

## Ontogeny of the deep-sea cranchiid squid *Teuthowenia pellucida* (Cephalopoda: Cranchiidae) from New Zealand waters

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*Teuthowenia pellucida* is a cosmopolitan southern sub-tropical species, and is abundantly represented in local New Zealand collections. However, because of the morphological similarities between this and other cranchiid genera at early ontogenetic stages, accurate identification of small specimens can be difficult. Herein, the morphological changes characterizing six pre-adult developmental stages (termed A–F) are reported in detail, as well as adult morphology; new information is provided on fecundity. These findings comprise a small contribution toward eventual resolution of the systematically unstable Cranchiidae.

**Keywords:** Cranchiidae; ontogeny; New Zealand; squid

### Introduction

*Teuthowenia* is a squid genus of the family Cranchiidae, whose largely transparent tissues have resulted in the common name “glass” squids; their crypsis is also aided by eye photophores (Herring et al. 2002), which counter-shade down-welling light from the surface (Young and Roper 1976; Voss 1985). Cranchiids have been reported from all oceans except the Arctic (Norman and Lu 2000), and are found primarily between the mesopelagic and bathypelagic zones; however, some species, including those of the genus *Teuthowenia*, migrate vertically within the water column depending on maturity and seasonality (Voss 1985; Moreno et al. 2009).

*Teuthowenia* contains three species (Voss 1980, 1985): *Teuthowenia maculata* and *Teuthowenia megalops* are found in the central and northern Atlantic, and *Teuthowenia pellucida* lives circum-globally in the southern sub-tropical belt (Voss 1985). This wide-spread generic distribution and the ability to migrate through the water column indicate that these animals probably form components of several different oceanic trophic systems. However, relatively little has been reported about cranchiid predator–prey interactions in the deep sea, although beaks representing many genera – including *Teuthowenia* – have been found in the stomachs of top marine predators, ranging from seabirds (e.g., Imber 1992) to cetaceans (e.g., MacLeod et al. 2003).

*Teuthowenia pellucida* (Chun 1910) has a complex systematic history. Since its original description by Chun in 1910, in which he attributed the species to the genus *Desmoteuthis*, it has been reported as part of eight different genera by different authors, and was eventually placed within *Teuthowenia* by Voss (1980, 1985), who recognized its affinity with the other two known members of the genus, *T. megalops*

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and *T. maculata*. All three species are characterized at maturity by their distinctive fin shape; large eyes, each with three ventral photophores; and the presence of tubercles located externally at the two ventral fusion points between the head and mantle, placing the genus within the subfamily Taoniinae. However, characters for reliably identifying immature specimens are needed, especially during the larval stages, which bear morphological resemblance to several other genera.

The most appropriate terminology for immature cephalopods has been the subject of some discussion (Young and Harman 1988; Sweeney et al. 1992). The term “larvae” was disputed because most cephalopods lack a definitive metamorphosis (Young and Harman 1988); however, Okutani (1987) described that, in contrast to octopods, “actively swimming oegopsid [squids] usually have a cylindrical or spindle-shaped muscular mantle in the adult stage, but a soft, saccular or dome-shaped mantle during juvenile stages,” showing that squid do exhibit some morphological changes during maturation, which could be interpreted as metamorphosis. The term “paralarval” was proposed, defined as post-hatchling cephalopods that display behavioural and/or morphological characters that differ from those of later ontogenetic stages, and pertain to their environment (Young and Harman 1988; Sweeney et al. 1992; Hanlon and Messenger 1996). As squid from several genera of Cranchiidae (*Teuthowenia*, *Helicocranchia*, *Sandalops* and *Leachia*) have been shown to migrate vertically into deeper waters with maturity (Young 1975, 1978; Voss 1985), young cranchiids were initially termed “paralarvae” (Young and Harman 1988); however, Sweeney et al. (1992) considered young cranchiids as being truly larval, indicating that some confusion remains. Both Young and Harman (1988) and Sweeney et al. (1992) agreed that after the post-hatchling stage, the squid should be considered a juvenile; for cranchiid squids, the juvenile phase begins when the eyes become sessile (Young and Harman 1988). The sub-adult stage follows, defined by Young and Harman (1988) as a morphologically developed animal that still requires sexual maturation and/or further growth to reach adulthood. The present study uses the term “larval” to refer to post-hatchling squid and aims to describe and illustrate the ontogenetic development of *T. pellucida* throughout the larval, juvenile, sub-adult and adult stages, enabling reliable identification of individuals of all sizes.

### Material and methods

Specimens of *T. pellucida* were examined from the National Institute of Weather and Atmospheric Research, Ltd. (NIWA) and the National Museum of New Zealand Te Papa Tongarewa (NMNZ) in Wellington, New Zealand (Appendix). Some specimens of *Megalocranchia* and *Liguriella* were also analysed (Appendix). All specimens were fixed in ~4% formalin and stored in 70–80% ethanol. Examinations and illustrations were made using a dissecting microscope with camera lucida. Morphological measures and counts were taken as per Roper and Voss (1983). Tentacle club suckers were imaged using scanning electron microscopy, after being critical-point-dried and sputter-coated in gold–palladium.

Larval and juvenile developmental stages were identified based on morphological differences (outlined in Table 1), with divisions made when several physical features changed markedly, or developed where absent in the previous stage (e.g. tubercles first appearing in stage C). Using these criteria, six stages were identified before the adult stage. Although chromatophore patterns have been found to have systematic

Table 1. Key morphological characteristics of developmental stages in *Teuthowenia pellucida*. \* Features viewed under microscope at 40x magnification.

Character		Mantle	Fins	Tubercles	Eyes	Eye photophores	Arms	Tentacles
Developmental stage								
Stage A (Larva)	Saccular	Semicircular	Absent	Pedunculate, contiguous with stalk	Absent	Short (less than 1 mm), about 3 suckers per arm	III=II=IV=I	No defined club, sucker; in proximal half in two series, distal half four series
Stage B (Larva)	Saccular	Paddle shaped	Absent	Pedunculate, contiguous with stalk	Absent	Arms extend past buccal mass, ~20 suckers per arm	III>II>IV=I	Tentacle tip pointed, no club definition. suckers in proximal half in two series, distal half four series
Stage C (Larva)	Tapered bell	Paddle shaped	1	Pedunculate, beginning differentiation	1 photophore	III>II>IV=I, 18-30 suckers per arm	Club defined with four series of suckers, stalk with two series in straight lines	Suckers on mid-manus expanded, rings visible*, zigzag sucker pattern on stalk, sucker counts remain same
Stage D (Juvenile)	Conical	Paddle shaped	2 or 3	Sessile, spherical	3 photophores (developing)	III>II>IV=I, 20-32 suckers per arm	8-10 large teeth visible on sucker rings*, stalk similar: sucker counts remain same	10-12 large teeth visible on sucker rings*.
Stage E (Juvenile)	Conical	Paddle shaped	2-5	Sessile, spherical	All 3 photophores developed	III>II>IV=I 22-32 suckers per arm	Stalks similar. Sucker counts remain the same	
Stage F (Sub-adult)	Conical	Ovular	2-5	Sessile, spherical	All 3 photophores developed	III>II>IV=I, membrane present, 24-40 suckers per arm		

use in young squids (Young and Harman 1987), the condition of the material examined herein varied considerably, preventing identification of consistent patterns. Chromatophore size and density have been noted where possible.

The fecundity of females was determined by removing the entire ovary of a mature female, separating the eggs from the supportive fibres, and weighing the egg mass; subsets were then counted and weighed in several trials, and the mean of all calculations was used to extrapolate the total number of eggs present.

## Results

A total of 110 specimens of *Teuthowenia* were examined (Appendix), ranging in size from 1.5 to 210 mm dorsal mantle length (ML). Twenty-nine of the specimens were adults, with 22 reproductively mature or mated. Previously reported maturity scales (Arkhipkin 1992) for squid have focused on gonad development, with “juvenile”/stage 0 encompassing all stages before visual sexual differentiation (Arkhipkin 1992); however, young squids (particularly cranchiids) can also undergo significant morphological changes unrelated to sexual maturity. Documenting the progression of these stages is necessary to ensure the correct identification of early life-stage specimens.

All stages of *Teuthowenia* possessed the head–mantle fusion characteristic of the cranchiids: one attachment site at the dorsal midline of the anterior mantle margin, and two ventrally, one on either side of the funnel. Other morphological characters were observed to develop through ontogeny (Figure 1), with their progression characterizing certain growth stages, as detailed below. Some variation was observed in the sizes at which these developments occurred, so mantle length ranges given are approximate, and overlap for certain stages (especially Stages E and F).

### *Pre-adult stages* (main characters summarized in Table 1)

Stage A (larval, ML ~ 1–10 mm; Figures 1A and 2A) – Mantle saccular; walls thin, gelatinous. Consistent localized patches of small, dark chromatophores (Figure 3), about three to five per mm<sup>2</sup>. Fins semi-circular, length and width < 10% ML, ~ 99% of length posterior to mantle tip. Stalked eye length ~ 10% ML, eyes contiguous with stalk. Funnel widely conical, base ~ 70% total mantle width (MW), funnel aperture (FA) ~ 25% base width (BW). Gladius not visually continuous along dorsal midline. Arms stubby, less than 1 mm in length, not extending past buccal mass, each with dense cluster of small chromatophores on aboral surface and few suckers (four per arm at ML 5 mm). Tentacle length approximately equal to mantle length; stalks with several patches of small chromatophores on aboral surface in distal half (Figure 3); 100–120 suckers present over each tentacle stalk and club: 12–20 present in two series on proximal portion of stalk, increasing to four series over distal portion (approximately 20 rows); club undifferentiated from stalk.

