A systematic review of the squid genus *Chiroteuthis* (Mollusca: Cephalopoda) in New Zealand waters

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***Chiroteuthis veranyi* (Férussac, 1835)**

Live animal, aquarium shot © Steve O'Shea

NIWA 48825, ♂, ML 64 mm, 42˚21.08'S, 176˚11.68'E, 30 m, 21/02/2001

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ATTESTATION OF AUTHORSHIP

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgments), 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.

Rebecca Mensch

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ABSTRACT

Collections of *Chiroteuthis* from New Zealand waters are reviewed for the first time. The distribution of available material spans 24°45–45°25.7'S, 163°29.3'E–165°13.75'W, depths 0–2000 m, with collections comprising 60 specimens attributed to three species, *C. mega* (3 specimens), *C. spoeli* (1 specimen from New Zealand waters, 2 additional specimens from waters north of New Zealand) and *C. veranyi* (54 specimens), each for the first time described from New Zealand waters on the basis of physical specimens, with *C. spoeli* being both first reported from New Zealand waters, in addition to which the male of this species is for the first time described. External and internal anatomy for each of the three species recognised from New Zealand waters are described, with each illustrated in series of photographs and drawings.

An uncritical compilation of *Chiroteuthis* species previously reported from New Zealand waters numbered eight taxa: four species and four form taxa previously reported on the basis of beaks recovered from stomach contents of potentially long-distance-foraging marine predators. Thus, the diversity of *Chiroteuthis* taxa actually occurring within New Zealand waters is lower than was expected, at least based upon *in situ* captured specimens represented in available museum collections.

Although all taxa recognised in collections can be allocated existing taxa, the current knowledge of *Chiroteuthis* diversity in New Zealand is hindered by both a lack of specimens, and the quality of available specimens. Recommendations are made to improve preservation and curation techniques to ensure cephalopods available for research purposes provide the most taxonomic information.

INTRODUCTION

The genus *Chiroteuthis* d'Orbigny, 1841 is the largest of four genera presently accommodated in the family Chiroteuthidae Gray, 1849. Chiroteuthid squid are widely distributed throughout the world's oceans, known from subarctic, temperate, tropical and subantarctic waters (Roper & Young 1998), but despite their wide distribution they have not been the subject of any monographic review. Identification of species assigned to this family is difficult.

All chiroteuthids have distinct tentacles and club morphology, but given the extreme length and fragility of these structures, they are often lost during capture, especially in nets, or when specimens have been recovered from fisheries bycatch. The shape, number, and distribution of eye photophores are also distinct in these species, but these too are often damaged during capture. All chiroteuthids also have a unique paralarval form, known as the doratopsis stage (Young 1991), that can reach sizes to 60 mm mantle length (Lu 2001, Roper & Young 1975); this form can be differentiated from the adult by its narrower and elongated head and mantle, and lack of grossly elongated tentacles (Berry 1963, Haimovici *et al*. 2002, Lu 2001); the clubs are not easily distinguished as suckers are present on a large distal portion of the tentacle (Berry 1963, Nesis 1971); photophores are entirely lacking (Berry 1963, Lu 2001, Nesis 1971); and the gladius is usually reported as protruding from the tip of the fins (Berry 1963, Haimovici *et al*. 2002, Lu 2001, Young 1991), although this is actually the remnant of a delicate tail that is invariably lost or damaged upon capture (Vecchione, *et al*. 1992).

Adults of the genus *Chiroteuthis* are easily differentiated from other chiroteuthids by the presence of photophores on the aboral surface of arms IV (Roper & Young 1998). Other

distinguishing characteristics of the adult are its nearly circular fins, ear-like funnel cartilages, photophores on the ventral surface of the eyes, greatly elongated arm pair IV, and tentacle clubs with symmetrical protective membranes (Roper & Young 1998, Salcedo-Vargas 1996).

New Zealand museum collections of squids have grown significantly over the past few decades, yet the last time the squid fauna of this region was the subject of any complete review was nearly 60 years ago (Dell 1952) — wherein 9 squid species were recognised, none of which was a chiroteuthid. Since Dell's review of the New Zealand Cephalopoda fauna a series of systematic reviews have been undertaken on the squid families Histioteuthidae (Hortskotte 2008, Voss 1969, Voss *et al*. 1998), Enoploteuthidae (Riddell 1985), Onychoteuthidae (Bolstad 2007, 2008, in press), monotypic Architeuthidae (Förch 1998), and Cranchiidae and Gonatidae (Imber 1978); the order Octopoda also has been revised in entirety (O'Shea 1999). As a consequence of these and other [non-monographic] works, 80 species of squid and 39 species of octopus were recently recognised from New Zealand waters (Spencer *et al*. 2009), including four chiroteuthid taxa. So how is it that chiroteuthids have been reported from New Zealand waters without this family ever having been revised?

Chiroteuthids as prey for marine predators

More research has been undertaken on the diets of locally occurring marine predators than there has been on the ecology and systematics of their cephalopod prey. However, due to the long-distance foraging nature of some of these predators, many cephalopod species have been included in local biodiversity inventories that probably were

consumed outside of New Zealand waters (O'Shea 1997). Inaccuracies in the biodiversity inventory of New Zealand may also arise due to inherent difficulties non-teuthologists experience in identifying often damaged or partially digested hard-part remains, such as squid beaks and gladii.

Squid beaks are consistently found in the stomach contents of marine predators that have been caught in our waters, or have stranded on New Zealand beaches. By identification of hard-part remains (beaks) from stomach contents of locally occurring cetaceans (Beatson 2007; Beatson *et al*. 2007a, b; Beatson & O'Shea 2009; Meynier *et al*. 2008), sea birds (Imber 1976, 1992; Imber & Ross 1975; James & Stahl 2000; Moore & Wakelin 1997), pinnipeds (Bando *et al*. 2006, Crawley & Wilson 1976, Meynier *et al*. 2009, Page *et al*. 2005), fish (Clark 1985; Jones 2008, 2009; Rosecchi *et al*. 1988), and other squids (Bolstad & O'Shea 2004, Jackson *et al*. 1998) each has been shown to prey on squid, some extensively. However, despite squid being an integral part of marine food webs, very little is known of their biology, abundance, systematics, and even distribution throughout New Zealand waters.

Hoki on the Campbell Plateau have been reported to have eaten *Chiroteuthis picteti* Joubin, 1894 (Clark 1985), while orange roughy on the Challenger Plateau were reported to have eaten *C. capensis* Voss, 1967 (Rosecchi *et al*. 1988). Clarke & MacLeod (1982) identified two chiroteuthid species from the stomach contents of sperm whales taken in the Tasman Sea: *C.* ?*joubini* Voss, 1967 and *C*. sp. C Clarke, 1980. Black petrels are reported to have consumed *C.* ?*joubini*, in addition to *C.* ?*veranyi* (Férussac, 1835), and *C*. sp. A (Imber 1976). The wandering albatross' prey includes *C*. spp. A and D (Imber & Russ 1975), although these identifications were later amended to include *C. capensis,* with *C*. sp. A attributed to *C. veranyi*, *C*. sp. D to *Mastigoteuthis* sp. (Imber 1992)

(and subsequently to *Asperoteuthis* sp., likely *A. nesisi* Arkhipkin & Laptikhovsky, 2008 [Arkhipkin & Laptikhovsky 2008]). Another sea bird, the southern Buller's albatross, was also found to have *C*. spp. A and D in its diet (James & Stahl 2000). Beatson (2007) identified three form taxa, identified as *C*. spp. 1, 2 and 4 from stomach contents of pygmy sperm whales that stranded on New Zealand shores in recent years; Gomez-Villota (2007) identified *C. veranyi*, *C*. sp. 2 (the same form taxon as Beatson 2007), from stomach contents of sperm whales that had stranded on New Zealand shores in recent years. To summarise, an uncritical inventory of the genus *Chiroteuthis* from New Zealand waters includes four described species, *C. capensis, C.* ?*joubini*, *C. picteti* and *C. veranyi*, in addition to four unresolved form taxa *C*. sp. C, and *C*. spp. 1, 2 and 4 — if uncritically accepted, 8 possible taxa.

The two most recent inventories of New Zealand molluscan taxa proffer different accounts of *Chiroteuthis* diversity in New Zealand waters, although both agree that three taxa occur in this region; Spencer & Willan (1995) cite *C. capensis*, *C.* cf. *joubini*, and one unidentified taxon; Spencer *et al*. (2009) cite *C. capensis* and two unidentified species (*C. capensis* is recognised as a junior synonym of *C. mega* (Joubin, 1932) (Salcedo-Vargas 1997)). These latter two accounts cite different taxa from New Zealand waters to those reported earlier (based on stomach content analyses of their predators), and they differ also in the number of taxa occurring in New Zealand waters (3 as opposed to 8). Given New Zealand collections of these species have not been the subject of systematic review, the primary objective of this thesis is to review those taxa represented in collections from New Zealand waters and try to resolve the confusion surrounding their specific identity.

This thesis constitutes the first systematic review of the squid genus *Chiroteuthis* from New Zealand waters, one of two chiroteuthid genera now formally reported from this region (the second being *Asperoteuthis*). Such systematic confusion is not limited to New Zealand representatives of this genus. There is confusion world-wide as to how many species are valid, and in their subgeneric attribution also.

Species inventory within the genus Chiroteuthis

Sweeney & Roper (1998) recognised 11 *Chiroteuthis* species, three considered to be of dubious nature; Roper & Young (1998) cited six valid species; Felley *et al*. (2002) recognised four species and two sub-species, one of which was of dubious status; Okutani (2005) recognised seven species. Each of Roper & Young (1998), Sweeney & Roper (1998), and Okutani (2005) agree on the validity of *C. calyx* Young, 1972; *C. joubini*; *C. mega* (=*C. capensis*); *C. picteti* and *C. veranyi*. Okutani (2005) and Roper & Young (1998) also consider *C. spoeli* Salcedo-Vargas, 1996 to be a valid taxon; Sweeney & Roper (1998) and Okutani (2005) consider *C. lacertosa* Verrill, 1881 to be valid; Sweeney & Roper (1998) further consider *C. imperator* Chun, 1908 and *C. macrosoma* Goodrich, 1896 to be valid, and *C. atlanticus* (MacDonald & Clench, 1934), *C. diaphana* (Verrill, 1884) and *C. pellucida* Goodrich, 1986 to be possibly valid, though questionable. Felley *et al*. (2002) recognised the valid species and sub-species as *C. imperator*, *C. picteti picteti* Joubin, 1894, *C. picteti somaliensis* Salcedo-Vargas, 1996 and *C. mega*, with *C. atlanticus* considered questionably valid. Okutani (2005) maintained *C. imperator* was a junior synonym of *C. picteti*, and *C. atlanticus* to be invalid.

Consensus would have it that *Chiroteuthis calyx*, *C. joubini*, *C. mega*, *C. picteti*, *C. spoeli* and *C. veranyi* were all valid taxa.

Subgeneric classifications

Two subgenera have been recently used, *Chirothauma* Chun, 1910, and *Chiroteuthis* d'Orbigny, 1841, although this classification is not universally followed. Salcedo-Vargas (1996) attributed *C. mega* (= *C. capensis*), *C. picteti*, and *C. imperator* into *Chirothauma*, and *C. calyx, C. veranyi, C. spoeli*, and *C. joubini* into *Chiroteuthis* (*s.s.*). Subgeneric allocation was based largely upon the shape of eye photophores and morphology of tentacle club trabeculae (Salcedo-Vargas 1996), with *Chirothauma* characterised by having eye photophores disposed in three series and *Chiroteuthis* in two series. Roper and Young (1998) refrained from attributing taxa in subgenera, but recognised three 'Groups' based on eye photophore and tentacle club morphology: Group 1 included *C. picteti* and *C. mega*, both with eye photophores in three series; Group 2 included *C. joubini*, *C. spoeli*, and an unknown species, all with eye photophores in two series and tentacle clubs with protective membranes in three sections; and Group 3, *C. veranyi* and *C. calyx*, both with eye photophores in two series, including stripes, and a tentacle club with protective membranes differentiated into two nearly equal sections.

Chirothauma was diagnosed by Salcedo-Vargas (1996) as: "Body long and slender, cylindrical anteriorly but abruptly tapered posteriorly, with swollen part in posterior end of fins; fins medium to large, heart shaped; anti-tragus strongly developed and usually larger than tragus; club-area strongly trabeculated, with 60–85 trabeculae; sucker stalk bears raised keel which ends at base; 9–18 sharp teeth on distal margin, but

central median tooth largest; eyeball has 22–27 photophores arranged in 3 rows of photophores; none or 2 ink sac photophores round or drop-like shaped; chromatophores arranged in circular pattern;" and *Chiroteuthis* as "Body short to medium; mantle tapering gradually, without swollen part in end of fin mantle-insertion; tail small; club-area bordered symmetrically with small trabeculae; wide trabeculated part or fin-like, non-trabeculated membrane present in first third of club-area; sucker stalk thick and cylindrical, thinner stalk that bears sucker protrudes from skirt, cup or ring-like thickened section; large sucker in arms II and III in some species; 2 stripes or rows of photophores on eyeball; 1 or 2 photophores on ink sac."

Roper & Young (1998) diagnosed their three 'Groups' of *Chiroteuthis* as: 1**,** eye photophores in three series; club membrane in two sections, proximal section much shorter; club pigmentation in chromatophores, not epithelial cells; club sucker ring with central tooth enlarged; 2**,** eye photophores in two series; club membrane in three sections; club pigmentation in epithelial cells, not chromatophores; club sucker ring without central tooth enlarged; and 3, eye photophores in two stripes accompanied by round photophores; club membrane in two, nearly equal parts; club sucker ring with central tooth enlarged.

Given two contrasting supraspecific classifications have been proposed in recent years, one involving subgenera and one form taxa of no recognised systematic status, all taxa referred to herein are attributed to the genus *Chiroteuthis* (*sensu lato*); more taxa need to be examined than presently are available for this regional review in order to critically evaluate the status of these supraspecific categories.

MATERIALS and METHODS

MATERIALS

Materials examined were loaned from the two major repositories of cephalopods in New Zealand: those of the National Institute of Water and Atmospheric Research Ltd., Wellington, New Zealand (NIWA), and Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ). Additional acronyms used in materials examined sections include: RV – Research Vessel, FV – Fishing Vessel, MWT – Mid Water Trawl.

NIWA collections comprised 32 specimens, those of NMNZ 53 specimens. Of these 85 specimens available for examination, 60 are attributed to species herein; other specimen lots could not be reliably identified due to a combination of factors: specimen incompleteness or damage, poor preservation, or juvenile status.

METHODS

A combination of stereo, compound, and scanning electron microscopes were used to examine and illustrate specimens; line drawings have been prepared using either a drawing tube or camera lucida. Abbreviations frequently used in photographs and drawings are: A – Anterior, P – Posterior, V – Ventral, D – Dorsal, M – Medial, L – Lateral.

Descriptions focus on hard and soft-part morphology of these animals (beaks, gladius, sucker ring dentition; and measurements, counts and indices of the body); anatomical descriptions are limited largely to the presence, absence or shape of visceral, tentacular, arm and eye photophores.

Counts and Measurements (Fig. 1)

Counts and measures used follow generally those of Roper & Voss (1983), as defined below. All indices are presented as percentages of mantle length. Arm measurements are taken from the right appendage unless otherwise noted.

ML – Mantle Length

TL – Total Length

MW/I – Mantle Width (farthest anterior, near funnel) / Index

FL/I – Fin Length / Index

FW/I – Fin Width (widest point) / Index

AF – Arm Formula

AL/I – Arm Length from first sucker / Index

ASC – Arm Sucker Count, on proximal half

ClL/I – Club Length / Index

- CrL – Carpus Length
- MnL – Manus Length
- DcL – Dactylus length

ClSI – Club Sucker Index

ClRC – Club Row Count (longitudinal)

TrRC – Transverse Row Count (club)

STC – Sucker Teeth Count

HL/I – Head Length / Index

HW/I – Head Width (at eyes, including lenses) / Index

TSL/I – Tentacle Stalk Length / Index

Photophores IV – Photophore count on left and right arms IV.

