasing greatly in size mid-arm, suckers lack dentition basally and mid-arm; suckers with 5–12 blunt/rounded teeth distally. Male Arms I–III modified at maturity (Fig. 10.9), arm modified with four series of large round suckers or lacking suckers entirely with triangular dermal pads with linear ridges (Fig. 10.9a), 15–20% arm length. Tentacles 40–43–45% ML, with five or six pairs of adentate suckers. Clubs 9–11–12% ML (22–26% TL) with 84–125 suckers. Largest manus suckers (Fig. 10.10) with 5–11 long, pointed, slightly curved teeth, medial two may be slightly enlarged.

**Known distribution:** Eastern Australian waters to Kermadec Islands (30°S–35°S; Fig. 10.1). Present material collected from 110–1071 meters depth.

**Remarks:** Often the basal-most arm sucker (or pair of suckers) was noticeably separated from the other sucker pairs. This species lacks enlarged primary cusps on the manus suckers (a feature shared by all other species in the genus, and unique among known cranchiid taxa).

In other morphological traits, however, it conforms with other *Taonius* taxa, and molecular analyses place it closely with other sequenced *Taonius* species (BIN ADH3662, see Fig. 11.1). The generic diagnosis above (slightly emended from other recent diagnoses, e.g., Young, 2014a) encompasses the tentacle morphology of *T. expolitus*. If the tentacular clubs are missing, it is possible that this species could be confused with a member of *Galiteuthis*, as the two genera superficially are quite similar and some species of *Galiteuthis* also lack dentition on the arm suckers. *Taonius* can usually be distinguished from *Galiteuthis* by the lack of pointed tubercles at the ventral funnel–mantle fusion.

**Etymology:** This species is named for the smooth (toothless) margins on the arm suckers (from the Latin ‘*expolitus*’ meaning ‘smooth’), a feature unique among the presently known *Taonius* species.

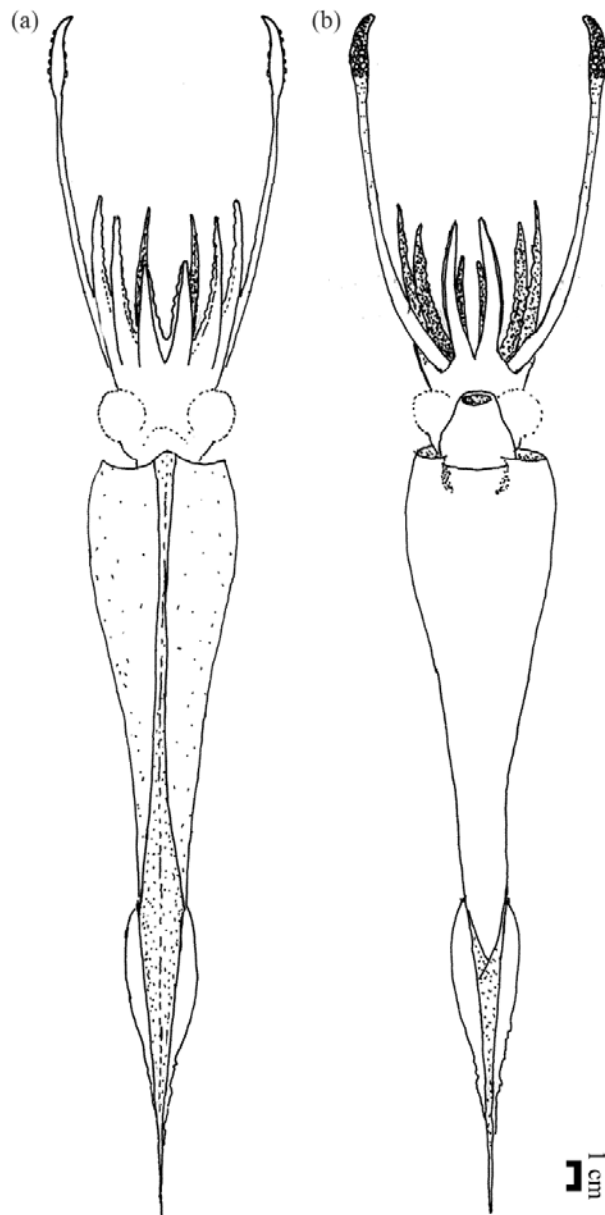


Fig. 10.8—*Taonius expolitus* sp. nov. (a) dorsal and (b) ventral view (composite illustration based on mantle and head of NIWA 95946; ML 285 mm; tentacles of NIWA 119227; CL 27 mm).



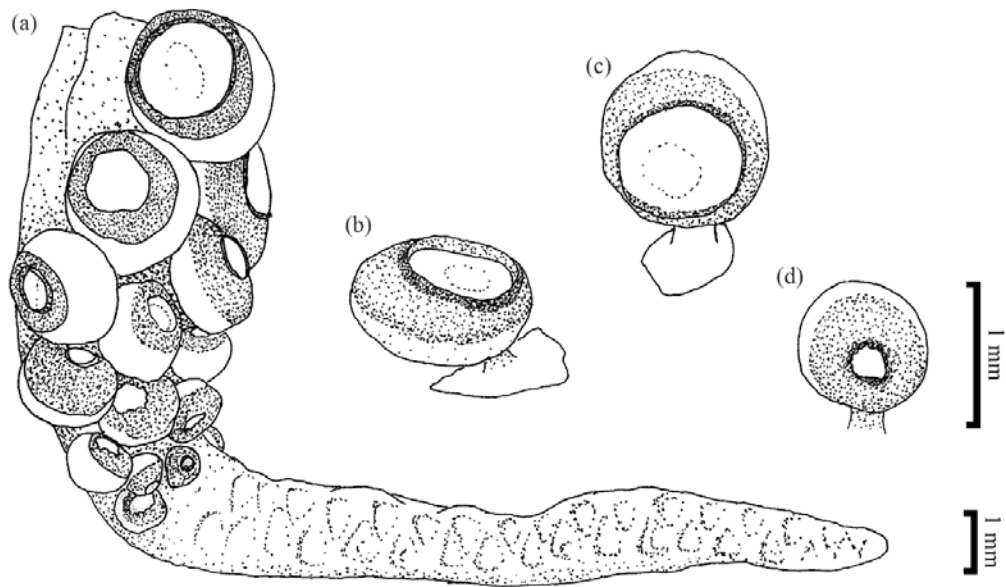


Fig. 10.9—Male *Taonius expolitus* sp. nov. arm suckers (a) hectocotylus? and (b–d) arm suckers: (b, c) medial suckers and (d) distal suckers (NIWA 95946; ML 285 mm).

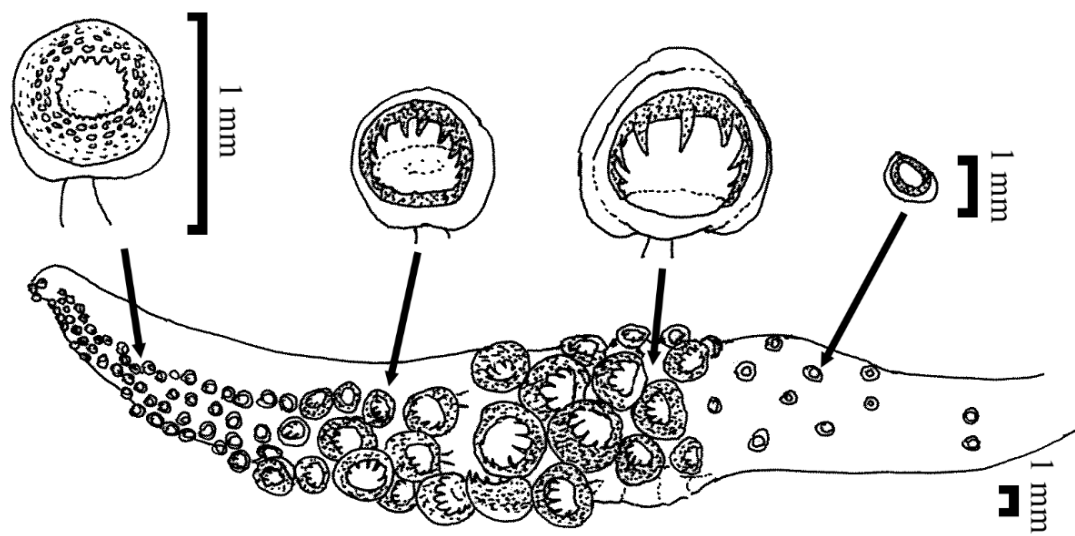


Fig. 10.10—*Taonius expolitus* sp. nov. right tentacle club and club armature (NIWA 119227; CL 27 mm).

***Taonius notalia*, sp. nov.** (Figs 10.11, 10.12, Table B23)

*Belonella* sp. Nesis, 1987: 274.

**Diagnosis:** Mantle slender (mean MW 15% ML); largest manus suckers on tentacle clubs with single enlarged primary cusp and approximately six smaller secondary cusps (usually three on each side); mid-arm suckers with 5–7 blunt teeth, basal arm suckers adentate. Gladius visible only as narrow line along dorsal midline, expands slightly at anterior margin.

**Type material:** [Holotype] **MV F54273**, ML 245 mm, 56.01°S, 155.00°W, S. E. of Tasmania, 1700 m, 29/11/1968.

**Material examined (5 specimens):** **MV F163703**, ML 307 mm, sex indet., 54.61°S, 158.74°E–54.87°S, 158.68°E, Tasmania, Macquarie Island, 802 m, 02/01/1995; **MV F163704**, ML 263 mm, sex indet., 54.72°S, 158.70°E, Tasmania, Macquarie Island, 815–875 m, 08/01/1995; **MV F163706**, ML 310 mm, sex indet., 54.72°S, 158.70°E–54.55°S 158.77°E, Tasmania, Macquarie Island, 700–915 m, FV *Austral Leader*, 29/01/1995; **ZMO, uncatalogued**: ML 265 mm, sex indet., 56.50°S, 158.70°W, 2000 m, SS *Norvegia*.

**Non-localised material examined:** **RSMAS #782-20**, ML 225, sex indet., “sub-Antarctic”, MWT, 3039 m, 20/10/63.

#### **Description:**

**Adult** (ML 225–310 mm; Figs 10.11, 10.12)—Mantle slender, MW 11–15–17% ML; fins narrow, lanceolate, FL 32–36–43% ML, FW ~13% ML. HL 8–12–17% ML, HW 10–20% ML, ED ~10% ML, inner photophore positioned slightly anteriorly. Funnel narrows to small distal aperture, FA 28% FB; ventral fusion window ‘angular’. Gladius barely visible through tissue; rachis expanded, sagittate, anterior tip pointed.

Arm formula  $III \approx II > IV > I$  (although lengths vary only slightly): Arm I 15–20–29% ML, Arm II 18–24–30% ML, Arm III 19–24–33% ML, Arm IV 16–21–27% ML. Protective membranes along entire arm length; short web present; keel absent from all arms. Arms with 18–24 sucker pairs, suckers decrease in size basal to mid-arm then increase slightly around pair 10, largest arm sucker with five to seven blunt teeth; several basal-most suckers adentate. Tentacles 32–44–61% ML, with 18 suckers. Clubs (Fig. 10.12) ~9% ML (16–23–29% TnL) with 80–100 suckers. Largest manus suckers with one enlarged primary cusp and 4–6 small secondary cusps (Fig. 10.12a).

**Known distribution:** Southern Pacific Ocean, south-east of New Zealand, possibly sub-Antarctic (Fig. 10.1). Material from this study caught between 700 and 3032 meters depth.

**Remarks:** Although both species from the highest latitudes (*T. notalia* and *T. borealis*) have similarly shaped tentacular clubs, their mantle shapes differ considerably. *Taonius borealis* is the stoutest member of this genus, while *T. notalia* has the more slender mantle (mean MW 15% ML) commonly associated with the other species in this genus. As limited material of *T. notalia* was available for study, it is difficult to infer the full geographic distribution of this species; however, it appears to overlap with *G. glacialis* (which can be differentiated by its small, spherical mantle tubercles and elongated hooks on the tentacle club). It is highly likely this was the species Nesis (1987) reported

as *Belonella* sp. from the notalian-Antarctic, since this taxon was characterised by a singular large tooth on the manus suckers and 1–5 smaller teeth along lateral ring and large protective membranes on the arms.

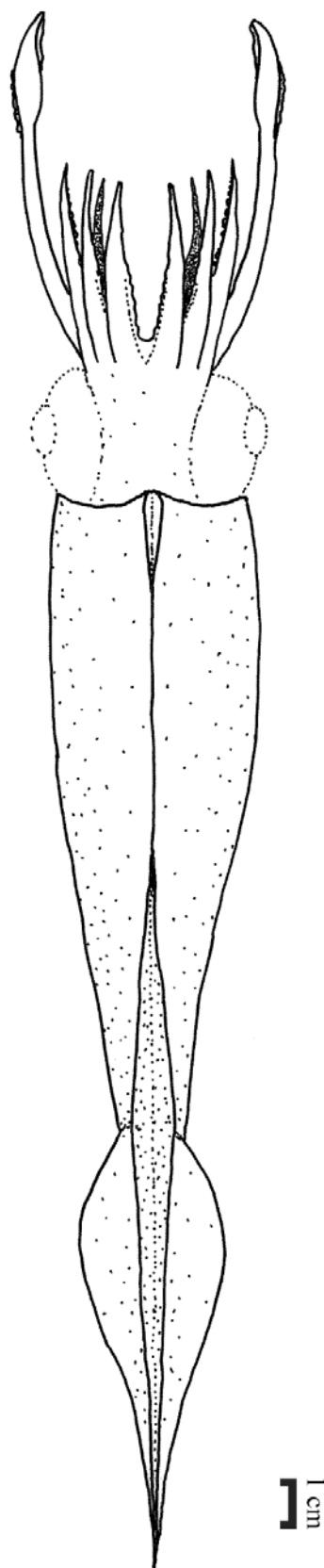


Fig. 10.11—Dorsal view of *Taonius notalia*, sp. nov. (RSMAS #782-20, ML 225 mm).

**Etymology:** The species name derives from the Notalian-Antarctic (the region of ocean between tropical waters and the Southern Ocean). This area includes southern New Zealand and Macquarie Island, where the type specimens were caught.

***Taonius robisoni*, sp. nov.** (Figs 10.13–10.16, Table B24).

*Taonius* sp. Young, 1972: 98.

**Diagnosis:** Mantle slender (mean MW 18% ML), arm suckers with three or four large blunt teeth; manus suckers with two enlarged cusps and about four smaller cusps along lateral margins. Greatest breadth of gladius conus posterior to fin insertion, gladius visible along entire dorsal mantle length.

**Type material:** [Holotype] **SBMNH 464424**, ML 143 mm, sex indet., 32.93°N, 120.42°W, USA, California, 3657 m, 16/02/1966.

**Material examined** (3 specimens): **SBMNH 464422**, ML 69 mm, sex indet., 33.38°N, 118.76°W, USA, California, Santa Catalina Island, 1280 m, 16/04/1964; **SBMNH 464421**, ML 96, sex indet., 29.97°N, 119.20°W, Mexico, Baja California, Isla Guadalupe, 07/08/1964; **SBMNH 460944**, ML 165, sex indet., 21.38°N, 158.30°W, USA, Hawaii, Oahu, FIDO XVI tow 85, 22/03/1980.

**Non-localised material examined** (1 specimen): **SBMNH 464982**, ML 210 mm, 02/10/1992.

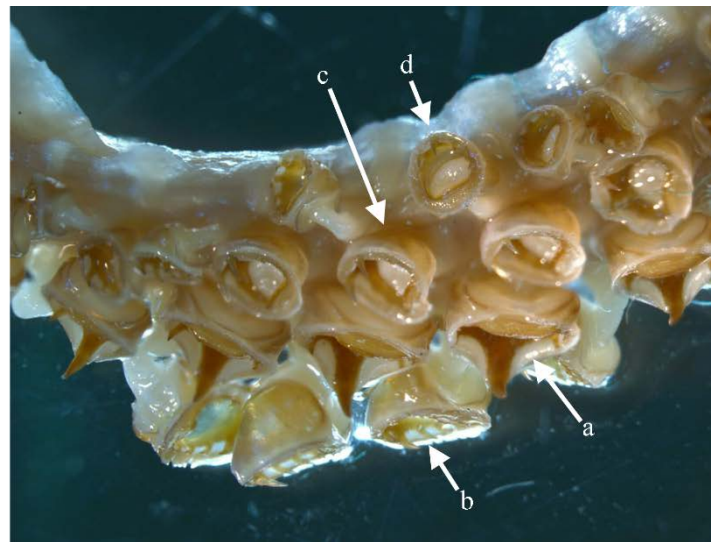
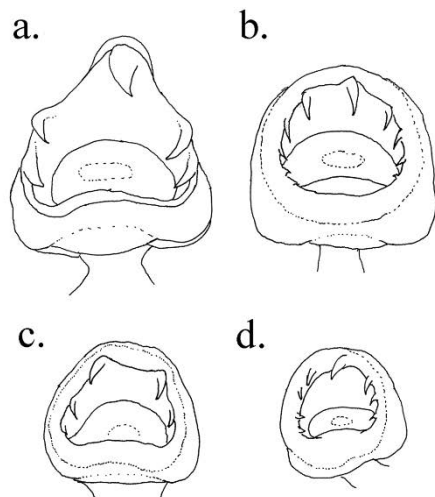


Fig. 10.12—*Taonius notalia*, sp. nov. tentacle armature (RSMAS #782-20; ML 225 mm): (left) schematic diagram of tentacular club suckers from (a,c) inner manus series and (b,d) outer manus series; (right) photograph of right tentacular club.

**Description:**

(ML 69–210 mm; Figs 10.13–10.16)—Mantle conical, MW 10–18–25% ML; gladius visible throughout mantle length, widening slightly at anterior margin; conus long, over 50% ML. Fins narrow, lanceolate, FL ~50% ML, FW 10% ML. HL 8–9–10% ML, HW 9–14–18% ML, eye diameter 4–7–10% ML with two crescentric photophores. Funnel tapers gradually from base to distal opening, funnel length 6–7–9% ML, FA 30–34–40% FB; cartilaginous fusion windows rounded (Fig. 10.14).

Arm formula  $III \geq II \geq IV > I$  (but nearly sub-equal): Arm I ~11% ML, Arm II 9–14–17% ML, Arm III 10–15–17% ML, Arm IV 10–13–16% ML. Sucker counts vary slightly, with 28–48 suckers on longest arm. Basal-most arm suckers lack dentition, sucker size increases slightly mid-arm, largest medial sucker with three or four blunt teeth (Fig. 10.13e), sucker size decreases distally, dentition remaining consistent on distal suckers. Tentacles ~35% ML; clubs (Fig. 10.15) ~5% ML (15–22% TnL) with ~60 suckers. Largest manus suckers with two enlarged primary cusps and two small secondary cusps (Fig. 10.16); smaller manus suckers with two primary cusps and six to eight smaller cusps.

**Known distribution:** Specimens examined herein from north-eastern sub-tropical Pacific Ocean (Fig. 10.1), from California to Mexico (29°N–33°N) and the Hawaiian Islands, elsewhere reported as *Taonius* sp. from southern Californian waters (Young, 1972).

**Remarks:** This taxon has, at most, four blunt teeth on the largest arm suckers and has largely been identified as *T. pavo* in museum collections. The two species do share some morphological similarities, as the holotype of *T. pavo* also has arm suckers with four or five blunt teeth on the distal ring margin. Unfortunately, the holotype of *T. pavo* lacks tentacles, so it was impossible to compare them to the clubs of *T. robisoni*; however, previous descriptions of *Taonius pavo* characterise it as having only two large curved teeth on the manus suckers, thus lacking the smaller cusps along the ring margin that are present on the manus suckers of *T. robisoni*. This is consistent with other non-type material of *T. pavo* (from the Atlantic) that I was able to examine briefly while visiting European collections. Therefore, recognition of these two species appears justified.

**Etymology:** This species is named in honour of American researcher Dr Bruce Robison, from the Monterey Bay Aquarium Research Institute (MBARI). Mid-water ecology research voyages, often led by Dr Robison, have captured fantastic ROV footage of cephalopods off the coast of California; some of the recorded *Taonius* encounters are believed to be this new species.