Stage B (larval, ML ~ 10–20 mm; Figures 1B and 2B) – Mantle saccular; walls thin, gelatinous. Fins paddle-shaped, length ~ 10–15% ML, width < 10% ML, ~ 99% of length posterior to mantle tip. Stalked eye length ~ 20% ML, eyes contiguous with stalk. Funnel conical, BW ~ 65% MW, FA ~ 20% BW. Gladius visible along entire length of midline, small conus visible just anterior to fins. Arms begin to extend past buccal mass; formula I = II = III = IV; arm length ~ 10–15% ML, each with about 10 pairs of small suckers by end of stage, beginning at about 25% arm length and

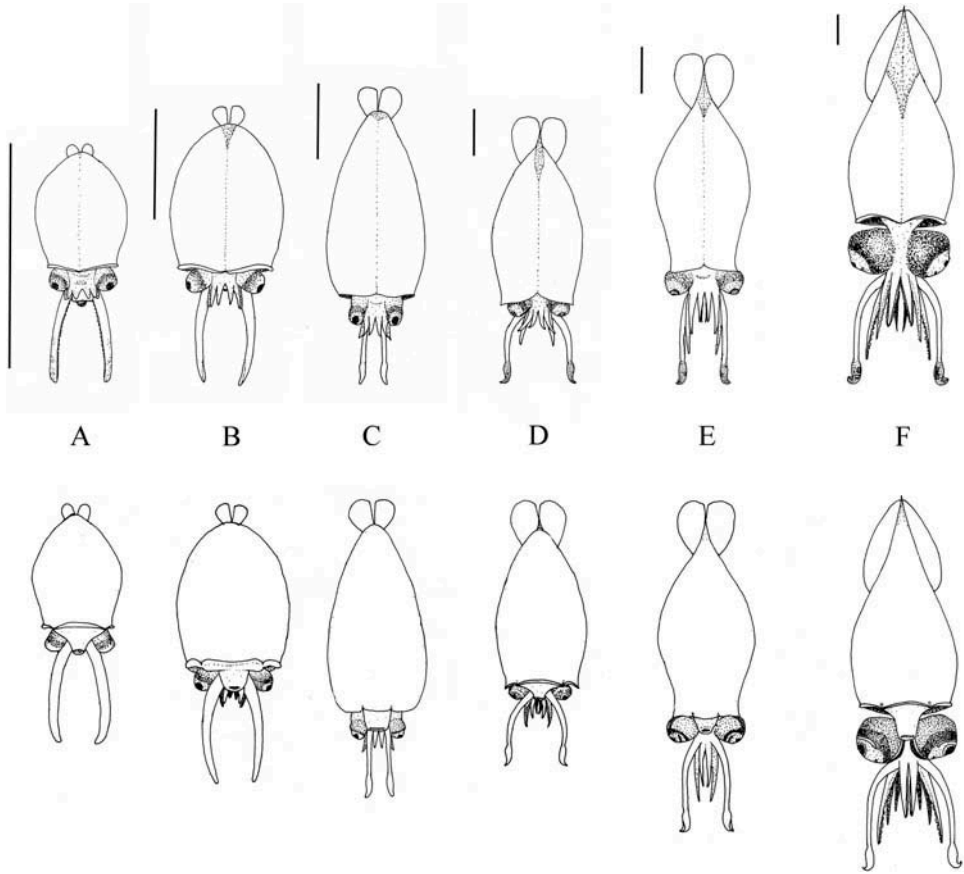


Figure 1. Ontogenetic series of *Teuthowenia pellucida*; dorsal (above) and ventral (below) views. Approximate mantle length range: (A) 1–10 mm; (B) 10–20 mm; (C) 20–28 mm; (D) 28–40 mm; (E) 40–70 mm; (F) 45–100 mm. Scale bar = 1 cm.

continuing to arm tip. Tentacles slightly shorter than ML; stalks thick, muscular, with small suckers along entire length, their numbers as in stage A. Club slightly differentiated from stalk, slightly concave along dorsal margin, tapering to distal point. Flethy membrane forming along dorsal club margin. Club suckers enlarged towards centre, with diameter of largest twice that of tentacle stalk suckers.

Stage C (larval, ML ~ 20–28 mm; **Figures 1C** and **2C**) – Mantle proportionally larger than in earlier stages, tapering to blunt end. Fins paddle-shaped, length ~ 10% ML, width ~ 15–20% ML, 95% of fin length posterior to mantle tip. Eyes on stout stalks, visually differentiated from stalk; first ventral photophore developing (**Figure 2C**). Funnel as in Stage B, but with single external tubercle present at each ventral mantle–funnel fusion point. Gladius as in Stage B. Arms as in Stage B but with arms II and III slightly longer; formula III = II > IV = I; arms III 10–20% ML. Tentacle length < 50% ML; club clearly differentiated; sucker counts and arrangement as in Stage B.

Stage D (juvenile, ML ~ 29–40 mm; **Figures 1D** and **2D**) – Mantle conical; outer dermal layer with oval chromatophores, each < 1 mm along long axis, sparsely spaced (about four per cm<sup>2</sup>). Fins paddle-shaped, length and width ~ 30–35% ML,

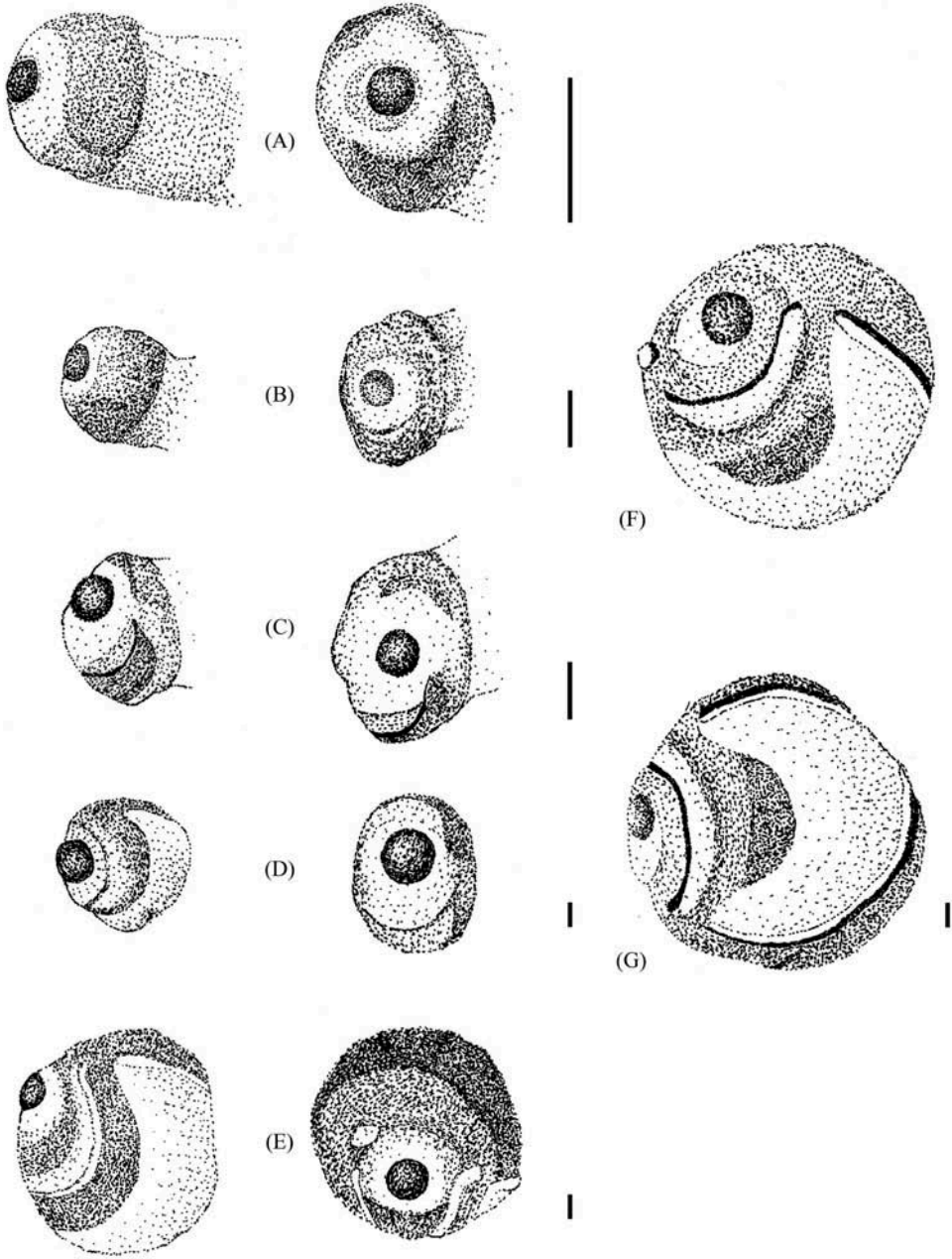


Figure 2. Development of *Teuthowenia pellucida* eyes through ontogeny showing both anterior (right) and lateral (left) perspective. Eye presented from (A) stage A; (B) stage B; (C) stage C; (D) stage D; (E) stage E and F; (F) adult (anterior); (G) adult (ventral). Scale bar = 1 mm.