FA – Fin Attachment (width between)

ED/I – Eye Diameter / Index

LD/I – Lens Diameter / Index

GlLm (in)&(out) – Gill Lamellae (inner) and (outer)

Descriptions, measurements and illustrations of the tentacle club (Fig. 2) are based upon available or best-condition clubs. The carpus commences at the first sucker or membrane insertion (whichever occurs first), and ends when suckers become paired; the manus commences where suckers become paired and ends where membrane trabeculae change form (includes undefined trabeculae between two distinct parts of membrane). The dactylus commences where the second part of membrane begins, where trabeculae are triangular, and ends at base of tip 'bud.'

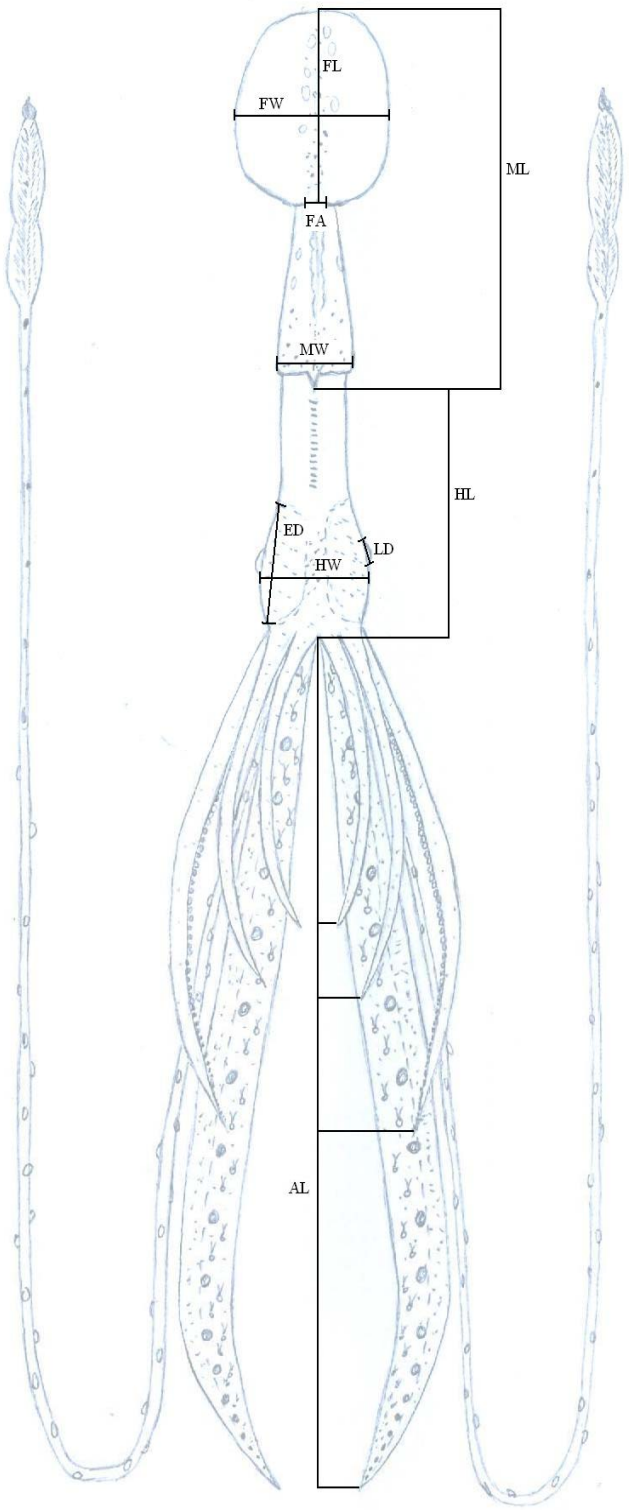

Figure 1. Whole animal external measurements

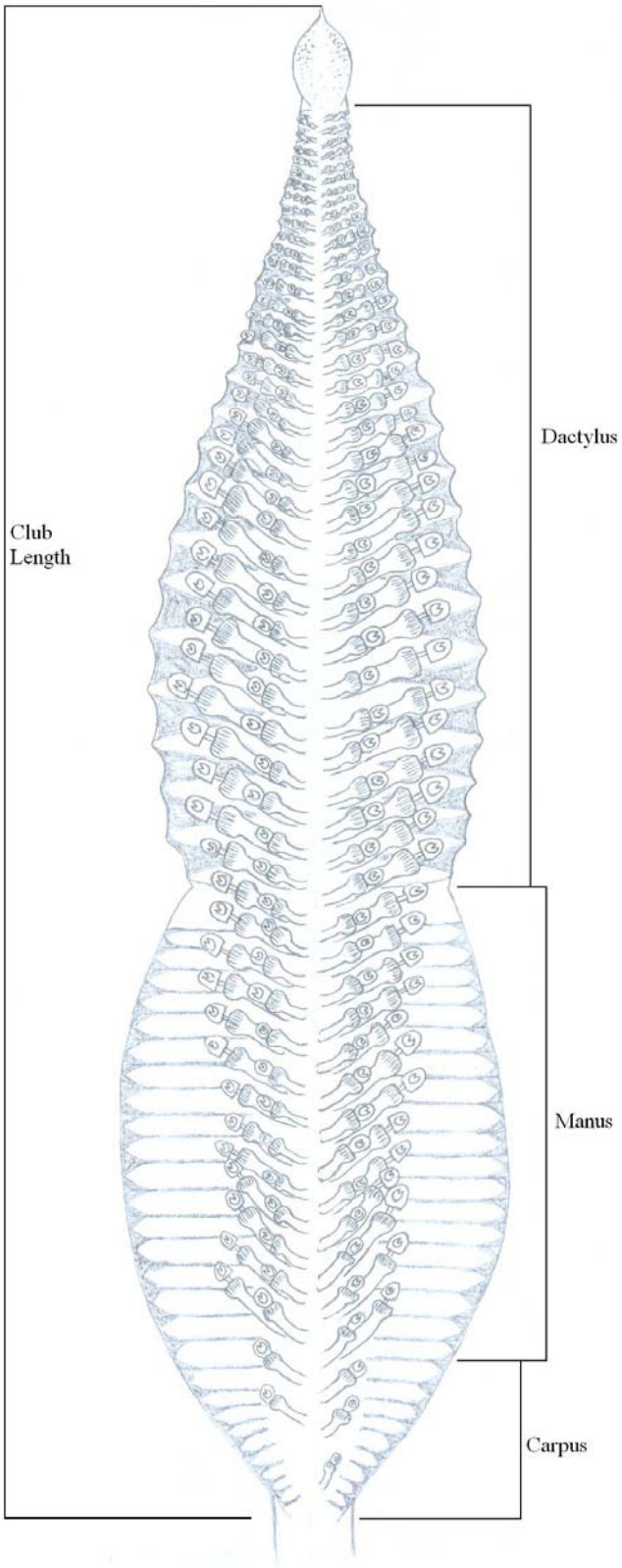

Figure 2. Tentacle club, oral

Lower beak

Drawings crated using a camera lucida with the use of a micrometer for a scale bar. Measurements were taken from drawings with all measurements in millimetres (mm), rounded to nearest 0.5 mm.

Lateral View (Fig. 3b): The base of the wing and lateral wall create a plane referred to as the baseline; beak width measured parallel to this baseline between the farthest points of the wing and lateral wall. A line at the top of the hood, parallel to the baseline, with the distance between these lines representing beak height. Beak length measured from the tip of the rostrum to the baseline at the lateral wall. At the end of the crest a line parallel to the baseline, the distance between these lines is the posterior lateral wall height. Lateral wall width measured perpendicular to the line for beak length, at the midpoint of the posterior lateral wall height. If a fold is present on the lateral wall, the height below where the fold intersects the posterior lateral wall is designated A, and the height above designated B; the line of this fold is extended until it intersects the baseline, this angle is the fold angle. Hood length is measured from the tip of the rostrum to the farthest point on the hood. Wing length is measured from the end point of the hood to the baseline point of the wing.

Oblique View (Fig. 3c): If the wing fold or shoulder is too thick or high to observe the jaw angle in lateral profile, the oblique view must be used to measure this angle. The lower rostral length is measured from the tip of the rostrum to the jaw angle. Wing width at the shoulder is measured perpendicular to the line drawn for wing length. The maximum wing width is taken by flattening the wing.

Aboral View (Fig. 3d): Baselines are drawn parallel to each other on either side of the beak. The distance between these two lines is the beak depth.

Lateral wall and rostral cuts (Fig. 3e): Rostral cuts (D, E, and F) were made somewhat horizontally (see figure) through the beak to determine the thickness of the rostrum at varying distances from the tip. Lateral wall cuts (A, B, and C) were made vertically through the lateral wall to show the thickness and contour of the lateral wall at varying distances from the rostral tip.

Frequently cited abbreviations in lower beak descriptions and illustrations:

LRL – Lower Rostral Length

BW – Beak Width

BH – Beak Height

BL – Beak Length

BD – Beak Depth

WnL – Wing Length

HdL – Hood Length

PLWlH – Posterior Lateral Wall Height

A – Height from baseline to lateral wall fold

B – Height from lateral wall fold to top of lateral wall

WnW – Wing Width at shoulder

MWnW – Maximum Wing Width

LtWlW – Lateral Wall Width

JA – Jaw Angle

FA – Fold Angle, angle of lateral wall fold to baseline

BH%BW – Beak Height % of Beak Width

HdL%BL – Hood Length % of Beak Length

HdL%WnL – Hood Length % of Wing Length

A/B – Ratio of A (height from baseline to lateral wall fold) to B (height from lateral wall fold to top of lateral wall

A%BH – A % of Beak Height

Upper beak (Fig. 3a)

Measurements were taken in the same manner as for the lower beak. The rostrum length is measured as the distance between the point of the rostrum and the jaw angle. The jaw angle is measured by extending the straight lines creating the angle, regardless

of how these edges may curve away. The hood length is measured between the rostrum tip and the upper posterior point of the hood. The crest length is measured between the rostrum tip and the upper posterior point of the crest. The rostrum to wing base length is measured from the tip of the rostrum to the point where the wing meets the lateral wall (this is used as a secondary reference measurement for specimens without a defined jaw angle, which therefore have no defined rostrum length).

Frequently cited abbreviations in upper beak descriptions and illustrations:

URL – Upper Rostrum Length

HdL – Hood Length

CL – Crest Length

WnBL – rostrum to Wing Base Length

JA – Jaw Angle

HdL%CL – Hood Length % of Crest Length

HdL%URL – Hood Length % of Upper Rostrum Length

CL%URL – Crest Length % of Upper Rostrum Length

HdL%WnBL – Hood Length % of Wing Base Length

CL%WnBL – Crest Length % of Wing Base Length

Hd Darkening – Hood darkening

RTA – Rostrum Tip Angle

Gladius (Fig. 4)

All measurements comply with methods detailed by Toll (1982). Indices (I) are percent of gladius length, except gladius length index, which is a percentage of mantle length. Indices of free rachis length (Ir) are used here as a secondary index, considering all examined gladii were incomplete.

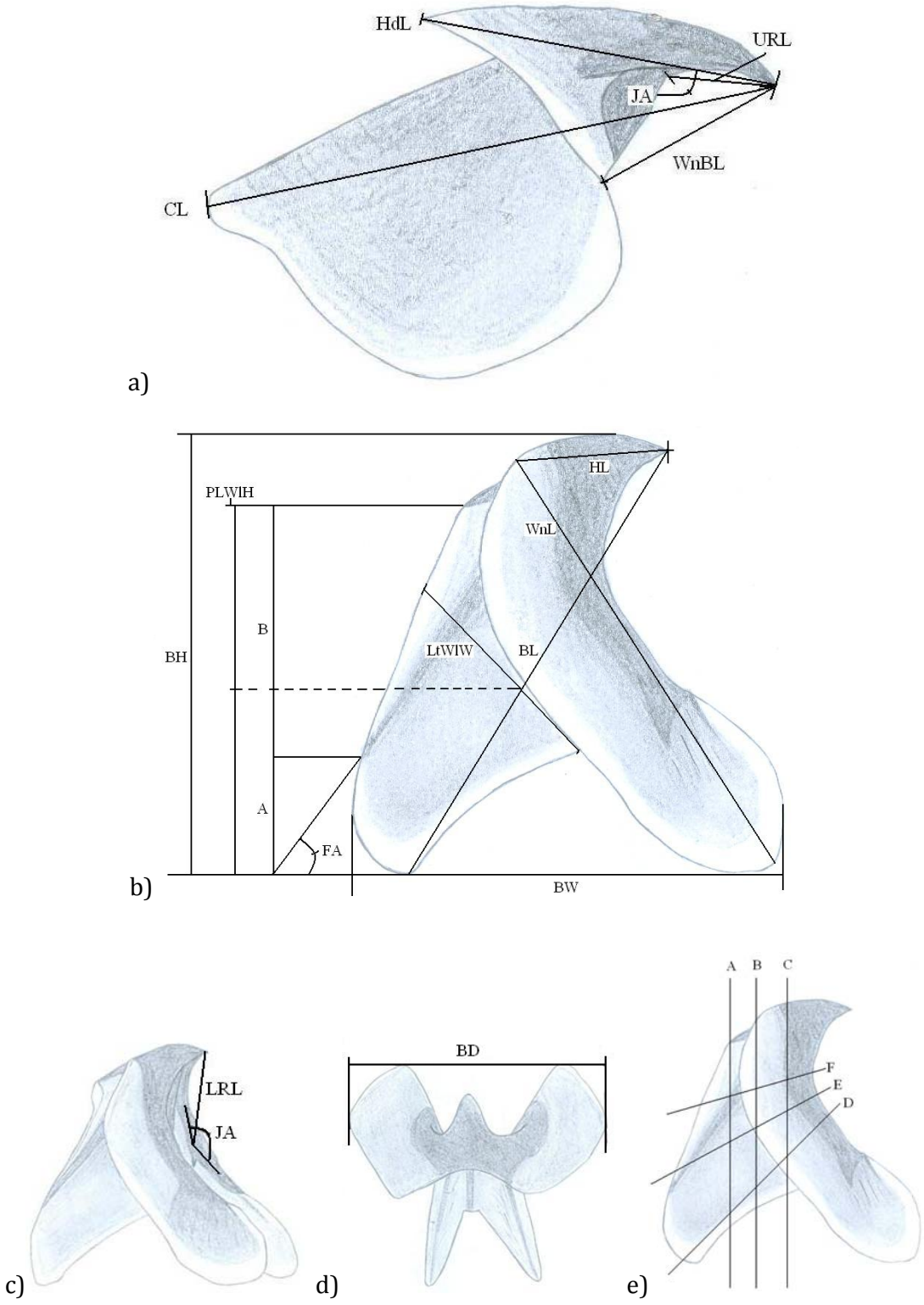

Figure 3. Beak measurements: a) upper beak lateral, b) lower beak lateral, c) lower beak oblique, d) lower beak aboral, e) lower beak cuts

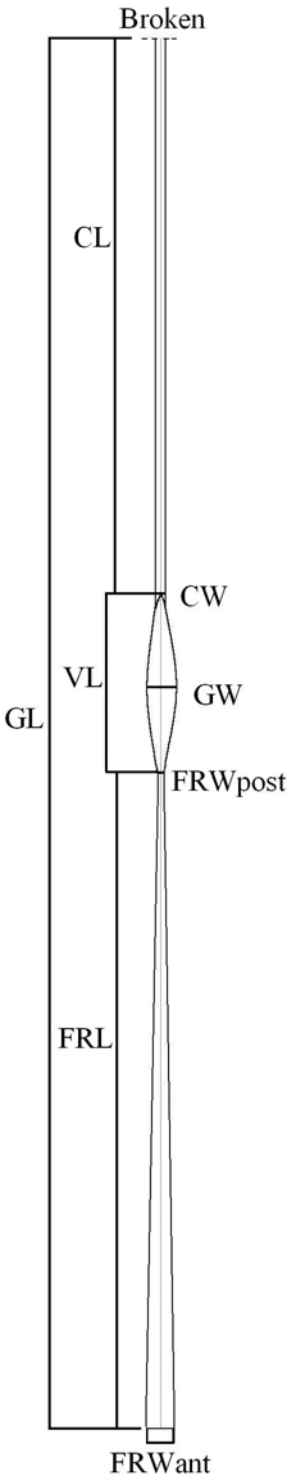

Figure 4. Gladius measurements

Gladius abbreviations

GL – Gladius Length

GLI – Gladius Length Index

GLIr – Gladius Length Index of free rachis length

FRL – Free Rachis Length – anterior tip to vane insertion

FRLI – Free Rachis Length Index

FRWant – Free Rachis Width anterior – for gladii which taper posteriorly; greatest width across free rachis.