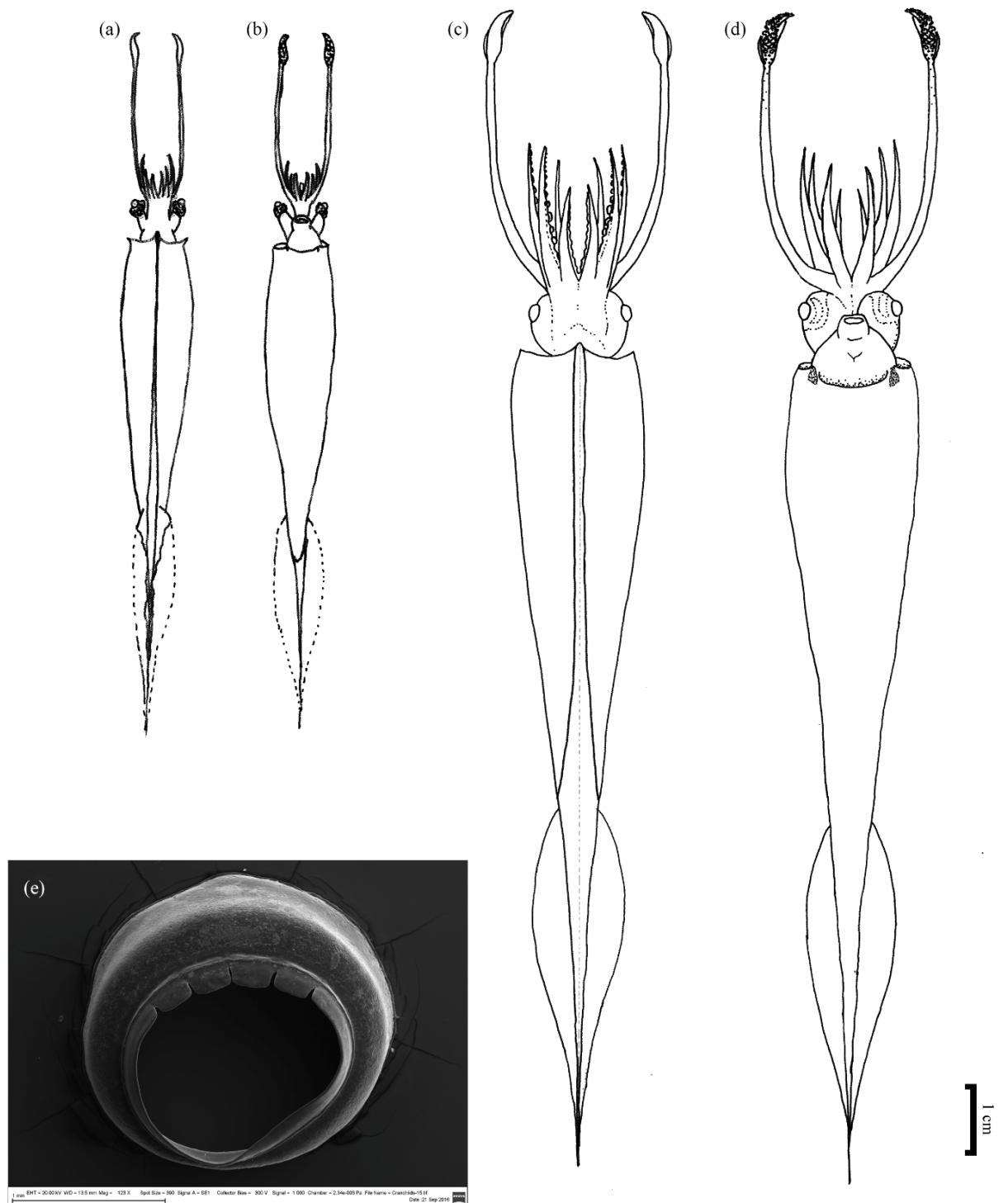


Fig. 10.13— *Taonius robisoni*, sp. nov. (a,b) juvenile (SBMNH 460944; ML 165 mm), (c–e) adult (SBMNH 464982; ML 210 mm) (a,c) dorsal and (b,d) ventral, (e) largest Arm III sucker.

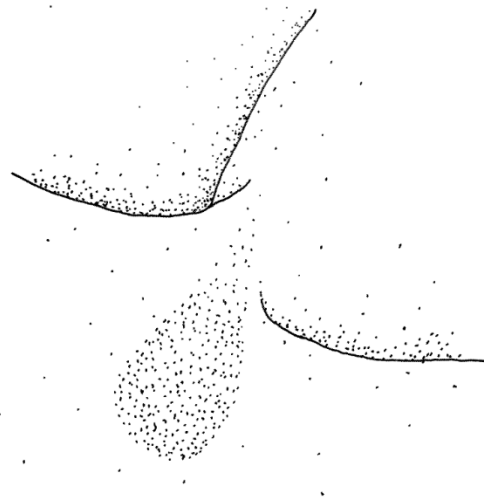


Fig. 10.14—Right funnel-mantle fusion window of *T. robisoni*, sp. nov. (SBMNH 464982, ML 210 mm).



Fig. 10.15— Right tentacle club of *T. robisoni*, sp. nov. (SBMNH 464982; ML 210 mm).

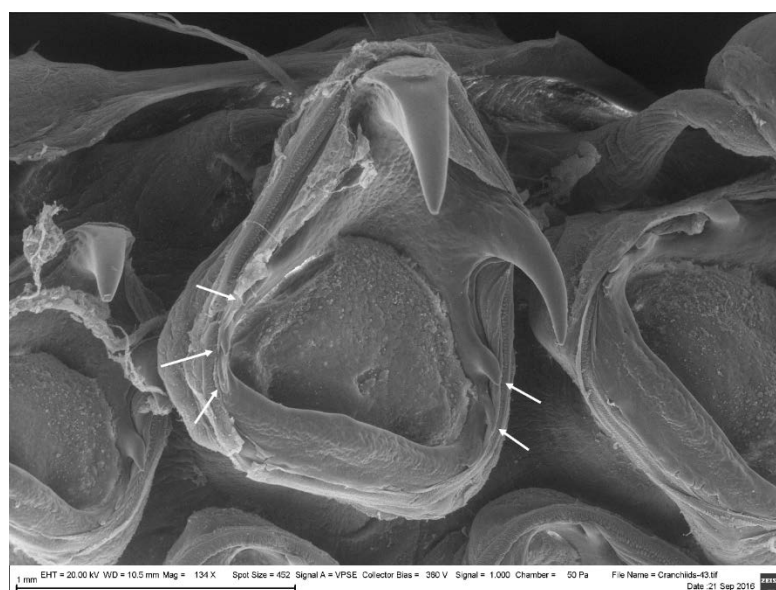


Fig 10.16— Mid-manus sucker of *Taonius robisoni*, sp. nov. (SBMNH 464982; 210 mm), arrows indicate secondary cusps.

***Taonius tanuki*, sp. nov.** (Figs 10.17–10.21, Table B25)

**Diagnosis:** Mantle slender (mean MW 19% ML); arm suckers with 12–18 blunt teeth; largest club manus suckers with two primary cusps and one or two small secondary cusps. Inner eye photophore resembles the typographical curly bracket symbol ( { ).

**Type material:** [Holotype] **NMNZ M.172913**, ML 395 mm, ♂, 29.53°S, 167.63°E, Norfolk Ridge, 200–1200 m, 15/05/2003.

**Material examined (12 specimens):** **NMNZ M.172910**, ML 453 mm, ♂, 28.83°S, 167.57°E, Norfolk Ridge, S of Norfolk Island, 1020–1045 m, RV *Tangaroa*, 16/05/2003, Stn.2003030, ethanol 80%, ff. **NMNZ M.172908** (7 specimens), ML 283, 276, 272, 270, 261, 260, 237 mm, ♂/♀, 32.43°S, 161.76°E, Lord Howe Rise SE of Lord Howe Island, 1171–1259 m, RV *Tangaroa*, Stn.2003074, 24/05/2003; **NMNZ M.09146**, ML 250 mm, sex indet., 40.07°S, 167.90°E, New Zealand, 920–922 m, RV *James Cook*, BT, Stn.J19/12/84, 14/11/1984; **NMNZ M.091403**, ML 208 mm, sex indet., 40.08°S, 168.11°E, New Zealand, 887–900 m, RV *James Cook*, BT, Stn.J19/06/84, 12/11/1984; **NMNZ M.091392**, ML 235 mm, sex indet., 44.69°S, 173.53°E, New Zealand, 700 m, RV *James Cook*, MWT, Stn.J15/52/83, 02/12/1983.

**Description:**

(ML 235–453 mm; Figs 10.17–10.21)—Mantle conical (MW 13–19–28% ML); fins narrow, lanceolate, FL 33–37–41% ML, FW <15% ML (fins damaged in majority of specimens). HL 8–13–22% ML, eyes large, ED 9% ML, HW 8–13–20% ML, with two near-crescent shaped photophores, outer photophore terminates just above arm crown, inner photophore ~40% ED, resembles curly bracket ( { ) (Fig. 10.18). Funnel narrows slightly, FA 26–49–73% FB, cartilaginous window at funnel fusion oval, curved towards ventral mid-line (Fig. 10.19).

Arms robust basally, slender distally; formula III>II>IV>I, although lengths vary only slightly: Arm I 11–18–26% ML, Arm II 15–21–30% ML, Arm III 18–24–30% ML, Arm IV 17–21–25% ML. Arms with up to 50 suckers, increasing slightly in size mid-arm, largest arm sucker with 12–18 teeth decreasing to four or five distally. Oral surface of arms narrow, causing biserial suckers to appear uniserial on proximal half of arm. Male arm modifications seen on Arms I–III (Fig. 10.20), multiple series of small oblong suckers, 25–30% arm length. Tentacles 42–57–67% ML, stalks with 11–24 pairs of adentate suckers (Fig. 10.21a). Clubs 7–9–11% ML (13–24% TnL) with 68–108 suckers. Largest manus suckers (Fig. 10.21d) with two enlarged primary cusps and one or two small secondary cusps.

**Known distribution:** Southern Pacific species presently known from Norfolk Island to southern New Zealand (28°S–45°S)(Fig. 10.1). Known from 200–1200 meters depth.

**Remarks:** Much Pacific *Taonius* material has previously been attributed to *T. 'pavo'*. The holotype of *T. pavo* (described as elongated with large eyes and short arms [Lesueur, 1821]) was examined to facilitate accurate comparisons, and while *T. pavo* and the South Pacific *Taonius* specimens share some morphological characteristics common to the genus (such as an elongated mantle and proportionally shorter arms), the holotype of *Taonius pavo* also has four square teeth on the basal arm suckers (unfortunately, the distal arm tips and tentacles had been removed). This differs from southern Pacific taxa that have at least 12 teeth (*T. tanuki*) or lack teeth (*T. expolitus*).



The recognition of this species is supported by COI. A single individual representing *T. tanuki* formed a unique BIN (BOLD:AAK0251), distinct from all other sequenced *Taonius* species including *T. pavo* (BOLD:AAM9951; the most morphologically similar species) from the Atlantic Ocean (Fig.11.1). No material was encountered in this study that appeared to represent Pacific records of *T. pavo sensu stricto*. *Taonius tanuki* does occur sympatrically with *T. expolitus*, sp. nov. around the Kermadec Islands, but *T. expolitus*, sp. nov. lacks teeth on the arm suckers, while *T. tanuki* has 12–18 blunt teeth. COI analyses of specimens representing these taxa from the Kermadec region confirm that they are genetically distinct.

**Etymology:** The tanuki is a mammal endemic to Japan, and a common trickster figure in Japanese myth and folklore, notorious for being a mischievous shape-shifter (which seems apt, given the historical systematic instability of this genus). This name additionally pays homage to the extensive Japanese contributions to cephalopod research, as was made evident at the 2015 Cephalopod International Advisory Council proceedings in Hakodate.

## Discussion

As many previous authors have noted, distinguishing among *Taonius* (and many other taoniin) species can be challenging. In the Pacific Ocean, where it appears that at least six distinct species have historically been attributed to ‘*T. pavo*’ (or less frequently *T. belone*), sucker armature (both arm and tentacle) seems to be the most reliable species-level character. In most species, mantle and fin shape and proportions are very similar, arm lengths vary only slightly, and eye photophore patterns are difficult to compare due to the delicacy of, and therefore frequent damage to, the eyes. Individual morphological characters are shared by multiple taxa, and it is often only through a combination of two or more characters that many species can be morphologically distinguished.

Historically, *Taonius pavo* was used as a cosmopolitan ‘catch-all’ name for many specimens (including some from other genera, e.g., *Galiteuthis phyllura*) that fit a broad set of characteristics: long, slender, conical mantle with lanceolate fins approximately half the length of the mantle. Lesueur’s (1821) original species, *Loligo* (*Taonius*) *pavo*, was briefly described as having an elongated and pointed mantle, being carmine-brown in colour, and having extremely large eyes that face slightly anteriorly; however, the description did not include specific details regarding sucker armature as both the distal arms and tentacles of the specimen had been removed prior to preservation. The extant holotype has deteriorated significantly; however, some of the larger remaining arm sucker rings have four or five blunt teeth on their distal margin, similar to those of *Taonius robisoni*.

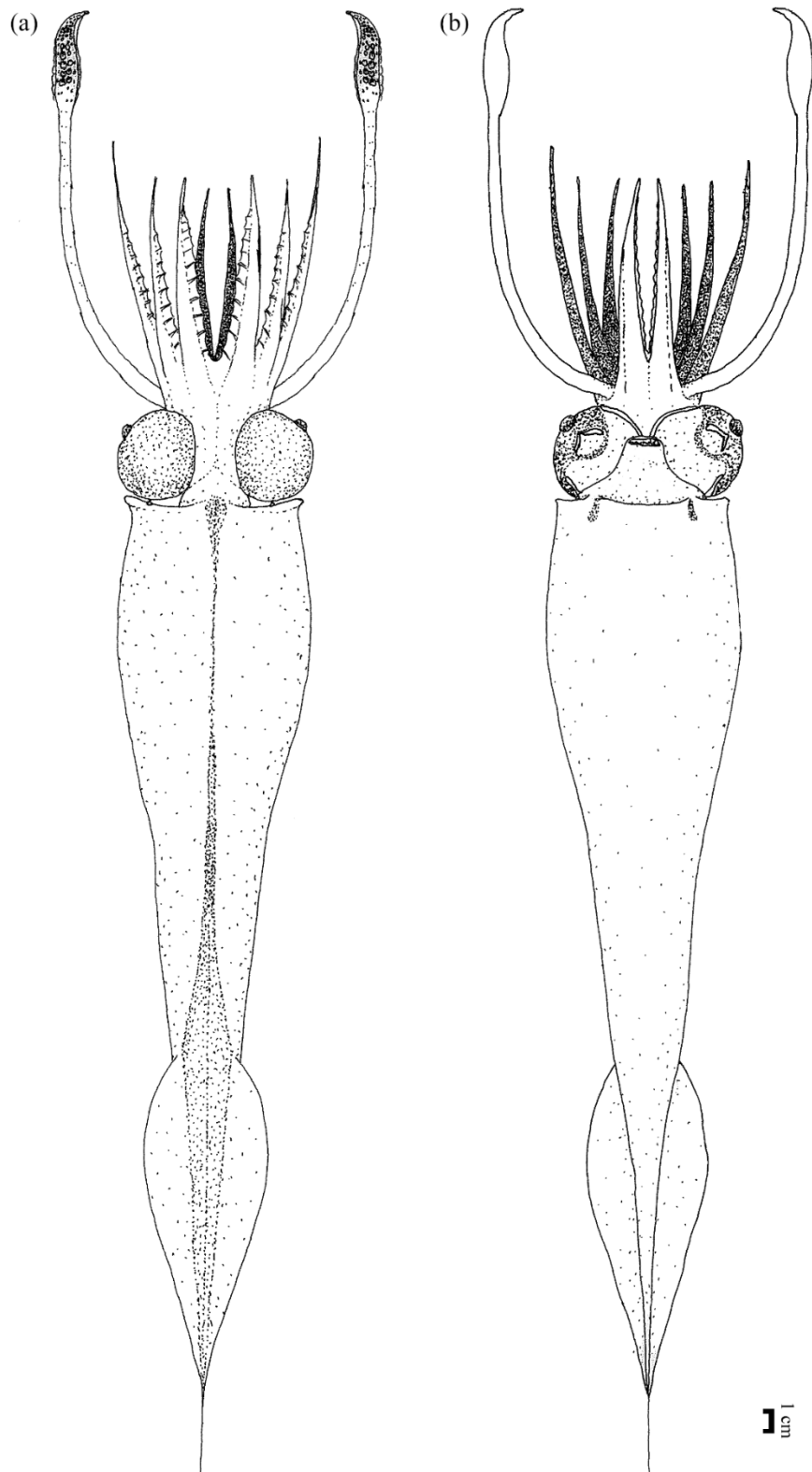


Fig. 10.17— *Taonius tanuki*, sp. nov. schematic (a) dorsal view, (b) ventral view (NMNZ M.172913; ML 395 mm).

The only locality data provided for the *T. pavo* holotype was that it was caught in ‘Sandy Bay’, somewhere along the east coast of North America. Recent authors (e.g., Young, 2014a) have examined additional, more complete specimens from the western North Atlantic and provided more detailed descriptions of the tentacle armature, which comprises two large, curved teeth on the central manus suckers, with no smaller cusps along the lateral margins. Comparative Atlantic material examined in this study (e.g., NMNH 1080249; ML 227 mm) aligned well with this description. Thus, although this material cannot be unequivocally confirmed as the same taxon described by Lesueur as ‘*L. pavo*’, a basis for comparison is established among Pacific material and Atlantic material from near the *T. pavo* type locality. A full redescription of *T. pavo* should be undertaken, and may help to finally resolve the some of the systematic challenges of this genus.

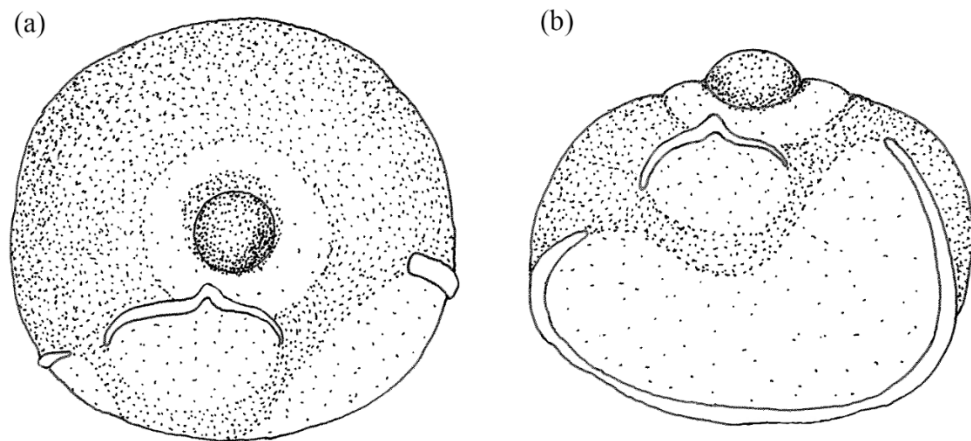


Fig. 10.18—Right eye schematic of *T. tanuki*, sp. nov. (a) lateral view, (b) ventral view (NMNZ M.172910; ML 453).

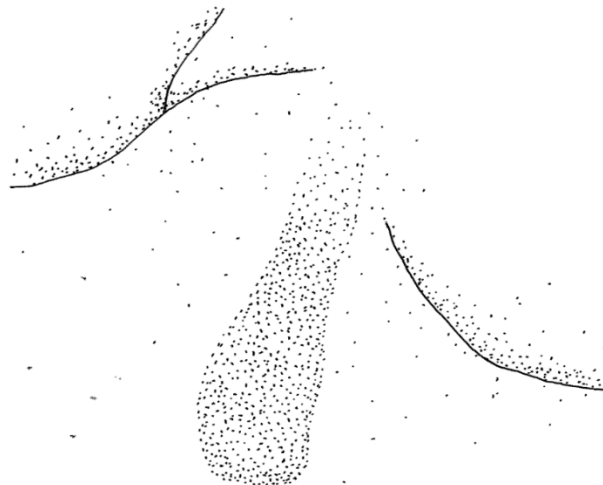


Fig. 10.19—Right funnel-mantle fusion window of *T. tanuki*, sp. nov. (NMNZ M.172938; ML 221 mm).

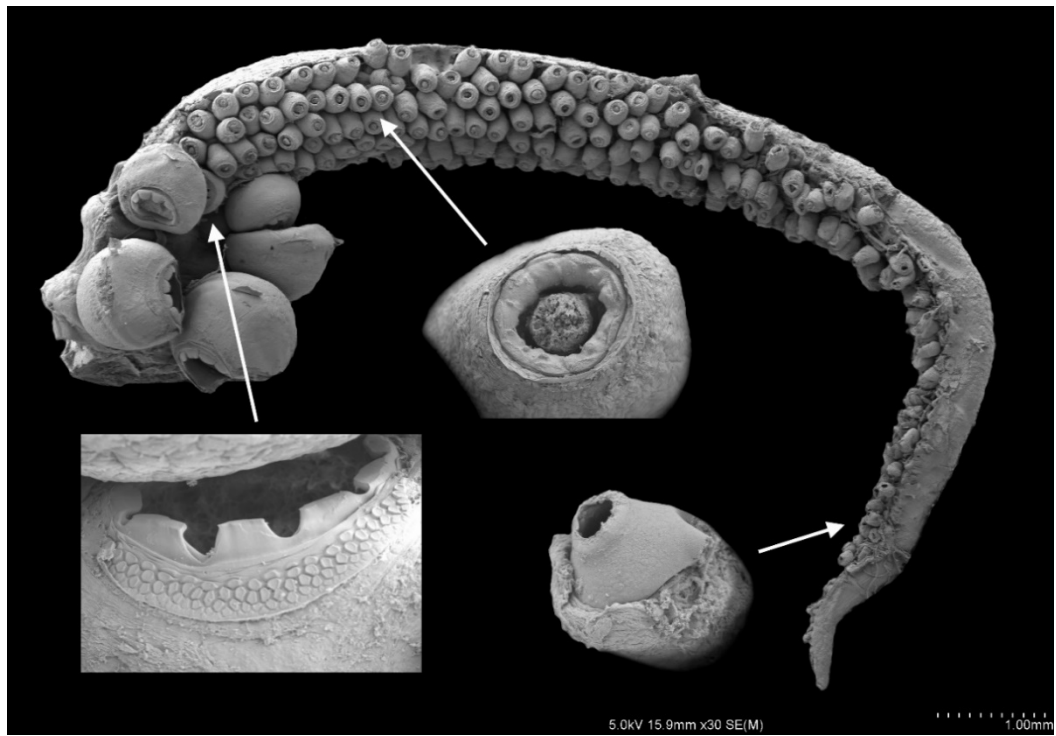


Fig. 10.20—*Taonius tanuki*, sp. nov. Arm III male modification (NMNZ 172913; ML 395 mm).