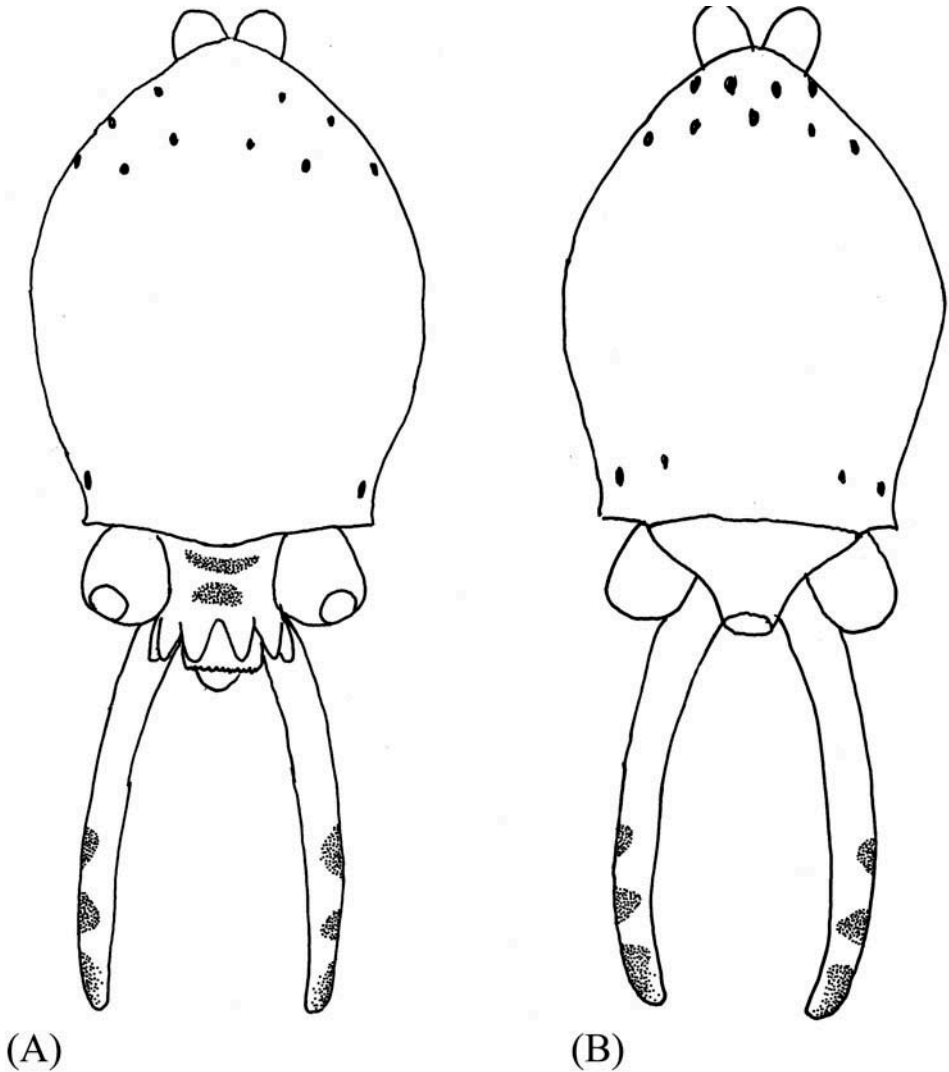


Figure 3. Common chromatophore patterns on (A) dorsal and (B) ventral side of stage A larvae of *Teuthowenia pellucida*.

40% of fin length posterior to mantle tip. Eyes spherical, stalks diminished, eye depth  $\sim 20\%$  head width; all three ventral photophores developing. Head width (HW) approximately equal to mantle width. Funnel base  $\sim 50\%$  MW, FA  $\sim 25\%$  BW. Multiple tubercles (two or three) on exterior mantle surface at funnel–mantle fusion points. Gladius remains unchanged. Arms with 10–15 pairs of suckers each; formula  $\text{III} > \text{II} > \text{IV} \approx \text{I}$ ; arms III 25–30% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Tentacles  $\sim 50\%$  ML; stalk with 12–20 pairs of suckers in zig-zag pattern along length (Figure 4); club well defined, curves toward dorsal side distally, with fleshy membrane on both dorsal and ventral margins. Approximately 80 suckers, enlarged at mid-manus, with visible rings.

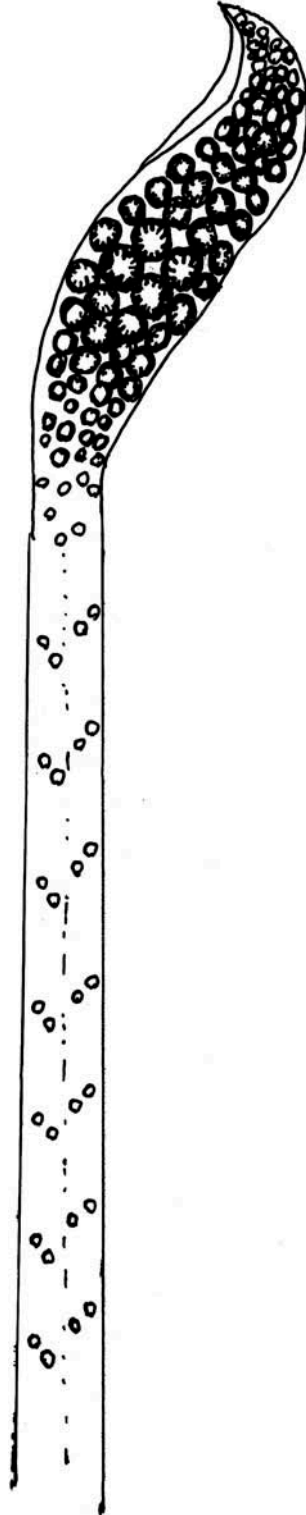


Figure 4. Schematic diagram of *Teuthowenia pellicida* tentacle showing paired zig-zag sucker pattern on stalk, visible from Stage D onwards.



Stage E (juvenile, ML ~ 41–70 mm; [Figures 1E and 2E](#)) – Mantle conical, with similar chromatophore patterns as in previous stage. Fins paddle-shaped, length 20–35% ML, width 13–15% ML, 20% of fins extend past mantle tip. Eyes bulbous, not stalked; all three ventral eye photophores fully developed. HW ~ 70–100% maximum MW. Funnel base ~ 25–30% MW, FA ~ 50% BW. Tubercles and gladius as in Stage D. Arms with ~ 15 pairs of suckers each; formula III > II > IV = I; arms III < 30% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Tentacles slender, length approximately 50% ML; stalk with zig-zag sucker pattern, club ~ 30% tentacle length, well defined, curving toward dorsal side distally, with dorsal membrane more pronounced than in previous stages. Approximately 80 suckers on club, largest in median two series at mid manus, with 8–10 large teeth visible.

Stage F (sub-adult, ML ~ 45–100 mm; [Figures 1F and 2E](#)) – Mantle conical; outer dermal layer with oval chromatophores, each 1–2 mm at longest axis, sparse (five or six per cm<sup>2</sup>). Fins thin, gelatinous, narrowly ovate in outline when taken together; length < 50% ML, width 20–30% ML, not extending past mantle tip. Eyes large, causing head width to exceed mantle width; all three ventral photophores developed. Funnel conical, BW ~ 40–50% MW, FA ~ 50% BW. Two to five tubercles present at funnel–mantle fusion points, mostly on external mantle surface but occasionally inside mantle cavity. Gladius fully developed, visible along entire length of dorsal midline. Arms with 12–18 pairs of suckers each; formula III > II > IV = I; arms III 30–50% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane; largest suckers on distal half of arms III. Tentacle length ~ 100% ML, with suckers as in Stage E; ~ 10–12 large teeth visible on sucker rings.

**Adult** (ML > 100 mm; [Figures 2F and G and 5](#))

Mantle conical, maximum width (~ 40–50% ML) attained within anterior 20% ML; walls thin, gelatinous. Outer dermal layer with oval, reddish brown chromatophores, approximately 1–2 mm along long axis, 10–20 per cm<sup>2</sup>. Fins fleshy, ~ 50% ML, narrow (greatest width roughly equal to maximum mantle width), rounded at insertions, tapering to rounded point posteriorly. Head width (measured from lens to lens) wider than maximum mantle width; outer surface of head covered with small, densely set chromatophores (about six per cm<sup>2</sup>). Eyes ([Figure 5](#)) large, oriented anteroventrally, each with three photophores ([Figures 2F and G and 6](#)): two large, crescent-shaped (one around lens, one longitudinally ventral); one small, oval, at anterior periphery slightly above centre. Funnel conical, BW ~ 30% MW, FA ~ 60% BW. Two to five tubercles present at funnel–mantle fusion points (often several on external surface of mantle and one on fused area inside cavity; see [Figure 7](#)). Gladius clearly visible along entire length of dorsal midline ([Figure 5B](#)). Conus visible over posterior 40–50% mantle length. Arm formula III > II > IV ≥ I, arms III 30–50% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Trabeculae on membranes align with pairs of suckers. Arms with ~ 15–20 pairs of adentate suckers; largest suckers present on arms II and III; four to six enlarged suckers near tip about twice diameter of those at arm base. In mature males, distal 15% of arms I and II modified, with four series of small suckers ([Figure 8B](#); see below). In mature females, distal 15% of all arms comprised of fleshy, pigmented brachial organs ([Figure 8A](#); see below). Tentacle length 80–100% ML; stalks thinner than bases of