FRWantI – Free Rachis Width anterior Index

FRWantIr – Free Rachis Width anterior Index of free rachis length

FRWpost – Free Rachis Width posterior – for gladii which taper posteriorly; width of free rachis at vane insertion.

FRWpostI - Free Rachis Width posterior Index

FRWpostIr – Free Rachis Width posterior Index of free rachis length

GW – Gladius Width – greatest distance across vanes

GWI – Gladius Width Index

GWIr – Gladius Width Index of free rachis length

CL – Conus Length – start at anterior most point of conus (rim), point where lateral vanes join.

CLI – Conus Length Index

CLIr – Conus Length Index of free rachis length

CW – Conus Width – measured perpendicular to midline; measured at anterior most point of conus (rim).

CWI – Conus Width Index

CWIr – Conus Width Index of free rachis length

VL – Vane Length – measured between vane insertion and conus formation

VLI – Vane Length Index

VLIr – Vane Length Index of free rachis length

SYSTEMATICS

Chiroteuthis d'Orbigny, 1841

Synonymy:

Bigelowia MacDonald & Clench, 1934

(Chiridioteuthis) Pfeffer, 1912

Chiropsis Joubin, 1932

Doratopsis Rochebrune, 1884

(Tankaia) Sasaki, 1929

DIAGNOSIS: Mantle variable in length, conical to cylindrical; fins nearly circular; funnel cartilage shaped like human ear; photophores on ventral side of eyes in two or three series; arm IV greatly enlarged; tentacle stalk long; club with trabeculated membrane; photophore in tip of club; suckers in four rows on tentacle club; buccal formula DDVV.

Chiroteuthis mega (Joubin, 1932)

Figures 5–18, 57; Table 1

New Zealand synonymy:

Chiroteuthis mega (Joubin, 1932)

Chiroteuthis sp. 2 Beatson, 2007: 143; Gomez-Villota 2007: 111.

Chiroteuthis sp. 4 Beatson, 2007: 144.

Chiroteuthis capensis Voss, 1967: 76–79, pl. IV & V — Spencer & Willan 1995: 52; Spencer *et al*. 2009: 219.

Material Examined: 3 specimens, 1 ♂, 2 sex indeterminate: NMNZ M.172951, sex indet., ML NA, 35°56.46'S, 170°01.01'E, 1975 m, 6/06/2003, RV *Tangaroa*, NORFANZ Stn 168; NMNZ M.52030, sex indet., ML NA, 37°25.6'S, 178°39.3'E, NZ, 0–429 m, 4/08/1976, RV *James Cook* Stn J11/101/76, MWT; NMNZ M.102109, ♂, ML 198 mm, 40°00.82'S, 178°03.79'E, 828–1000 m, 5/10/1989, FV *Wilwatch* Stn WIL/88/89.

Recognised distribution (New Zealand): 35°56.46–40°00.82'S, 170°01.01–178°39.3'E, 0–1975 m (Fig. 57).

DIAGNOSIS

Lacks visceral photophores. Tentacle club protective membrane divided into two parts: proximal part with only about a dozen very narrow trabeculae; distal part long with 58–70 broad triangular trabeculae. Club sucker stalks vaguely in two portions; without 'pleated skirt'; medial and lateral stalks with lateral keel. Club sucker rings with 15–17 teeth with central one enlarged. Eye photophores in three series: lateral series with eight photophores; intermediate series stripe with posterior end almost separate photophore; medial series stripe. Arms lack globular suckers; arm suckers with 20–30 teeth around circumference of the ring.

DESCRIPTION

Colour

Ontogenetically variable. Specimens NMNZ M.102109 (Fig. 5) and NMNZ M.172951 (Fig. 6) almost entirely dark purple, with exceptions being sucker stalks on arm IV, distal portion of sucker stalks on tentacle club, and aboral photophore on tip of tentacle club. Chromatophores on dorsal and ventral sides of fins and mantle less densely spaced; buccal membrane purple. The smaller NMNZ M.52030 (Figs 7, 8) is beige-coloured, with purplish-brown chromatophores most dense between and around eyes ventrally; largest on head, extending posteriorly past funnel; on aboral surfaces of all arms as well as oral surface of arm IV membrane; not apparent along tentacle stalk or on club.

Photophores

Eye photophores (Fig. 9) in three series: lateral series with eight small, round photophores; medial series with five separate photophores, anterior and posterior photophores rounded, central three medially elongated; medial series stripe with one separate round photophore on posterior margin. Arm IV photophores (Fig. 10i) gold-coloured , apparent in transparency along oral surface of arm in smaller specimen, extending arm length , between sucker pairs; on larger specimens photophores not immediately obvious (Fig. 10h), buried beneath dark-coloured epithelium. Aboral photophore at base of tentacle stalk absent. Large, superficial pad to sucker-like organs (Figs 10e–g), presumed to be photophores, on tentacle stalks. Tip of club (Fig. 10a–d) with large, dark purple “bud” with thin white stripe photophore running medially on centre of aboral surface. Ink sac photophores absent.

Figure 5. *Chiroteuthis mega* (NMNZ M.102109)

Figure 6. *Chiroteuthis mega* (NMNZ M.172951)

Figure 7. *Chiroteuthis mega* (NMNZ M.52030)

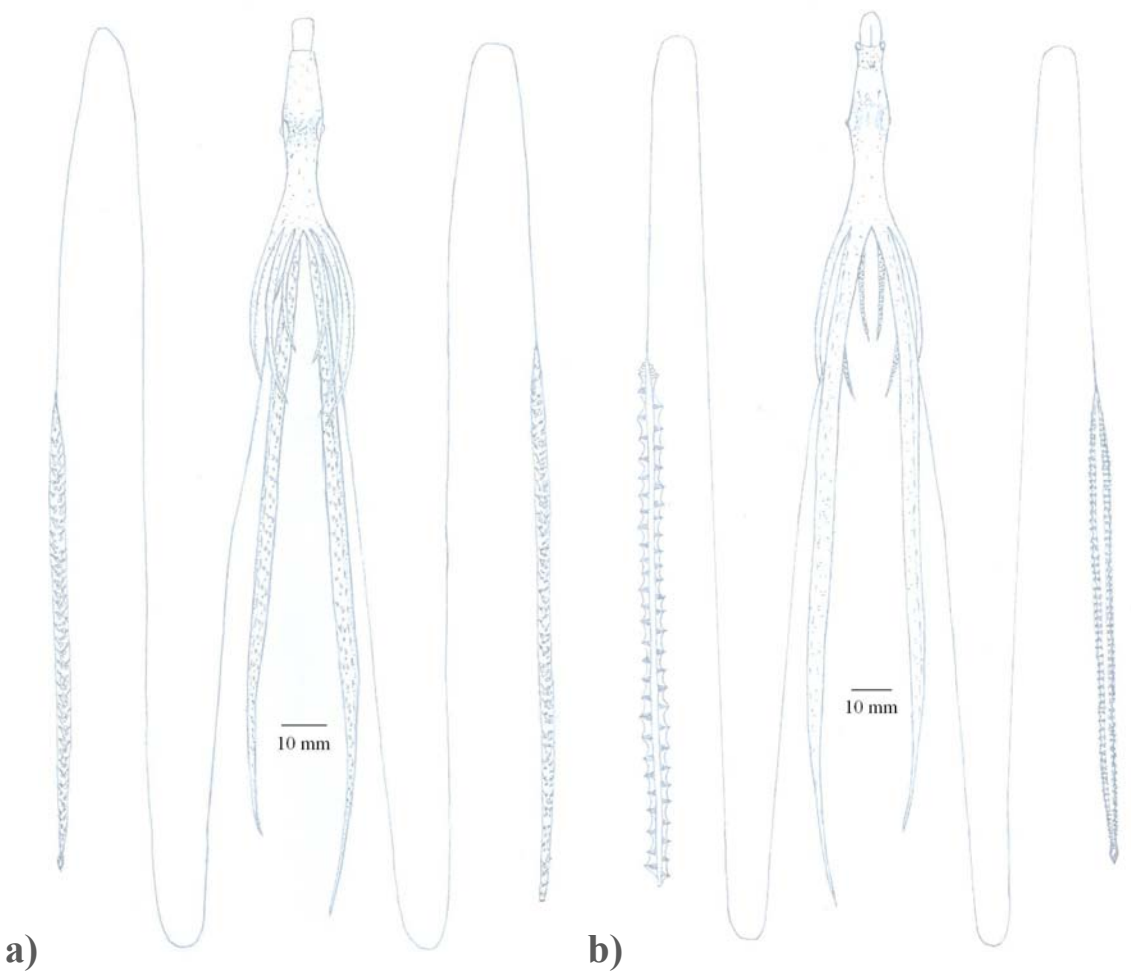

Figure 8. *Chiroteuthis mega* (NMNZ M.52030), schematic: a) dorsal, b) ventral

Mantle (Fig. 5)

Only NMNZ M.102109 with intact mantle; wider than head, conical, attaining greatest diameter at level of mantle aperture, broadening rapidly anterior to point of fin insertion; musculature thick.

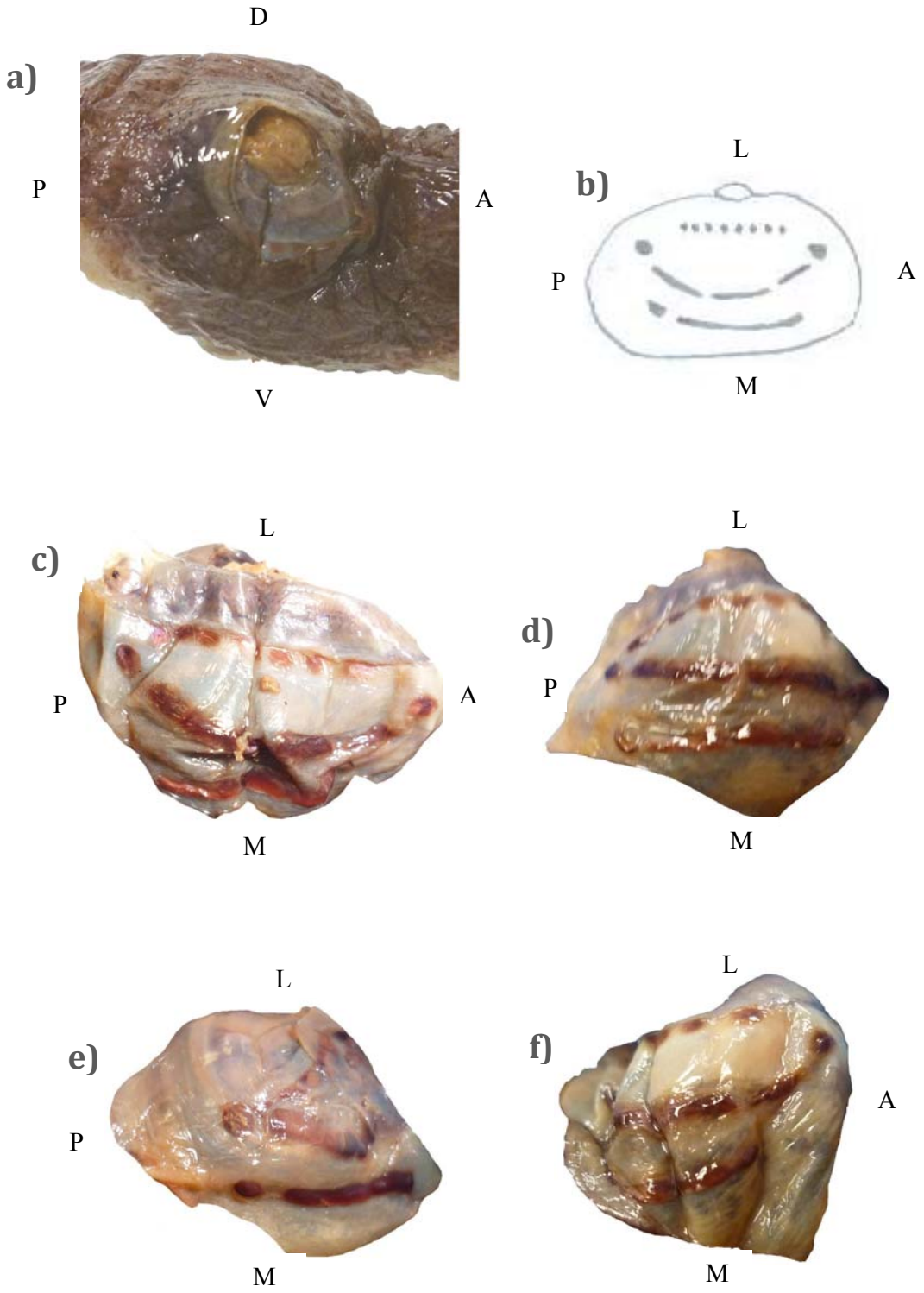

Figure 9. *Chiroteuthis mega* eye photophores: a) NMNZ M.102109 lateral with skin intact, b) ventral, c) NMNZ M.102109 ventral, d) NMNZ M.102109 ventro-posterior, e) NMNZ M. 172951 ventro-posterior, f) NMNZ M.102109 anterior-ventral.