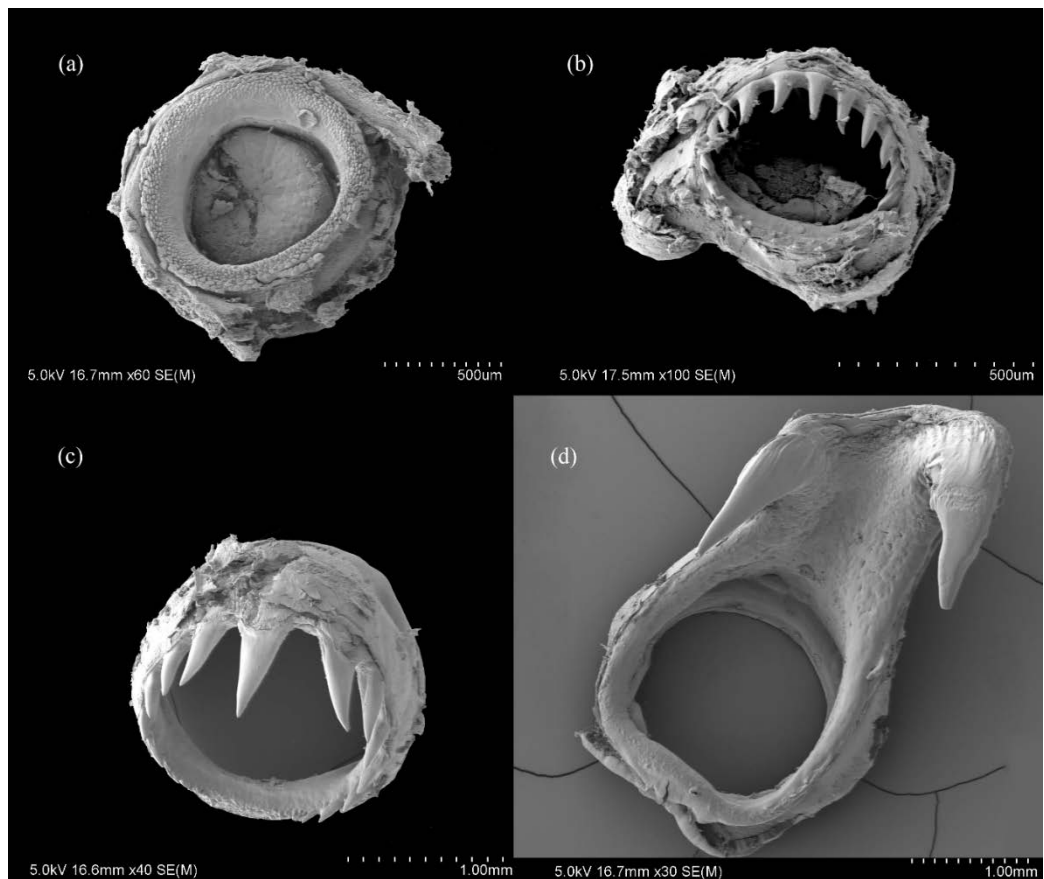


Fig. 10.21—*Taonius tanuki*, sp. nov. tentacle suckers: (a) tentacle stalk, (b) small manus sucker, (c) dactylus sucker, (d) largest manus sucker (NMNZ 172913; ML 395 mm).

The six species of *Taonius* present in the Pacific Ocean are all morphologically distinct from our current understanding of *T. pavo* (s.s.). *Taonius borealis* (Nesis, 1972) is noticeably stouter than other species of *Taonius*, and differs from *T. pavo* in that it has two enlarged primary cusps (often unequal in size) and three to six smaller cusps on the largest manus suckers. The number of teeth on the arm suckers of *T. borealis* (16–22) also differs from that observed in *T. pavo* (four or five); however, arm sucker dentition decreases distally, so care must be taken to compare suckers from similar locations on the arms. Nesis (1972) also described *T. belone* (as ‘*Belonella pacifica pacifica*’) in the Pacific Ocean. Of all known Pacific *Taonius* taxa, *T. belone* is the species most similar to *T. pavo*, possessing similar manus sucker morphology. However, *T. belone* differs in the arm sucker dentition, as the arm suckers have 20–30 small blunt teeth around the entire sucker ring margin (whereas *T. pavo* has a few teeth only on the distal margin).

This research also found four additional Pacific *Taonius* species that are morphologically distinct from the three established taxa. *Taonius robisoni* has similar arm-sucker dentition to *T. pavo* (three or four large blunt teeth distally); it has also been documented in the wild with red-brown chromatophores. However, the manus suckers of *T. robisoni* have two to four small secondary cusps along the lateral margin, which *T. pavo* lacks. The second new species described herein, *T. notalia*, sp. nov., is the first known *Taonius* species known to occur in sub-Antarctic waters. The manus suckers of this taxon resemble those of *T. borealis*; however, there is only a single primary cusp and four to six smaller secondary cusps along the lateral margins (progressively decreasing in size proximally). This species also differs from *T. borealis* in that it is long and slender (mean MW 15% ML) whereas *T. borealis* is often more stout (mean MW 27% ML). Although the available material for *T. notalia* was limited, the gladius of specimens appeared as a narrow line through the outer integument, whereas most other *Taonius* species have a gladiol vane visibly wider than two millimetres.

The two new species of *Taonius* from the waters surrounding New Zealand and Australia (*T. tanuki* and *T. expositus*) have similarly been previously reported as ‘*T. pavo*’, but are now recognised as distinct and can be morphologically distinguished as follows. *Taonius tanuki* possesses a unique combination of arm and manus sucker dentition: the largest manus suckers have two large distal cusps and one or two smaller teeth along the lateral margins, and the largest arm suckers have approximately 18 teeth which do not completely encompass the entire sucker ring margin. In addition, the inner eye photophore of *T. tanuki* resembles a pinched crescent (or a curly bracket), also a unique character within the genus. It is possible that this species may be an ontogenetic stage of *T. belone* (whose eye morphology remains poorly documented); however, as shown in Fig. 11.1, *T. tanuki* is genetically distinct from all other sequenced species of *Taonius* (BIN ADH3663). *Taonius expositus* can also be distinguished from all known congeners using both molecular and morphological characters. Although the existing material for this taxon is severely damaged, *T. expositus* is the only known *Taonius* species to lack dentition on the arm suckers. The manus suckers of this taxon also differ from other known *Taonius*, as they lack enlarged primary cusps, instead having 5–11 subequal pointed teeth set around the distal margin. Both of these characters are unique within the genus *Taonius*, and the combination of the two characters is not seen in any other cranchiid.

*Taonius* appears to be widely distributed throughout the Pacific, and sympatric species appear to occur in some regions (e.g. *T. tanuki* and *T. expolitus* in the southwestern Pacific, and *T. borealis* and *T. robisoni* off the west coast of North America). While only a single species is presently known from other regions, future research may reveal additional taxa and/or wider distributions than those currently recognised. It seems likely that, given the diversity seen in the Pacific Ocean, undescribed species remain to be discovered in other major bodies of water, and future research could focus on a worldwide systematic revision of *Taonius*.

## Genetic Analysis

Morphology has been the traditional basis for classification of taxa; however, reliance on these characters alone can be challenging as specimens can be damaged or morphologically similar, as is commonly the case with cranchiid taxa. In these instances, it can be helpful to compare molecular data to support species distinctions. This combination of physical and genetic analysis is called integrative taxonomy, and is increasingly recognised as a useful tool in differentiating cephalopod taxa (Allcock, Cooke, & Strugnell, 2011; Braid & Bolstad, 2015).

DNA sequencing can reveal taxon-specific nucleotide sequences at specific nuclear and mitochondrial loci. There are several regions which are more commonly used; however, cytochrome *c* oxidase subunit I (COI) has been shown to vary sufficiently to facilitate species-level identifications, and has assisted in the resolution of several historically unstable families of deep-sea squid (Braid et al., 2014; Braid & Bolstad, 2015; Braid et al., 2017). It has been particularly helpful in families where morphology is highly conserved (leading to cryptic taxa) and/or where specimens and their features are frequently damaged during capture. Combining molecular and morphological characters can substantially strengthen systematic revisions.

Much of the existing molecular data from the family Cranchiidae has been compiled as components of wider phylogenetic analyses of cephalopods. In many instances these molecular analyses focussed on only a single representative from a given genus, and there remains little agreement on the position of the Cranchiidae within the Oegopsida, or which families are considered the cranchiids' closest relatives. Carlini and Graves (1999) found that the two cranchiid genera they included in their phylogeny, *Cranchia* and *Liocranchia*, grouped together as a family but were not strongly supported (bootstrap value [BS] 54%); additionally, these taxa grouped in a wider clade with *Ancistrocheirus* and *Pyroteuthis*. The lack of support may have been because only two of the thirteen valid genera of this family were included. Later analyses showed stronger support for the Cranchiidae as a monophyletic family. For example, Lindgren, Pankey, Hochberg, and Oakley (2012) used a combination of five genes (COI, histone H3, 18S rRNA, 28S rRNA, and 16S rRNA) to investigate the phylogenetic relationships in the Cephalopoda. In this study, the Cranchiidae were positioned basally to most other oegopsid squids (with only the Ommastrephidae and Thysanoteuthidae being more basal), which could imply that this family diverged early in oegopsid evolution. Support was strong at the species level, with both *Leachia atlantica* and *L. lemur* having 100% bootstrap support. Each subfamily was strongly supported in this analysis (BS 90–99%) while the relationships among genera within the Taoniinae showed lower support (BS below 70%), and therefore better resolution is needed.

A recent expedition provided fresh tissue from cranchiid specimens in the south Atlantic, allowing Bolstad et al. (2015) to generate a Bayesian topology for the family Cranchiidae. This was the first instance where the phylogenetic relationships within the Cranchiidae had been analysed. Genera such as *Cranchia*, *Leachia*, *Teuthowenia*, and *Galiteuthis* were strongly supported, while others such as *Taonius* and *Helicocranchia* were weakly supported. This phylogeny also showed some distinction between the two sub-

families—although, this was not strongly supported—and there were some interesting anomalies (such as *Megalocranchia* grouping with the Cranchiinae). Although the 23 sequences used in the phylogeny from Bolstad et al. (2015) provided the most comprehensive analysis of cranchiid relationships to date, the authors concluded that further molecular and systemic research was needed to further clarify the lack of support for the deeper nodes in their phylogenetic tree.

## Methods

### *Specimens*

Sequences have been generated as part of a larger genetic study on the Cranchiids, and are included herein for comparison with the morphological characters discussed in this thesis. The specimens used in this chapter (Appendix C), were extracted, amplified, and sequenced following Braid (2017). Sequences were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007) in a project titled ‘New Zealand Cranchiids’ (project code: NZCRA). All sequences used in this analysis were added to the dataset titled ‘Molecular Analysis of the Cranchiid Squids’ (dataset code: DS-CRANCH).

### *Phylogenetic analysis*

Species boundaries were tested using the Barcode Index Number (BIN) system, which uses a clustering algorithm to generate operational taxonomic units based on COI, which have a high concordance with species (Ratnasingham & Hebert, 2013). BINs are automatically generated by BOLD for barcode sequences (Ratnasingham & Hebert, 2013). COI sequences were aligned using the Multiple Alignment using Fast Fourier Transform (MAFFT) online server (Katoh & Standley, 2013), and a neighbour-joining phylogeny was created using MEGA 7.0.26 (Kumar, Stecher, & Tamura, 2016) with the Kimura 2-parameter (K2P) model with 1000 bootstrap replicates to create an unrooted tree (Fig. 11.1).

## Results

This analysis represents the most complete phylogenetic analysis of the Cranchiidae to date (Fig. 11.1), with 34 BINs generated, and includes all the publicly available cranchiid sequences on BOLD and GenBank, as well as sequences generated for the wider genetic analysis of the cranchiids (in prep.). In *Galiteuthis*, seven BINS were recovered representing four named species (*G. glacialis*, *G. suhmi*, and *G. armata*, and *G. phyllura*), and three species with uncertain identifications (*G. sp. NZ1*, *G. sp. NZ2*, and *G. sp. KER*), which grouped together as a single clade, with low support (bootstrap support [BS] 53). The monotypic genus *Mesonychoteuthis* formed a sister relationship to this clade (BS 54), and a BIN analysis of 11 individuals revealed a single species of *M. hamiltoni*. The genus *Taonius* presently appears polyphyletic. One clade of *Taonius* species was made up of four



named species (*T. borealis*, *T. pavo*, *T. cf. robsoni*, and *T. tanuki*) and two unnamed species (*T. sp. PO1* and *T. sp. PO2*) and is strongly supported (BS 81). This clade showed a poorly supported relationship with the previously mentioned *Galliteuthis*/*Mesonychoteuthis* clade (BS 33). The other *Taonius* clade was represented by a single named species, *T. expolitus*, and showed a poorly supported sister relationship to the other *Taonius*/*Galliteuthis*/*Mesonychoteuthis* clade.

A single clade was formed of all *Teuthowenia* species, with three BINS formed representing two named species (*T. megalops* and *T. pellucida*) and one currently unnamed species (*T. aff. pellucida*) with strong support (BS 100).

The monotypic genus *Bathothauma* (represented by three specimens of *B. lyromma* representing a single BIN) formed a poorly supported clade with the unidentified species ‘Cranchiidae sp.’ (BS 46). The identity of ‘Cranchiidae sp.’ is currently considered to be a species of *Liguriella*; however, material should be morphologically examined in further detail to confirm the generic identity of these sequences. Another monotypic genus, *Sandalops*, was represented by six individuals identified as *S. melancholicus* from the Kermadec Islands region, which formed a single BIN.

*Helicocranchia* was represented by four BINs that were only identified to the genus level (*H. sp. SA*, *H. sp. RJ2009*, *H. sp. KER*, and *H. sp. NP*), which formed a single, well-supported clade (BS 83). *Megalocranchia* was represented by three BINs from one named species (*M. cf. fisheri*) and two unidentified species (*M. sp. ARL-2008* and *M. sp. PO*), which formed a well-supported clade (BS 91).

A well-supported sister-relationship was found between *Liocranchia* and *Cranchia* (BS 89). *Liocranchia* contained two BINs and was represented by one named species (*L. reinhardti*) and a presently unidentified species (*L. sp. PO*). The monotypic genus *Cranchia* was represented by six individuals of *C. scabra* from Hawaii and New Zealand, which formed a single BIN. *Leachia* formed a separate clade with three BINS that represented by three named species (*L. atlantica*, *L. lemur*, and *L. separata* sp. nov.).

## Discussion

This phylogeny is the most comprehensive comparison of cranchiid sequences to date, with 18 of the 34 taxa being sequenced for the first time. Twelve of the thirteen genera treated by Voss (1980) were recovered; no sequences were available for *Egea inermis* (the sole species in the monotypic genus *Egea*), and although *Liguriella* is thought to be present, this requires confirmation. The subfamily Taoniinae was recovered with very low support (BS 35), while the genera in the subfamily Cranchiinae did not form a single clade. However, two genera in the Cranchiinae (*Liocranchia* and *Cranchia*) formed a clade of with strong support (BS 89). There has been some speculation that these two sub-families may represent two separate families of squid; however, there is currently not enough evidence to support this separation. This phylogeny includes roughly half of the known (or hypothesised) cranchiid species, and the inclusion of additional taxa as material becomes available may well alter our understanding of the family’s relationships. In

addition, the current phylogeny was created using a single mitochondrial gene, and the relationships that were recovered may differ if more genes were included or with different types of phylogenetic analyses. However, as with any phylogeny, these results represent a hypothesis that can be tested further in the future.

In two genera, a sufficient number of representative species were included that subgroups have begun to emerge: both *Galiteuthis* and *Taonius* each appear to have clades of at least two or three particularly closely related species within them. Interestingly, *Taonius* did not form a monophyletic clade, with *T. expolitus* appearing basal to the *Galiteuthis*/*Mesonychoteuthis*/*Taonius* clade. It is likely that similar subgroups will emerge within *Leachia* (which contains seven known species, only three of which have been sequenced to date) and perhaps *Helicocranchia* (with four BINs were recovered in the present analysis, and Voss et al. (1992) have suggested that up to 14 species may exist).

For most of the previously published sequences, voucher specimens were not available for examination. It was therefore not possible to assign corresponding taxon names (for species with known morphology) to all BINs; some of the genetically distinct groupings in Fig. 11.1 will almost certainly prove to represent additional novel taxa. However, some insights can be gained and some inferences drawn from even this preliminary phylogeny. Remarks follow for each of the eleven genera represented in Fig. 11.1.

### *Bathothauma*

Although only one named species of *Bathothauma* is known, Voss et al. (1992) postulated that up to four might exist. Three specimens identified as *B. lyromma* formed a poorly supported clade with an unidentified cranchiid (BS 46). It is possible that this unidentified cranchiid represents an additional species of *Bathothauma*. At least two morphologically distinct taxa occur in Hawaiian waters and one of those is also found in (and has been sequenced from) New Zealand waters.

### *Cranchia*

The sequences of *Cranchia scabra* formed a single BIN (AAJ6514) based on COI sequences of specimens obtained from New Zealand, Hawaiian, and Japanese waters, supporting the cosmopolitan distribution of this taxon (Voss, 1980; Nesis, 1987). Unfortunately, there were no sequences available for *Enigmocranchia nipponica* (Kubodera & Okutani, 2014) for comparison, as morphological analysis has revealed similarities in *C. scabra* and *E. nipponica*.

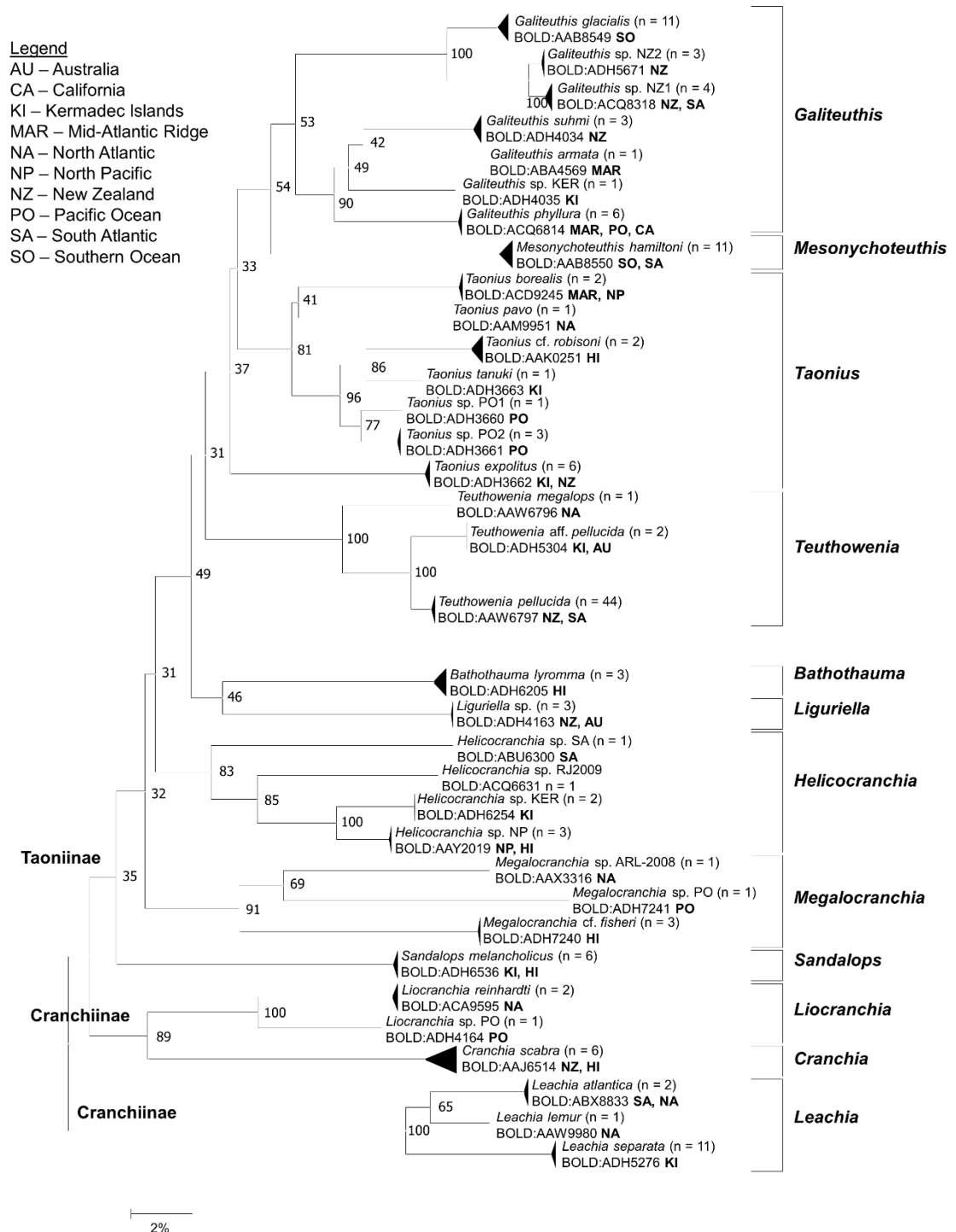


Fig. 11.1—Neighbour-joining phylogeny (K2P) for all cranchiids sequences in the present study and previously published 658 bp sequences (see Appendix C) from the mitochondrial cytochrome c oxidase subunit I region, based on 1000 bootstrap replicates. Barcode Index Numbers (BINs) are indicated.

### *Galiteuthis*

One surprising result of this analysis was the emergence of two distinct groupings within the genus *Galiteuthis*. *Galiteuthis glacialis* and two unidentified *Galiteuthis* species (both from the Chatham Rise off the east coast of New Zealand) form a distinct clade and *G. phyllura* and (what is thought to be) *G. suhmi* group together. Unfortunately, there are no known sequences of *G. pacifica*; however, should tissue from this species be obtained, this would further clarify the apparent groupings within this genus.

Six distinct BINs (likely representing species) of *Galiteuthis* were recovered in this analysis. In New Zealand, *G. suhmi* and *G. glacialis* formed distinct BINs, and, rather unexpectedly, two additional BINs were formed by several specimens from the Chatham Rise, but were encountered too recently to have been included in the morphological component of this study. In the North Pacific, *G. phyllura* has been sequenced; in the Atlantic, a sixth BIN was formed by material attributed by its collectors to *G. armata*.

### *Helicocranchia*

This genus remains challenging. In keeping with its reputation as a group of small-bodied, hard-to-identify squids, likely containing many undescribed taxa (Voss, et al., 1992), sequences from just seven individuals formed four BINs. In the Pacific, material analysed from Hawaii (BIN AAY2019) was distinct from two specimens collected in the Kermadec Islands (BIN ADH6254). Two unidentified Atlantic taxa were also available for comparison. These results support the status of this genus as one of the cranchiid groups most in need of a detailed worldwide revision.

### *Leachia*

Most published *Leachia* sequences represented Atlantic material (one BIN formed by specimens attributed by collectors to *L. lemur*, and a second BIN formed by a closely related, possibly undescribed species from the Sargasso Sea). In the Pacific, only *Leachia separata* was available for sequencing.

### *Liocranchia*

Two BINs were recovered from available material, most likely representing the two known species of *Liocranchia*: *L. reinhardti* and *L. valdiviae*; however, material from what is likely *L. valdiviae* ('unidentified' *L. sp.* PO, Fig. 11.1) was not examined during this research.