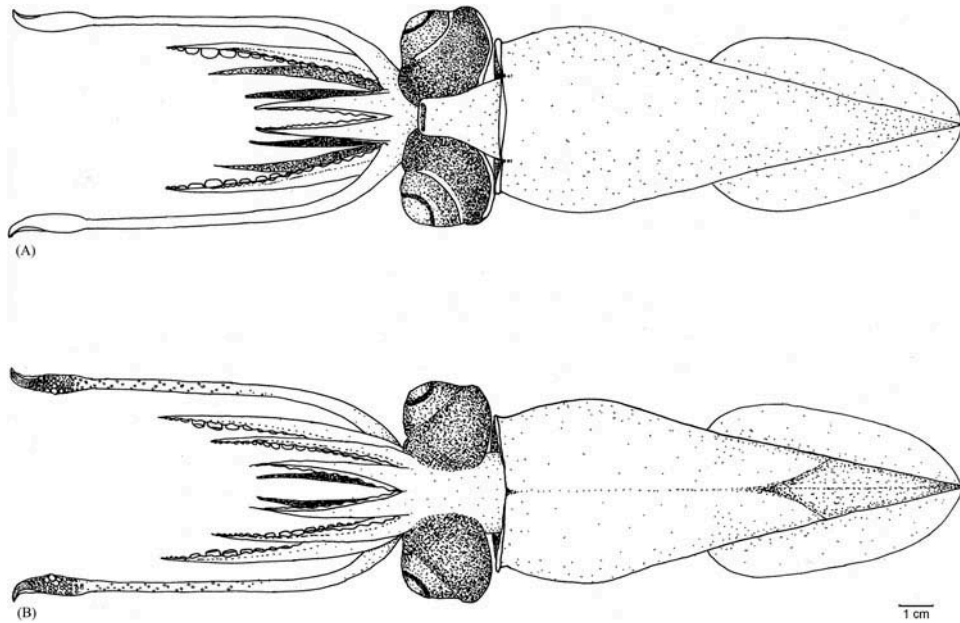


Figure 5. Sub-mature adult *Teuthowenia pellucida* (NIWA 71688, male, ML = 135 mm), (A) ventral and (B) dorsal view. Scale bar = 1 cm.

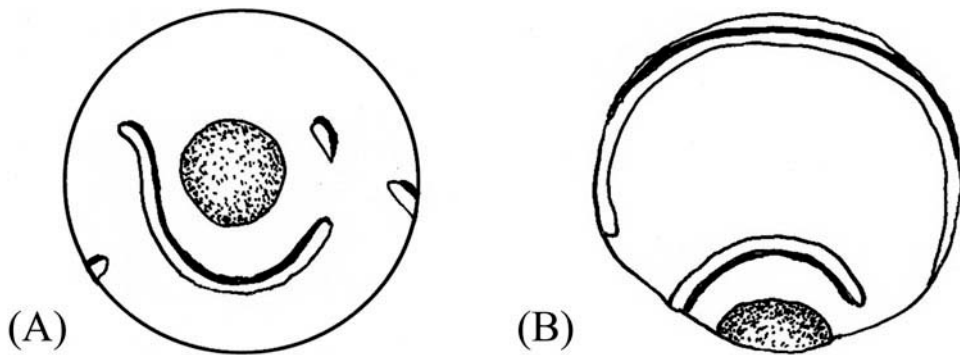


Figure 6. Simplified diagram of eye photophores and lens from (A) anterior view and (B) ventral side of the eye in adult *Teuthowenia pellucida*.

adjacent arms, narrowing toward clubs, with alternating pairs of small suckers (zig-zag pattern) down length of stalk (Figure 4). Clubs slightly expanded (Figure 5), ~ 20% tentacle length, with fleshy dorsal and ventral membranes, the latter more pronounced; about 80 suckers present. Carpal area poorly defined, with suckers appearing randomly distributed proximally, then arranged in four series and increasing in size to mid manus, then quickly decreasing again distally. Suckers (Figure 9) stalked, each with 24–30 teeth, longest distally.

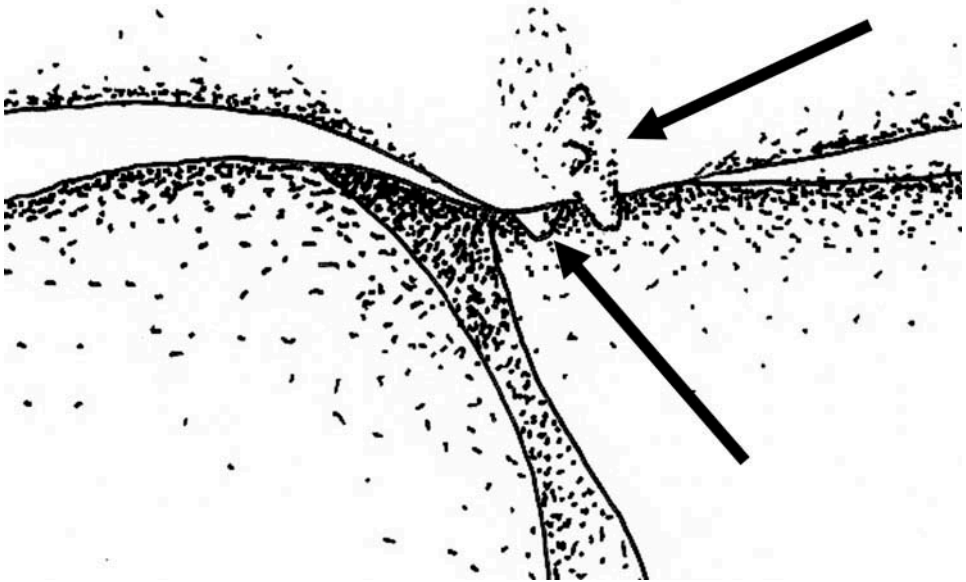


Figure 7. Tubercles at the funnel–mantle fusion point in adult *Teuthowenia pellucida* (three on the exterior and one on the interior mantle surface indicated by arrows).

### *Sexual modifications*

*Teuthowenia pellucida* exhibits secondary sexual characteristics on the arms in both males and females. The suckers on the tips (distal ~ 15%) of arms I and II in males increase from two to four densely set series (Figure 8B). Females have distal brachial organs, consisting of two flaps of skin that overlap along the oral surface of all arms (Figure 8A); these lack pigment during development, and darken to a deep red in mature specimens. This appearance is similar among the six genera of cranchiids (*Cranchia*, *Liocranchia*, *Leachia*, *Teuthowenia*, *Megalocranchia* and *Egea*) that display this feature (Herring et al. 2002). Several examined females were reproductively mature, and three possessed large ovaries with near-mature eggs. The eggs were 1.6–2.8 mm along the longest axis, and an intact ovary was estimated to hold approximately 18,000 eggs. Nidamental glands from these three females were swollen and appeared to have encysted suckers attached to the outer membrane.

### **Discussion**

#### *Ontogenetic development*

In the most recent revision of the genus *Teuthowenia*, Voss (1985) summarized the larval stages of *T. pellucida* and *T. megalops*. However, the abundance of larval, juvenile and sub-adult specimens of *T. pellucida* in New Zealand collections has

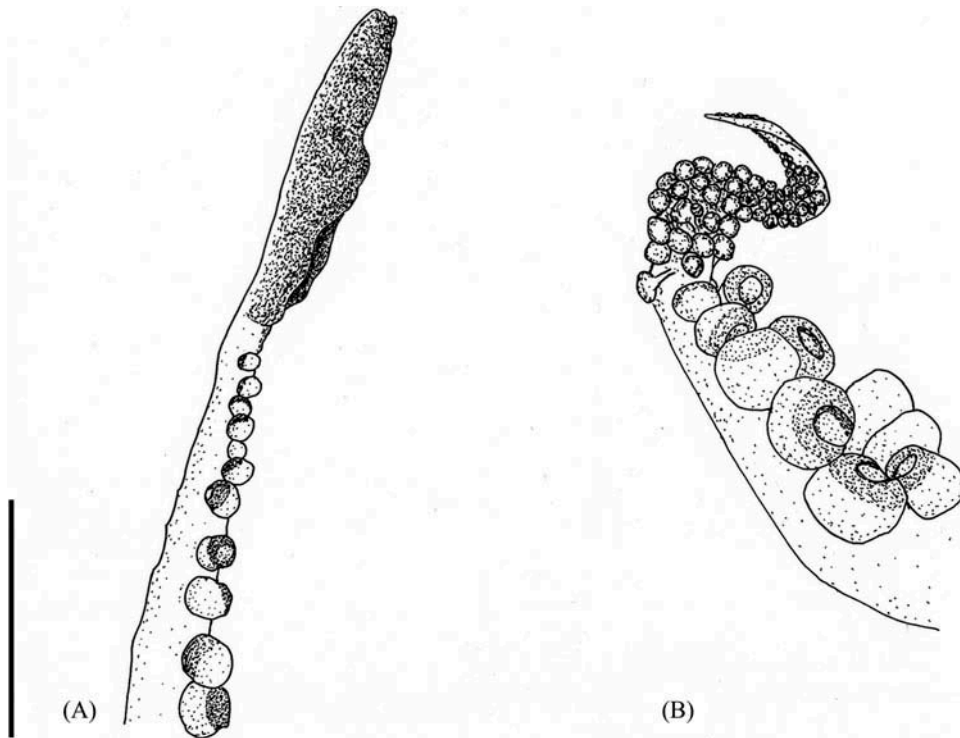


Figure 8. Arm modifications in adult *Teuthowenia pellucida*. Brachial end organ (A) on the tips of all arms in mature females; (B) four series of small suckers on the distal tip of arms I and II in adult males. Scale bar = 1 cm.

permitted the present detailed investigations into the morphological development of this species through early ontogeny, resulting in the identification of seven developmental stages (whose key features are summarized in Table 1). As *Teuthowenia* larvae are often misidentified in collections or simply labelled “cranchiid sp.,” it is hoped that the present findings will assist in the accurate identification of small specimens.