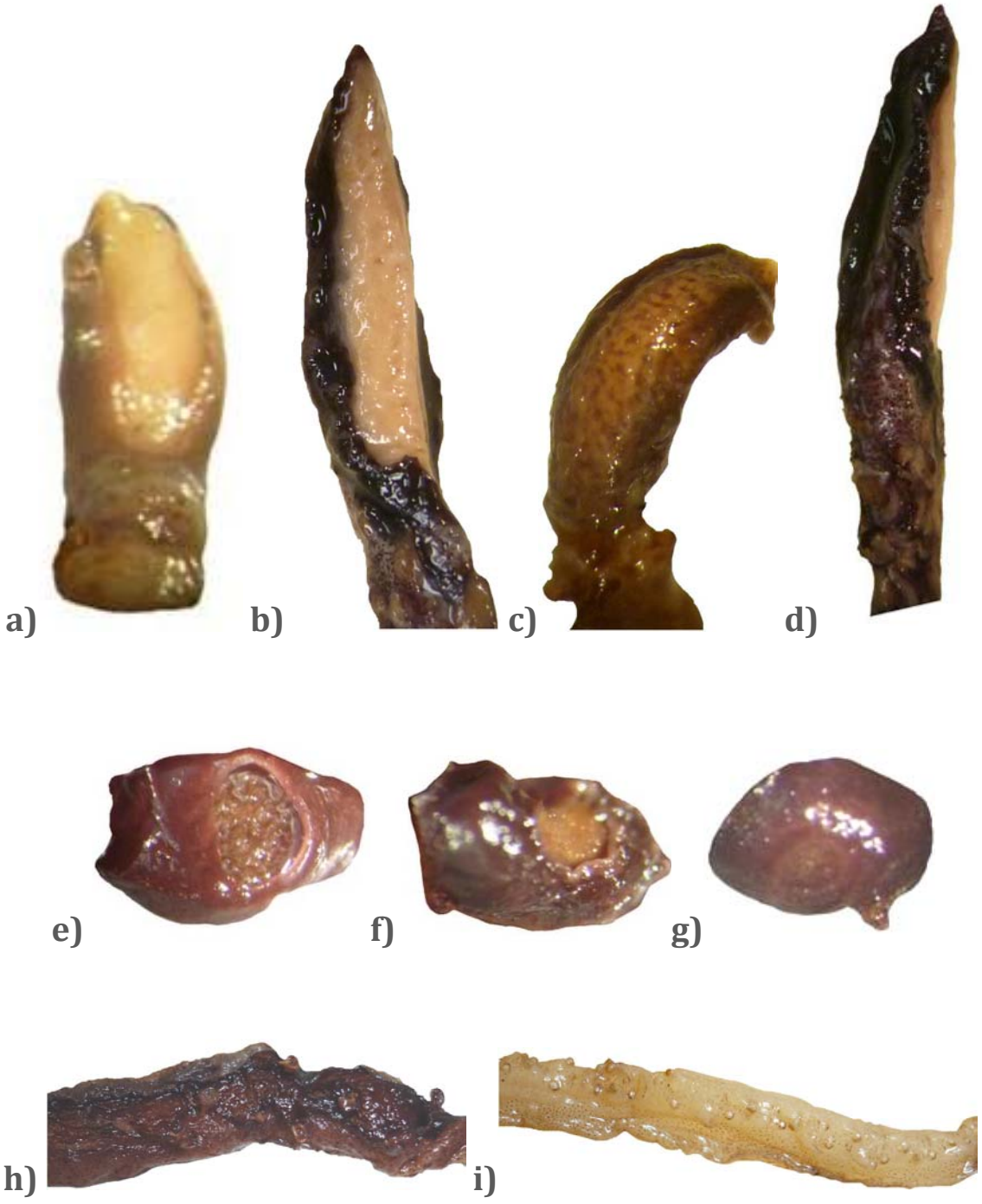

Figure 10. *Chiroteuthis mega* tentacle and arm IV photophores: a) NMNZ M.52030 tip aboral, b) NMNZ M.102109 tip aboral, c) NMNZ M.52030 tip oral, d) NMNZ M.102109 tip oral, e) NMNZ M.172951 stalk proximal, f) NMNZ M.172951 stalk proximal, g) NMNZ M.172951 stalk distal, h) NMNZ M.102109 arm IV, i) NMNZ M.52030 arm IV

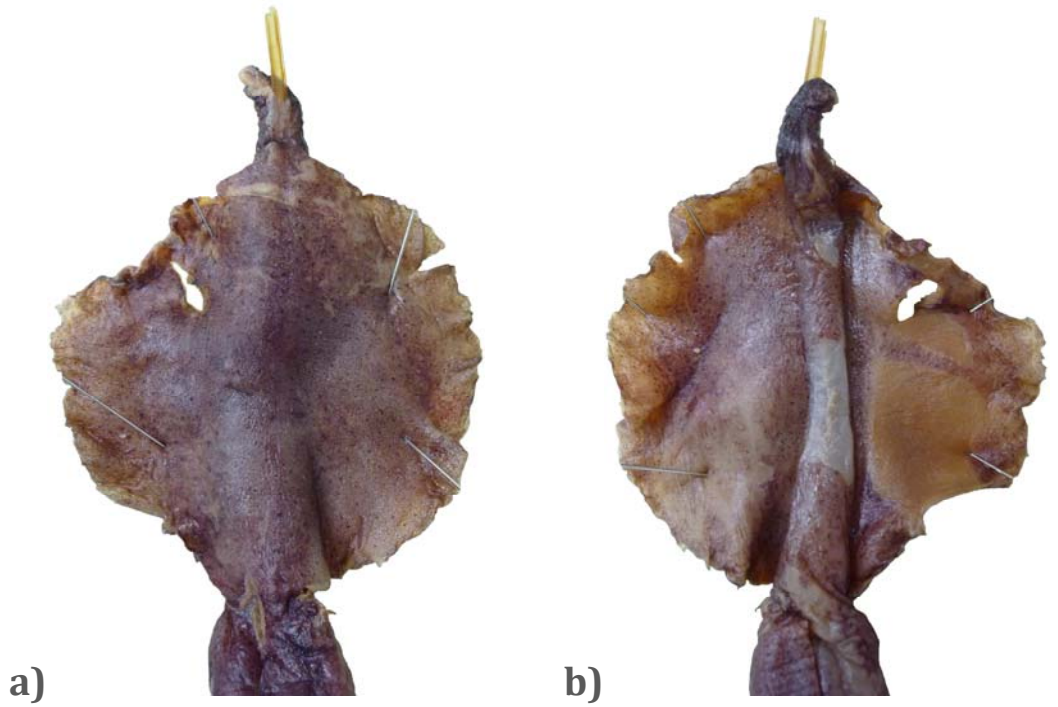

Figure 11. *Chiroteuthis mega* (NMNZ M.102109) fins: a) dorsal, b) ventral

Head (Figs 5–8)

Cylindrical, long, narrow, widest at or just posterior of eyes. Brachial pillar long in small specimen, short in large specimen. Funnel short, conical or cylindrical. Olfactory papillae with slightly rounded tip, located half-way between posterior edge of eye and funnel opening.

Fins (Fig. 11)

Nearly circular, their length 39.4% ML, width 41.9% ML, without anterior lobe. Tail thick, length 14% ML, gladius broken, protruding from end of tail.

Arms

Formula IV>>III≥ II>I. All arms thin. Arm I shortest; aboral keel on NMNZ M.102109. In NMNZ M.52030 arm L II about equal length to L III, but R II 5 mm longer than R III; in larger specimens arm II slightly shorter than arm III, with aboral keel. Arm III much shorter than IV, with aboral keel or membrane. Arm IV very long (R 322% HL, L 378% HL), more robust than arms I–III; thin, wide membrane along entire dorso-lateral side of arm to sheathe of tentacle stalk.

Arm suckers (Figs 12, 13)

With variable tooth count, dentate around entire circumference; rings present only on smallest specimen (NMNZ M.52030). Teeth narrow and acutely pointed distally, becoming curved and saw-like laterally, and low and squared proximally. Arm I largest sucker between basal and mid-arm portion (Fig. 12c) with 25 teeth. Arm II largest sucker between basal and mid-arm portions (Fig 12d, e) with 27 teeth; mid-arm suckers (Fig. 13b) with 13 distal and lateral teeth, and 10 proximal teeth; arm tip sucker (Fig. 13c) with 22 distal and lateral teeth, and 10 proximal teeth. Arm III largest sucker between basal and mid-arm portions (Figs 12f, g) with 16 teeth; arm tip sucker (Fig. 13d) with about 22 distal and lateral teeth, and 10 proximal teeth. Arm IV largest suckers on basal portion (Figs 12h, i) with 26 teeth; basal sucker suckers with about 26 distal and lateral teeth, and 10 proximal teeth (Fig. 13e); mid-arm sucker (Fig. 13f) deformed.

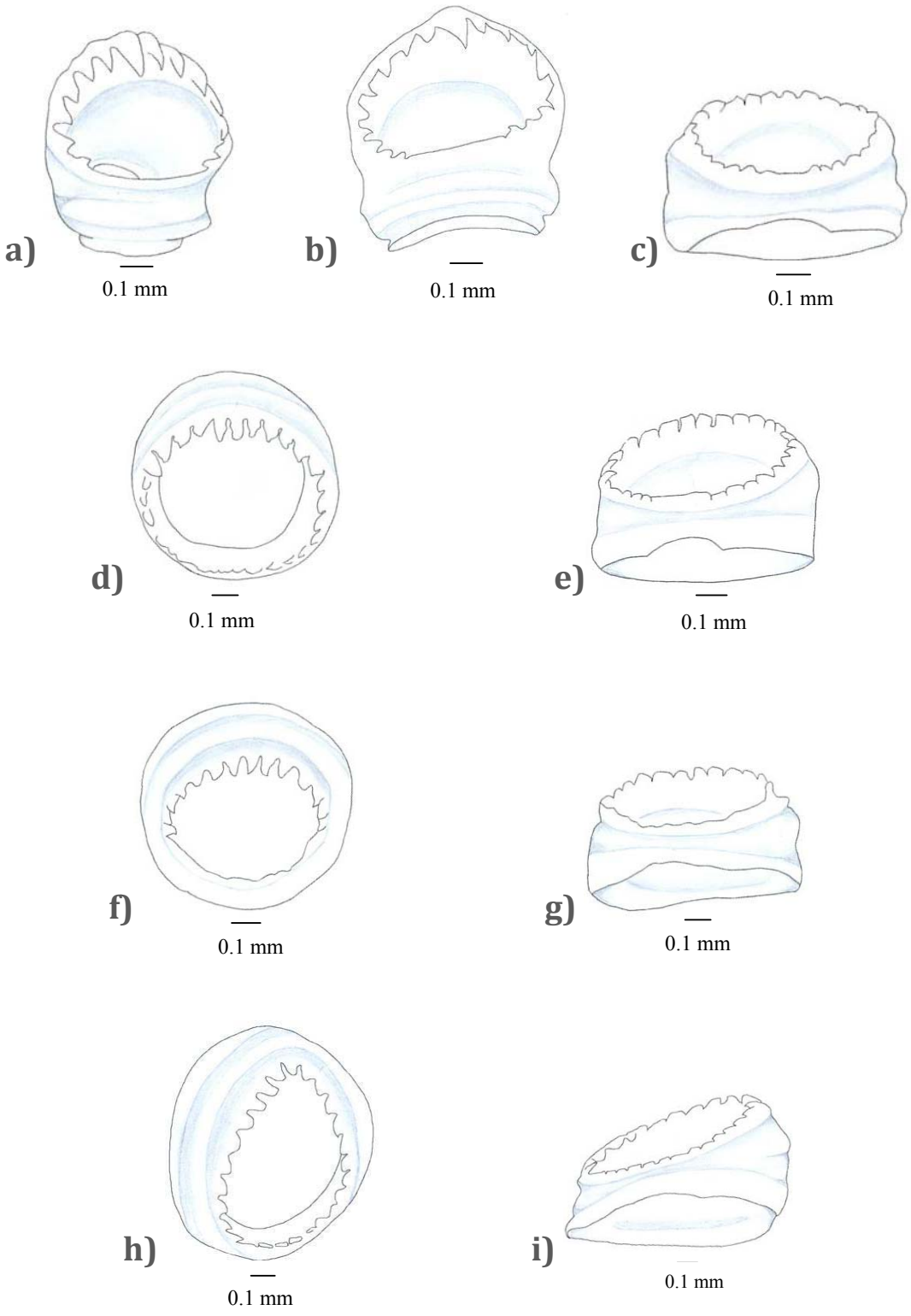

Figure 12. *Chiroteuthis mega* (NMNZ M.52030) sucker rings: a) manus, b) dactylus; c–i) largest arm suckers, c) I side, d) II, e) II side, f) III, g) III side, h) IV, i) IV side

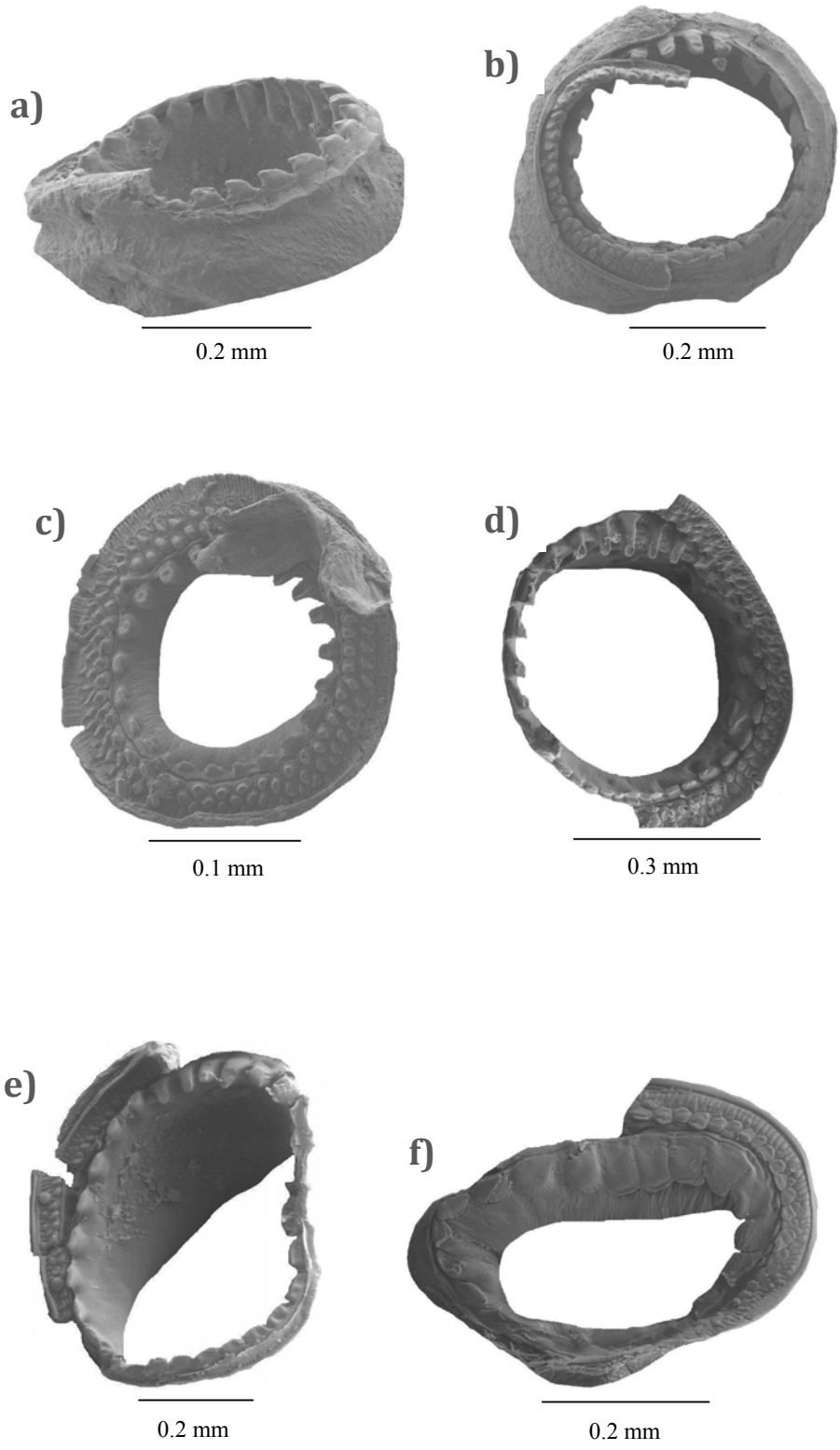

Figure 13. *Chiroteuthis mega* (NMNZ M.082030) arm sucker rings: a) II, b) II, c) II, d) III, e) IV, f) IV; a & e) base, b & f) middle, c & d) tip

Tentacle (Figs 14–16)

Stalks aborally flattened (NMNZ M.102109), long. Club long, well developed (Fig. 14) with protective membrane (Figs 14, 15a–d) extending its length, differentiated into two sections: manus with seven or eight narrow, closely spaced trabeculae; dactylus with 64 wide, triangular trabeculae. Carpus with three suckers (Fig. 14c); manus with 10 alternating small suckers (Fig. 14c); dactylus with 64 rows of alternating, paired suckers (Fig. 14a). Sucker stalks (Figs 15e, f; 16f, g) not having two clearly defined parts; have lateral keels on basal ¼ of medial stalk and basal ½ of lateral stalk; becoming very thin and white distal to keel. Medial stalks about ⅔ as long as lateral; distal ½ of lateral sucker stalk becoming very thin. Club sucker ring dentition (Figs 12a, b; 16) with 15–17 distal and lateral teeth, and one or two proximal scallops, with distal central tooth enlarged; proximal portion smooth or weakly scalloped.