### *Megalocranchia*

Material from *Megalocranchia* was also limited and is notoriously difficult to identify. Three BINs were recovered in this analysis, but the voucher specimens could not be examined, and it would be imprudent to attribute them to any known species based solely on geography. It is possible that the Hawaiian material (BOLD:ADH7240) represented *M. cf. fisheri*, but equally possible that it did not. The remaining BINs were formed by material from Japanese waters and from the North Atlantic.

### *Mesonychoteuthis*

Eleven individuals were available for the monotypic genus *Mesonychoteuthis*, which all formed a single BIN for *M. hamiltoni*.

### *Sandalops*

Six *Sandalops* sequences from Hawaii and New Zealand formed a single BIN. Voss et al. (1992) suggested that up to four closely related species may exist, however, and comparison with additional material (particularly from the Atlantic and Indian Oceans) may provide further insight into this relatively poorly studied taxon.

### *Taonius*

Among the available *Taonius* material, six BINs were recovered, five of which were from the Pacific Ocean and showed high congruence with species identified morphologically herein. No sequences were available for *Taonius notalia* sp. nov. Two other southern Pacific species *T. expolitus* sp. nov. (from the Kermadec Islands and Eastern Australian waters) and *T. tanuki* sp. nov. (from temperate New Zealand waters) appeared genetically distinct from each other and all currently sequenced species in this genus. In the North Pacific, three BINs were formed, representing *T. borealis* (BIN ACD9245), *T. cf. robisoni* sp. nov. (BIN AAK0251, and potentially *T. belone* (BIN ADH3661), although voucher specimens for this BIN ADH3661 could not be examined so the morphological identity remains unconfirmed.

### *Teuthowenia*

Within this phylogenetic tree, the best-represented single taxon was *Teuthowenia pellucida*, which is a southern sub-tropical circumglobal species (Voss, 1985) and was represented by Pacific and Atlantic material, which formed a single BIN (BOLD:AAW6797). However, there appears to be a second sympatric species in northern New Zealand waters (herein referred to as *T. aff. pellucida*). The two specimens (one from

NIWA and the other from the Australian Museum) were not available for examination in time for inclusion within this study; therefore, future morphological analysis is required to confirm the distinct features of this potential new taxon. This phylogeny also recovered *Teuthowenia megalops* (Prosch, 1849) (a GenBank sequence from the Atlantic Ocean) as a distinct species from *T. pellucida*. Although these two species have long been understood to be morphologically distinct (Voss, 1985), this is the first time that sequences have been directly compared.

Overall, this analysis forms the most complete phylogeny of the family Cranchiidae to date. There is strong support for many of the nominal taxa, as well as evidence of several additional taxa that are likely to be new to science. However, many taxa are not yet available for sequencing, and further sampling of fresh material will be very beneficial for a more comprehensive understanding of this family.

This research compares favourably to some previous analyses of the cranchiids. For instance, the relationship between *Cranchia* and *Liocranchia* is well supported here ([BS] 89%), in comparison to Carlini and Graves (1999) who found the relationship to be weakly supported. These results (Fig. 11.1) show some similarities to the relationships found by Lindgren et al. (2012) and Bolstad et al. (2015) as *Teuthowenia*, *Liocranchia*, and *Cranchia* are still strongly supported, and there appears to be general grouping of the sub-families (as well as the hooked cranchiids). However, as the phylogenetic tree in Fig. 11.1 was created with the largest number of sequences to date, many clades formed that did not appear in any of these previous molecular analyses. The inclusion of further genetic sequences will continue to improve understanding of the relationships within this morphologically confusing family. Of equal importance is a better understanding of the position of the Cranchiidae in comparison to the rest of the Cephalopoda, as was evident in Sanchez et al. (2018).

A few particular aspects of the phylogeny presented by Sanchez et al. (2018) invite commentary. In terms of cranchiid interrelationships, several peculiarities were noted. In their Figure 1 (combined tree of all cephalopods), a clade formed by *Leachia* and *Cranchia* fell separately not only to the other Cranchiidae (including *Liocranchia*, which should be part of the same subfamily, Cranchiinae) but basal to a hypothetical clade that included all other oegopsids, plus myopsids, sepiolids, and cuttlefishes. The authors identified *Liocranchia* as being ‘misplaced’ (in that it grouped with Taoniinae, rather than with *Leachia* and *Cranchia*) but did not comment on the far more unexpected placement of these two genera basal to most of the Decabrachia. In their Figure 2 (Decabrachia), the *Leachia*–*Cranchia* clade fell within a strange grouping of oegopsid families that included Psychroteuthidae (but not its closest relative, Histiotuteuthidae), Cycloteuthidae, and some enoploteuthid genera (but not others). On this tree, *Cranchia* and *Leachia* were identified as ‘misplaced’ but their position and apparent nearest neighbours were not further discussed. The authors acknowledged that the positions of many genera conflicted with previous phylogenetic research, and previous morphological and genetic analysis has shown that *Liocranchia* and *Cranchia* appear to be closely related (Bolstad et al., 2015; Voss, 1988).

The decabrachian phylogenetic tree in Sanchez et al. (2018) was annotated with symbols that represent (mostly) morphological characteristics shared by species within, or sometimes across several, genera. This enabled comparison of select morphological data with the relationships hypothesised according to genetic characters. This type of annotation is difficult to apply to family Cranchiidae because the morphology in this family is so variable. The three morphological features attributed to some of the cranchiid genera were the funnel valve, arm or tentacle hooks, and eye photophores. The funnel valve was said to be present in *Cranchia* and absent in *Leachia*, which agrees with previous generic descriptions by Voss (1980). However, the other two morphological characters were not accurately represented. Arm/club hooks were correctly labelled as present in *Galiteuthis* and *Mesonychoteuthis* (but notably not *Taonius*, which is generally grouped as part of the hooked cranchiids as it has noticeably enlarged cusps on the manus suckers). Hooks were additionally mapped as ‘present’ in *Helicocranchia* and *Teuthowenia*, although no taxa from these genera are reported to have hooks on the arms or tentacles. Hooks were also attributed to the *Cranchia–Leachia* clade, within which *L. danae* is the only known hooked species (out of seven generally accepted species).

The mapping of photophores in the cranchiids by Sanchez et al. (2018) also created some confusion. They listed the possible decabrachian photophore character states as: Absent, Present/external (mantle, arms), and Present/internal (viscera). It is unclear whether the ventral eye photophores common to many oegopsid genera—*Brachioteuthis*, *Chroteuthis*, and all 13 cranchiid genera (see, e.g., Herring, Dilly, & Cope, 2006), to name a few—were overlooked, or simply deemed unimportant. If ‘external photophores’ does only specifically refer to those present on the mantle and/or arms, then the symbol indicating presence in *Teuthowenia* is erroneous (and has been incorrectly mapped for a number of other taxa including *Chroteuthis*, *Mastigoteuthis*, *Octopoteuthis*, and all enoploteuthid and pyroteuthid genera). The placement of many of the symbols on the phylogenetic tree of Sanchez et al. (2018) was not entirely clear, as often these symbols were placed in areas with very little free space. The combined visualisation of genetic and morphological data can be powerful (e.g., Braid & Bolstad, 2015; Bolstad et al., 2018), but care must be taken that morphological characters are accurately and unambiguously mapped. Unfortunately, in this case, inaccuracies in character mapping and genus placement within the Oegopsida may suggest artificial uncertainties in cranchiid systematics, where in fact the family’s stability is finally improving.

## Concluding Discussion

Due to the problematic nature of Cranchiidae taxonomy, this is the first systematic review of any kind in nearly 40 years (with the most recent major revision being undertaken by Voss [1980]). This research examined over 400 specimens collected throughout the Pacific (plus comparative Atlantic material) and, as per the hypothesis, re-describes 21 species from 10 genera, names and describes five novel taxa, and reports four additional morphotypes that may prove to represent new species, pending additional observations and material. The descriptions of ontogenetic stages for previously described species provide detailed morphometric indices and helpful characters for differentiating among taxa at various stages of development (including previously undescribed systematically important male modifications). Finally, this research presents a preliminary phylogeny of the family and more than doubles the number of COI sequences publicly available on the Barcode of Life Data System (BOLD).

The results herein compare favourably to the (relatively few) recently published studies of this family. Voss (1980) concluded that 13 of the nominal 41 genera were valid within the family Cranchiidae and that the family itself should be divided into two sub-families, the Cranchiinae and Taoniinae (as originally proposed by Pfeffer, 1912). This study found general support for generic distinctions of Voss (1980) (however, no *Egea* material was examined in this present research), and supports the division, both by morphological and molecular traits, between the two sub-families.

Further study by Voss et al. (1992) resulted in the identification of some useful morphological characters for several taxa within the Cranchiidae, but this work was primarily focussed on paralarval morphology and did not go into significant detail regarding species-level distinctions. Additionally, in the remarks section of each generic description, Voss provided hypotheses regarding the total number of taxa globally, several of which have been encountered and described in this research (e.g. *Bathothauma* sp. HI and several species of *Taonius*), and many others of which remain undescribed. Voss et al. (1992) speculated that *Taonius* was made up of five species globally, an uncharacteristic underestimate; however, there are at least six distinct species now recognised in the Pacific Ocean alone. Similarly, *Galiteuthis* was believed to have around six species globally. The present study re-describes four known species from the Pacific Ocean, but genetic analysis indicates that two more are likely present in the South Pacific; therefore, it is possible that this genus could also have been underestimated in previous literature. Both *Bathothauma* and *Liguriella* were thought to have multiple species (Voss, et al., 1992); unfortunately, there was not enough material to confirm the number of Pacific species of *Liguriella*, although a new species of *Bathothauma* has been hypothesised herein, due to the unique morphology of the male arm modifications. Some of the distinctions made by Voss et al. (1992) remain to be confirmed. For instance, they proposed that *Sandalops* contained three or four species; however, the current research was only able to identify one through both morphology and limited molecular sequencing (from both the New Zealand region and Hawaii).

Currently, one of the most up-to-date repositories for worldwide cephalopod diversity and taxonomic information is the online Tree of Life web project



(www.tolweb.org). This web database provides some preliminary information regarding genus-level characters and some specific characters for some of the taxa within the family; however, as there has been little taxonomic work undertaken on this family in recent years, Tolweb pages for many taxa are still lacking substantial detail. Several genera (especially those thought to have been monotypic), such as *Cranchia*, *Liocranchia*, *Bathothauma*, and *Sandalops*, have information on distinguishing characters, life history information (although this is often very minimal), and geographic and vertical distribution records. Other genera, like *Leachia*, *Taonius*, *Galiteuthis*, and *Helicocranchia*, include this information for some species, while others are named only. Information is provided at the generic level for *Megalocranchia*, but due to the systematic instability of this family no specific information is available for any of the currently accepted taxa. This research will provide additional details for many of the unpopulated species pages, and provide character descriptions for several taxa that do not yet have any information.

#### *Relatively Stable Genera:*

The systematics of several of the cranchiid genera were not altered by this revision; however, the descriptions provided in this research have added significant detail to our knowledge of the morphology of these taxa. Both *Cranchia* and *Liocranchia* have been well-established genera, with comparatively few invalid taxa being described throughout history. *Cranchia* remains monotypic; little morphological variation was observed across material from a wide geographic range, and all sequenced *Cranchia* material (including Pacific and Atlantic specimens) fall within a single BIN (AAJ6514). The *Liocranchia* material examined herein is also consistent with the previous morphological descriptions of the two known species. Although both of these genera appear stable, given the limited understanding of the Cranchiidae, further research may identify additional morphologically similar, or cryptic species.

*Sandalops* is another genus believed to be monotypic. Morphological analysis of material from around the Pacific supported this; however, many specimens examined lacked tentacles, whose morphology can reveal specific differences in some other cranchiid genera specific variations. Morphological and molecular comparisons among Atlantic, Pacific, and Indian material would provide further insight into *Sandalops*' taxonomy and zoogeography.

Species of *Galiteuthis* in the Pacific Ocean appear to be well described and systematically stable; however, like several of the other genera already discussed, further examination of Atlantic material may reveal the presence of new taxa. Currently, *G. armata* is the only accepted species from the Atlantic Ocean; however, given the diversity seen in the Pacific (four accepted species), it is possible that additional taxa may be discovered in the other oceans as well.

#### *Some instability/More work needed:*

The known diversity of several genera has increased as a direct result of this research. Three species of *Leachia*: *L. danae*, *L. dislocata*, and *L. pacifica*, were redescribed, although more material of *L. pacifica* should be examined to gain a better understanding of its morphological changes throughout ontogeny. One new species of *Leachia*, *L. separata*, was recognised and a second species is hypothesized from New Zealand waters. As only two specimens of this second species were available for examination (one of which was badly damaged) it would be premature to describe this as a new species, especially given the vast array of junior synonyms already attributed to this genus. *Leachia cyclura*, a species previously considered to be circumglobal, was not identified in the material examined herein, and several additional proposed taxa from this genus are considered *nomen dubia*, due to type descriptions lacking sufficient details (see Discussion in Chapter 2).

Like *Leachia*, the known diversity of *Taonius* has increased (in fact, more than doubled) through the descriptions of *T. robisoni*, *T. tanuki*, *T. notalia*, and *T. expolitus*. These four new species each have unique combinations of characters not seen in the three currently accepted *Taonius* taxa. Through the recognition of *T. notalia*, the known range of *Taonius* has also been extended into the Southern Ocean.

In *Bathothauma*, *Helicocranchia*, and *Megalocranchia*, material was examined that suggested the existence of unnamed species, but these have not been formally described or named due to the limited number of specimens known at present. *Bathothauma*, for instance, has long been considered monotypic; however, two specimens from the central Pacific had morphological characters that distinguished them from the original description of *Bathothauma lyromma*. These specimens (presently called *Bathothauma* sp. HI) appeared to have proportionally fewer teeth on the arm sucker rings, and the male had modified elongated Arms I with two series of swollen suckers along most of the arm length.

In the genus *Helicocranchia*, morphological differences were observed in northern Pacific and southern Pacific material. The Californian and Hawaiian specimens agree with published descriptions of the North Atlantic *H. pfefferi* and have been attributed to this name (although further research on this genus, including molecular characters, may well separate these groups in the future). Given the high number of hypothesized species in this genus (see Voss et al. 1992), the New Zealand/Australian material (herein called *Helicocranchia* sp. 'NZ') will likely prove novel, but without additional comparative material from other oceans and a better understanding of species-level characters in this genus, formal description would be premature.

Similarly, *Megalocranchia* remains in need of further (ideally, global) revision. Although there were several apparent morphologically distinct species examined in the present work, prior descriptions of species in this genus often lacked specific details regarding morphological characters. Earlier revisions focussed solely on the presence of the internal photophore and few details were recorded of other potentially useful characters (such as ventral ocular photophore shape or sucker dentition). This lack of detail made species-level identifications in this study challenging, and several of the *Megalocranchia* species reported herein may be later reidentified, or may split into several regional species.

when more specimens become available (as was stated in chapter 8). An important next step in resolving relationship within this genus will be examining material from the Atlantic and western Indian Oceans (around the Cape of Good Hope), as several type specimens were described from those regions; Pacific material can then be re-examined subsequently, to determine which taxa, if any, occur across the Atlantic, Indian, and Pacific Oceans.

Although this research supported the validity of the two currently accepted species of *Liguriella* (*L. podophthalma* and *L. pardus*), the material available for study for both species was extremely limited. Voss et al. (1992) hypothesized that ‘several’ species of *Liguriella* existed globally; however, this research has only identified two species, one of which (*L. pardus*) was provisionally placed into the genus until further material can be examined. The data collected herein for *L. pardus* was based solely on the type material, making it difficult to infer the systematic placement of this taxon. *Liguriella* remains one of the most enigmatic and poorly understood genera in this enigmatic and poorly understood family.

Three of the 13 genera considered valid by Voss (1980), which was the last generic revision of this family, were not examined. *Teuthowenia pellucida*, which is the only species of *Teuthowenia* reported to date from the Pacific Ocean, was recently reviewed based on material from the New Zealand region by Evans and Bolstad (2014). Preliminary molecular analyses (see Fig. 11.1) now suggest that a second *Teuthowenia* species may, in fact, co-occur with *T. pellucida* in far northern New Zealand waters. However, sufficient material is not yet available to examine the morphology of this purported taxon’s morphology and compare it in detail with *T. pellucida*. The two remaining genera are both believed to be monotypic and are not known from the Pacific Ocean: *Egea inermis* is believed to be a species found only in the Atlantic and *Mesonychoteuthis hamiltoni* is known only from Antarctic waters. No material examined in this study appeared referable to either of these species and these genera were accordingly not treated herein.

#### *Characters:*

Cranchiids can be difficult to identify morphologically, even to a generic level; however, certain morphological characters (such as fin shape and eye photophore arrangement) can assist in this process. The fins can be round, lanceolate, lobed, or sagittate, and these morphological differences can assist in identifying a specimen to genus (or to a limited number of genera). Mantle proportions can also be a useful character at the generic level, as some cranchiid genera are stout and round (e.g. *Cranchia*, *Helicocranchia*, or *Sandalops*) while others are more slender and elongated (e.g. *Taonius*, *Galiteuthis*, or *Leachia*). This character can be more variable due to the elasticity of the cranchiid mantle, and possible distortion during capture and preservation, but can be a useful first step in narrowing possible genera when making an identification.

Previous literature rarely mentions the ventral cartilaginous windows (outside of the Cranchiinae). This character is more noticeable in the subfamily Cranchiinae (as both *Liocranchia* and *Leachia* have long, tuberculate cartilaginous strips); however, the cartilaginous areas (called ‘windows’ due to their translucent nature once preserved) can be

useful in generic level determinations in the Taoniinae as well. For instance, *Megalocranchia* has a distinctive ‘wing-shaped’ window (Fig. 8.4) which can be used for identifying this genus even before locating the internal photophores. Those of *Taonius* and *Liguriella* were often elongated and rounded (Figs. 7.5, 10.8), while those of *Galiteuthis* were usually more triangular in shape (Fig. 5.10a) (although *Galiteuthis* did have the most variability in ventral window shape). *Sandalops* often has very narrow windows, usually appearing as short lines or ovals, while *Helicocranchia* and *Bathothauma* often lack ventral windows altogether. Rachis window shape can also be helpful in distinguishing genera, but to a lesser extent. The rachis window in both *Taonius* and *Galiteuthis* expands anteriorly; in *Taonius* this expansion continues directly to the mantle margin, while in *Galiteuthis* the rachis curves outward, slightly before the margin, giving the rachis a lobed appearance. *Megalocranchia* and *Liguriella* both have an ovate or diamond-shaped rachis window (in *Megalocranchia* this translucent area occurs just posterior to the anterior margin, with the narrow visible gladius continuing on to the margin itself, while in all other genera the expanded rachis is located directly at the anterior margin). *Sandalops*, *Helicocranchia* and *Bathothauma* show significantly less expansion in the rachis area, often with the visible glacial line only expanding slightly, or with a very narrow oval at the anterior margin.

Characters that can be helpful for distinguishing among species often require the use of a microscope, as they are usually quite small. In some genera (e.g. *Liocranchia*, *Galiteuthis*, and *Leachia*) the presence, location, and shape of tubercles can distinguish among taxa. For instance, Table 5 shows that the presence of dorsal tubercles can distinguish *L. reinhardti* from *L. valdiviae*. This research has also shown how sucker dentition (both arm and tentacle club) can be a useful character for distinguishing between species. In *Taonius*, the morphology of the tentacle clubs’ largest manus suckers are extremely important for distinguishing among *Taonius* species (Table 9), and in almost all genera, arm sucker dentition (both tooth shape and number) was helpful in distinguishing between species. Although eye photophores can be a character for distinguishing among genera and (to a lesser extent) species of Taoniinae, this character is most helpful in distinguishing between Cranchiinae taxa. Species of *Leachia* and *Liocranchia* have different numbers of ocular photophores that can be used to identify species (Tables 4, 5). However, many of the above features are easily damaged during capture, handling, and (to a lesser extent) preservation. If damage has occurred (as is the case with all largely soft-bodied animals) species identification may be difficult.

#### *Pacific Biodiversity:*

As has been shown throughout this research, the systematics of the family Cranchiidae has been historically unstable, leading to a large number of previously proposed taxa and genera ultimately being considered invalid (Voss, 1980). None of the available names that have been considered junior synonyms by previous authors could be confidently resurrected for any of the apparently novel taxa recognised in this study. For this reason, new species are described herein from several genera. Further systematic research, particularly using an integrative approach, may uncover additional new species. Several newly described taxa, such as *Taonius robisoni* and *Leachia separata*, had been

documented previously (either in historical descriptions or on digital media), but had been attributed incorrectly to known species. These have now been recognised as distinct species and named accordingly, in the hopes of improving the accuracy of our zoogeographic knowledge of the Cranchiidae.

Too little information is available to identify with any confidence possible areas of particularly high cranchiid diversity in the Pacific. Regions with apparently higher biodiversity have often been the focus of targeted sampling efforts (such as the Hawaiian Islands, or the Kermadec Islands between New Zealand and Tonga); many other regions are likely no less diverse, but may appear so at present as an artefact of low sampling effort. It is likely that cranchiid diversity decreases toward polar regions (a trend that is fairly common for most cephalopod families; Rosa, Dierssen, Gonzalez, & Seibel, 2008). At present, this proves true in the Cranchiidae, as only two cranchiid species are known from the northern Pacific north of 40°N (*Taonius borealis* and *Galiteuthis phyllura*) while only three have been found in the southern Pacific, south of 60°S (*Galiteuthis glacialis*, *Mesonychoteuthis hamiltoni*, and *Taonius notalia*). In contrast, material representing 18 species was examined in this study from tropical Pacific waters. With our current, limited knowledge of cranchiid distribution, it is unwise to make any further claims to whether certain areas of the Pacific are more diverse than others.