While examining larval *Teuthowenia*, it became apparent that certain body structures (e.g. arm crown, eyes, mantle) do not develop uniformly, but rather undergo rapid changes during certain larval stages. For example, the mantle appears much larger relative to other body structures in larvae of Stage C than Stage B (Figure 1), a result of the head and arms undergoing little absolute growth during this period, although structural changes are apparent. The eyes in Stage C, although still stalked, become more spherical in outline and the eye can be visually distinguished from the stalk itself. At this stage the larger crescent photophore is also developing on the ventral surface of the eye, the arm tips become pointed rather than blunt, and the tentacle club begins to differentiate from the stalk. Another dramatic change is observed between stages E and F (Figure 1), where the fins change rapidly from the characteristic paddle shape seen in larvae to the approximately ovate juvenile/adult form. While several

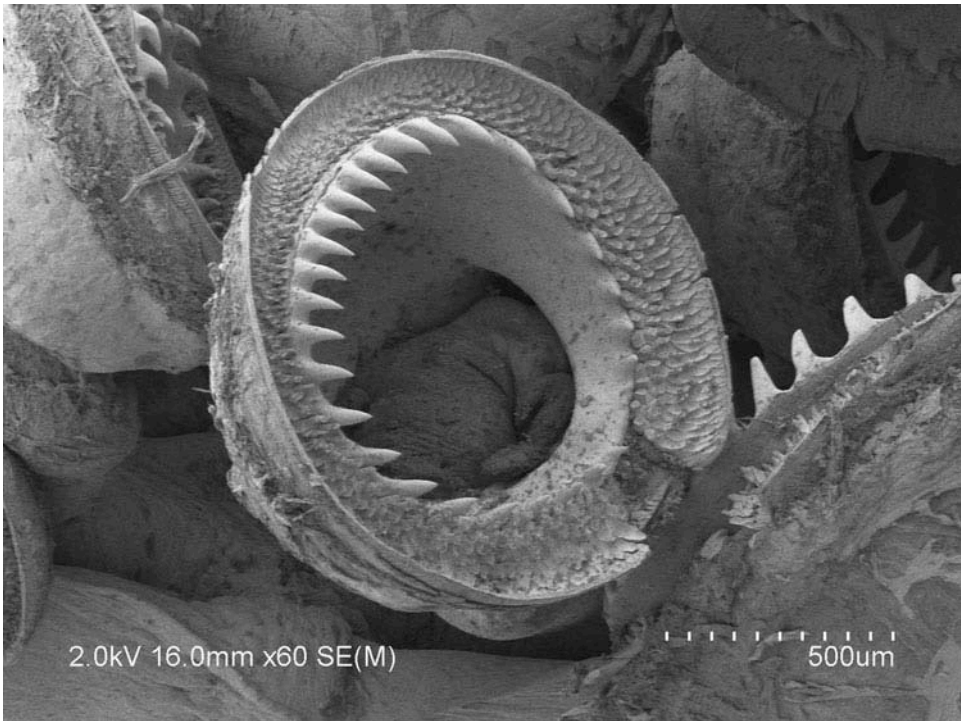


Figure 9. Mid-manus tentacle club sucker ring of adult *Teuthowenia pellucida* showing 28 teeth.

intermediate stages can be recognized during this change in shape (Figure 10), they do not characterize separate larval developmental stages because the other morphological characters remain relatively constant. As animals mature at slightly different rates, minor overlap was observed at the beginning and end of consecutive developmental stages; however, the transition between stages E and F had the greatest overlap, with the development characterizing Stage F beginning as early as 45 mm ML in some specimens and as late as 75 mm ML in others.

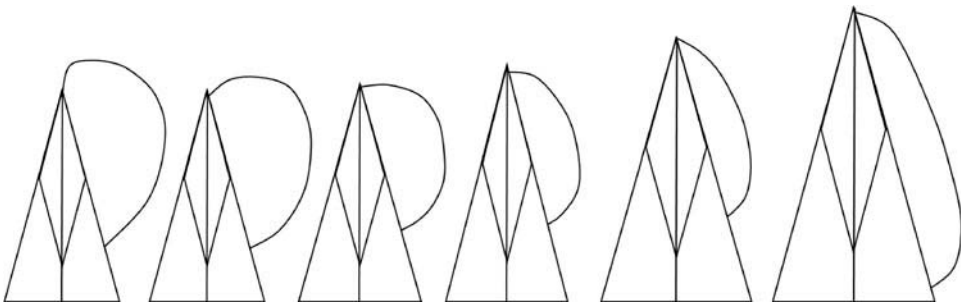


Figure 10. Development of fin shape between juvenile and sub-adult stages (stages E and F) of *Teuthowenia pellucida*. Specimen maturation from left to right.

Recognition of these stages and their sometimes rapid transitions should make identifications of young *Teuthowenia* more reliable. Small individuals of other genera are often attributed to *Teuthowenia*, particularly if true *Teuthowenia* specimens of a given size are poorly represented in collections, precluding direct comparison. Much local confusion appears to occur in particular among *T. pellucida* at Stage C and similar-sized individuals of *Liguriella* and *Megalocranchia*, compounded by the relative scarcity of Stage C specimens (only three were identified during this study). However, at this size (ML 20–28 mm), *Liguriella* and *Megalocranchia* each possess an elongated arm crown and eyes on long stalks (Figure 11) with eyes narrowing ventrally in both genera, although this character is more noticeable in *Megalocranchia* specimens (Figure 11B). Differences in the gladius visibility through the anterior part of the dorsal midline can also be observed: the rhachis in *Megalocranchia* can be seen through a very distinctive diamond-shaped translucent patch at the dorsal mantle fusion, while the same patch in *Liguriella* is distinctly oval, and in *T. pellucida* the area appears as a narrow point (Figure 12).

Difficulties in differentiating these and other cranchiid genera at various life stages have historically complicated the family's systematics. While Voss (1980) considerably stabilized the Cranchiidae, by appraising the 41 nominal genera and rediagnosing the 13

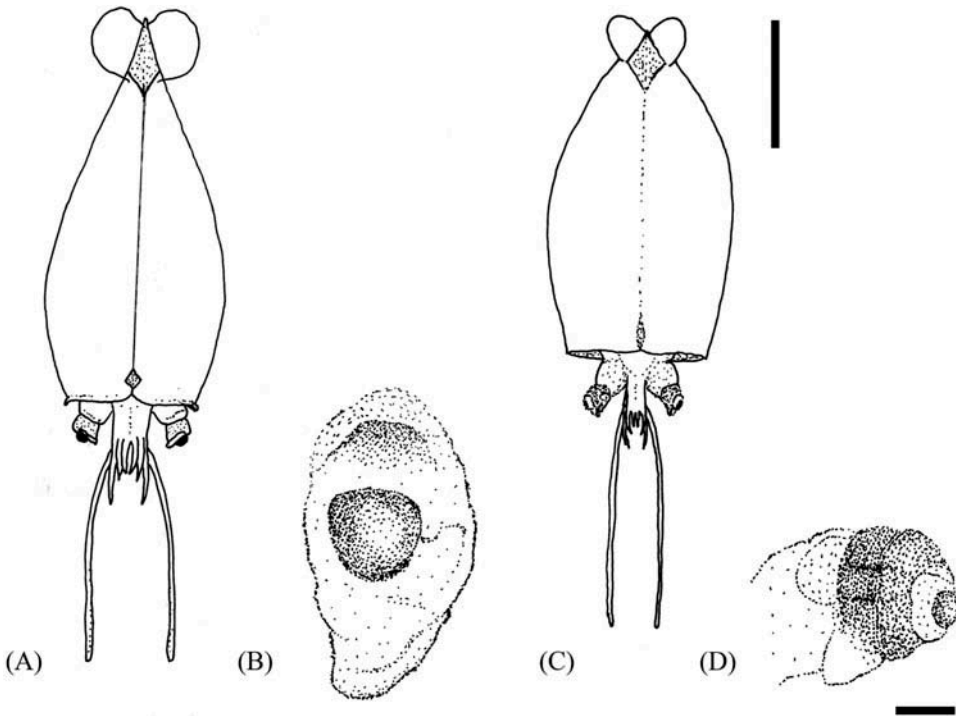


Figure 11. Larval cranchiids with similar morphological characteristics. (A) *Megalocranchia* (ML = 29 mm) with enlarged diagram of (B) the eye viewed anteriorly. (C) *Liguriella* (ML = 24 mm) with enlarged diagram of (D) the eye viewed laterally. Vertical bar (A, C) = 1 cm, horizontal bar (B, D) = 1 mm.