Lower beak (Fig. 17a–c, e)

Wider than high; wing fold obscures jaw angle in lateral profile. Hood closely adpressed to crest; visible crest shorter than or equal to hood length. Wall fold extends to posterior edge of lateral wall at an angle of 40–60˚ from baseline; ratio of A to B ~ 37–57%; jaw angle obtuse (124–128˚); shoulder without tooth. At LRL 2.5 mm, hood darkened 80%, wing darkened 57.1% of length; at shoulder darkened laterally 75%; margins translucent. Oral surface lightly darkened down shoulder. At LRL 4 mm, entire rostrum and hood darkened, wing darkened 80% length; darkened laterally 50% at shoulder. Rostrum thickened with keel (Fig. 17e iv–vi). Lateral wall with thickened fold, but without keel (Fig. 17e i–iii).

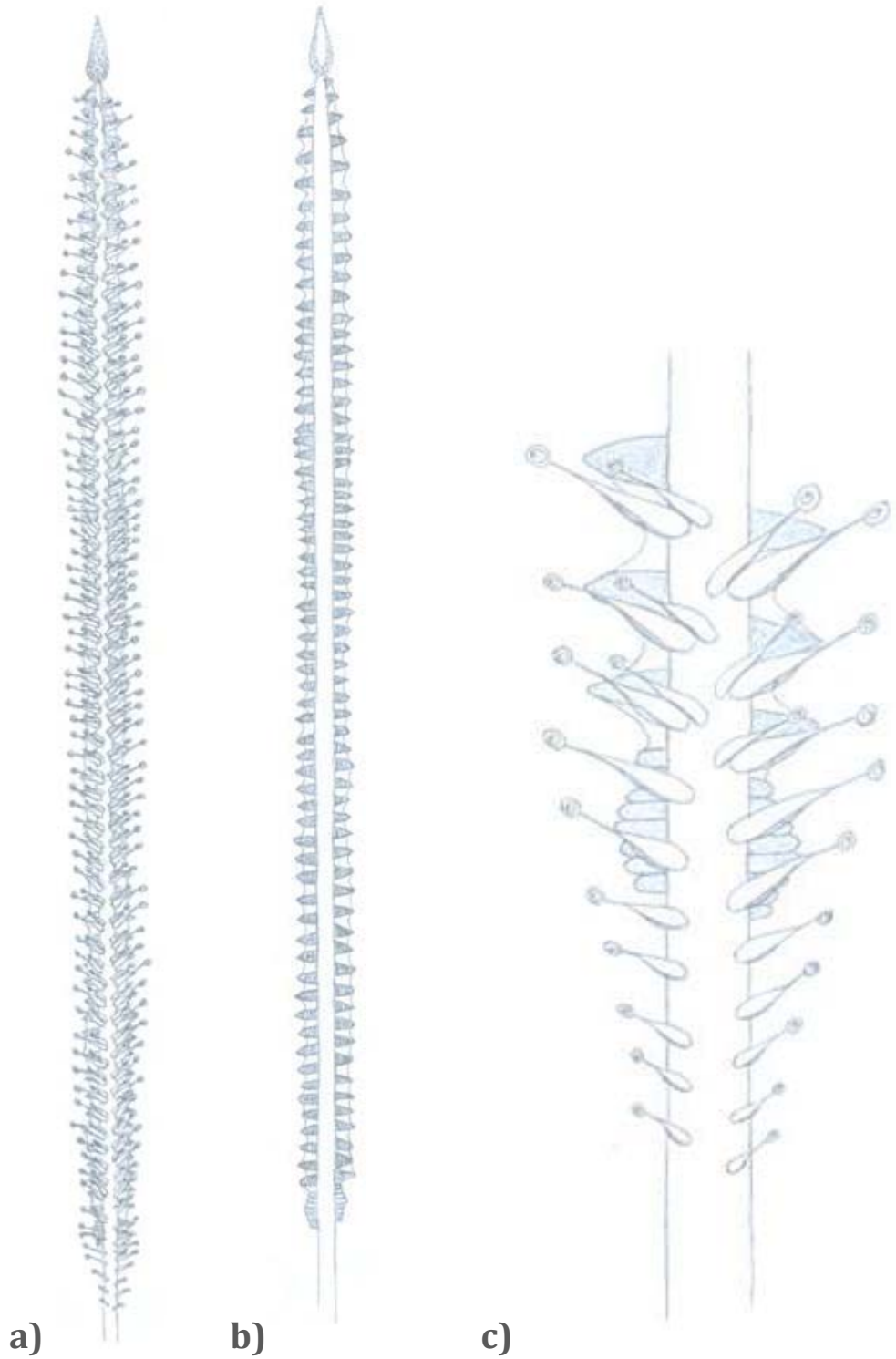

Figure 14. *Chiroteuthis mega* tentacle club: a) oral, b) aboral, c) oral carpus and manus

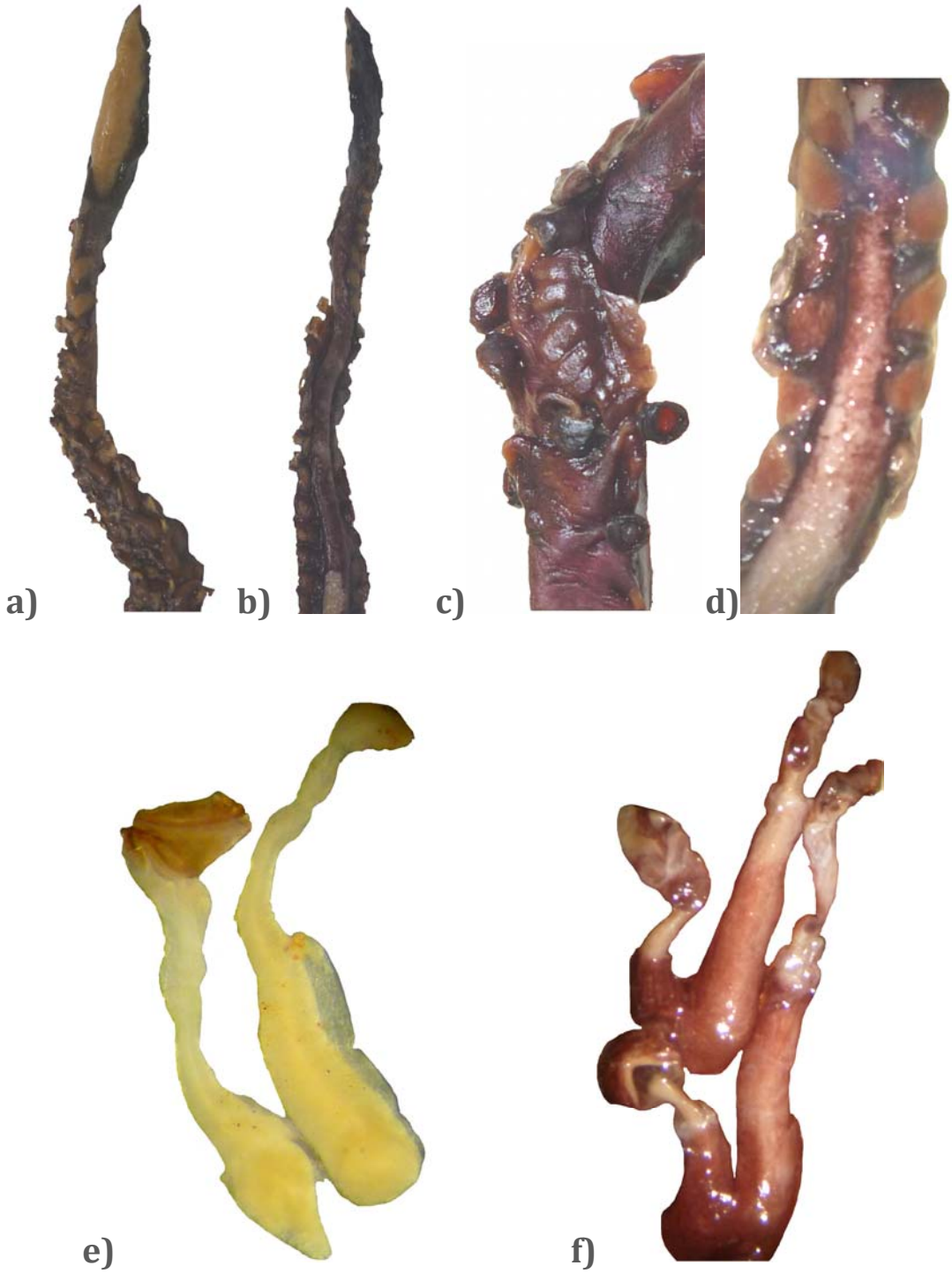

Figure 15. *Chiroteuthis mega* tentacle clubs: a) NMNZ M.102109 oral (aboral photophore), b) NMNZ M.102109 aboral (oral photophore), c) NMNZ M.172951 proximal trabeculae, d) NMNZ M.102109 distal trabeculae, e) NMNZ M.52030 dactylus sucker stalks, f) NMNZ M.102109 dactylus sucker stalks

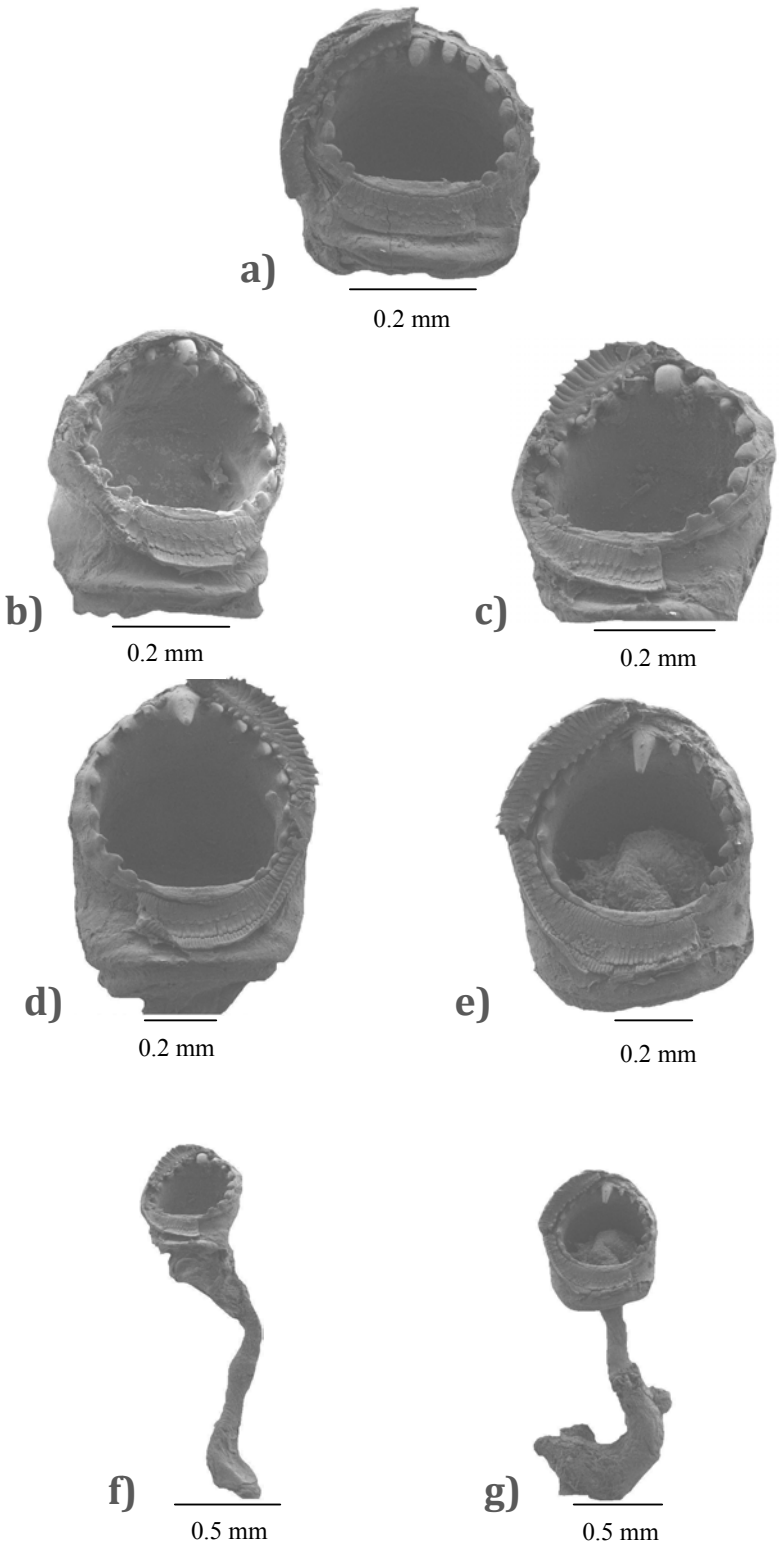

Figure 16. *Chiroteuthis mega* (NMNZ M.52030) tentacle club suckers and stalks: a) carpus; b, c, f) manus; d, e, g) dactylus. b & d) lateral, c & e–g) medial

Upper beak (Fig. 17d)

With pointed rostrum. No distinct jaw angle; shoulder concave. Hood length 66% crest length. Hood darkened 87% from rostral tip; outer margin of hood translucent.

Radula (Fig. 17f) **and palatine palp**

Rachidian with three cusps, the central the largest, with pronounced groove between central and lateral cusps. First lateral bi-cusped, the medial cusp larger, variably medially curved, with pronounced groove between cusps. Second lateral with long, dagger-like medial cusp, its length greater than that of rachidian, but shorter than marginal. Marginal blocks sabre-like, long, narrow, may alternate with rows of teeth.

Internal anatomy (Fig. 18a)

Outer demibranch of gill with 33 lamellae, inner demibranch with 25 lamellae. Penis (Fig. 18a) prominent, beige-coloured, terminally with spade-like modification.

Gladius (Fig. 18b)

Long, thin and translucent. Tip of conus broken, protruding from tail. Long free rachis (47.5% present GL), widest anteriorly, tapering posteriorly, narrowest at vane insertion (FRWantIr: 2.8%, FRWpostIr: 1.4%). Conus long (Ir 77%) but incomplete. Vane length Ir 32.6%.