It is marginally more plausible to comment on vertical distribution trends in the family. It has been generally shown that cranchiid squid undergo ontogenetic descent, with paralarvae most often encountered in epipelagic waters, moving deeper into the water column as they grow (and presumably mature). This behaviour has been reported for *Galiteuthis phyllura* (Roper and Young, 1975), *Leachia pacifica* and *Bathothauma lyromma* (Young, 1978), and *Teuthowenia pellucida* (Voss, 1985; Evans, 2013). Although there was limited material available for smaller paralarval size ranges in this research, *Leachia dislocata*, *Liocranchia reinhardti*, *Bathothauma lyromma*, and *Taonius borealis*, all appear to show ontogenetic descent with increased size (Figs 2.13, 3.2, 4.7, 10.2). *Helicocranchia pfefferi* and *Leachia separata* both show no apparent difference in vertical distribution over a range of sizes (Figs 2.15, 6.4); many of these were additionally collected using non-closing nets, rendering the depth of capture uncertain. Insufficient depth records are available at present to draw any conclusions regarding depth distributions in the remaining Pacific cranchiids.

#### *Ecology:*

Very little is known regarding the ecology or trophic roles cranchiid squid play in marine ecosystems. Some, such as *Mesonychoteuthis hamiltoni*, have been previously shown to make up a high proportion of whale diets in some regions (Clarke, 1980). However, *M. hamiltoni* is significantly larger than most other members of this family and likely occupies an atypical trophic niche, and should probably not be used to infer possible trophic roles of the smaller species in the family. In predator gut contents, beaks from cranchiid squid can be numerous but often represent a much lower percentage of wet weight (West, Walker, Baird, Mead, & Collins, 2017), presumably due their ‘relatively’

smaller size, and the gelatinous nature of their tissue. The family Cranchiidae has been shown to be abundant in predator diets and several species, such as *Taonius 'pavo'* or *Teuthowenia megalops* are often listed as prey in ecological studies of marine mammals (MacLeod, Santos, & Pierce, 2003), sometimes constituting up to 60% of the predator's diet. *Taonius 'pavo'*, in particular, appears in ecological studies from both the Atlantic and Pacific Ocean, indicating a need for further research into beak morphology for commonly preyed upon taxa. Hopefully, this research will enable more accurate appraisal of the trophic roles of *Taonius* species, by recognising the presence of four additional species from the Pacific Ocean. Given the delicate nature of their tissue and our limited knowledge of cranchiid beaks, identifying specimens from gut contents can be challenging. Some preliminary work has been done on beak morphology (Imber, 1978; Clarke & Roper, 1998), but the systematic instability of the family has made it challenging to correctly match beaks to species. Where material was available (e.g., *Leachia dislocata*, *Galiteuthis pacifica*, *Sandalops melancholicus*) this study has reported beak morphology, but for many taxa this has not yet been possible. Hopefully this can be rectified in the future now that there is a greater understanding of the species present in the Pacific Ocean.

Even less is known about the reproductive strategies of the cranchiids. Voss (1980) provided some explanation of the secondary sexual modifications present in males and females of each genus; observations made herein generally agree with her descriptions, and in some cases species-level characters could also be reported (e.g., *Leachia danae*). Males of the Cranchiinae generally show an enlarged arm tip (of a single arm), that curls in on itself and bears reduced suckers. The most extreme example of this modification known to date is seen on males of *L. danae* (Fig. 2.3b), where the curved arm tip also has a widened membrane along the aboral surface, making it appear disc-like. Mature males of the Taoniinae possess one or more modified arm pairs, and show greater variation in hectocotylus morphology. Many taxa (such as *Taonius*, *Helicocranchia*, *Teuthowenia* and *Bathothauma*) often have modified arms that have two series of suckers proximally and four series of smaller, elongated suckers on the distal third of one or more arm pairs. In several taxa, the relative length and/or armature of the modified arms varied further. In *Bathothauma* sp. HI nearly the entire length of Arms I is modified, possessing two series of enlarged swollen suckers (Fig. 4.10). *Galiteuthis suhmi* has large flattened papillae on the distal third of the arm (Fig. 5.20). *Taonius expolitus* sp. nov. appears to lack suckers on the arm modification altogether, instead having only triangular pads on Arms I–III (Fig. 10.9); however, it is unclear yet whether this modification is natural or the result of damage. Overall, very few mature females were examined in collections; however, those that were seem appeared very similar to *Teuthowenia pellucida* (Evans & Bolstad, 2014), wherein spermatangia were implanted into the mantle and head tissue and small suckers were encysted into the inner surface of the mantle cavity (observed in spent specimens of *Taonius* and *Galiteuthis*). However, aside from that, very little is known regarding the mating and spawning habits of taxa in this family.

### *Limitations:*

Taxonomic studies are necessarily limited by the material available for study. Cranchiids are a particularly difficult group due to their combination of high species diversity, relatively poor representation in many collections, and the delicate nature of their tissues, often leading to significant damage on capture and further distortion through preservation. Ideally, this study would have provided detailed descriptions of all ontogenetic stages of each species, as was done by Evans and Bolstad (2014) for *Teuthowenia pellucida*, but this is not yet possible for many taxa due to a lack of available paralarval material. The morphology of paralarval cranchiids remains even more poorly understood than that of adults, and many appear morphologically similar upon preliminary examination. The most accurate method for identifying these specimens is to compare morphological features among progressively smaller specimens (starting from an adult); however, the material examined herein was often limited to larger sizes (with the smallest specimens being around 30 mm ML in many taxa). Many of the paralarval specimens encountered in collections had (understandably) only been identified to family, making them harder to place in a specific taxon.

Many cranchiid squid are damaged during capture, due to the fragile and gelatinous nature of their tissue, so much of the material examined is in poor condition. Cranchiid squid are typically easier to examine once they have been preserved, as the fresh tissue is often delicate, soft, and flaccid (often making them appear like a crumpled plastic bag or deflated balloon). The preservation process, while firming up the mantle tissue and allowing better examination of some morphological characters, may also distort and shrivel the body, and fracture the gladius. The large, bulbous eyes that characterise many genera of cranchiid were often imploded or missing entirely. This created many problems, given the value of eye photophore patterns in specific identification.

Specimens were primarily examined from New Zealand, Australia, Japan, and the west coast of North America, with a smaller number of specimens being examined from the central Pacific Ocean. Little material was available from the west coast of South America or the western-tropical Pacific; the Hawaiian region was also relatively poorly represented in available material. Given the regional diversity seen herein (particularly in genera such as *Leachia* and *Taonius*), it would not be surprising to see further new species described from these areas. Several type specimens (many of which were synonymised with other taxa by Nesis, 1987) had previously been described from these areas, and it is unfortunate that this material has not been examined recently (or in some instances is no longer extant).

### *Future directions:*

Most, if not all, of the genera within the family Cranchiidae would be further stabilised by global generic revisions, examining and directly comparing material from all oceans. The ability to compare species between the Atlantic and Pacific Oceans would help to clarify species delineations made in previous revisions, and provided further insight into genera thought to be monotypic (such as *Sandalops* and *Egea*). Several taxa (*Cranchia scabra*, *Bathothauma lyromma*, *Liguriella podophthalma*, and *Sandalops melancholicus*)

were thought to be cosmopolitan monotypic species; however, a least two of these genera (*Bathothauma* and *Liguriella*) have been shown in this study to comprise at least two species. This shows the importance of comparative taxonomy, as many of the accepted cranchiid taxa were described from the Atlantic Ocean. It may be found, given further systematic research that *Cranchia* and *Sandalops* also differ between these two major bodies of water.

In addition, this research focussed primarily on the external morphology of the taxa. Internal structures, such as beak and radula morphology, can be useful in ecological and trophic studies, and more focus should be placed on those features to progress our knowledge of the Pacific cranchiids. Other features of internal anatomy, such as the structure of the gills, viscera, mantle chambers and coelom may also prove useful. Further observations on reproductive structures, when available, will likely also prove invaluable.

This study has contributed significantly to the stability of the notoriously problematic family Cranchiidae in the Pacific region, by providing detailed descriptions of its known (and several new) species. However, it is clear that this will be far from the last word on these taxa, as much remains to be learned about their ontogeny, distribution, ecology, biology, and global distribution. It is likely that some species found in the Pacific also occur in other regions, but close scrutiny of the cranchiid fauna in the Atlantic and Indian Oceans (integrating molecular characters, where possible) will be needed in order to clarify the global zoogeography of the family. Given the diversity presently observed in the Pacific Ocean, research into cranchiid squid in other oceans will almost certainly reveal additional taxa, leaving plenty of work for enthusiasts of cranchiid taxonomy.



## Acknowledgements

I would like to thank all of the institutions who allowed me to visit their collections and conduct my research. I would also like to acknowledge the National Institute of Weather and Atmospheric Research, Ltd. (NIWA) and the Museum of New Zealand Te Papa Tongarewa, the Royal British Columbia Museum (RBCM), the Santa Barbara Museum of Natural History (SBMNH), Melbourne Museum (MV), and the Australian Museum (AM) for loaning the specimens in their collections. Special thanks to Bruce Marshall (Te Papa), Sadie Mills and Diana MacPherson (NIWA), Heidi Gartner (RBCM), Daniel Geiger (SBMNH), Chris Rowley (MV) and Mandy Reid (AM) for their assistance with my numerous specimen loans.

Throughout a majority of this research I was funded by the Auckland University of Technology's Vice-Chancellor Scholarship. This funding was critical to my accomplishment of this thesis, as it allowed me to do research without the additional stress of finding employment. I would like to thank the scholarship committee for selecting me as one of the recipients for this prestigious award. I have also been blessed with several opportunities to conduct research and present my findings overseas during the course of my degree, and I would like to thank the Auckland University of Technology for financial support for some of these expeditions. Special thanks to Brid Lorigan, and Winnie Zhu who handled all the travel and registration documentation.

The inspiration for both this topic and degree is due to Steve O'Shea, without whom, this adventure would never have begun. I will always admire your passion and dedication to the pursuit of cephalopod knowledge.

There are so many people who supported me through this tumultuous journey. I would like to thank all of my friends, both in New Zealand and Canada, who got to learn far more about 'glass squid' than they ever wanted to know from my incessant rants and musings. Although this research was sometimes a bit monotonous, it was always improved by the knowledge and humor (and also baking) of the rest of the ALCES team: Heather, Jesse, and Alex. My love and appreciation to my grandparents, Frank and Mona Boydell, for their enduring belief that I can achieve all of my aspirations in life. My parents have been an anchor throughout my entire life, and I know that it is only through their continuing love and support that I was able to have this amazing opportunity to complete this research.

I would like to sincerely thank Mandy Reid, who provided so much valuable input into my writing, especially joining my supervisory team at such a late point in the PhD journey. I know that you have made me a better scientist. Finally, this thesis would never have come to completion without the assistance of my primary supervisor, Kat Bolstad. She encouraged me when I was doubting my own abilities, celebrated my accomplishments, and challenged me to continue improving my academic writing. I am proud to say that no baby ducklings were harmed in the creation of this thesis. Thank you Kat for the support, optimism, and professionalism you have shown over these past few years. It was an honor to be your student.

Let's go study some squid!

## References

- Adams, A., & Reeve, L. (1848). *Mollusca Part 1. The Zoology of the Voyage of H.M.S. "Samarang" under the Command of Captain Sir Edward Belcher during the years 1843-46*. Paris.
- Aldred, R. G. (1974). Structure, growth and distribution of the squid *Bathothauma lyromma* Chun. *Journal of the Marine Biological Association of the United Kingdom*, 54, 995–1006.
- Allan, J. K. (1940). A rare stalk-eyed squid (*Bathothauma lyromma* Chun) new to Australian waters. *Records of the Australian Museum*, 20(5), 320–324.
- Allan, J. K. (1945). Planktonic cephalopod larvae from the eastern Australian coast. *Records of the Australian Museum*, 21(6), 317–350.
- Allcock, A. L., Cooke, I. R., & Strugnell, J. M. (2011). What can the mitochondrial genome reveal about higher-level phylogeny of the molluscan class Cephalopoda? *Zoological Journal of the Linnean Society*, 161(3), 573–586.
- Anderson, F. E. (2000). Phylogeny and historical biogeography of the loliginid squids (Mollusca: Cephalopoda) based on mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution*, 15(2), 191–214.
- Arkhipkin, A. (1996a). Age and growth of planktonic squids *Cranchia scabra* and *Liocranchia reinhardtii* (Cephalopoda, Cranchiidae) in epipelagic waters of the central-east Atlantic. *Journal of Plankton Research*, 18(9), 1675–1683.
- Arkhipkin, A. (1996b). Statolith microstructure and age of early life stages of planktonic squids *Galiteuthis phyllura* and *Belonella borealis* (Oegopsida, Cranchiidae) from the northern North Pacific. *Journal of Plankton Research*, 18(1), 123–132.
- Beatson, E. (2007). The diet of pygmy sperm whales, *Kogia breviceps*, stranded in New Zealand: implications for conservation. *Reviews in Fish Biology and Fisheries*, 17(2–3), 295–303.
- Berry, S. S. (1909). Diagnosis of new cephalopods from the Hawaiian Islands. *Proceedings of the United States National Museum*, 37(1713), 407–419.
- Berry, S. S. (1911). Preliminary notice of some new Pacific cephalopods. *Proceedings of the United States National Museum*, 40, 589–592.
- Berry, S. S. (1912). Some necessary changes in cephalopod nomenclature. *Science*, 36, 643–646.
- Berry, S. S. (1914). The cephalopods of the Hawaiian Islands. *Bulletin of the Bureau of Fisheries*, 32(789), 257–362.

- Berry, S. S. (1916). Cephalopoda of the Kermadec Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68(1), 45–66.
- Berry, S. S. (1920). Light production in Cephalopods, II: an introductory survey. *Biological Bulletin*, 38, 171–195.
- d’Blainville, H. D. (1823). Mémoire sur les espèces du genre Calmar (Loligo, Lamarck). *Journal de Physique, de Chimie et d’Histoire Naturelle*, 96, 116–135.
- Bolstad, K. S. (2008). Two new species and a review of the squid genus *Onychoteuthis* Lichtenstein, 1818 (Oegopsida: Onychoteuthidae) from the Pacific Ocean. *Bulletin of Marine Science*, 83(3), 481–529.
- Bolstad, K. S. R. (2010). Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Zootaxa*, 9626 [186 pp].
- Bolstad, K. S. R., Perez, J. A. A., Strugnell, J. M., & Vidal, E. A. G. (2015). Cranchiids of the South Atlantic mid-oceanic ridge: results from the first southern MAR-ECO expedition. *Journal of Natural History*, 40(21–24), 1351–1371.
- Bolstad, K. S. R., Braid, H. E., Strugnell, J. M., Lindgren, A. R., Lischka, A., Kubodera, T., Laptikhovsky, V. L., & Roura Labiaga, A. (2018). A mitochondrial phylogeny of the family Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Molecular Phylogenetics and Evolution*. (In press).
- Braid, H. E. (2017). Resolving the taxonomic status of *Asperoteuthis lui* Salcedo-Vargas, 1999 (Cephalopoda, Chiroteuthidae) using integrative taxonomy. *Marine Biodiversity*, 47(3), 621–635.
- Braid, H. E., & Bolstad, K. S. R. (2015). Systematics of the Mastigoteuthidae Verrill, 1881 (Cephalopoda: Oegopsida) from New Zealand waters. *New Zealand Journal of Zoology*, 42(3), 187–256.
- Braid, H. E., Kubodera, T., & Bolstad, K. S. R. (2017). One step closer to understanding the chiroteuthid families of the Pacific Ocean. *Marine Biodiversity*, 47(3), 659–683.
- Braid, H. E., McBride, P. D., & Bolstad, K. S. R. (2014). Molecular phylogenetic analysis of the squid family Mastigoteuthidae (Mollusca, Cephalopoda) based on three mitochondrial genes. *Hydrobiologia*, 725(1), 145–164.
- Bucklin, A., Ortman, B. D., Jennings, R. M., Nigro, L. M., Sweetman, C. J., Copley, N. J., ... & Wiebe, P. H. (2010). A “Rosetta Stone” for metazoan zooplankton: DNA barcode analysis of species diversity of the Sargasso Sea (Northwest Atlantic Ocean). *Deep Sea Research Part II: Topical Studies in Oceanography*, 57(24–26), 2234–2247.

- Carlini, D. B., & Graves, J. E. (1999). Phylogenetic analysis of cytochrome *c* oxidase I sequences to determine higher-level relationships within the coleoid cephalopods. *Bulletin of Marine Science*, 64(1), 57–76.
- Chun, C. (1906). System der Cranchien. *Zoologischer Anzeiger*, 31(2):82–86.
- Chun, C. (1910). Die Cephalopoden. I. Oegopsida. *Wissenschaftliche Ergebnisse Der Deutschen Tiefsee-Expedition Valdivia*, 18, 1–401.
- Clarke, M. R. (1962). Respiratory and swimming movements in the cephalopod *Cranchia scabra*. *Nature*, 196, 351–352.
- Clarke, M. R. (1966). A review of the systematics and ecology of oceanic squid. *Advances in Marine Biology*, 4, 91–300.
- Clarke, M. R. (1980). Cephalopoda in the diet of the sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports*, 37, 1–324.
- Clarke M. R. (1986). *A handbook for the identification of cephalopod beaks*. Clarendon Press, Oxford.
- Clarke, M., Denton, E., & Gilpin-Brown, J. (1979). On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom*, 59(2), 259–276.
- Clarke, M. R. & Roper, C. F. E. (1998). Cephalopods represented by beaks in the stomach of a sperm whale stranded at Paekakariki, North Island, New Zealand. *South African Journal of Marine Science*, 20(1), 129–133.
- Croxall, J. P. & Prince, P. A. (1994). Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science*, 6(2), 155–162.
- De Silva-Dávila, R., Avendaño-Ibarra, R., García-Domínguez, F., & Saldierna-Martínez, R. (2010). New records of *Drechselia danae* (Joubin, 1931)(Cephalopoda: Cranchiidae) off the Pacific coast of Mexico. *CICIMAR Océánides*, 25(1), 89–93.
- Dell, R. K. (1959). Some additional New Zealand cephalopods from Cook Strait. *Zoology Publications from Victoria University of Wellington*, 25, 1–12.
- Evans, A. B. (2013). *Ecology and ontogeny of the cranchiid squid Teuthowenia pellucida in New Zealand waters*. (Masters thesis, Auckland University of Technology, Auckland, New Zealand) Retrieved from: <http://aut.researchgateway.ac.nz/handle/10292/5747>
- Evans, A. B., & Bolstad, K. S. R. (2014). Ontogeny of the deep-sea cranchiid squid *Teuthowenia pellucida* (Cephalopoda: Cranchiidae) from New Zealand waters. *Journal of Natural History*, 49(21–24):1327–1349.

- Ferussac, A. d', & d'Orbigny, A. (1834). *Histoire naturelle générale et particulière des céphalopodes acétabulifères vivants et fossiles*. Paris.
- Filippova, J. A. (1972). New data on the squids (Cephalopoda: Oegopsida) from the Scotia Sea (Antarctic). *Malacologia*, 11(2), 391–406.
- Glaubrecht, M., & Salcedo-Vargas, M. A. (2000). Annotated type catalogue of the Cephalopoda (Mollusca) in the Museum für Naturkunde, Humboldt University of Berlin. *Zoosystematics and Evolution*, 76(2), 269–282.
- Goodrich, E. S. (1896). Report on a collection of Cephalopoda from the Calcutta Museum. *Transactions of the Linnean Society of London*, 7(1), 1–24.
- Grant, R. E. (1833). On the structure and characters of *Loligopsis*, and an account of a new species (*Lol. guttata* Grant) from the Indian Seas. *Transactions of the Zoological Society of London*, 1, 21–28.
- Gray, J. E. (1849). *Catalogue of the Mollusca in the collection of the British Museum: part I Cephalopoda antepedia*. London, England: British Museum.
- Grimpe, G. (1922). Systematische Übersicht der europäischen Cephalopoden. *Sitzungsberichte der naturforschenden Gesellschaft zu Leipzig*, 45–48, 36–52.
- Guerrero-Kommritz, J. (2001). Catalogue of the cephalopod type specimens in the Zoological Museum Hamburg. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 98, 171–174.
- Hernández-García, V. (1995). The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic with emphasis on the role of cephalopods. *Fishery Bulletin*, 93(2), 403–411.
- Herring, P. J. (2000). Bioluminescent signals and the role of reflectors. *Journal of Optics A: Pure and Applied Optics*, 2(6), R29–R38.
- Herring, P. J., Dilly, P. N. & Cope, C. (2002). The photophores of the squid family Cranchiidae (Cephalopoda: Oegopsida). *Journal of Zoology*, 258, 73–90.
- Hoyle, W. E. (1885). On *Loligopsis* and some other genera. *Proceedings of the Royal Physical Society of Edinburgh*, 8, 313–333.
- Hoyle, W. E. (1886). Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. *Zoology*, 16(44), 1–245.
- Hoyle, W. E. (1904). Reports on the Cephalopoda. *Bulletin of the Museum of Comparative Zoology at Harvard College, in Cambridge*, 43(1), 1–72.

- Imber, M. J. (1978). The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidea) in the New Zealand region. *New Zealand Journal of Zoology*, 5(3), 445–484.
- Imber, M. J. (1992). Cephalopods eaten by wandering albatross (*Diomedea exulans* L.) breeding at six circumpolar localities. *Journal of the Royal Society of New Zealand*, 22(4), 243–263.
- Issel, R. (1908). Diagnosi preliminari di un nuovo genere e di due nuove specie di Cefalopodi appartenenti alla fam. Cranchiidae raccolti dalla R. Nave "Liguria." *Monitore Zoologico Italiano*, 19(4), 102–104.
- Joubin, L. (1895). Contribution a l'étude des céphalopodes de l'Atlantique Nord. *Résultats des Campagnes Scientifiques Accomplies sur Yacht par Albert I Prince Souverain de Monaco*, 9, 1–63.
- Joubin, L. (1898). Note sur une nouvelle famille de Céphalopodes. *Annales des Sciences Naturelles, Zoologie*, 8(6), 279–292.
- Joubin, L. (1905). Note sur les organes photogènes de l'oeil de *Leachia cyclura*. *Bulletin du Musée Océanographique de Monaco*, 1(23–56), 1–13.
- Joubin, L. (1912). Sur les céphalopodes capturés en 1911 par S. A. S. le Prince de Monaco. *Comptes Rendus des Séances de l'Académie des Sciences*, 154, 395–397.
- Joubin, L. (1920). Céphalopodes provenant des campagnes de la Princesse-Alice (1898–1910). *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert I Prince Souverain de Monaco*, 54, 1–95.
- Joubin, L. (1924). Contribution a l'étude des Céphalopodes de l'Atlantique nord (4e Série). *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert I Prince Souverain de Monaco*, 67, 1–113.
- Joubin, L. (1931). Notes préliminaires sur les céphalopodes des croisières du DANA (1921–1922), 3e partie. *Annals de l'Institut Océanographique*, 10(7), 169–211.
- Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30(4), 772–780.
- Kristensen, T. K. & Knudsen, J. (1983). A catalogue of the type specimens of Cephalopoda (Mollusca) in the Zoological Museum, University of Copenhagen. *Steenstrupia*, 9(10), 217–227.
- Kubodera, T. & Okutani, T. (2014). An unusual squid from the Sea of Japan, *Enigmocranchia nipponica*, new genus and new species (Cephalopoda: Decembrachiata: Cranchiidae). *National Museum of Nature and Science Monographs*, 44, 149–156.