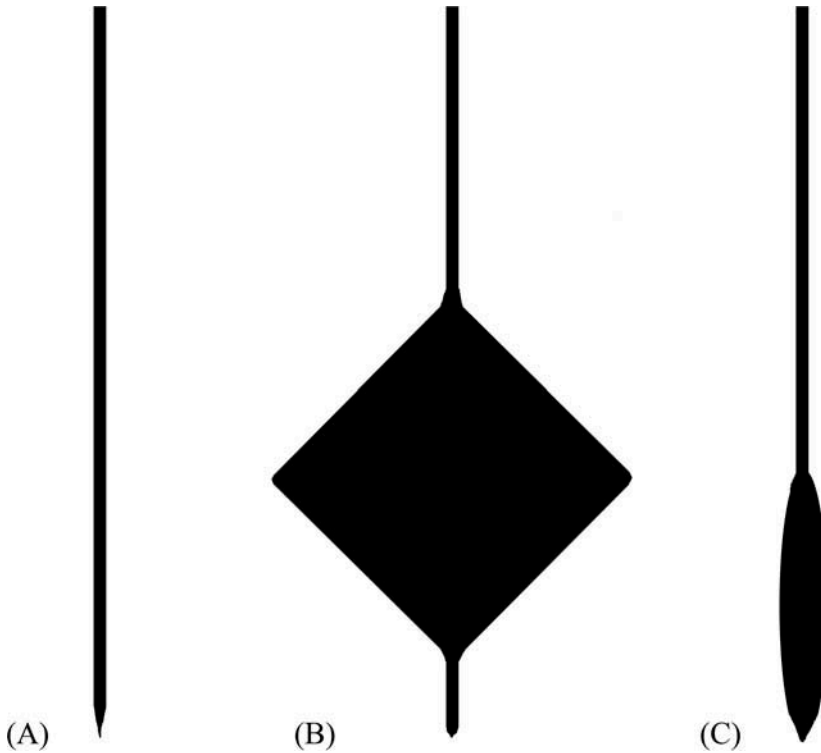


Figure 12. Difference in visible rachis shape at anterior dorsal midline of (A) *Teuthowenia*; (B) *Megalocranchia*; (C) *Liguriella* (ML range: 17–29 mm).

genera considered valid today, much work is still required at the lower taxonomic levels. Although not within *Teuthowenia*, undescribed species are known to exist – *Liguriella*, *Egea* and several other cranchiid genera are believed to contain presently unnamed species (Voss et al. 1992) – and these can only be recognized where named taxa are well understood and described through as many life stages as possible.

### **Sexual maturity**

In mature individuals, apart from the coelom, the mantle lumen was dominated by reproductive tissues. Mating and spawning behaviours are largely undocumented for cranchiids; of the 13 genera, reproductive structures have only been completely described for *T. pellucida* and *Galiteuthis glacialis*, and this information is still largely speculative. Voss (1985) outlined the internal sexual structures of female *T. pellucida*, the post-spawning anatomy of *G. glacialis* was described by Nesis et al. (1998) and the pre-spawning anatomy was later described by Laptikhovsky and Arkhipkin (2003). The gaps between these three studies, the fact that fecundity estimates from this study are nearly three times higher than those previously reported for *T. pellucida*, and the fact that size at sexual maturation has only been estimated in males to date (Voss 1985), all indicate the need for further investigation of cranchiid reproduction.

One mature female (ML = 190 mm, NIWA 71690) contained approximately 18,000 eggs, which is a significant increase from the previous estimate of 6000–8000 reported for this species (Voss 1985). However, this number is relatively low compared with some other species of squid; *Illex illecebrosus* can produce up to 400,000 ova (Durward et al. 1979) and *G. glacialis*, another cranchiid, is estimated to produce approximately 20,000 eggs (Nesis et al. 1998). Additional mature females should be examined, if possible, to assess the variability in fecundity within *T. pellucida*; for this study, the remaining mature females examined were slightly damaged, precluding accurate egg counts, although their ovaries appeared to have been similar in size to that of the intact specimen.

Secondary sexual features consisted of brachial end organs on all arm tips of females and modified arm tips on arms I and II in males; in both sexes, suckers proximal to modifications did not change, compared with sub-mature specimens lacking these sexual features. Some females lacked brachial organs due to damaged arm tips; this is consistent with results from Herring et al. (2002), who found that all examined specimens of *T. megalops* lacked all arm tips. Male arm modifications were more often retained, and most mature males exhibited the tight cluster of numerous suckers on the first two pairs of arms (Figure 8B). Voss (1985) suggested that these modified arms could be used to caress the swollen nidamental glands in the female, with the suckers becoming encysted there; encysted suckers found on the nidamental glands of mature females examined herein support this theory. The function of sexual modifications in both males and females has not been confirmed; however, it is believed that the female's brachial organ may act as an attractant, either by emitting light (Herring et al. 2002), by pheromone release (Voss 1985), or possibly a combination of both. Live observation of mating behaviours is needed to help confirm the function of these modifications.

Arkhipkin (1992) presented a scale for classifying cephalopod maturity based on reproductive features. Since all juveniles fall into his "Stage 0" there is little direct overlap between his findings and the presently identified larval stages (although it is possible that some currently unknown morphological character also indicates the onset of his Stage 1). Both findings from Arkhipkin and those herein draw attention to the rapid growth and morphological changes that squid undergo during their early and late life stages, and serve as a reminder that, even for many species where the sub-adult and adult animals are reasonably well described, much remains to be observed about other stages of maturity.

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**Appendix.** Specimens examined.*Teuthowenia*

Stage	Specimens
<b>Stage A</b>	<b>30 specimens (all sex indet.):</b>
<b>(larval)</b>	NMNZ M.302130, ML 1.5 mm, NZ, RV <i>James Cook</i> , Stn J11/26/80, 1980 NMNZ M.102180, ML 3.0 mm, 45°28.2'S, 164°50.9'E, NZ, 231 m over 4540 m, RV <i>Kaiyo Maru</i> , Stn KM/231B/85, 29/08/1985 NMNZ M.102209, ML 3.0 mm, 44°45.3'S, 167°1.1'E, NZ, 205 m over 2520 m, RV <i>Kaiyo Maru</i> , Stn KM/230A/85, 29/08/1985 NMNZ M.302138, ML 3.0 mm, NZ, RV <i>James Cook</i> , Stn J13/08/81, 1981 NMNZ M.286202, NZ, RV <i>James Cook</i> , Stn J11/54/81 NMNZ M.302148, ML 3.4 mm, NZ, RV <i>James Cook</i> , Stn J10/**/80, 1980 NMNZ N.102151, ML 3.6 mm, 45°59.7'S, 165°37.3'E, NZ, RV <i>Kaiyo Maru</i> , Stn KM/212C/85, 30/08/1985 NMNZ M.302155, ML 4.0 mm, RV <i>James Cook</i> , Stn J11/11/81, 1981 NMNZ M.302142, ML 4.0 mm, NZ, RV <i>James Cook</i> , Stn J10/**/80, 1980 NMNZ M.102239, ML 5.0 mm, 46°45.8'S, 165°54.2'E, NZ, RV <i>Kaiyo Maru</i> , Stn KM/112B/85, 31/07/1985 NMNZ M.302157, sex indet., ML 5.0 mm, RV <i>James Cook</i> , Stn J11/06/81, 1981 NMNZ M.302135, ML 5.0 mm, NZ, RV <i>James Cook</i> , Stn J10/**/80, 1980 NMNZ M.302149, ML 5.0 mm, NZ, RV <i>James Cook</i> , Stn J13/08/81, 1981 NMNZ M.302147, ML 6.0 mm, NZ, RV <i>James Cook</i> , Stn J13/07/81, 1981 NMNZ M.302144, ML 6.0 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980 NMNZ M.302150, ML 6.2 mm, NZ, RV <i>James Cook</i> , Stn J16/05/80, 1980 NMNZ M.302146, ML 7.0 mm, NZ, Stn ACH/61/80, 1980 NMNZ M.302156, ML 7.5 mm, NZ, RV <i>James Cook</i> , Stn J11/**/80, 1980 NMNZ M.302129, ML 7.8 mm, NZ, RV <i>James Cook</i> , Stn J11/**/80, 1980 NMNZ M.091777, ML 8.0 mm, 38°8.7'S, 173°37.6'E, NZ, 216 m over 782 m, RV <i>Kaiyo Maru</i> , Stn KM/201C1/85, 23/08/1985 NMNZ M.302130, ML 8.0 mm, NZ, RV <i>James Cook</i> , Stn J11/26/80, 1980 NMNZ M.302145, ML 8.0 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980 NMNZ M.302131, ML 8.0 mm, NZ, RV <i>James Cook</i> , Stn J16/04/80, 1980 NMNZ M.302143, ML 8.0 mm, NZ, RV <i>James Cook</i> , J11/**/80, 1980 NMNZ M.302132, ML 8.0 mm, NZ, RV <i>James Cook</i> , Stn J11/26/80, 1980 NMNZ M.302141, ML 8.2 mm, NZ, RV <i>James Cook</i> , J16/08/80, 1980 NMNZ M.302133, ML 8.7 mm, NZ, RV <i>James Cook</i> , Stn J16/103/80, 1980 NMNZ M.09159, ML 9.0 mm, 36°46.8'S, 176°18.5'E, NZ, 114 m over 620 m, RV <i>James Cook</i> , Stn J11/38/76, 31/07/1976 NMNZ M.302151, ML 10.0 mm, NZ, RV <i>James Cook</i> , Stn J09/16/83, 1983
<b>Stage B</b>	<b>3 specimens (all sex indet.):</b>
<b>(larval)</b>	NMNZ M.302139, ML 9.5 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980 NMNZ M.287201, ML 13.0 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980 NMNZ M.287202, ML 15.0 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980
<b>Stage C</b>	<b>3 specimens (all sex indet.):</b>
<b>(larval)</b>	NMNZ M.286197, ML 19.0 mm, NZ, <i>HMAS Cook</i> , 06/1984 NMNZ M.091551, ML 21.0 mm, 39°14.9'S 178°45.5'E, NZ, 30 m over 3000 m, RV <i>James Cook</i> , Stn J12/11/87, 14/09/1987 NMNZ M.287201, ML 27.0 mm, NZ, RV <i>James Cook</i> , Stn J16/**/80, 1980