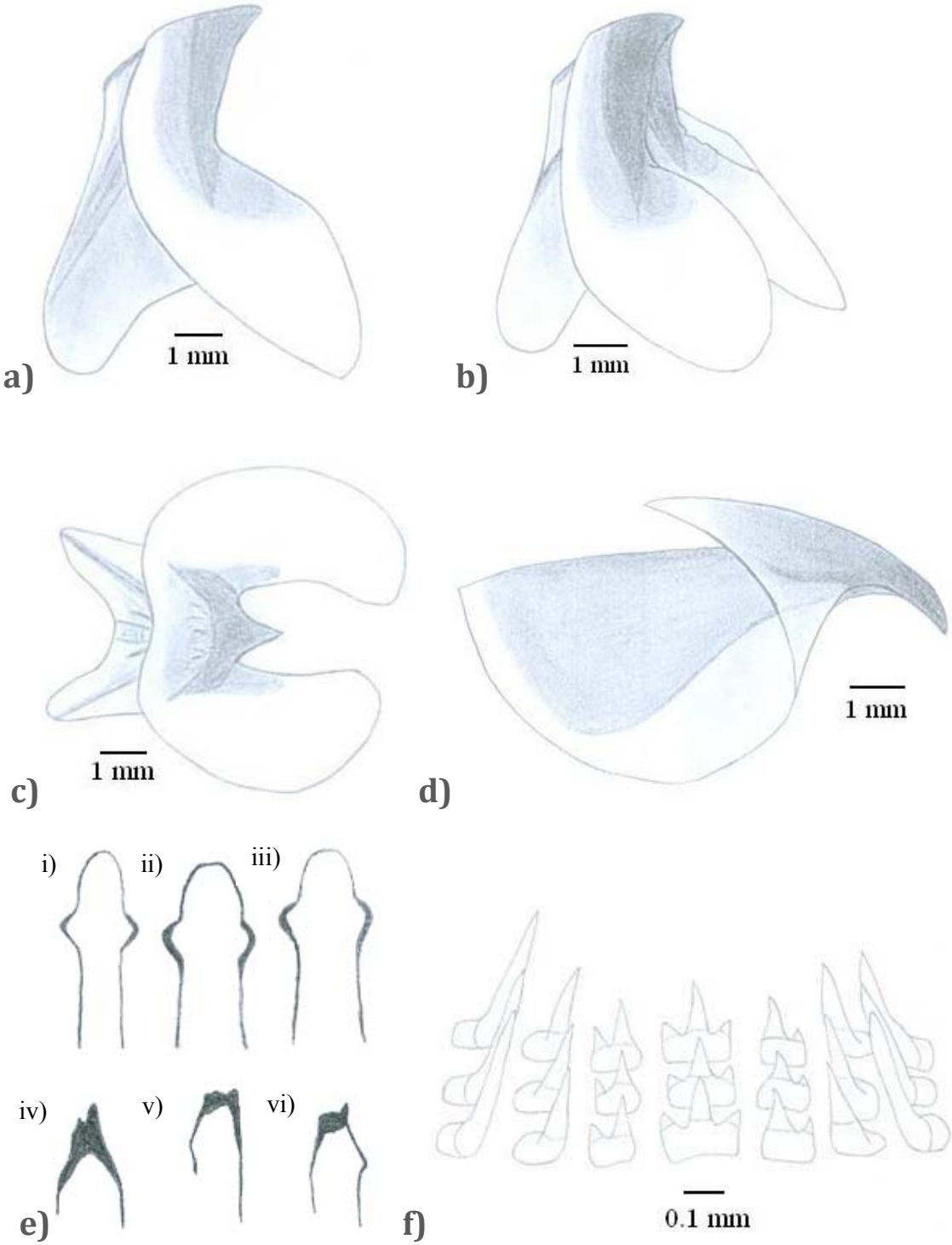

Figure 17. *Chiroteuthis mega* (NMNZ M. 52030) mouth parts: a) lower beak lateral, b) lower beak oblique, c) lower beak aboral, d) upper beak lateral, e i–iii) lower beak lateral wall cuts, e iv–vi) lower beak rostral cuts, f) radula, e i) cut A, e ii) cut B, e iii) cut C, e iv) cut D, e v) cut E, e vi) cut F

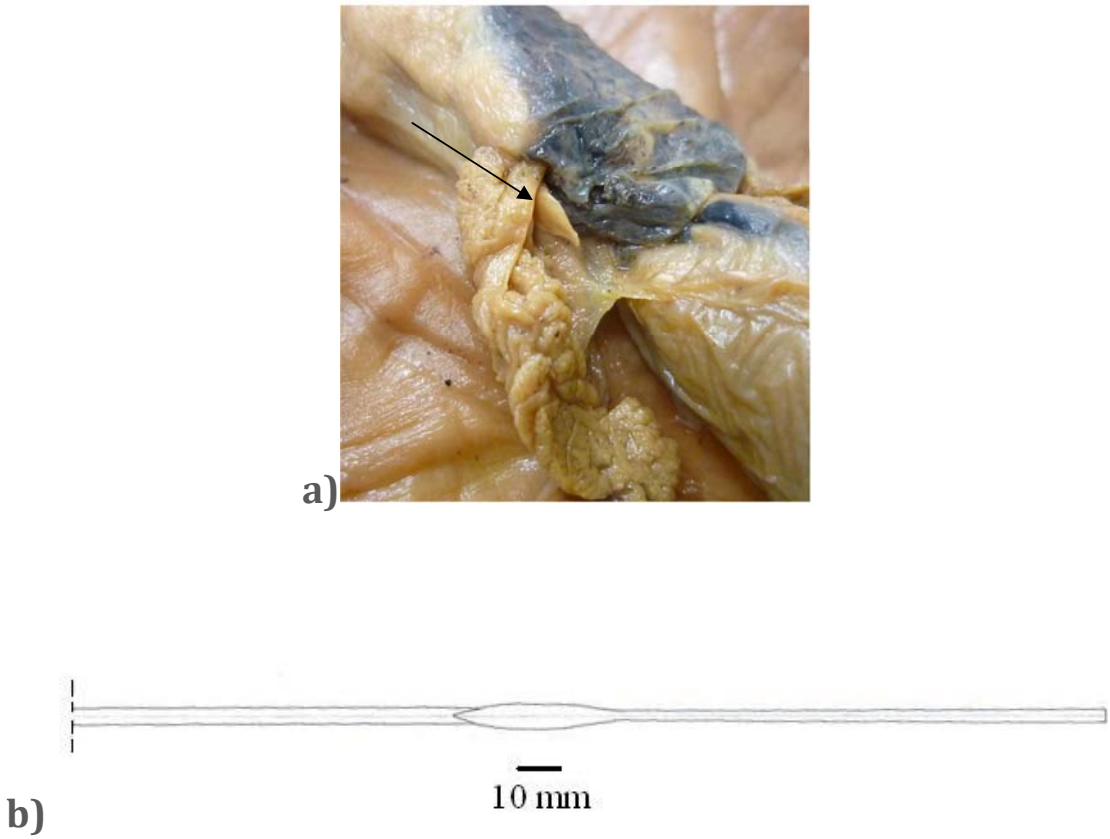

Figure 18. *Chiroteuthis mega* NMNZ M.102109 internal anatomy: a) penis, b) gladius

REMARKS

The first description of *Chiroteuthis mega* (Joubin 1932) focused on penis morphology; in a redescription the following year (Joubin 1933a) recognised that the specimen earlier described by him had experienced pre-mortem trauma to the ventral arms, which were in the process of re-growing; the unique tentacle club morphology described for this specimen is also likely an artefact of pre-mortem trauma re-growth. The single photophore on the liver also described for this species was likely a bend in the cephalic vein (Roper & Young 1999a). Voss described a complete specimen in 1967 which he concluded to be a new species, *C. capensis*, given the lack of visceral

photophores and unique tentacle club morphology. Both these species were considered valid until *C. capensis* was recognised to be a junior synonym of *C. mega* (Salcedo-Vargas 1997). *Chiroteuthis mega* remains the only recognised species in this genus to lack visceral photophores.

Of the three specimens in New Zealand collections, only one had an intact mantle (NMNZ M.102109), the buccal mass of this specimen had been previously extracted, and the radula removed and not returned to the sample. Because of the incomplete nature of the three specimens available the description of this species is necessarily limited. From previous descriptions of this species, most notably that of Voss (1967) for *C. capensis*, the New Zealand specimens differ slightly in the arm sucker dentition and club proximal trabeculae count. Some arm suckers have a few more teeth than that reported for this species previously (20–30), and the proximal part of the club membranes have four or five fewer trabeculae than that described for the type of *C. capensis* (12). These differences are minimal and may be indicative of a regional morphology, or may simply represent a slight broadening of the currently known range of characters for this species.

Of greater interest are differences in eye photophores for specimens referred to as *C. capensis* and those herein to its senior synonym, *C. mega*. Eye photophores were present on a single eye of each NMNZ M.102109 and NMNZ M.172951; on NMNZ M.172951 the lateral and intermediate series were damaged and difficult to count and describe accurately; the eye of NMNZ M.102109 was slightly miss-shapen. This damage and distortion may have caused the three central photophores of the intermediate series to appear elongated, rather than 'stripe like;' the posterior and anterior photophores were distinctively separate and circular. Both specimens clearly had a separate photophore

on the posterior end of the medial series, although this species is described with this photophore as "nearly separate" (Roper & Young 1999a). To determine whether these differences represent a regional morphology, a broadening in the recognised state of eye photophores for the species as a whole, or are simply due to capture damage, requires more and better-condition specimens from New Zealand waters than are presently available to be more fully evaluate.

This species has been previously reported from New Zealand waters from stomach contents of pygmy sperm whales, *Kogia breviceps* (Beatson 2007) and sperm whales, *Physter macrocephalus* (Gomez-Villota 2007). All cephalopods reported from the stomachs of *Kogia* were recognised to occur within New Zealand waters on the basis of *in situ* captured specimens, whereas those of *Physeter* were not, given the recognised extensive migratory behaviour of the latter. Spencer & Willan (1995) reported this species (as *C. capensis*) from New Zealand waters on the basis of beaks recovered from stomach regurgitations of wandering albatross (Imber 1992), the capture of which could not conclusively be sourced to New Zealand waters (*fide* O'Shea 1997); Spencer *et al*. 2009 reported this species (as *C. capensis*) from New Zealand waters on the basis of a single *in situ* captured specimen (NMNZ M.102109) — a specimen herein re-examined and confirmed to belong to this species. Based on its representation in New Zealand marine collections this species would not appear to be particularly common.

These are the first *in situ* captured specimens to be described from New Zealand waters (including that specimen referred to from these waters by Spencer *et al*. (2009). With the limited number of specimen lots available it is difficult to know the real distribution of this species throughout these waters, but available specimens have all been collected from waters north of the Subtropical Convergence, off both east and west coasts of New

Zealand (Fig. 57). This species is previously known from the North and South Atlantic, as well as the eastern North Pacific (Roper & Young 1999a).

Table 1. Measurements of *Chiroteuthis mega* (mm)

	M.52030	M.102109	M.172951
ML	NA	198	NA
MW	NA	29.5	NA
TL	NA	NA	NA
FL	NA	78	NA
FW	NA	83	NA
ALI	(L) 170	358	320
ALII	(L) 48	125	132
ALIII	(L) 45	110	100
ALIV	(L) 31	84	84
ASCI	26	42	41
ASCII	14	26	28
ASCIII	19	24	22
ASCIV	15	16	20
CL	115	235	221
Carpus L	6	5	6
Manus L	2	11	13
Dactylus L	102	219	192
CRC	71	69	70
T Stalk L	520	NA	NA
HL	45	60	52
HW	10	27	18
ED	9*	18	NA
LD	4	5	NA
GLC (inner)	NA	25	NA
GLC (outer)	NA	33	NA
free lobe	NA	N	NA
sex	Indet	♂	Indet

* = Damaged. NA = Not Applicable, either too damaged or absent. Indet = indeterminate.

Chiroteuthis spoeli Salcedo-Vargas, 1996

Figures 19–29, 57; Tables 2 & 3

Material Examined: 3 specimens: 2 ♀, 1 ♂; NMNZ M.286109, ♀, ML 165 mm, 24˚45'S, 167˚40'E, 20/11/1996, HALIPRO2, BT074; NMNZ M.172949, ♀, ML 82 mm, 26°23.5'S, 167˚01.21'E, 1019–1030 m, 18/05/2003, RV *Tangaroa*, NORFANZ Stn 44; NMNZ M.152619, ♂, ML 144 mm, 28˚45.6'S, 179˚20.0'E, 19/06/1976, RV *James Cook* Stn J9/60/76.

Recognised Distribution (New Zealand): 24˚45–28˚45.6'S, 167˚01.21–179˚20.0'E, 1019–1030 m (Fig. 57).

DIAGNOSIS

Tentacle club long with protective membrane divided into three almost equal parts, intermediate portion without trabeculae, distal and proximal sections with narrow trabeculae. Club sucker stalks in two portions with some pleating, stalks lack lateral keels; club suckers with 5–7 sharp teeth, the central not enlarged. Eye photophores round, in two series: lateral and medial series both with seven photophores, the anterior- and posterior-most photophores slightly larger and farther away from central five. Largest suckers globular with 8–14 low, square teeth.

DESCRIPTION

Colour (Figs 19–21)

Entire animal purple; blueish on dorsal surface between eyes, ventral surface around eyes, in spots on the aboral surfaces of arms III and IV, and dorsal surface of mantle; small to large dark-purple chromatophores covering entire body; head and mantle with many small, dark chromatophores, especially on dorsal surface of head; chromatophores on funnel. Dorsal and ventral surfaces of fins completely covered in

various sized chromatophores. All arms with chromatophores on oral and aboral surfaces, especially dark on oral surface of IV arms. Buccal membrane off-white, without apparent chromatophores.

Photophores (Figs 22, 23)

Eye photophores (Figs 22a–e; 23a–e) rounded, in two series on ventral side: medial series with six or seven photophores, five or six in centre, one anterior; lateral series with eight photophores, seven starting at posterior-most portion, one at anterior-most portion. Arm IV (Fig. 22f) photophores iridescent, gold to white coloured on oral surface, extend arm length, between sucker pairs; largest basal, become smaller and more closely spaced towards tip. Aboral photophore at base of tentacle stalk absent. Large, superficial pad to sucker-like organs (Fig. 23f), presumed to be photophores, on tentacle stalks. Two rounded photophores covering entire ink sac (Fig. 23g).

Mantle (Figs 19–21)

Conical, attaining greatest diameter at level of mantle aperture, broadening rapidly anterior to point of fin insertion; musculature thick.

Head (Figs 19–21)

Round, its length ~ 45–57% ML, widest at eyes; brachial pillar wide and long; eye diameter ~ 8–13% ML. Funnel small, cylindrical. Olfactory papillae long.