- Kubodera, T., Watanabe, H., & Ichii, T. (2007). Feeding habits of the blue shark, *Prionace glauca*, and salmon shark, *Lamna ditropis*, in the transition region of the Western North Pacific. *Reviews in Fish Biology and Fisheries*, 17(2-3), 111.
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular Evolutionary Genetics Analysis version 7.0. *Molecular Biology and Evolution*, 33(7), 1870–1874.
- Lamarck, J. B. (1798). Sur les genres de la sèche, du calmar et du poulpe, vulgairement nommés polypes de mer. *Mémoires de la Société d'Histoire Naturelle de Paris*, 1(7), 1–25.
- Lamarck, J. B. (1812). Présentant la distribution et la classification de ces animaux, les caractères des principales divisions, et une simple liste des genres; à l'usage de ceux qui suivent ce cours. *Extrait du cours de Zoologie du Museum d'Histoire Naturelle, sur les Animaux Sans Vertébrat*, 2–127.
- Lane, F. W. (1957). *Kingdom of the Octopus, the life-history of the Cephalopoda*. London: Jarrolds Publishers Ltd.
- Lankester, E. R. (1884). On *Procalistes*, a young cephalopod with pedunculate eyes, taken by the "Challenger" expedition. *Quarterly Journal of Microscopical Science*, 24(2), 311–318.
- Leach, W. E. (1817). Synopsis of the orders, families, and genera of the class Cephalopoda. *The Zoological Miscellany; descriptions of new or interesting animals*, 3(30), 137–141.
- Leach, W. E. (1818). Sur plusieurs espèces nouvelles de la classe des céphalopodes et sur une nouvelle distribution systématique des ordres, familles et genres de cette classe. *Journal de Physique, de Chimie et d'Histoire Naturelle*, 86, 393–396.
- Lesueur, C. A. (1821). Description of several new species of Cuttlefish. *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1), 86–101.
- Lichtenstein, H. C. (1818). Onychoteuthis, Sepien mit Krallen. *Isis*, 1818, 1591–1592.
- Lindgren, A. R. (2010). Molecular inference of phylogenetic relationships among decapodiformes (Mollusca: Cephalopoda) with special focus on the squid order Oegopsida. *Molecular Phylogenetics and Evolution*, 56, 77–90.
- Lindgren, A. R., Pankey, M. S., Hochberg, F. G., & Oakley, T. H. (2012). A multi-gene phylogeny of Cephalopoda supports convergent morphological evolution in association with multiple habitat shifts in the marine environment. *BMC Evolutionary Biology*, 12, 129.

- Lipinski, M. R., Naggs, F.A. & Roeleveld, M. A. (2000). Catalogue of types of Recent cephalopods in the collection of the Natural History Museum, London. *Annales Zoologici (Warszawa)*, 50(1), 101–120.
- Lönnberg, E. (1896). Notes on some rare cephalopods. *Öfversigt af Kongl. Vetenskaps-akademiens förhandlingar*, 8, 603–611.
- Lu, C. C. & Clarke, M. R. (1974). Two new species of cranchiid cephalopod from the North Atlantic, *Uranoteuthis bilucifer* n. gen., n. sp. and *Galiteuthis triluminosa* n. sp. *Journal of the Marine Biological Association of the United Kingdom*, 54, 985–994.
- MacLeod, C. D., Santos, M. B., & Pierce, G. J. (2003). Review of the data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association of the United Kingdom*, 83, 651–665.
- Massy, A. L. (1907). Preliminary notice of new and remarkable cephalopods from the south-west coast of Ireland. *Annals and Magazines of Natural History*, 20(7), 377–384.
- McSweeney, E. S. (1971). Morphology and distribution of the Antarctic cranchiid squid *Galiteuthis glacialis* (Chun) (Doctoral dissertation, University of Miami, Miami, USA).
- Nesis, K. N. (1972). A review of the squid genera *Taonius* and *Belonella* (Oegopsida, Cranchiidae). *Zoologicheskyy Zhurnal*, 51(3), 341–350.
- Nesis, K. N. (1974). A revision of the squid genera *Corynomma*, *Megalocranchia*, *Sandalops*, and *Liguriella* (Oegopsida, Cranchiidae). *Transactions of the Institute of Oceanology, USSR*, 96, 6–22.
- Nesis, K. N. (1987). *Cephalopods of the world; Squids, cuttlefishes, octopuses, and allies*. Neptune City, NJ, USA: T.F.H. Publications.
- Nesis, K. N., Nigmatullin, C. M., & Nikitina, I. V. (1998). Spent females of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *Journal of Zoology*, 244(2), 185–200.
- Odhner, N. H. (1923). Die Cephalopoden. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*, 1(4), 1–7.
- Okutani, T. (1975). A probable advanced stage of *Bathothauma lyromma*. *The Veliger*, 17(3), 243–246.
- d'Orbigny, A. (1834). Mollusques. *Voyage dans l'Amerique Meridionale*, 5(3), 1–758.
- d'Orbigny, A. (1845). *Mollusques vivants et fossiles ou description de toutes les espèces de Coquilles et de Mollusques*. Paris.



- Ormseth, O. A. (2017). *Assessment of the squid stock complex in the Gulf of Alaska*. Gulf of Alaska Stock Assessments: NOAA.
- Owen, R. (1836). Descriptions of some new and rare Cephalopoda. *The Transactions of the Zoological Society of London*, 2(2), 103–130.
- Pearson, P. (1969). Cartilaginous dermal scales in cephalopods. *Science*, 164, 1404–1405.
- Petrov, A. F., & Tatarnikov, V. A. (2011). Results of investigation of the diet of Antarctic toothfish *Dissostichus mawsoni* (Nototheniidae) in the Lazarev Sea. *Journal of Ichthyology*, 51(1), 131–135.
- Pfeffer, G. (1884). Die cephalopoden des Hamburger Naturhistorischen Museums. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1), 1–30.
- Pfeffer, G. (1900). Synopsis der oegopsiden Cephalopoden. *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2), 147–198.
- Pfeffer, G. (1912). Die Cephalopoden der Plankton-Expedition. Zugleich eine Monographische Übersicht der Oegopsiden Cephalopoden. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2, 1–815.
- Piatkowski, U. & Hagen, W. (1994). Distribution and lipid composition of early life stages of the cranchiid squid *Galiteuthis glacialis* (Chun) in the Weddell Sea, Antarctica. *Antarctic Science*, 6(2), 235–239.
- Prince, P. A. (1980). The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophris*. *Ibis*, 122(4), 476–488.
- Prosch, V. (1849). Nogle nye Cephalopoder. Kongelige Danske Videnskabernes Selskab, 5(1), 53–72.
- Ramakrishna, A. D. & Mitra, S. C. (2004). Catalogue of type species (Bivalvia, Scaphopoda & Cephalopoda) present in the Mollusca section of Zoological Survey of India. *Records of the Zoological Survey of India*, 228, 1–97.
- Rathke, H. (1833). *Perothis*, ein neues genus der Cephalopoden. *Mémoires Présentés à l'Académie Impériale des Sciences de St. Petersbourg par Divers Savans*, 2(1/2), 149–175.
- Ratnasingham, S., & Hebert, P. D. (2007). BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Resources*, 7(3), 355–364.
- Ratnasingham, S., & Hebert, P. D. (2013). A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PloS one*, 8(7), e66213.
- Reid, A. (2016). *Cephalopods of Australia and sub-Antarctic territories*. Clayton South, Australia: CSIRO.

- Remeslo, A. V., Yakushev, M. R., & Laptikhovsky, V. (2015). Alien vs. Predator: interactions between the colossal squid (*Mesonychoteuthis hamiltoni*) and the Antarctic toothfish (*Dissostichus mawsoni*). *Journal of Natural History*, 49(41–42), 2483–2491.
- Robson, G. C. (1921). On the cephalopoda obtained by the Percy Sladen Trust Expedition to the Indian Ocean in 1905. *Transactions of the Linnean Society of London (series 2, Zoology)*, 17(4), 429–442.
- Robson, G. C. (1924). Preliminary report on the Cephalopoda (Decapoda) procured by the S.S. "Pickle." *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3, 1–14.
- Robson, G.C. (1925). On *Mesonychoteuthis*, a new genus of oegopsid Cephalopoda. *Annals and Magazine Natural History*, 9(16), 272–277.
- Robson, G. C. (1948). The Cephalopoda Decapoda of the "Arcturus" Oceanographic Expedition, 1925. *Zoologica*, 33(3), 115–132.
- de Rochebrune, A. T. (1884). Etude monographique sur la famille des Loliopsidae. *Bulletin de la Societe Philomathique de Paris*, 8(1), 7–28.
- Rodhouse, P. G., Arnbom, T. R., Fedak, M. A., Yeatman, J., & Murray, A. W. A. (1992). Cephalopod prey of the southern elephant seal, *Mirounga leonina*. *Canadian Journal of Zoology*, 70(5), 1007–1015.
- Rodhouse, P. G. & Clarke, M. R. (1985). Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. *Vie et Milieu*, 35(3/4), 223–230.
- Roper, C. F. E. & Lu, C. C. (1990). Comparative morphology and function of dermal structures in oceanic squids (Cephalopoda). *Smithsonian Contributions to Zoology*, 493, 1–40.
- Roper, C. F. E., & Voss, G. L. (1983). Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum Victoria*, 44, 48–63.
- Roper, C. F. E., & Young, R. E. (1975) Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology*, 209, 1–51.
- Roper, C. F. E., Young, R. E., & Voss, G. L. (1969) An illustrated key to the families of the order Teuthoidea (Cephalopoda). *Smithsonian Contributions to Zoology*, 13, 1–32.
- Rosa, R., Diersen, H. M., Gonzalez, L., & Seibel, B. A. (2008). Large-scale diversity patterns of cephalopods in the Atlantic open ocean and deep sea. *Ecology*, 89(12), 3449–3461.

- Russell, E. S. (1909). Preliminary notice on the Cephalopoda collected by the Fishery Cruiser Goldseeker 1903–1908. *Annals and Magazine of Natural History*, 3, 446–455.
- Sanchez, G., Setiamarga, D. H., Tuanapaya, S., Tongtherm, K., Winkelmann, I. E., Schmidbaur, H., ... & Gleadall, I. (2018). Genus-level phylogeny of cephalopods using molecular markers: current status and problematic areas. *PeerJ*, 6, e4331.
- Sasaki, M. (1920). Report on cephalopods collected during 1906 by the United States Bureau of Fisheries steamer "Albatross" in the northwestern Pacific. *Proceedings of the United States National Museum*, 57(2310), 163–203.
- Sasaki, M. (1929). A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *Journal of the Faculty of Agriculture, Hokkaido Imperial University, Sapporo, Japan*, 20, 42–43.
- Scott, P. H., Hochberg, F. G., & Roth, B. (1990). Catalog of Recent and fossil molluscan types in the Santa Barbara Museum of Natural History. I. Caudofoveata, Polyplacophora, Bivalvia, Scaphopoda and Cephalopoda. *The Veliger*, 33(Suppl. 1), 1–27.
- Seapy, R. R. & Young, R. E. (1986). Concealment in epipelagic pterotracheid heteropods (Gastropoda) and cranchiid squids (Cephalopoda). *Journal of Zoology, London (A)*, 210, 137–147.
- Steenstrup, J. (1856). Hectocotyldannelsen hos Octopodslægterne Argonauta og Tremoctopus, oplyst ved Iagttagelse af lignende dannelser hos blæksprutterne i almindelighed. *Kongelige Danske Videnskabernes Selskabs Skrifter*, 5 Raekke, Naturvidenskabelig og Mathematisk, 4, 185–216.
- Steenstrup, J. (1861). Overblik over de i Kjobenhavns Museer opbevarede Blæksprutter fra det aabne Hav (1860–61). *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling*, 1861, 69–86.
- Sweeney, M. J., Roper, C. F. E., & Hochberg, F. G. (1988). Catalog of the type specimens of Recent Cephalopoda described by S. Stillman Berry. *Malacologia*, 29(1), 7–19.
- Sweeney, M. J., Roper, C. F.E., Mangold, K. M., Clarke, M. R., & Boletzky, S. V. (1992). "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513, 1–282.
- Sweeney M. J. & Vecchione M. (1998). *Generic and specific names introduced in the squid family Loliginidae*. Pp. 223–237, in: Voss N. A., Vecchione, M. Toll, R. B. & Sweeney, M. J. eds. (1998). Systematics and biogeography of cephalopods. *Smithsonian Contributions to Zoology* 586(1), 1–276; (2), 277–599.
- Thiele, J. (1934). Handbook of systematic malacology. Pts 3–4, 1476–1485.

- Thomas, G. & Friend, G. R. (1982). The food and feeding ecology of the Light-mantled Sooty Albatross at South Georgia. *Emu*, 82, 92–100.
- Tripathy, B., Mukhopadhyay, A., Hafiz, Md., & Venkitesan, R. (2013). Cephalopoda in NZC of the Zoological Survey of India, Kolkata. *Records of the Zoological Survey of India*, 342, 1–60.
- Verrill, A. E. (1881). The cephalopods of the north-eastern coast of America. Part II. The smaller cephalopods, including the "squids" and the octopi, with other allied forms. *Transactions of the Connecticut Academy of Sciences*, 5(6), 259–446.
- Voight, J. R. (2008). A mature female of *Bathothauma* Chun, 1906 (Cephalopoda: Cranchiidae) from Hawaii. *American Malacological Bulletin*, 26(1-2), 133–138. doi:10.4003/006.026.0213
- Voight, J. R., Pörtner, H. O., & O'Dor, R. K. (1995). A review of ammonia-mediated buoyancy in squids (Cephalopoda: Teuthoidea). *Marine and Freshwater Behaviour and Physiology*, 25(1–3), 193–203.
- Voss, G. L. (1960). Bermudan Cephalopoda. *Fieldiana, Zoology*, 39(40), 419–446.
- Voss, G. L. (1962). *Ascocranchia joubini*, a new genus and species of cranchiid squid from the North Atlantic. *Bulletin de L'Institut Oceanographique, Monaco*, 1242, 1–6.
- Voss, G. L. (1963). Cephalopods of the Philippine Islands. *Bulletin of the United States National Museum*, 234, 1–180.
- Voss, G. L. (1977). Present status and new trends in cephalopod systematics. *Symposia of the Zoological Society of London*, 38, 49–60.
- Voss, N. A. (1980). A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). *Bulletin of Marine Science*, 30(2), 365–412.
- Voss, N. A. (1985). Systematics, biology, and biogeography of the cranchiid cephalopod genus *Teuthowenia* (Oegopsida). *Bulletin of Marine Science*, 36(1), 1–85.
- Voss, N. A. (1988). Evolution of the cephalopod family Cranchiidae (Oegopsida). *The Mollusca*, 12, 293–314.
- Voss, N. A., Stephen, S. J., & Dong, Zh. (1992). Family Cranchiidae Prosch, 1849. In Sweeney, M. J., Roper, C. F. E., Mangold, K. M., Clarke, M. R., & Boletzky, S. V. (eds.). *"Larval" and juvenile cephalopods: a manual for their identification*. (pp. 187–210). Washington, D. C.: Smithsonian Institution Press.
- Voss, N. A. & Voss, R. S. (1983). Phylogenetic relationships in the cephalopod family Cranchiidae (Oegopsida). *Malacologia*, 23(2), 397–426.

- Watanabe, H., Kubodera, T., Moku, M., & Kawaguchi, K. (2006). Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. *Marine Ecology Progress Series*, 315, 187–197.
- West, K. L., Walker, W. A., Baird, R. W., Mead, J. G., & Collins, P. W. (2017). Diet of Cuvier's beaked whales *Ziphius cavirostris* from the North Pacific and a comparison of their diet world-wide. *Marine Ecology Progress Series*, 574, 227–242.
- Young, J. Z. (1970). The stalked eyes of *Bathothauma* (Mollusca, Cephalopoda). *Journal of Zoology, London*, 162, 437–447.
- Young, R. E. (1972). The systematics and aerial distribution of pelagic cephalopods in the seas off Southern California. *Smithsonian Contributions to Zoology*, 97, 1–159.
- Young, R. E. (1975). Transitory eye shapes and the vertical distribution of two midwater squids. *Pacific Science*, 29(3), 243–255.
- Young, R. E. (1975). *Leachia pacifica* (Cephalopoda, Teuthoidea): Spawning habitat and function of the brachial photophores. *Pacific Science*, 29(1), 19–25.
- Young, R. E. (1978). Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fisheries Bulletin*, 76, 583–615.
- Young, R. E. (2014a). *Taonius pavo* (Lesueur, 1821). Version 06 December 2014 (under construction). Retrieved from [http://tolweb.org/Taonius\\_pavo/19611](http://tolweb.org/Taonius_pavo/19611).
- Young, R. E. (2014b). *Taonius belone* (Chun, 1906). Version 21 January 2014 (under construction). Retrieved from [http://tolweb.org/Taonius\\_belone/120159](http://tolweb.org/Taonius_belone/120159).
- Young, R. E. & Mangold, K. M. (2018). *Helicocranchia pfefferi* Massy 1907. Banded piglet squid. Version 29 March 2018 Retrieved from [http://tolweb.org/Helicocranchia\\_pfefferi/19580/](http://tolweb.org/Helicocranchia_pfefferi/19580/)

## Appendix A: List of Pacific cranchiid taxa

### Cranchiinae

- Cranchia* Leach, 1817
  - Cranchia scabra* Leach, 1817
  - ?*Cranchia nipponica* (Kubodera & Okutani, 2014)
- Leachia* Lesueur, 1821
  - Leachia danae* (Joubin, 1931)
  - Leachia dislocata* Young, 1972
  - Leachia pacifica* (Issel, 1908)
  - Leachia separata*, sp. nov.
  - Leachia* sp. NZ (?novel taxon)
- Liocranchia* Pfeffer, 1884
  - Liocranchia reinhardti* (Steenstrup, 1856)
  - Liocranchia valdiviae* Chun, 1910

### Taoniinae

- Bathothauma* Chun, 1906
  - Bathothauma lyromma* Chun, 1906
  - Bathothauma* sp. HI (?novel taxon)
- Galiteuthis* Joubin, 1898
  - Galiteuthis glacialis* (Chun, 1906)
  - Galiteuthis pacifica* (Robson, 1948)
  - Galiteuthis phyllura* Berry, 1911
  - Galiteuthis suhmi* (Hoyle, 1886)
- Helicocranchia* Massy, 1907
  - Helicocranchia pfefferi* Massy, 1907
  - Helicocranchia* sp. NZ (?novel taxon)
- Liguriella* Issel, 1908
  - Liguriella podophtalma* Issel, 1908
  - Liguriella pardus* (Berry, 1916)
- Megalocranchia* Pfeffer, 1884
  - Megalocranchia abyssicola* (Goodrich, 1896)
  - Megalocranchia fisheri* (Berry, 1909)
  - Megalocranchia maxima* Pfeffer, 1884
  - Megalocranchia* sp. NZ (?novel taxon)
- Sandalops* Chun, 1906
  - Sandalops melancholicus* Chun, 1906
- Taonius* Steenstrup, 1861
  - Taonius belone* (Chun, 1906)
  - Taonius borealis* (Nesis, 1972)
  - Taonius expolitus*, sp. nov.
  - Taonius notalia*, sp. nov.
  - Taonius robisoni*, sp. nov.
  - Taonius tanuki*, sp. nov.
- Teuthowenia* Chun, 1910
  - Teuthowenia pellucida* (Chun, 1910)

## Appendix B: Measures and counts

The following tables show measures and counts for cranchiid taxa with more than three specimens examined. Mean indices have been calculated as a percentage of ML. Asterisks (\*) indicate damaged features, with the value representing the intact portion of that character (not included in mean index calculations). A dash (-) indicates that the feature was absent or too damaged to accurately measure.