(Continued)

## Appendix. (Continued).

Stage	Specimens
<b>Stage D (juvenile)</b>	<b>9 specimens (all sex indet.):</b> NIWA 71677, ML 28.0 mm, 42.92°S, 175.87°E, NZ, 50.0 m, TAV002/20, Stn Z10384, 8/02/2001 NIWA 71678, ML 30.1 mm, 42.93°S, 175.93°E, NZ, 50.0 m, TAV002/19, Stn Z10383, 8/02/2001 NMNZ M.286142, ML 32.0 mm, 40°55.6'S, 176°50.3'E, NZ off Cape Turnagain, 30.0 m, RV <i>James Cook</i> , Stn J15/19/87, 09/12/1987 NMNZ M.287274, ML 33.4 mm, 42°39.9'S, 174°48.1'E, NZ, 30 m, RV <i>James Cook</i> , Stn J15/20/87, 9/12/1987 NMNZ M.286206, ML 34.0 mm, 40°55.4'S, 176°58.0'E, NZ, 30 m, RV <i>James Cook</i> , J15/18/87, 9/12/1987 NIWA 71679, ML 36.8 mm, 42.73°S, 176.37°E, NZ, 10.0 m, TAV002/33, Stn Z10397, 10/02/2001 NIWA 71681, ML 36.9 mm, 43.02°S, 175.37°E, NZ, 30.0 m, TAV002/1, Stn Z10365, 05/02/2001 NIWA 71680, ML 38.7 mm, 43.35°S, 175.55°E, NZ, 30.0 m, TAV002/16, Stn Z10380, 08/02/2001 NIWA 71713, ML 42.1 mm, Stn TAN0012/61, 01/12/2000
<b>Stage E (juvenile)</b>	<b>14 Specimens (all sex indet.):</b> NMNZ M.287275, ML 40.0 mm, 39°16.3'S, 178°34.6'E, NZ, 30.0 m, RV <i>James Cook</i> , Stn J15/05/87, 06/12/1987 NIWA 71718, ML 42.1 mm, 42.28°S, 176.08°E, NZ, 25.0 m, TAV002/87, Stn Z10525, 21/02/2001 NIWA 71676, ML 42.1 mm, 42.64°S, 176.76°E, NZ, 20.0 m, TAV002/18, Stn Z10456, 16/02/2001 NIWA 71714, ML 42.4 mm, 42.54°S, 176.47°E, NZ, 20.0 m, TAV002/35, Stn Z10473, 18/02/2001 NMNZ M.091421, ML 43.0 mm, 40°8.3'S 160°14.9'E, NZ, 45–35 m over 4700 m, RV <i>James Cook</i> , Stn J16/08/85, 16/10/1985 NIWA 71714, ML 46.3 mm, 42.54°S, 176.47°E, NZ, 20.0 m, TAV002/35, Stn Z10473, 18/02/2001 NIWA 71704, ML 49.6 mm, TAN802/213, 01/02/1998 NMNZ M.067849, ML 50.0 mm, 38°22.15'S, 178°57.18'E, NZ 30.0 m, RV <i>James Cook</i> , Stn J13/09/79, 30/09/1979 NMNZ M.091562, ML 50.0 mm, 39°14.5'S, 179°50.1'E, NZ, 30 m, over 3600 m, RV <i>James Cook</i> , Stn J12/17/87, 14/09/1987 NIWA 71715, ML 51.7 mm, NZ, 50.0 m, TAN9202/100, Stn Z8779, 24/02/1992 NMNZ M.286141, ML 60.0 mm, 41°10.9'S, 176°38.6'E, NZ, 1148–1170 m, RV <i>James Cook</i> , Stn J12/57/88, 24/10/1988 NMNZ M.091544, ML 62.0 mm, 39°14.9'S, 178°35.4'E, NZ, 30.0 m, RV <i>James Cook</i> , Stn J12/09/87, 13/09/87 NMNZ M.286199, ML 70.0 mm, 44°38.3'S, 173°40.2'E, NZ, 350 m over 887–924 m, RV <i>James Cook</i> , Stn J21/18/84, 10/12/1984 NMNZ M.286208, ML 73.0 mm, 39°15.6'S, 179°49.6'E, NZ, 30 m, RV <i>James Cook</i> , Stn J15/11/87, 07/12/1987
<b>Stage F (sub-adult)</b>	<b>42 specimens (all sex indet.):</b> NMNZ M.286140, ML 34.6 mm, 42°36.6'S, 174°36.4'E, NZ, 30.0 m, RV <i>James Cook</i> , Stn J15/21/87

(Continued)

**Appendix.** (Continued).

Stage	Specimens
	NMNZ M.091544, ML 45.6 mm, 39°14.9'S, 178°35.4'E, NZ, 30.0 m, RV <i>James Cook</i> , Stn J12/09/87, 13/09/1987
	NIWA 71706, ML 45.6 mm, TAN9802/179, 01/02/1998
	NIWA 71693, ML 48.8 mm, 100.0–20.0 m, TAN9802/133, 01/02/1998
	NMNZ M.067250, ML 50.0 mm, 37°50.9'S, 179°8.1'E, NZ, 40.0 m, RV <i>James Cook</i> , Stn J01/78/80, 11/01/1980
	NMNZ M.074213, ML 50.0 mm, 42°0.80'S, 174°52.80'E, NZ, 1292–1395 m, RV <i>Tangaroa</i> , Stn 1979671, 14/01/1979
	NIWA 71717, ML 52.0 mm, 42.55°S, 174.75°E, 80.0 m, TAV002/106, Stn Z10544, 22/02/2001
	NIWA 71682, ML 54.0 mm, <i>NZI</i> , Stn u2308
	NMNZ M.286151, ML 54.0 mm, 39°26.44'S, 179°51.83'E, NZ, 21–103 m over 2405 m, RV <i>Tangaroa</i> , Stn TAN9503/46, 28/03/1995
	NMNZ M.091513, ML 54.0 mm, 32°10.2'S, 167°54.7'E, NZ, 60.0 m over 750–1125 m, RV <i>James Cook</i> , Stn J16/23/85, 24/10/1985
	NMNZ M.091619, ML 54.0 mm, 38°48.8'S, 172°24.4'E, NZ, 120–180 m over 832–833 m, RV <i>Kaiyo Maru</i> , Stn KM/102B/85, 19/07/1985
	NMNZ M.286163, ML 56.0 mm, 38°58.87'S, 170°7.38'W, NW of Valerie Guyot Louisville Ridge, 20–101 m over 4600 m, RV <i>Tangaroa</i> , TAN9503/14, 21/03/1995
	NIWA 71708, ML 58.0 mm, TAN9802/189, 01/02/1998
	NMNZ M.067845, ML 58.0 mm, 38°22.05'S, 179°35.35'E, NZ, 30 m over 1700 m, RV <i>James Cook</i> , Stn J13/11/79, 01/10/1979
	NIWA 71699, ML 59.0 mm, TAN9802/211, Stn Z11021
	NMNZ M.091599, 32°15.3'S, 167°45.6'E, NZ, 125 m over 1640–1678 m, RV <i>James Cook</i> , Stn J16/21/85, 24/10/1985
	NMNZ M.286162, ML 61.0 mm, 40°0.83'S, 177°58.41'E, NZ, 14–99 m over 1529 m, RV <i>Tangaroa</i> , Stn TAN9503/35, 29/03/1995
	NMNZ M.286188, ML 61.0 mm, 39°14.76'S, 179°18.36'W, NZ, 31–102 m over 3500 m, RV <i>Tangaroa</i> , TAN9503/1, 19/03/1995
	NIWA 71687, ML 63.0 mm, 42.76°S, 179.99°W, 1064.0–750.0 m, TAN0104/43, 16/04/2001
	NMNZ M.074361, ML 63.0 mm, 39°9.5'S, 179°22.5'E, NZ, 30 m over 1200 m, RV <i>James Cook</i> , Stn J08/45/80, 23/04/1980
	NMNZ M.286139, ML 64.0 mm, 39°45.40'S, 178°34.46'E, NZ, 22–109 m over 2711 m, RV <i>Tangaroa</i> , Stn TAN9503/50, 28/03/1995
	NMNZ M.286203, ML 65.0 mm, 40°28.71'S, 170°21.80'W, W of Valerie Guyot Louisville Ridge, 16–104 m over 4300 m, RV <i>Tangaroa</i> , Stn TAN9503/35, 25/03/1995
	NIWA 71702, ML 65.2 mm, 41.57°S, 179.67°E, 100.0 m, TAN9802/164, Stn Z10311
	NMNZ M.074303, ML 67.0 mm, 37°30.80'S, 177°32.50'E, NZ, 715–755 m, RV <i>Tangaroa</i> , Stn 1979763, 24/01/1979
	NMNZ M.286143, ML 67.0 mm, 43°33.7'S, 167°7.6'E, NZ, 170–250 m over 1250 m, RV <i>James Cook</i> , Stn J15/52/87, 16/12/1987
	NMNZ M.074309, ML 68.0 mm, 37°28.3'S, 177°13.0'E, NZ, 80–386 m over 194–994 m, RV <i>James Cook</i> , Stn J07/56/75, 09/05/1975

(Continued)