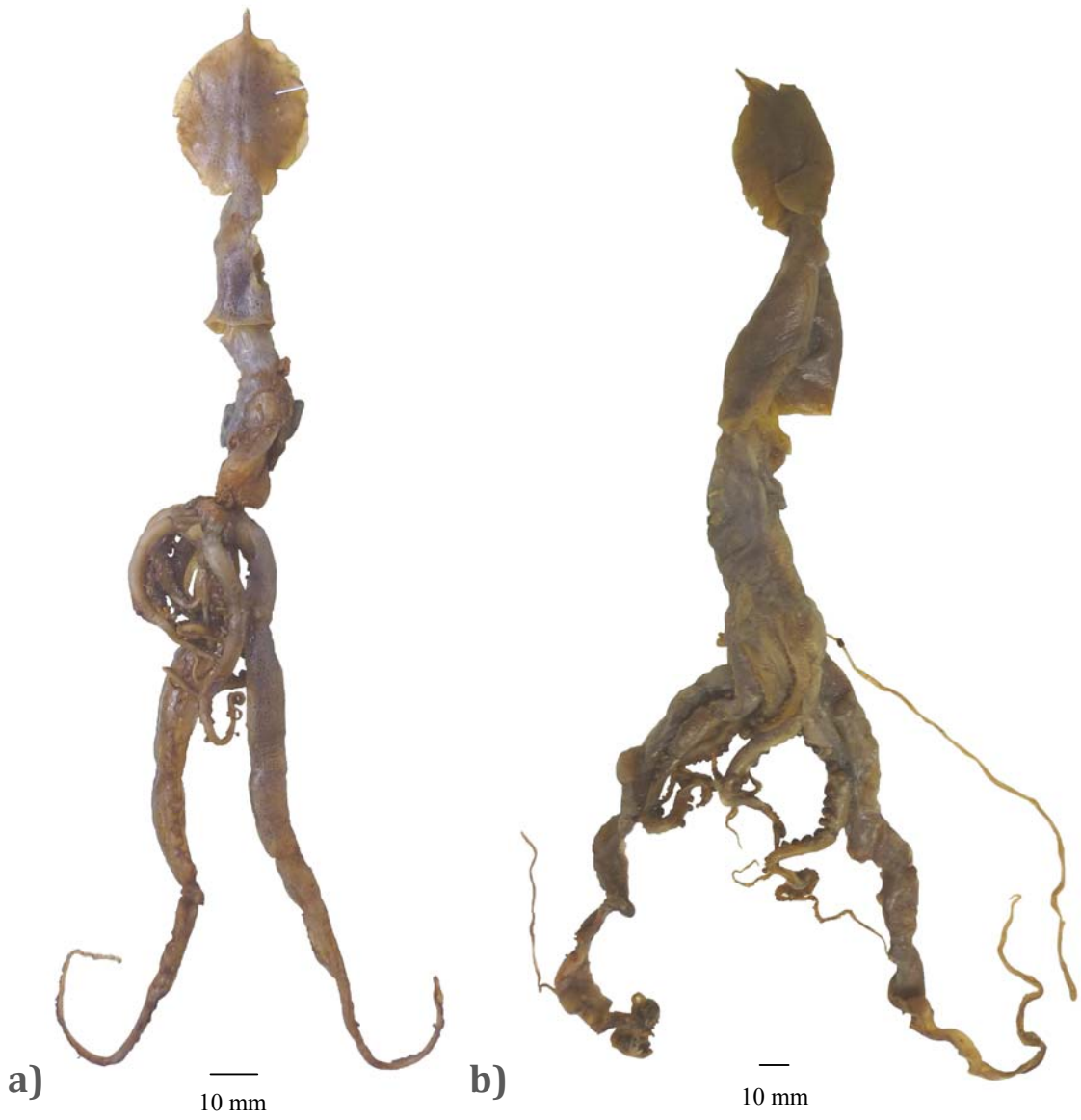

Figure 19. *Chiroteuthis spoeli*: a) NMNZ M.172949, b) NMNZ M.286109

Fins (Fig. 24)

Nearly circular, their length ~ 44–46% ML, width ~ 37–40% ML; very small tail.

Anterior lobe absent or free for small portion.

Figure 20. *Chiroteuthis spoeli* (NMNZ M.172949), schematic: a) dorsal, b) ventral

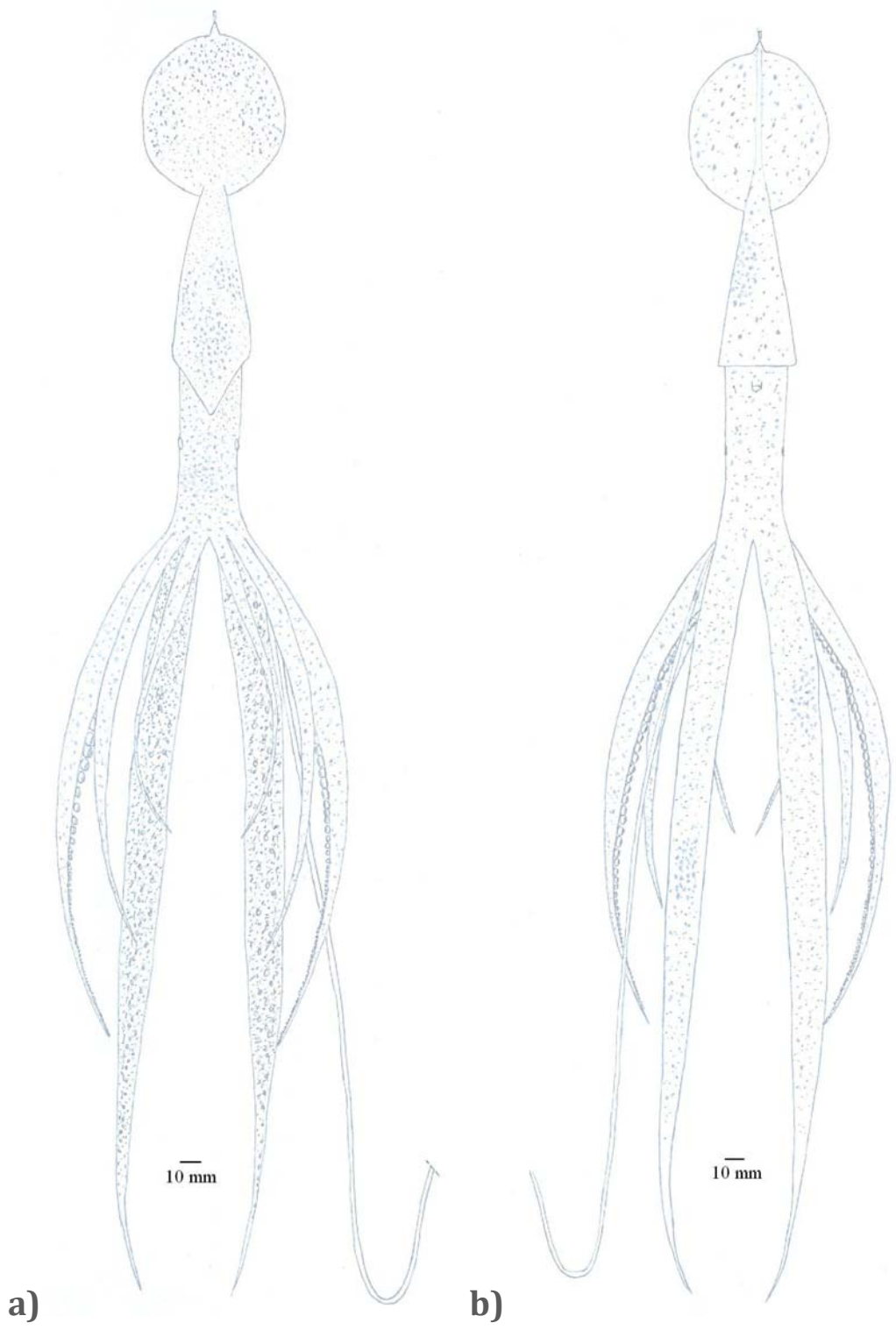

Figure 21. *Chiroteuthis spoeli* (NMNZ M.286109), schematic: a) dorsal, b) ventral

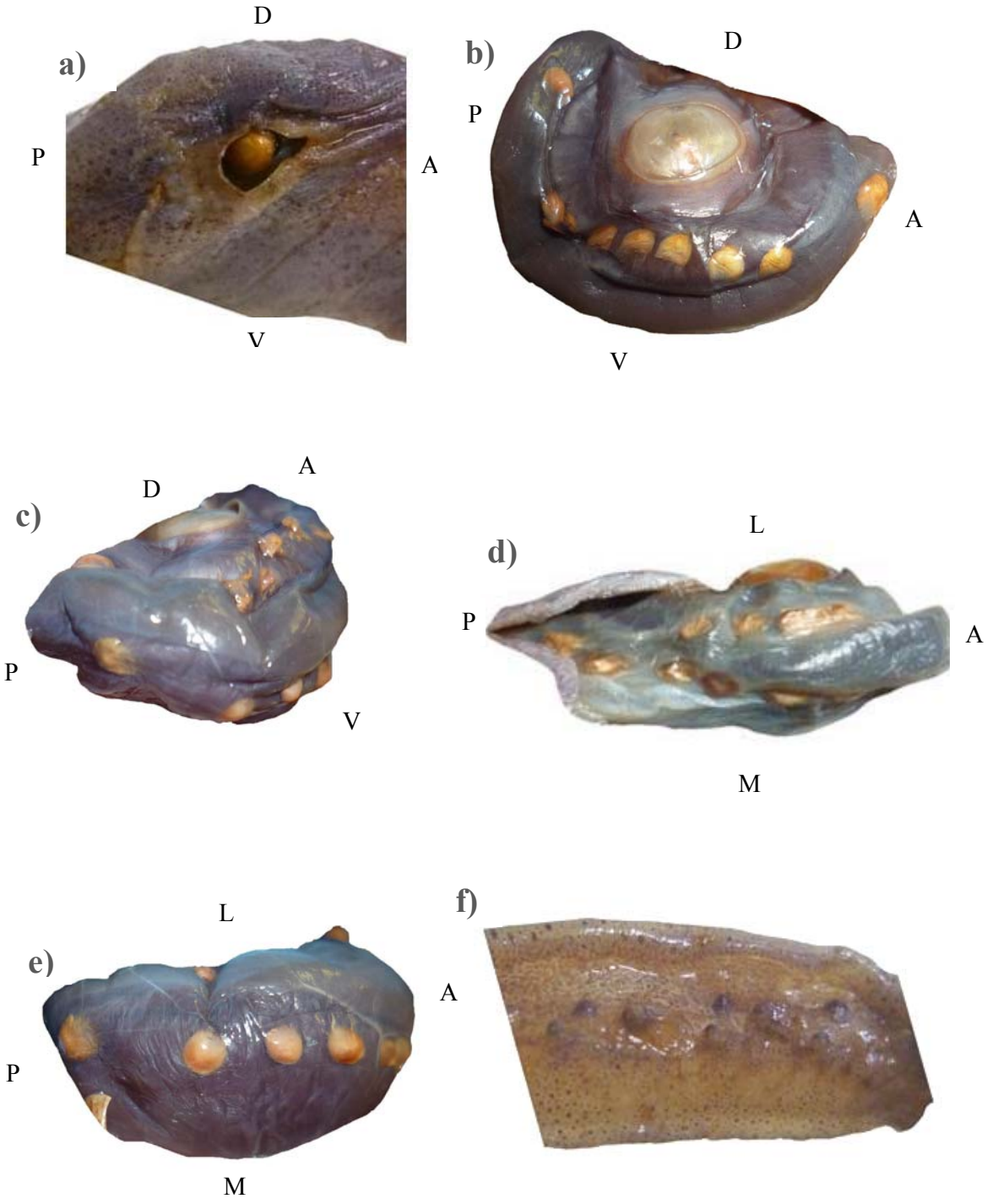

Figure 22. *Chiroteuthis spoeli* photophores: a) NMNZ M.286109 eye (lateral) with skin intact, b) NMNZ M.152619 lateral, c) NMNZ M.152619 posterior, d) NMNZ M.286109 posterior-ventral, e) NMNZ M.152619 posterior-ventral, f) NMNZ M.172949 arm IV photophores

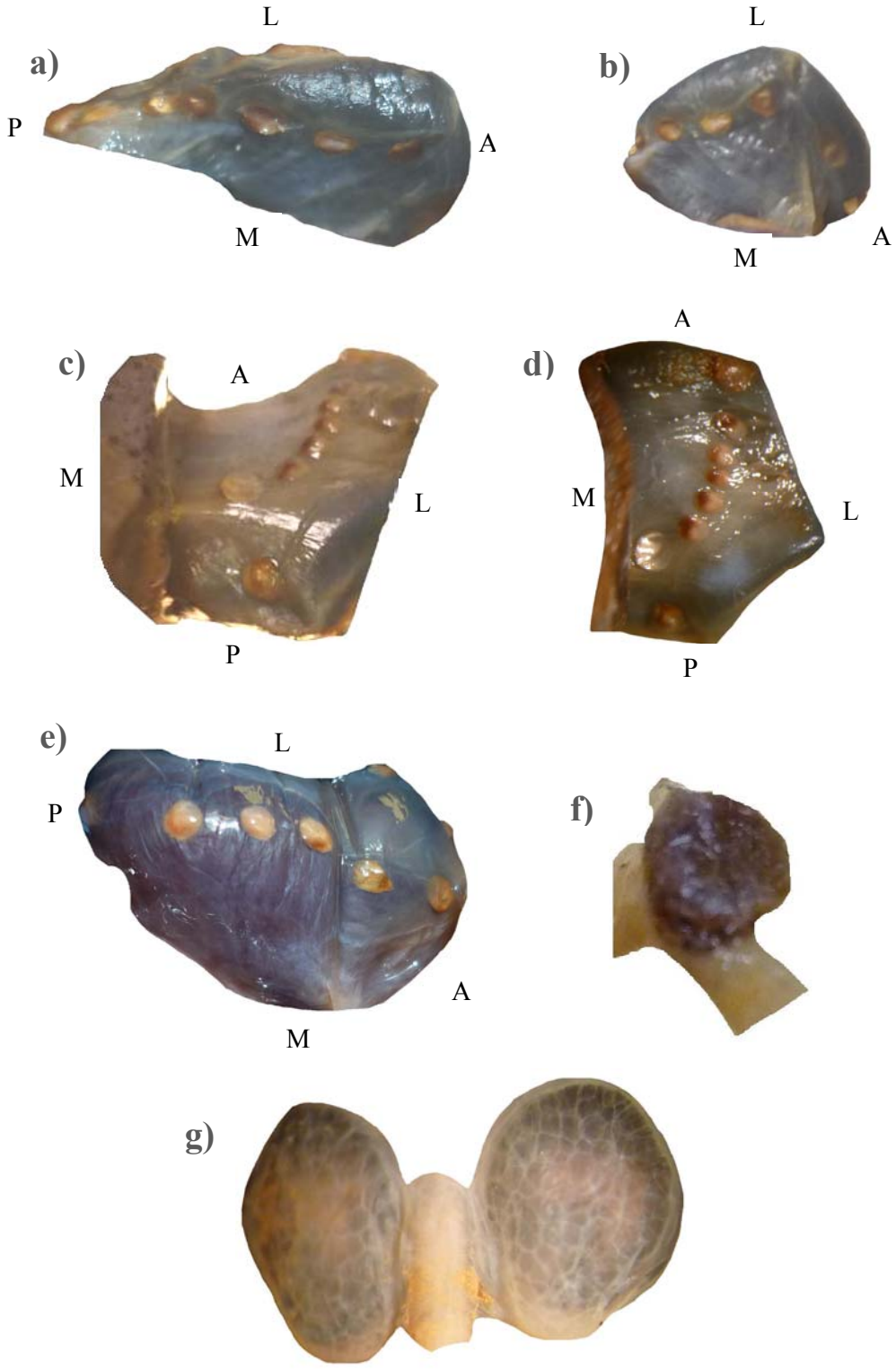

Figure 23. *Chiroteuthis spoeli* photophores: a) NMNZ M.286109 posterior-ventral, b) NMNZ M.286109 anterior-ventral, c) NMNZ M.172949 anterior-ventral, d) NMNZ M.172949 anterior-ventral, e) NMNZ M.152619 anterior-ventral, f) NMNZ M.286109 tentacle stalk photophore, g) NMNZ M.172949 ink sac; a–e) eye photophores

Arms (Fig. 25g–j)

Formula IV>>III>II>I. Arm I thin. Arm II thin; membrane on aboral surface, begins abruptly at mid-arm, extends to distal 1/5th. Arm III much shorter (AL III ~ 98–122% ML), less robust than IV; membrane or keel running along aboral proximal ½–¾ of arm length. Arm IV very long (~ 191–210% ML) and robust; well-developed, with wide membrane extending along entire dorso-lateral surface of arm to sheathe tentacle stalk; with narrow keel extending the entire ventral-lateral surface of arm.

Suckers (Figs 25a–f; 26)

All suckers with eight or nine low, broad, squared distal teeth, and two or three lateral scallops; proximal portion irregular, except on tip. Suckers on tip with about 20 teeth around circumference of ring, squared teeth around entire sucker, longer on distal portion, shorter on proximal. Arm I (Figs 25a, 26a–e) basal suckers medium sized and somewhat globular, gradually becoming larger and more globular mid-arm, then rapidly becoming smaller distally, with transition less pronounced on arms II and III. Arm II (Figs 25b, 26f–i) basal suckers large and somewhat globular, gradually becoming very large and more globular mid-arm, then rapidly becoming smaller distally; largest suckers along proximal ⅓ of arm. Arm III (Figs 25c–e, 26j–m) basal suckers large and somewhat globular, gradually becoming very large and more globular mid-arm, then rapidly becoming smaller distally; largest suckers along mid–portion of arm. Arm IV (Figs 25f, 26n–p) largest suckers a few pairs from base; no globular suckers.