B1—Measures and counts of *Cranchia scabra* Leach, 1817

Specimen ID	NSMT-Mo:85213	NIWA 90026	Mean Indices	NMNZ M.074331	NMNZ M.074464	NSMT-Mo:67381	Mean Indices	NSMT-Mo:68168	MV F163416	NMNZ M.287288	Mean Indices
Type status	none	none		none	none	none		none	none	none	
ML	4	14	<b>5–15</b>	19	28	48	<b>15–60</b>	60	72	127	<b>60–160</b>
Sex	Indet.	Indet.		Indet.	Indet.	Indet.		Indet.	Indet.	F	
MW	2.5	10	<b>76</b>	17	20	34	<b>67</b>	40	27	76	<b>62</b>
FL	0.3	2.4	<b>15</b>	2.5	4	6	<b>15</b>	7	11	28	<b>17</b>
FW	1.01	5	<b>34</b>	5	8	12	<b>28</b>	14	21	48	<b>31</b>
HL	-	3	<b>15</b>	4	3	6	<b>15</b>	11	8	25	<b>15</b>
HW	-	3	<b>29</b>	5	6	14	<b>24</b>	18	18	40	<b>29</b>
ED	0.33	1.2	<b>11</b>	2	2.5	8	<b>12</b>	11	10	29	<b>18</b>
Arms I	0.5	1	<b>8</b>	1.5	1.5	5	<b>9</b>	7	6	21	<b>14</b>
Arms II	0.5	1.5	<b>8</b>	3	3	10	<b>16</b>	12	13	40	<b>24</b>
Arms III	0.5	2	<b>17</b>	5	5.2	15	<b>25</b>	19	16	60	<b>36</b>
Arms IV	0.5	1.2	<b>8</b>	2	3	9	<b>15</b>	12	12	45	<b>24</b>
TnL	1	14	<b>72</b>	22	23	51	<b>81</b>	58	46	111	<b>85</b>
CL	N/A	N/A	<b>19</b>	4	4.5	10	<b>16</b>	11	9	16	<b>15</b>

B2—Measures and counts of *Leachia danae* (Joubin, 1931)

Specimen ID	SBMNH 464531	NMNH 814880	Mean Indices	NMNH 814874	SBMNH 464531	SBMNH 49616	SBMNH 464442	SBMNH 464519	Mean Indices
Type status	none	none		none	none	none	none	none	
ML	44	62	<b>40–70</b>	70	84	103	112	159	<b>70–160</b>
Sex	Indet.	Indet.		Indet.	Indet.	Indet.	M	F	
MW	9	12	<b>20</b>	12	21	18	20	46	<b>20</b>
FL	17	22	<b>38</b>	28	33	38	34	58	<b>37</b>
FW	20.5	27	<b>42</b>	26	37	43	43	70	<b>44</b>
HL	6	7	<b>11</b>	4	10	7	9	8	<b>10</b>
HW	8	9	<b>20</b>	14	15	16	20	32	<b>19</b>
ED	3	3	<b>6</b>	5	11	12	13	19	<b>11</b>
Arms I	2	2	<b>6</b>	4	10	14	15	36	<b>16</b>
Arms II	2.7	4	<b>8</b>	5	15	19	22	51	<b>22</b>
Arms III	12	12	<b>25</b>	18	32	34	44	75	<b>38</b>
Arms IV	5	6	<b>12</b>	7	16	19	18	40	<b>21</b>
TnL	22	21	<b>41</b>	29	43	41	52	56	<b>45</b>
CL	4	4	<b>8</b>	5.5	8	7	9	12	<b>8</b>

B3—Measures and counts of *Leachia dislocata* Young, 1972

Specimen ID	SBMNH 464398	USNM 814864	SBMNH 464398	Mean Indices	USNM 729793	SBMNH 35001	SBMNH 35006	SBMNH 35005	USNM 729790	Mean Indices
Type status	none	none	none		none	paratype	paratype	paratype	none	
ML	20	31	51	<b>30–70</b>	76	91	96	107	121	<b>70–140</b>
Sex	Indet.	Indet.	Indet.		Indet.	Indet.	M	F	M	
MW	7	7	16	<b>23</b>	17	18	22	28	21	<b>21</b>
FL	2.5	7	16	<b>27</b>	23	19	28	37	31	<b>27</b>
FW	3	9.5	22	<b>38</b>	30	24	39	49	40	<b>36</b>
HL	3.5	4	4	<b>11</b>	4	4	7	13	5.5	<b>7</b>
HW	5.5	9	9	<b>18</b>	16	12	20	23	18	<b>17</b>
ED	2	1	3	<b>4</b>	7	3	11	11	10	<b>8</b>
Arms I	1	1.3	3.5	<b>6</b>	5	2	13	17	13	<b>10</b>
Arms II	1	2	5	<b>9</b>	9	5	24	24	16	<b>16</b>
Arms III	2	5	13	<b>24</b>	21	15	49	49	34	<b>33</b>
Arms IV	1	4	6	<b>11</b>	8*	5	16	22	12	<b>13</b>
TnL	10	17	33	<b>55</b>	28	32	-	-	37	<b>34</b>
CL	2.5	2	4.5	<b>8</b>	5	4	-	-	6	<b>6</b>

B4—Measures and counts of *Leachia separata*, sp. nov.

Specimen ID	MV F163526	NMNZ M.91560	MV F163517	NMNZ M.091543	NIWA 90004	NMNZ M.067263	Mean Indices
Type status	none	none	none	none	none	none	
ML	35	62	77	83	102	112	<b>35–117</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	F	
MW	3	16	20	20	20	26	<b>21</b>
FL	9	26	20	25	21	36	<b>29</b>
FW	10	32	29	31	34	46	<b>38</b>
HL	4	10	10	11	12	9	<b>13</b>
HW	5	10	14	12	13	17	<b>15</b>
ED	1.5	-	4	3.5	5	8	<b>5</b>
Arms I	0.7	6	5	4	9	11	<b>7</b>
Arms II	1	10	8	8	15	18	<b>13</b>
Arms III	4	26	22	22	25	35	<b>30</b>
Arms IV	0.8	7	6	8	11	17	<b>11</b>
TnL	18	46	36	58	45	55	<b>55</b>
CL	2	4	6	5	8	9	<b>7</b>



B5—Measures and counts of *Liocranchia reinhardti* (Steenstrup, 1856)

Specimen ID	NSMT-Mo:85214	NSMT-Mo:85216	SBMNH 461574	MNHN 2492	Mean Indices	MV F71691	MV F71691	NSMT-Mo:71607	Mean Indices
Type status	none	none	none	none		none	none	none	
ML	8.8	14	38	64	<b>15–65</b>	92	119	148	<b>65–148</b>
Sex	Indet.	Indet.	Indet.	Indet.		M	M	M	
MW	5.1	6	16	27	<b>45</b>	42	51	38	<b>33</b>
FL	0.8	3	9	16	<b>18</b>	30	36	47	<b>32</b>
FW	3.5	5	14	23	<b>31</b>	33	47	52	<b>37</b>
HL	0.6	2	4.5	10	<b>10</b>	12	15	30	<b>17</b>
HW	1.9	4	9	15	<b>26</b>	13	26	30	<b>21</b>
ED	-	1.5	4.5	9	<b>11</b>	17	19	22	<b>14</b>
Arms I	0.5	0.8	1	2	<b>4</b>	11	18	7	<b>12</b>
Arms II	0.5	1.3	2	9	<b>8</b>	18	28	19	<b>18</b>
Arms III	0.5	2	5.5	11	<b>16</b>	22	37	43	<b>28</b>
Arms IV	0.5	1	4	9	<b>11</b>	17	25	31	<b>21</b>
TnL	94	9	23	36	<b>52</b>	-	91	94	<b>60</b>
CL	17	1.4	5	7	<b>11</b>	10	13	17	<b>12</b>

B6—Measures and counts of *Liocranchia valdiviae* (Chun, 1910)

Specimen ID	MV F163698	SBMNH 460921	ZMB 110038a	SBMNH 461173	F16370 9	NMNZ M.172990	Mean Indices
Type status	none	none	none	none	none	none	
ML	13	26	28	34	63	82	<b>13–82</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	
MW	9	11	12	11	20	24	<b>37</b>
FL	1.5	4	6	4.5	15	21	<b>17</b>
FW	3	7	8	11	21	27	<b>29</b>
HL	1	3	5	4	6	15	<b>13</b>
HW	3.5	6	8	9	14	15	<b>25</b>
ED	1	2.5	3	4	5.5	6	<b>10</b>
Arms I	1	2	2	2	7	10	<b>8</b>
Arms II	1.5	3	3	4	10	16	<b>12</b>
Arms III	2.5	5	6	8	21	35	<b>23</b>
Arms IV	2	3	4	5	9	19	<b>14</b>
TnL	11	11	14	21	31	62	<b>58</b>
CL	2	2	3	3.5	6	10.5	<b>11</b>

B7—Measures and counts of *Bathothauma lyromma* Chun, 1906

Specimen ID	MV F163804	NIWA 90016	MV F163800	Mean Indices	NSMT- Mo:85212	NIWA 95913	Mean Indices	SBMNH 461081	AM C. 108566	NMNZ M.172937	Mean Indices
Type status											
ML	4	17	30	≤ 30	45	75	30–75	85*	102	144	75–150
Sex	Indet.				M			M	M	F	
MW	4	9	20	73	24	26	60	37	52	45	44
FL	2	4	5	23	5	11	18	12	20	17	16
FW	3.5	9.2	21	67	24	37	47	27	55	44*	43
HL	4	5.7	12	51	12	10	31	11	25	31	22
HW	6	7	26	90	35	34	64	24	38	23	33
ED	1	1	2.5	10	4	8	16	8	18	11	19
Arms I	1	1.4	2	10	5	10	21	10	44	39	32
Arms II	1	1.4	3	12	8	12	32	13	51	46	39
Arms III	1	1.4	3	13	9	13	36	15	56	54	44
Arms IV	1	1.2	2.3	11	5	12	30	14	46	48	37
TnL	7	24	41	156	68	87	186	63	40	155	121
CL	3	-	-	53	12	19	44	18	45	48	35

B8—Measures and counts for *Galiteuthis glacialis* (Chun, 1906)

Specimen ID	NIWA 70997	NIWA 44332	NIWA 44345	NIWA 44588	SBMNH 464506	Mean Indices	NMNZ M.286166	NMNZ M.277836	Mean Indices
Type status	none	none	none	none	none		none	none	
ML	8.7	10	41	46	67	40–75	169	374	>75
Sex	Indet.	Indet.	Indet.	Indet.	Indet.		Indet.	F?	
MW	5	5.5	13	15	19	28	32	78	19
FL	0.8	0.4	15	11	22	31	75	165	43
FW	1.2	0.6	5	5	10	12	42	78	18
HL	1.6	1	4.5	3	6	9	19	38	11
HW	4.2	3.7	9	9	13	18	16*	50	14
ED	1.3	1.2	4	2.5	6	7	-	29	10
Arms I	0.4	0.5	4	3.5	6	11	31	110	22
Arms II	0.4	0.5	6	5	11	15	40	125	26
Arms III	0.4	0.5	7	6	13	18	44	131	28
Arms IV	0.4	0.6	7	7.5	14	19	49	139	29
TnL	4.3	16	28	24	33	64	103	174	64
CL	N/A	N/A	6	3	7	9	13	35	10

B9—Measures and counts of *Galiteuthis pacifica* (Robson, 1948)

Specimen ID	SBMNH 49647	SBMNH 49343	SBMNH 51341	SBMNH 464473	SBMNH 464476	SBMNH 49324	SBMNH 464475	SBMNH 51342	Mean Indices
Type status	none	none	none	none	none	none	none	none	
ML	24	40	62	78	91	120	135	244	<b>60–244</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	
MW	10	14	18	24	22	36	18	63	<b>26</b>
FL	6	14	21	30	37	52	61	105	<b>41</b>
FW	5	6	12	11	15	23	24	50	<b>18</b>
HL	2	6	5	5	8	11	10	19	<b>8</b>
HW	5.5	11*	12*	13	18	22	25	38	<b>18</b>
ED	1.4	3	5	6	8	11	12	24	<b>9</b>
Arms I	3	5	8	8	9*	18	17	27	<b>12</b>
Arms II	3.4	7	11	9*	18	21	22	33	<b>16</b>
Arms III	4.2	9	13	13	21	28	25	45	<b>20</b>
Arms IV	4	10	14	13*	21	27	27	47	<b>21</b>
TnL	18*	33	50	32	48	65	72	-	<b>56</b>
CL	-	4.5	4	5	8	9	12	-	<b>8</b>

B10—Measures and counts for *Galiteuthis phyllura* Berry, 1911

Specimen ID	RBCM 979-11233-004	RBCM 979-11245-003	RBCM 979-11245-003	CAS 2328	CAS 2306	Mean Indices	NMNZ M.317512	RBCM 979-11242-002	RBCM 010-00295-002	Mean Indices
Type status	none	none	none	none	none		none	none	none	
ML	7.5	33	35	61	90	<b>35–100</b>	107	157	295	<b>100–295</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.		Indet.	Indet.	Indet.	
MW	5	9	14	18	21	<b>26</b>	18	24	57	<b>16</b>
FL	0.2	5	17	23	45	<b>40</b>	47	76	160	<b>49</b>
FW	1	3.5	6	10	14	<b>14</b>	13	23	54	<b>15</b>
HL	0.5	2	2	5	8	<b>10</b>	6	9	21	<b>7</b>
HW	2	9	11	11	15	<b>19</b>	15	22	36	<b>14</b>
ED	-	1.5	3	4	8	<b>7</b>	7	9	25	<b>8</b>
Arms I	1	1.5	4	5	11	<b>9</b>	12	16	46	<b>14</b>
Arms II	1	2	5.5	7	14	<b>12</b>	15	25	60	<b>17</b>
Arms III	1	2.5	6	9	16	<b>16</b>	18	31	71	<b>20</b>
Arms IV	1	3	5	11	21	<b>18</b>	23	34	75	<b>22</b>
TnL	4	16	28	35	42	<b>62</b>	52	65	137	<b>44</b>
CL	N/A	3	5	8	7	<b>12</b>	11	11	23	<b>8</b>

B11—Measures and counts of *Galiteuthis suhmi* (Hoyle, 1886)

Specimen ID	MV F78129	MV F78309	NIWA 90029	NIWA 90030	NMNZ M.091735	NIWA 92491	Mean Indices
Type status	none	none	none	none	none	none	
ML	25	62	212	265	267	410	<b>62–410</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	M	
MW	8.5	20	36	50	38	85	<b>21</b>
FL	2.5	20	97	119	127	179	<b>43</b>
FW	2	12	44	56	58	65	<b>20</b>
HL	1.5	8	28	33	27	67	<b>13</b>
HW	5	12	17	21*	37	38*	<b>13</b>
ED	-	5	-	24*	17	40*	<b>8</b>
Arms I	1	12	42	53	60	101	<b>21</b>
Arms II	1.5	17	51	73	71	118	<b>27</b>
Arms III	2	18*	54	75	76	123	<b>28</b>
Arms IV	2	18	56	81	74	120	<b>29</b>
TnL	13.5	-	124	143	119	312	<b>58</b>
CL	N/A	-	16	-	20	33	<b>8</b>

B12—Measures and counts of *Helicocranchia pfefferi* Massy, 1907

Specimen ID	SBMNH 47541	SBMNH 49502	SBMNH 45741	SBMNH 464233	Mean Indices	SBMNH 464210	SBMNH 464220	Mean Indices
Type status	none	none	none	none		none	none	
ML	4.4	16	27	41	<b>&lt; 50</b>	61	74	<b>&gt; 50</b>
Sex	Indet.	Indet.	Indet.	Indet.		M	F	
MW	3.2	9	10	25	<b>46</b>	25	31	<b>41</b>
FL	0.3	2.5	1.5	5	<b>10</b>	5	4.5	<b>8</b>
FW	0.9	6	6	10	<b>26</b>	12	11	<b>21</b>
HL		1	1	1	<b>5</b>	3	6	<b>5</b>
HW	2.5	5	6	10	<b>26</b>	13	14	<b>21</b>
ED	0.5	1	1.5	2	<b>7</b>	4	5	<b>6</b>
Arms I	0.4	2	3.5	6	<b>13</b>	12	9	<b>18</b>
Arms II	0.6	3	7	12	<b>21</b>	15	13	<b>23</b>
Arms III	1.2	3.5	9	14	<b>26</b>	18	21	<b>26</b>
Arms IV	0.2	2	3	6.5	<b>15</b>	9	12	<b>15</b>
TnL	-	14	21	36	<b>105</b>	48	-	<b>64</b>
CL	-	2	3	4	<b>11</b>	7	-	<b>9</b>

B13—Measures and counts of *Helicocranchia* sp. NZ

Specimen ID	NIWA 95902	NIWA 95955	Mean Indices	MV F163937	MV F163946	MV F163932	Mean Indices
Type status	none	none		none	none	none	
ML	18.3	24	< 40	42	49	63	> 40
Sex	Indet.	Indet.		Indet.	M	F?	
MW	6	10	48	25	18	19	48
FL	2.3	3	10	-	4	6	10
FW	4	8	25	-	12	11	25
HL	2	2.5	40	6	4	7	10
HW	4.5	6	25	13	11	12	25
ED	1.5	2	8	-	2.5	4	8
Arms I	4	3.5	23	14	10	14*	29
Arms II	5	6	30	15	13	15*	32
Arms III	7.5	8	37	19	14	15*	36
Arms IV	3.5	5	23	11	10	8*	18
TnL	18	31	110	58	43	-	111
CL	3	5	15	7	5	-	15

B14—Measures and counts of *Liguriella podophtalma* Issel, 1908

Specimen ID	NSMT-Mo:85233	NIWA 95898	NSMT-Mo:85252	NSMT-Mo:85232	NIWA 2257	NIWA 95923	NMNZ M.286166	Mean Indices
Type status	none	none	none	none	none	none	none	
ML	9	21	21	34	68	83	123	9–123
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	
MW	3	9	8	9	32	40	45	43
FL	1	3	2	5	12	15	32	16
FW	3	2	6	9	20	22	40	26
HL	3	2	5	5	12	12	28	17
HW	-	5	6	8	23	24	38*	31
ED	1	2	2	1.5	6	15	-	10
Arms I	<1	2.5	1.5	3	8	16	43	14
Arms II	<2	3	2	4	13	25	53	20
Arms III	<3	4	4	5	17	31	65	27
Arms IV	<4	3.5	3	4.5	12	27	55	22
TnL	8	20	22	21	51	-	104	96
CL	N/A	4	7	3.5	13	-	32	24

B15—Measures and counts of *Megalocranchia abyssicola* (Goodrich, 1896)

Specimen ID	MU 332928	USNM 730789	NSMT-Mo:67203	NSMT-Mo:67345	Mean Indices
Type status	none	none	none	none	
ML	57	92	186	263	<b>57–263</b>
Sex	Indet.	Indet.	Indet.	Indet.	
MW	21	35	38	40	<b>38</b>
FL	17	32	93	152	<b>31, 55<sup>^</sup></b>
FW	12	20	34	51	<b>20</b>
HL	6	10	16	24	<b>10</b>
HW	15*	30*	38	48	<b>25</b>
ED	6*	18	22	28	<b>13</b>
Arms I	9	17	27	43	<b>16</b>
Arms II	13	23	34	56	<b>22</b>
Arms III	18*	30	39	61	<b>27</b>
Arms IV	16	26	35	50	<b>24</b>
TnL	24	41	46	81	<b>36</b>
CL	7	13	17	30	<b>12</b>

<sup>^</sup> Indices differed in material above 150 mm ML.

B16—Measures and counts of *Megalocranchia fisheri* (Berry, 1909)

Specimen ID	SBMNH 464905	SBMNH 460924	Mean Indices	SBMNH 460969	SBMNH 464761	SBMNH 460755	Mean Indices	SBMNH 460742
Type status	none	none		none	none	none		none
ML	20	26	<b>20–40</b>	43	51	60	<b>40–60</b>	154
Sex	Indet.	Indet.		Indet.	Indet.	Indet.		Indet.
MW	6.5	7	<b>37</b>	26	18*	28	<b>44</b>	37
FL	2.5	3.5	<b>14</b>	8	8	16	<b>20</b>	61
FW	6	6	<b>24</b>	10	11	13	<b>18</b>	28
HL	1.5	1.5	<b>10</b>	3.5	5	10	<b>11</b>	18
HW	4.6	9.5	<b>27</b>	12	11	19	<b>27</b>	42
ED	1.1	2.1	<b>7</b>	3.2	4.5	8	<b>10</b>	30
Arms I	0.8	2.1	<b>7</b>	5	5	11	<b>13</b>	34
Arms II	1.1	3.8	<b>10</b>	6	8	12	<b>16</b>	40
Arms III	1.4	6.7	<b>15</b>	10	11	18	<b>24</b>	49
Arms IV	1.7	5.1	<b>13</b>	9	10	14	<b>20</b>	39
TnL	4.3	21	<b>73</b>	24	19	27	<b>48</b>	69
CL	2.5	6	<b>16</b>	7	9	9.5	<b>17</b>	18

B17—Measures and counts of *Megalocranchia maxima* Pfeffer, 1884

Specimen ID	SBMNH 464902	NMNH 815199	NMNH 815194	Mean Indices	MV F71717	NMNZ M.67228	MV F163948	Mean Indices
Type status	none	none	none		none	none	none	
ML	87	100	123	94–200	300	410	666	300–666
Sex	Indet.	M	M		F	F	M	
MW	30	41	55	38	40*	80	134	17
FL	28	29	42	31	138*	234	300*	49
FW	22	22	32	24	72*	70		21
HL	11	10	27	17	35	40	90	14
HW	24	43	40	34	30*	-	-	27
ED	14	18	27	18	35	-	-	10
Arms I	17	26	48	28	84	109	242*	31
Arms II	20	31	58	37	87	120	240	34
Arms III	32	43	61	44	101	134	245	35
Arms IV	25	35	56	36	85	122	224	32
TnL	38	72	115	73	178	200	330	53
CL	13	19	28	20	42	47	86	13

B18—Measures and counts of *Megalocranchia* sp. NZ

Specimen ID	NMNZ M.286201	NIWA 95951	SBMNH 460939	NMNZ M.074320	USNM 815097	NMNZ M.074305	Mean Indices
Type status	none	none	none	none	none	none	
ML	60	61	71	82	124	225	60–225
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	F	
MW	20	15	18	30	38	40*	33
FL	22	20	18	13	39	104	29
FW	7*	12	15	20	22	32	22
HL	13	7	7	19	22	33	16
HW	18	14	18*	20	33	-	26
ED	11	9	9*	18	20	-	16
Arms I	15	11	9	23	25	58	19
Arms II	18	14	11.5	28	25*	60	23
Arms III	24	18	18	35	36	85	33
Arms IV	24	15	14	31	30	63	28
TnL	-	47	29	-	47	131	47
CL	-	12	7	-	16	42	13

B19—Measures and counts of *Sandalops melancholicus* Chun, 1906

Specimen ID	NMNZ M.074324	NMNZ M.074316	SBMNH 460893	MV F163722	NSMT- Mo:66705	Mean Indices	MV F78244	NIWA 95896	Mean Indices
Type status	none	none	none	none	none		none	none	
ML	41	47	51	67	71	<b>40–75</b>	78	87	<b>&gt; 75</b>
Sex	Indet.	Indet.	Indet.	Indet.	M		Indet.	Indet.	
MW	23	19	18	48	28	<b>52</b>	45	46	<b>57</b>
FL	5.5	6	7	14	8	<b>14</b>	9	12	<b>12</b>
FW	9	9	12	24	14	<b>24</b>	18	21	<b>23</b>
HL	6	6	1	-	3	<b>14</b>	18	11	<b>14</b>
HW	9	9	12	-	20	<b>27</b>	25	28	<b>33</b>
ED	6	4	4	-	8	<b>11</b>	13	13	<b>14</b>
Arms I	6	7*	5	11	7	<b>15</b>	12	17	<b>19</b>
Arms II	4	6.5	5	12	8	<b>16</b>	15	17	<b>21</b>
Arms III	5	7	5.5	9*	8	<b>17</b>	17	18	<b>22</b>
Arms IV	6	7	6	12	7	<b>16</b>	12	18	<b>21</b>
TnL	-	-	24	59	38	<b>69</b>	-	95	<b>100</b>
CL	-	-	4	8	6	<b>16</b>	-	13	<b>15</b>

B20—Measures and counts of *Taonius belone* (Chun, 1906)

Specimen ID	NSMT-Mo:75114	NSMT-Mo:67349	NSMT-Mo:67349	NSMT-Mo:75441	Mean Indices
Type status	none	none	none	none	
ML	113	116	121	270	<b>113–270</b>
Sex	Indet.	Indet.	Indet.	Indet.	
MW	20	21	18	72	<b>20</b>
FL	51	46	47	51	<b>40, 20^</b>
FW	19	-	16	35	<b>14</b>
HL	10	9	9	29	<b>9</b>
HW	22	19	24	49	<b>18</b>
ED	7*	11	12	28	<b>9</b>
Arms I	12	12	16	43	<b>13</b>
Arms II	17	17	17	69	<b>17</b>
Arms III	23	21	21	69	<b>20</b>
Arms IV	16	20	16	63	<b>17</b>
TnL	51	37	25	114	<b>35</b>
CL	8	9	8	33	<b>9</b>

^ Indices differed in material above 200 mm ML.