## Appendix. (Continued).

Stage	Specimens
	NIWA 71717, ML 69.0 mm, 42.55°S, 174.75°E, 80.0 m, TAV002/106, Stn Z10544, 22/02/2001
	NMNZ M.287271, ML 74.0 mm, 44°41.59'S, 173°18.92'E, NZ, 750 m over 890–987 m, RV <i>James Cook</i> , Stn J21/21/84, 11/12/1984
	NIWA 71716, ML 76.0 mm, 42.44°S, 174.74°E, 100.0 m, TAV002/119, Stn Z10557, 23/02/2001
	NMNZ M.286156, ML 76.0 mm, 40°31.91'S, 178°59.33'E, NZ 17–107 m over 3000 m, RV <i>Tangaroa</i> , Stn TAN9503/59, 30/03/1995
	NMNZ M.286144, ML 77.0 mm, 40°30.64'S, 169°53.89'W, W of Valerie Guyot Louisville Ridge, 17–103 m over 4350 m, RV <i>Tangaroa</i> , Stn TAN9503/33, 24/03/1995
	NMNZ M. 074329, ML 78.0 mm, 37°34'S, 177°15'E, NZ, 420 m over 840 m, RV <i>James Cook</i> , Stn J07/50/75, 08/05/1975
	NMNZ M.286152, ML 80.0 mm, 45°11.3'S, 165°20.7'E, NZ, 30 m, RV <i>James Cook</i> , Stn J15/46/87, 15/12/1987
	NIWA 71707, sex indet., ML 81.0 mm, TAN9802/190, 01/02/1998
	NMNZ M.012942, ML 84.0 mm, 41°47'S, 175°2'E, NZ, 732 m over 1463 m, 19.04.1957
	NMNZ M.286189, ML 84.0 mm, 40°17.61'S, 179°36.19'E, NZ, 15–96 m over 3200 m, RV <i>Tangaroa</i> , Stn TAN9503/54, 29/03/1992
	NMNZ M.091505, ML 87.0 mm, 32°18.9'S, 167°40.5'E, NZ, 150 m over 1451–1565 m, RV <i>James Cook</i> , Stn J16/20/85, 24/10/1985
	NMNZ M.091411, ML 87.0 mm, 39°42.1'S, 168°0.1'E, NZ, 832–844 m, RV <i>James Cook</i> , Stn J05/46/84, 15/03/1984
	NIWA 71700, ML 90.0 mm
	NMNZ M.074306, ML 94.0 mm, 41°39'S, 175°14.48'E, NZ 140 m, RV <i>James Cook</i> , Stn J10/10/75, 28/06/1975
	NMNZ M.074311, ML 94.0 mm, 30°58.0'S, 175°12.8'W, NZ, 971 m over 5000 m, RV <i>James Cook</i> , Stn J17/76/76, 15/12/1976
	NMNZ M.286178, ML 96.0 mm, 39°20.23'S, 179°40.72'E, NZ, 20–105 m over 3958 m, RV <i>Tangaroa</i> , Stn TAN9503/45, 28/03/1995
<b>Adult</b>	<b>28 specimens, (9 ♀, 13 ♂, 6 sex indet.):</b>
	NIWA 71686, sex indet., ML 100.0 mm, 700 m, Stn Z9917, 02/07/1997
	NMNZ M.172982, ♂, ML 120.0 mm, 32°32.25'S, 169°43.56'E, Norfolk Ridge, 1275 m, RV <i>Tangaroa</i> , Stn 10, 12/05/2003
	NIWA 71691, sex indet., ML 122.0 mm, SWA 9501/073, 26/07/1995
	NIWA 71688, ♂, ML 135.0 mm, TAN9708/037
	NMNZ M.286176, sex indet., ML 138.0 mm, 42°50.2'S, 177°32.3'W, NZ, 821–863 m, RV <i>James Cook</i> , Stn J12/42/84, 29/07/1984
	NMNZ M.287267, ♂, ML 140.0 mm, 41°10.9'S, 176°38.6'E, NZ, 1148–1170 m, RV <i>James Cook</i> , Stn J12/57/88, 24/10/1998
	NMNZ M.074307, ♂, ML 150.0 mm, 41°50.4'S, 175°44.0'E, NZ, 210 m over 2000 m, RV <i>James Cook</i> , Stn J10/03/75, 27/06/1975
	NMNZ M.286159, ♂, ML 150.0 mm, 37°39.8'S, 168°58.4'E, NZ, 878–895 m, RV <i>James Cook</i> , Stn J04/41/83, 23/02/1983
	NIWA 71672, ♀, ML 155.0 mm, 43.15°S, 174.29°W, 980–1021 m, Z8548, 07/08/1996
	NIWA 71684, ♀, ML 155.0 mm, 44.00°S, 178.00°W, TAN9713/53, 13/12/1997

(Continued)

**Appendix.** (Continued).

Stage	Specimens
	NMNZ M.144084, ♀, ML 156.0 mm, 42°51.2'S, 175°33.1'E, NZ, 695 m, Stn 1112/62, 02/07/1998
	NIWA 71694, sex indet., ML 159.0 mm, 42.45°S, 170.11°E, 826 m, Stn Z9845, 05/09/1999
	NMNZ M.102592, ♀, ML 160.0 mm, 40°18.74'S, 173°15.93'E, North of Tasman Bay, 75–78 m, RV <i>Cordella</i> , COR9001/035, 19/02/1990
	NMNZ M.172926, ♂, ML 160 mm, 32°32.25'S, 169°43.56'E, Norfolk Ridge, 1275 m, RV <i>Tangaroa</i> , Stn 10, 12/05/2003
	NMNZ M.067224, sex indet., ML 165.0 mm, 43°6.77'S, 174°15.97'E, NZ, 494–508 m, RV <i>James Cook</i> , Stn J07/05/79, 02/06/1979
	NMNZ M.286186, ♂, ML 167.0 mm, 37°32.9'S, 169°25.9'E, West of Cape Egmont, 1075–1106 m, RV <i>Arrow</i> , Stn A04/174/83, 26/10/83
	NIWA 71695, sex indet., ML 170.0 mm, 44.63°S, 176.02°W, 948–931 m, Stn Z8551
	NMNZ M.091717, ♂, ML 170.0 mm, 39°46'S, 178°4'E, NZ, 1050–1089 m, FV <i>Wanaka</i> , Stn WK4/71/86, 20/04/1986
	NMNZ M.286160, ♂, ML 173.0 mm, 40°32.8'S, 168°40.5'E, NZ, 937–942 m, RV <i>James Cook</i> , Stn J02/33/87, 09/02/1987
	NIWA 71670, ♂, ML 178.0 mm, 42.81°S, 176.73°E, 1063–1069 m, Stn Z8311, 19/07/1995
	NIWA 71675, ♀, ML 180.0 mm, 42.70°S, 177.35°E, 950 m, Stn Z9565, 02/12/1998
	NMNZ M.286191, ♂, ML 184.0 mm, 41°18.3'S, 176°23.9'E, Wairarapa coast, 1175–1191 m, RV <i>James Cook</i> , Stn J9/7/89, 12/09/1989
	NIWA 71674, ♀, ML 185.0 mm, Stn Z11124
	NIWA 71691, ♂, ML 185.0 mm, SWA 9501/073, 26/07/1995
	NMNZ M.283190, ♀, ML 185.0 mm, 41°21.50'S, 176°20.90'E, NZ, 1073–1116 m, RV <i>James Cook</i> , Stn J06/14/84, 03/04/1984
	NIWA 71690, ♀, ML 190.0 mm, RV <i>Tangaroa</i> , TAN 9708/13
	NIWA 71671, ♀, ML 200.0 mm, 42.92°S, 179.41°E, 759 m, Stn Z8501, 19/06/1996
	NMNZ M.117199, ♀, ML 201.0 mm, 42°44.26'S, 176°34.27'W, 1196–1203 m, RV <i>Tangaroa</i> , Stn TAN9206/207, 14/07/1992
	NMNZ 287265, ♂, ML 210.0 mm, 42°28.4'S, 169°31.9'E, NZ, 1016–1020 m, RV <i>James Cook</i> , Stn J04/12/83, 17/02/1983

<i>Liguriella</i>	<b>3 specimens (all sex indet.)</b> Specimens
	NMNZ M.288175, GL 17 mm, 38°59.16'S, 170°19.80'W, NW of Valerie Guyot, Louisville Ridge, 19–98 m over 4500 m, RV <i>Tangaroa</i> , Stn TAN9503/13, 21/03/1995
	NMNZ M.074335, ML 25 mm, 37°34.00'S, 177°15.30'E, NZ, 305 m over 520 m, RV <i>James Cook</i> , Stn J04/54/76, 07/03/1976
	NMNZ M.288175, ML 26 mm, 38°59.16'S, 170°19.80'W, NW of Valerie Guyot, Louisville Ridge, 19–98 m over 4500 m, RV <i>Tangaroa</i> , Stn TAN9503/13, 21/03/1995
<i>Megalocranchia</i>	<b>3 specimens (all sex indet.)</b> Specimens
	NMNZ M.288168, ML 23 mm, 38°59.37'S, 164°36.67'W, N of Valerie Guyot, Louisville Ridge, 16–102 m over 5000 m, RV <i>Tangaroa</i> , Stn TAN9503/24, 23/03/1995
	NMNZ M.287200, ML 28 mm, 35°7.0'S, 179°22.0'W, NZ, 774 m over 3000 m, RV <i>James Cook</i> , Stn J17/03/76, 03/12/1976
	NMNZ M.074175, ML 29 mm, 33°9.0'S, 176°6.0'W, NZ, 732–869 m over 3508 m, RNZFA <i>Tui</i> , 23/07/1962