B21—Measures and counts of *Taonius borealis* (Nesis, 1972)

Specimen ID	RBCM 010-00251-008	RBCM 988-212-003	SBMNH 464441	RBCM 979-11252-004	RBCM 010-00264-001	NSMT-Mo:71705	Mean Indices
Type status	none	none	none	none	none	none	
ML	118	141	144	154	245	450	<b>118–450</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	Indet.	
MW	24	26	36	41	78	125	<b>27</b>
FL	46	58	54	66	95	141	<b>39</b>
FW	15*	17	20	24	25*	60*	<b>12</b>
HL	13	16	18	21	38	50	<b>13</b>
HW	26	31	33	42*	72	60*	<b>94</b>
ED	12	15	19	20	35	35	<b>12</b>
Arms I	19	18	30	31	65	127	<b>21</b>
Arms II	24	25	37	32	76	156	<b>26</b>
Arms III	26	27	41	38	82	150	<b>28</b>
Arms IV	24	23	28	30	66	110	<b>22</b>
TnL	75	47	68	67	167	286	<b>56</b>
CL	12	10	15	13	39	75	<b>12</b>

B22—Measures and counts of *Taonius exopolitus*, sp. nov.

Specimen ID	AM C.009070	AM C.009070	AM C.009070	NIWA 119227	AM C.009070	NIWA 95946	Mean Indices
Type status	none	none	none	paratype	none	holotype	
ML	223	233	250	-	282	285	<b>223–285</b>
Sex	M	Indet.	M	indet	F	M	
MW	42	41	40	-	34	51	<b>17</b>
FL	-	76*	64*	-	80	65*	<b>28</b>
FW	-	-	22*	-	24	-	<b>9</b>
HL	32	29	25	-	30	36	<b>12</b>
HW	30	30*	28*	-	27	-	<b>12</b>
ED	29	18*	21*	-	18*	-	<b>9</b>
Arms I	49	37	32	50	42	47	<b>16</b>
Arms II	56	48	40	58	43	54	<b>19</b>
Arms III	63	53	44	66	52	68	<b>22</b>
Arms IV	48	49	43	50*	52	52	<b>19</b>
TnL	99	105*	103	197	113	-	<b>43</b>
CL	22	27	27	27	25	-	<b>11</b>

B23—Measures and counts of *Taonius notalia*, sp. nov.

Specimen ID	RSMAS 782-20	MV F54273	MV F163704	ZMO; uncatalogued	MV F163706	Mean Indices
Type status	none	holotype	none	none	none	
ML	225	245	263	265	310	<b>225–310</b>
Sex	Indet.	Indet.	Indet.	Indet.	Indet.	
MW	38	35*	52	28*	-	<b>15</b>
FL	92	106	87	86	92	<b>36</b>
FW	32	31	32	34	36	<b>13</b>
HL	26	25	44	20	-	<b>12</b>
HW	44*	35	47	28*	-	<b>15</b>
ED	24	20	-	-	-	<b>10</b>
Arms I	37	44	-	41	90	<b>20</b>
Arms II	41	49	80	49	93	<b>24</b>
Arms III	42	46	86	51	91	<b>24</b>
Arms IV	39	44	70	43	84	<b>21</b>
TnL	72	84	-	127	188	<b>44</b>
CL	21	24	-	20	35	<b>9</b>

B24—Measures and counts of *Taonius robisoni*, sp. nov.

Specimen ID	SBMNH 464422	SBMNH 464421	SBMNH 464424	SBMNH 464982	Mean Indices
Type status	none	none	holotype	none	
ML	69	96	143	210	<b>69–210</b>
Sex	Indet.	Indet.	Indet.	Indet.	
MW	13	10*	36	36	<b>18</b>
FL	21	-	75	102	<b>50</b>
FW	-	-	-	20	<b>10</b>
HL	6	9	15	17	<b>9</b>
HW	11	9	26	28	<b>14</b>
ED	4	4	11	18	<b>7</b>
Arms I	8	8	18	26	<b>11</b>
Arms II	9	9	21	36	<b>14</b>
Arms III	11	10*	24	35	<b>15</b>
Arms IV	8	10	20	33	<b>13</b>
TnL	23	-	-	74	<b>35</b>
CL	5	6	-	11	<b>5</b>

B25—Measures and counts of *Taonius tanuki*, sp. nov.

Specimen ID	NMNZ M.174789	NMNZ M.172938	NMNZ M.091392	NMNZ M.172908	NMNZ M.172913	NMNZ M.172910	Mean Indices
Type status	none	none	none	none	holotype	none	
ML	180	221	235*	276	395	453	<b>235–453</b>
Sex	Indet.	Indet.	Indet.	Indet.	M	F	
MW	36	33	39	66	55	80	<b>19</b>
FL	70	83	91	94	187	186	<b>37</b>
FW	-	-	18	-	50	59	<b>15</b>
HL	39	28	30	30	53	47	<b>13</b>
HW	-	19	48	30	33*	71	<b>13</b>
ED	-	-	21	-	-	42	<b>9</b>
Arms I	32	25	38	57	78	82	<b>18</b>
Arms II	35	37	42	60	87	100	<b>21</b>
Arms III	41	45	54	66	77	112	<b>24</b>
Arms IV	37	38	49	61	74	88	<b>21</b>
TnL	76	144	147*	-	149	182	<b>57</b>
CL	12	21	20	-	43	48	<b>9</b>

**Appendix C: Specimens and COI sequences used in molecular analyses in Chapter 11 (see Fig. 11.1).**

Taxon ID		BIN	BOLD Process ID	Specimen ID	Locality	Reference
<i>Bathothauma</i>						
	<i>B. lyromma</i>		NZCRA002-17	Anela 315	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>B. lyromma</i>	BOLD:ADH6205	NZCRA003-17	FMNH 286571	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>B. lyromma</i>	BOLD:ADH6205	NZCRA001-17	Anela 457	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
<i>Cranchia</i>						
	<i>C. scabra</i>	BOLD:AAJ6514	KERCE002-17	NIWA 118124	New Zealand (Kermadec Islands)	Cranchiid study (in prep.)
	<i>C. scabra</i>	BOLD:AAJ6514	GBCPH1106-13	GQ853499		Elliger et al. (unpublished)
	<i>C. scabra</i>	BOLD:AAJ6514	GBCPH0061-06	AF000035	N Pacific Ocean	Carlini & Graves (1999)
	<i>C. scabra</i>	BOLD:AAJ6514	GBCPH1107-13	GQ853498		Elliger et al. (unpublished)
	<i>C. scabra</i>	BOLD:AAJ6514	NZCRA019-17	Anela 562	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>C. scabra</i>	BOLD:AAJ6514	NZCRA020-17	NSMT 027	Pacific Ocean	Cranchiid study (in prep.)
<i>Galiteuthis</i>						
	<i>G. armata</i>	BOLD:ABA4569	GBCPH1042-10	EU735396	Mid-Atlantic Ridge	Lindgren (2010)
	<i>G. glacialis</i>	BOLD:AAB8549	BASMC077-09	JR161-114-1	Southern Ocean (Scotia Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	BASMC078-09	JR161-114-1	Southern Ocean (Scotia Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CAOII681-09	KL_05_0786	Southern Ocean	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CAOII680-09	KL_05_0785	Southern Ocean	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CCWW011-11	MO_K11	Southern Ocean (Atka Bay)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA167-08	NIWA 44279	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA161-08	NIWA 44336	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA140-08	NIWA 44596	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA165-08	NIWA 44306	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)

	<i>G. glacialis</i>	BOLD:AAB8549	CANTA125-08	NIWA 44343.1	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA141-08	NIWA 44597	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA163-08	NIWA 44342	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA126-08	NIWA 44343.2	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	CANTA132-08	NIWA 44341	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>G. glacialis</i>	BOLD:AAB8549	BASMC076-09	JR161-114-1	Southern Ocean (Scotia Sea)	Cranchiid study (in prep.)
	<i>G. phyllura</i>	BOLD:ACQ6814	GBCPH1767-14	KF309245	Mid-Atlantic Ridge	Bolstad et al. (2015)
	<i>G. phyllura</i>	BOLD:ACQ6814	GBCPH1766-14	KF309246	Mid-Atlantic Ridge	Bolstad et al. (2015)
	<i>G. phyllura</i>	BOLD:ACQ6814	GBCPH1768-14	KF309247	Mid-Atlantic Ridge	Bolstad et al. (2015)
	<i>G. phyllura</i>	BOLD:ACQ6814	NZCRA036-17	NSMT 085	Pacific Ocean	Cranchiid study (in prep.)
	<i>G. phyllura</i>	BOLD:ACQ6814	NZCRA024-17	FMNH 330012	N Pacific Ocean (California)	Cranchiid study (in prep.)
	<i>G. phyllura</i>	BOLD:ACQ6814	NZCRA033-17	FMNH 330070	N Pacific Ocean (California)	Cranchiid study (in prep.)
	<i>G. suhmi</i>	BOLD:ADH4034	NZCRA034-17	NIWA 92491	New Zealand	Cranchiid study (in prep.)
	<i>G. suhmi</i>	BOLD:ADH4034	NZCRA046-17	TAN1401/106	New Zealand	Cranchiid study (in prep.)
	<i>G. suhmi</i>	BOLD:ADH4034	NZCRA047-17	NIWA 105554	New Zealand	Cranchiid study (in prep.)
	<i>G. sp. KER</i>	BOLD:ADH4035	KERCE082-17	NIWA 118845	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>G. sp. NZ1</i>	BOLD:ACQ8318	GBCPH1518-14	GU145078	SE Atlantic Ocean	Bucklin et al. (unpublished)
	<i>G. sp. NZ1</i>	BOLD:ACQ8318	NZCRA031-17	NIWA 105576	New Zealand	Cranchiid study (in prep.)
	<i>G. sp. NZ1</i>	BOLD:ACQ8318	NZCRA029-17	NIWA 105558	New Zealand	Cranchiid study (in prep.)
	<i>G. sp. NZ1</i>	BOLD:ACQ8318	NZCRA028-17	NIWA 105557	New Zealand	Cranchiid study (in prep.)
	<i>G. sp. NZ2</i>	BOLD:ADH5671	NZCRA027-17	NIWA 105550A	New Zealand	Cranchiid study (in prep.)
	<i>G. sp. NZ2</i>	BOLD:ADH5671	NZCRA026-17	NIWA 106489	New Zealand	Cranchiid study (in prep.)

	<i>G. sp. NZ2</i>	BOLD:ADH5671	NZCRA030-17	NIWA 105572	New Zealand	Cranchiid study (in prep.)
<i>Helicocranchia</i>						
	<i>H. sp. NP</i>	BOLD:AAAY2019	GBCPH0128-06	AF075412	N Pacific Ocean (Hawaii)	Anderson (2000)
	<i>H. sp. NP</i>	BOLD:AAAY2019	NZCRA039-17	FMNH 278110	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>H. sp. NP</i>	BOLD:AAAY2019	NZCRA038-17	Anela 475	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>H. sp. SA</i>	BOLD:ABU6300	CEPHW098-11	KF369197	S Atlantic Ocean	Bolstad et al. (2015)
	<i>H. sp. RJ2009</i>	BOLD:ACQ6631	GBCPH1535-14	GU145061	NW Atlantic Ocean	Bucklin et al. (2010)
	<i>H. sp. KER</i>	BOLD:ADH6254	KERCE084-17	NIWA 118847	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>H. sp. KER</i>	BOLD:ADH6254	KERCE028-17	NIWA 118486 C	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
<i>Leachia</i>						
	<i>Leachia atlantica</i>	BOLD:ABX8833	CEPHW104-11	KF369200	S Atlantic Ocean	Bolstad et al. (2015)
	<i>Leachia atlantica</i>	BOLD:ABX8833	GBCPH1530-14	GU145067	NW Atlantic Ocean	Bucklin et al. (2010)
	<i>Leachia lemur</i>	BOLD:AAW9980	GBCPH1049-10	EU735389	N Atlantic Ocean	Lindgren (2010)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE014-17	NIWA 118134 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE060-17	NIWA 118606 B	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE059-17	NIWA 118606 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE071-17	NIWA 118817	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE083-17	NIWA 118845 B	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE132-17	NIWA 119228 C	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE130-17	NIWA 119228 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE101-17	NIWA 119200 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE007-17	NIWA 118129	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE131-17	NIWA 119228 B	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>Leachia separata</i>	BOLD:ADH5276	KERCE061-17	NIWA 118606 C	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)

<i>Liocranchia</i>						
	<i>L. reinhardtii</i>	BOLD:ACA9595	CEPAR185-11	G16DOM/G16-1	Morocco	Cranchiid study (in prep.)
	<i>L. reinhardtii</i>	BOLD:ACA9595	CEPAR163-11	G14NOM/G14-1	Morocco	Cranchiid study (in prep.)
	<i>L. sp. PO</i>	BOLD:ADH4164	NZCRA041-17	NSMT 263	Pacific Ocean	Cranchiid study (in prep.)
<i>Megalocranchia</i>						
	<i>M. cf. fisheri</i>	BOLD:ADH7240	NZCRA043-17	FMNH 286594	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>M. cf. fisheri</i>	BOLD:ADH7240	NZCRA040-17	FMNH 286610	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>M. cf. fisheri</i>	BOLD:ADH7240	NZCRA042-17	Anela 535	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>M. sp. ARL-2008</i>	BOLD:AAX3316	GBCPH1056-10	EU735382	N Atlantic Ocean	Lindgren (2010)
	<i>M. sp. PO</i>	BOLD:ADH7241	NZCRA005-17	NSMT 119	Pacific Ocean	Cranchiid study (in prep.)
<i>Mesonychoteuthis</i>						
	<i>M. hamiltoni</i>	BOLD:AAB8550	CAOII852-09	Mesonychoteuthis _KEP_2005	S Atlantic Ocean (South Georgia)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	GBCPH1041-10	EU735397	Southern Ocean	Lindgren (2010)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA179-08	MH04	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA181-08	MH06	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA171-08	KL01	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA162-08	NIWA 44346	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA146-08	NIWA 44347	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA145-08	NIWA 44349	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA177-08	MH01	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	CANTA160-08	NIWA 44348	Southern Ocean (Ross Sea)	Cranchiid study (in prep.)
	<i>M. hamiltoni</i>	BOLD:AAB8550	NZCRA045-17	NSMT 374	Southern Ocean	Cranchiid study (in prep.)
<i>Sandalops</i>						
	<i>S. melancholicus</i>	BOLD:ADH6536	KERCE040-17	NIWA 118602 B	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)

	<i>S. melancholicus</i>	BOLD:ADH6536	KERCE080-17	NIWA 118843	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>S. melancholicus</i>	BOLD:ADH6536	KERCE039-17	NIWA 118602 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>S. melancholicus</i>	BOLD:ADH6536	KERCE124-17	NIWA 119226	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>S. melancholicus</i>	BOLD:ADH6536	KERCE085-17	NIWA 118848	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>S. melancholicus</i>	BOLD:ADH6536	NZCRA073-17	FMNH 286531	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
<i>Taonius</i>						
	<i>T. cf. robisoni</i>	BOLD:AAK0251	GBCPH0131-06	AF075415	N Pacific Ocean (Hawaii)	Anderson (2000)
	<i>T. cf. robisoni</i>	BOLD:AAK0251	NZCRA050-17	FMNH 278101	N Pacific Ocean (Hawaii)	Cranchiid study (in prep.)
	<i>T. pavo</i>	BOLD:AAM9951	GBCPH1057-10	EU735381	N Atlantic Ocean	Lindgren (2010)
	<i>T. borealis</i>	BOLD:ACD9245	GBCPH1829-14	KF309244	Mid-Atlantic Ridge	Bolstad et al. (2015)
	<i>T. borealis</i>	BOLD:ACD9245	RBCMI492-14	RBCM: 011-00132-002	NE Pacific Ocean (BC)	Cranchiid study (in prep.)
	<i>T. sp. PO1</i>	BOLD:ADH3660	NZCRA035-17	NSMT 245	Pacific Ocean	Cranchiid study (in prep.)
	<i>T. sp. PO2</i>	BOLD:ADH3661	NZCRA004-17	NSMT 016	Pacific Ocean	Cranchiid study (in prep.)
	<i>T. sp. PO2</i>	BOLD:ADH3661	NZCRA049-17	NSMT 030	Pacific Ocean	Cranchiid study (in prep.)
	<i>T. sp. PO2</i>	BOLD:ADH3661	NZCRA074-17	NSMT 254	Pacific Ocean	Cranchiid study (in prep.)
	<i>T. expolitus</i>	BOLD:ADH3662	KERCE125-17	NIWA 119227 A	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. expolitus</i>	BOLD:ADH3662	KERCE127-17	NIWA 119227 C	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. expolitus</i>	BOLD:ADH3662	KERCE126-17	NIWA 119227 B	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. expolitus</i>	BOLD:ADH3662	KERCE128-17	NIWA 119227 D	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. expolitus</i>	BOLD:ADH3662	KERCE129-17	NIWA 119227 E	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. expolitus</i>	BOLD:ADH3662	NZCRA018-17	NIWA 92488	New Zealand	Cranchiid study (in prep.)
	<i>T. tanuki</i>	BOLD:ADH3663	KERCE062-17	NIWA 121868	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
<i>Teuthowenia</i>						



	<i>T. megalops</i>	BOLD:AAW6796	GBCPH0308-06	AY617064	N Atlantic Ocean	Strugnell et al. (2005)
	<i>T. pellucida</i>	BOLD:AAW6797	CEPHW109-11	KF369198	S Atlantic Ocean	Bolstad et al. (2015)
	<i>T. pellucida</i>	BOLD:AAW6797	CANTA251-08	Teupell6	New Zealand (Chatham Rise)	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA076-17	NIWA 105555	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA007-17	NIWA 92487	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA008-17	NIWA 105547	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA058-17	NIWA 92474	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA053-17	NIWA 92481	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA060-17	NIWA 92486	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA082-17	NIWA 106182 B	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA081-17	NIWA 106170	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA054-17	NIWA 92471	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA067-17	TAN1401/MWT3-1	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA069-17	NIWA 105543	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA078-17	NIWA 105570	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA077-17	NIWA 105559	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA006-17	NIWA 92492	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA016-17	TAN1401/MWT1-NE	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA055-17	TAN1401/101-5	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA068-17	TAN1401/102-1	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA064-17	TAN1401/40	New Zealand	Cranchiid study (in prep.)

	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA063-17	TAN1401/35	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA009-17	NIWA 105549	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA066-17	TAN1401/TM	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA072-17	TAN1401/102-2	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA062-17	TAN1401/30	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA071-17	NIWA 106172	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA070-17	NIWA 105551	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA013-17	TAN1601/7-2	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA080-17	NIWA 106164	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA059-17	NIWA 92479	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA014-17	TAN1401/MWT1-E	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA075-17	NIWA 106175	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA065-17	TAN1401/69	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA015-17	TAN1401/42	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA017-17	TAN1401/47	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA083-17	NIWA 106182 A	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA012-17	TAN1401/MWT1-2	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA079-17	NIWA 105588	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA056-17	TAN1401/101-6	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA052-17	NIWA 92478	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA051-17	TAN1401/101-1	New Zealand	Cranchiid study (in prep.)

	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA061-17	NIWA 92480	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA011-17	TAN1601/7-1	New Zealand	Cranchiid study (in prep.)
	<i>T. pellucida</i>	BOLD:AAW6797	NZCRA057-17	TAN1401/101-7	New Zealand	Cranchiid study (in prep.)
	<i>T. aff. pellucida</i>	BOLD:ADH5304	KERCE038-17	NIWA 118601	New Zealand (Kermadec Islands)	Braid & Bolstad (submitted)
	<i>T. aff. pellucida</i>	BOLD:ADH5304	NZCRA022-17	AM C.500821	Australia	Cranchiid study (in prep.)
Unknown genus						
	Cranchiidae sp.	BOLD:ADH4163	NZCRA048-17	NIWA 96179	New Zealand	Cranchiid study (in prep.)
	Cranchiidae sp.	BOLD:ADH4163	NZCRA023-17	AM C.500830	Australia	Cranchiid study (in prep.)
	Cranchiidae sp.	BOLD:ADH4163	NZCRA021-17	AM C.500796	Australia	Cranchiid study (in prep.)