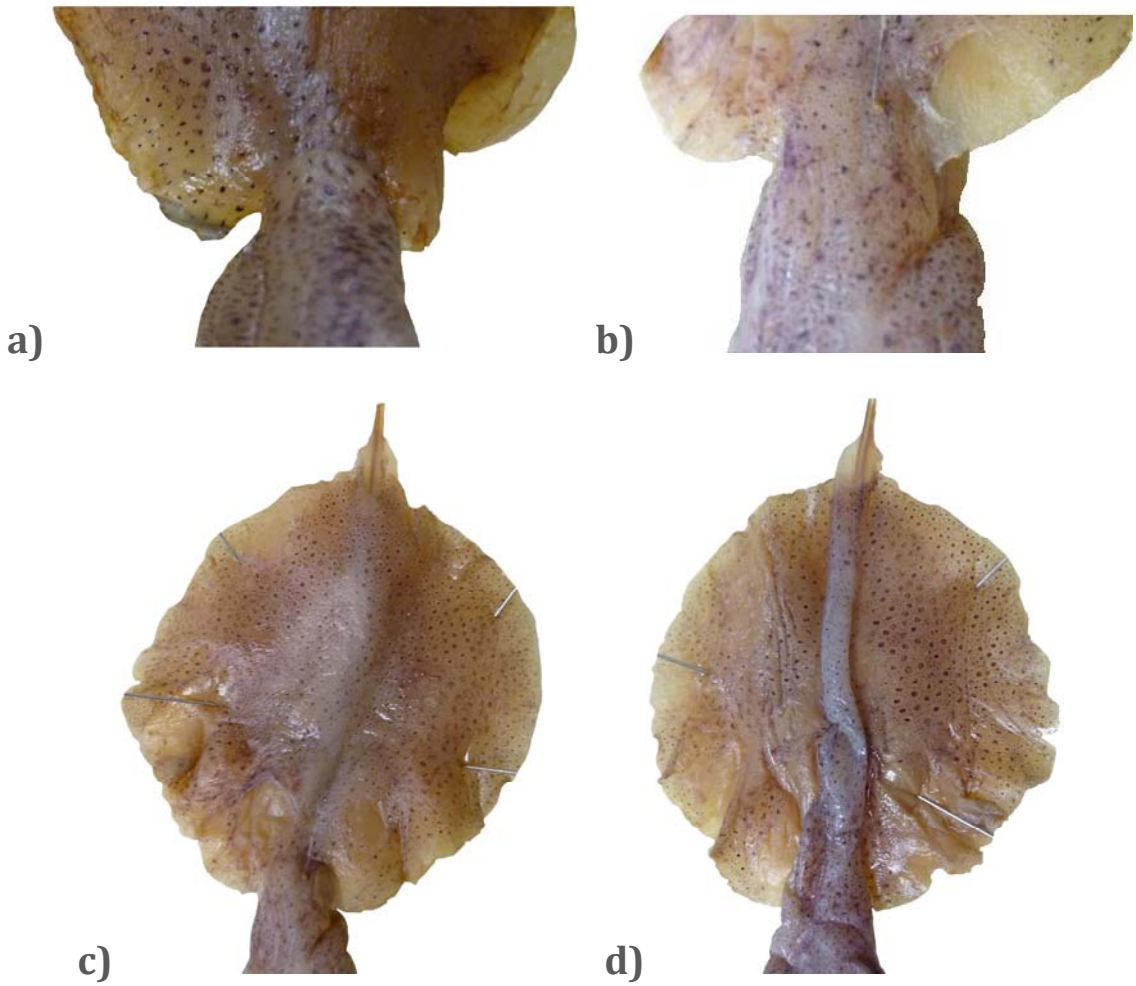

Figure 24. *Chiroteuthis spoeli* fins: a) NMNZ M.172949 anterior attachment, b) NMNZ M.286109 anterior attachment, c) NMNZ M.286109 dorsal, d) NMNZ M.286109 ventral

Tentacles

Thin, incomplete on all specimens.

Lower beak (Fig. 27a–c)

Width slightly less to greater than height; wing fold obscuring jaw angle and shoulder in lateral profile. Hood closely adpressed to crest; visible crest shorter than hood. Wall fold

extends to posterior edge of lateral wall at an angle of 52–62˚ from baseline; ratio of A to B ~ 43–50%; jaw angle obtuse (118–123˚); shoulder without tooth. Hood almost completely darkened; oral surface darkened down shoulder. At LRL 5.5 mm wing darkened 92.2% of length; at shoulder darkened laterally 82%; margins translucent. At LRL 2.5 mm, wing darkened 47% of length; at shoulder darkened laterally 61%; margins translucent. Rostrum thickened, but without keel (Fig. 27e iv–vi). Lateral wall with thickened fold, without keel (Fig. 27e i–iii).

Upper beak (Fig. 27d)

Greatly damaged in NMNZ M.172949, no evidence of distinct jaw angle. In NMNZ M.286109 clearly defined jaw angle; rostrum length 4 mm; jaw angle 130˚; shoulder concave. Hood length 12 mm; hood darkened 90%; hood length 3.2 times rostrum length.

Radula (Figs 27f, 28a) **and palatine palp** (Fig. 28b)

Rachidian with three cusps, the central the largest, with pronounced groove between central and lateral cusps, lateral cusps oriented admedially. First and second laterals variable; first lateral with large central tooth and slightly smaller lateral tooth, medial area may have shoulder or small tooth; second lateral with large central tooth, medial area may have shoulder or small tooth. Marginal blocks alternate with teeth rows; sabre-like, long, and narrow.

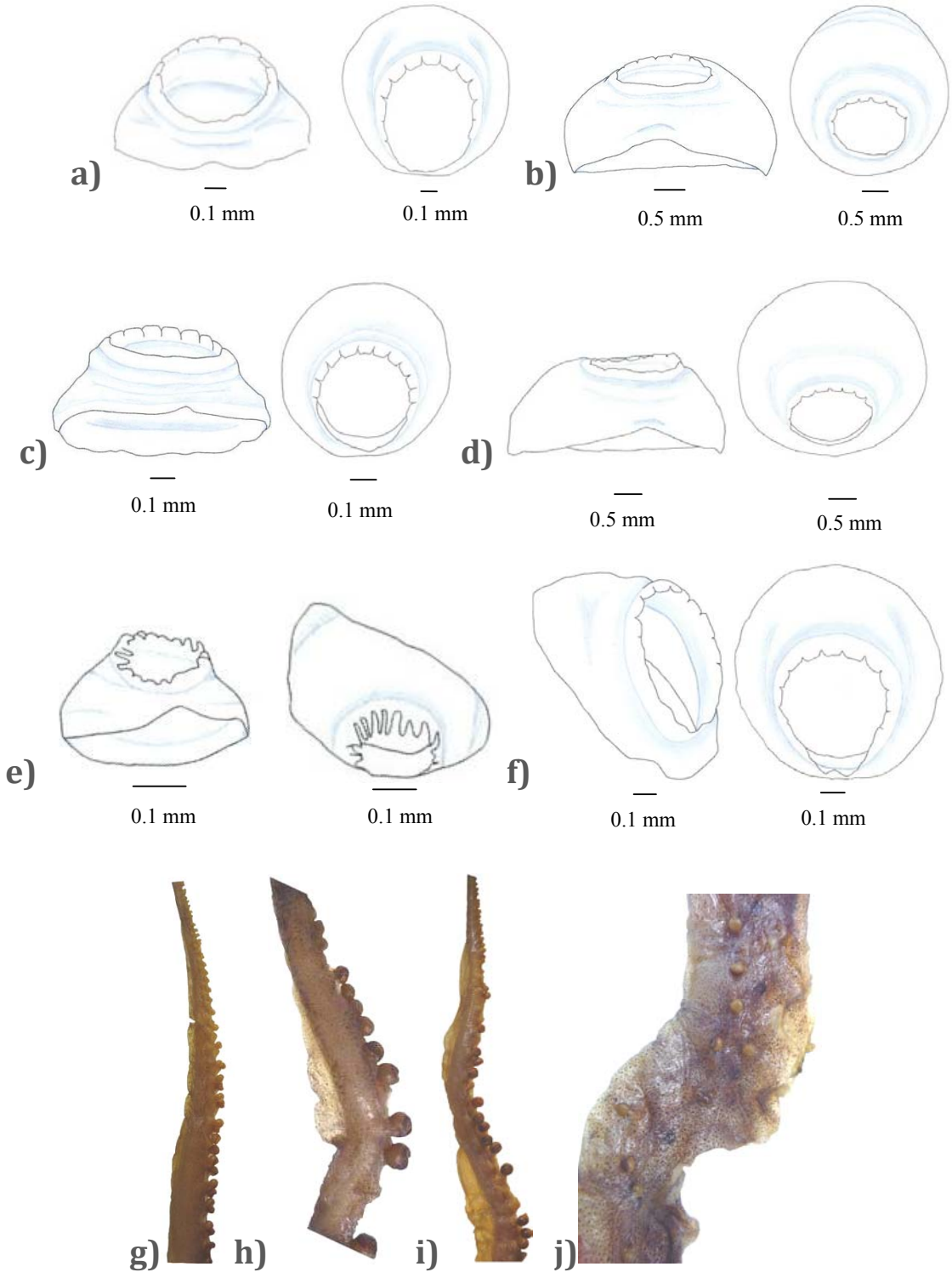

Figure 25. *Chiroteuthis spoeli* a–f arm sucker drawings: a) I NMNZ M.172949, b) II NMNZ M.286109, c) III NMNZ M.172949, d) III NMNZ M.286109, e) III NMNZ M.286109, f) IV NMNZ M.172949; g–j arms, g, i)NMNZ M.152619, h, j) NMNZ M.286109: g) I, h) II, i) III, j) IV; a, b, d, & f) largest, c) basal, e) tip

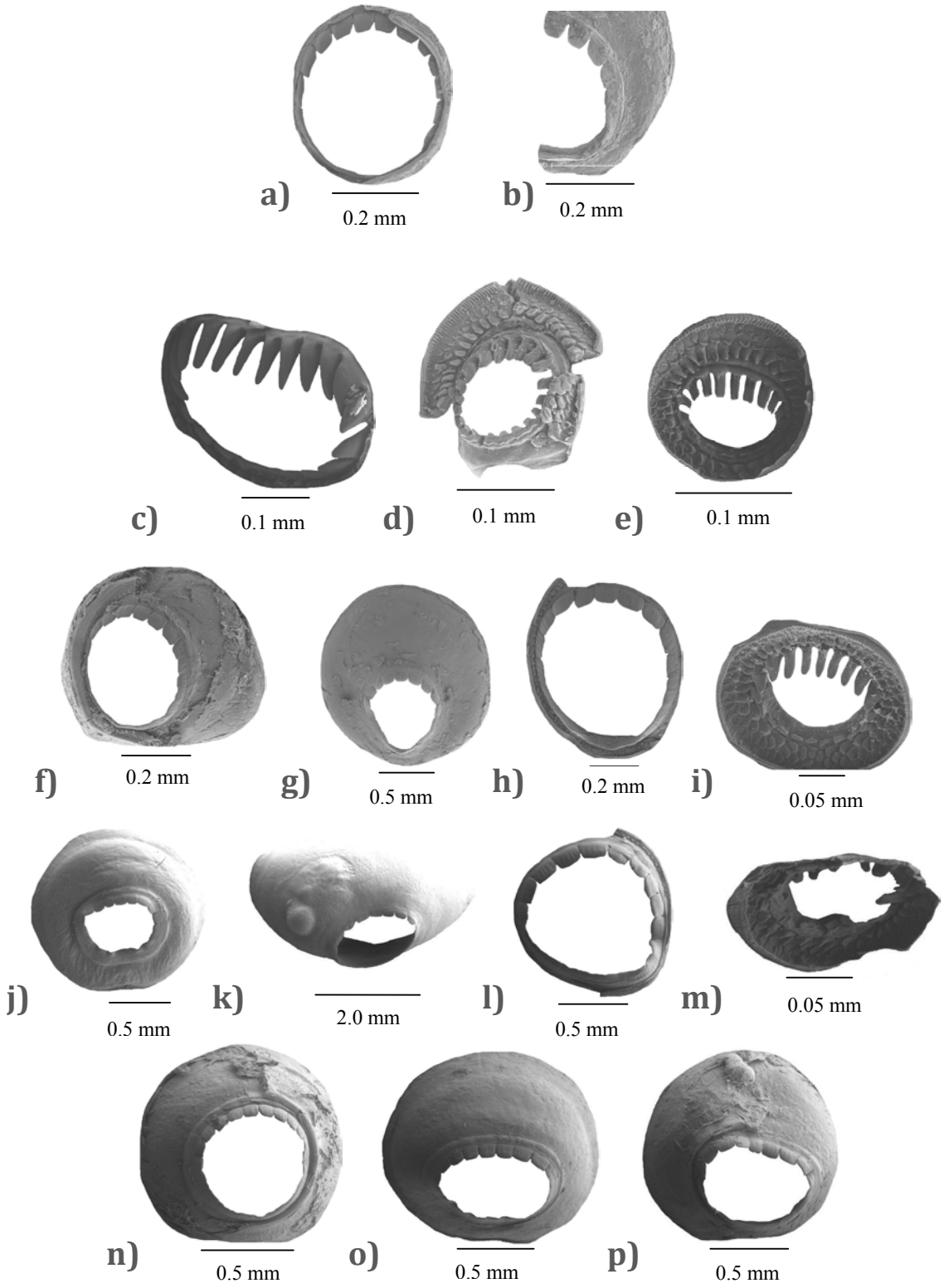

Figure 26. *Chiroteuthis spoeli* sucker rings: a–e arm I: a) NMNZ M.172949, b) NMNZ M.172949, c) NMNZ M.286109, d) NMNZ M.172949, e) NMNZ M.286109; f–i NMNZ M.172949 arm II; j–m NMNZ M.286109 arm III; n–p NMNZ M.286109 arm IV; a, f, j, & n) base, b, c, h, l, & p) middle, d, e, i & m) tip, g, k, & o) largest

Internal Anatomy (Fig. 29)

Outer demibranch of gill with 25 or 28 lamellae, inner demibranch of gill with 23 or 26 lamellae. Two small, white, very long and thin nidamental glands in NMNZ M.172949; larger and brown in NMNZ M.286109. Penis prominent (Fig. 29c, d) protruding from mantle of NMNZ M.152619; with terminal spade-like modification.

Gladius (Fig. 29e)

Long, thin and translucent. Tip of conus broken, protruding from fins. Free rachis long (~ 45–55% present GL), widest anteriorly, tapering posteriorly, narrowest at vane insertion (FRWantIr: 1.9%, FRWpostIr: 0.7–1.0%). Conus long (Ir 60.4–68.9%) but broken. Vane length variable (Ir 21.7–51.4%).

REMARKS

This is the most recently described species in this genus, with only two immature females previously known (Salcedo-Vargas 1996). Of the three specimens reported herein, none had a tentacle club, limiting the description of this taxon proffered herein. However, one of these three is also the first-described male of the species.

The eye photophores on specimen NMNZ M.286109 appear to be in series of six and eight, in contrast to type material with seven and seven. The eye is slightly misshapen, so it is possible that a photophore, which appears to be in the lateral series, may have actually been in the medial series before capture. The eyes on NMNZ M.152619 were slightly deflated, but otherwise in good condition; photophores were undamaged and

distinct; there is no question that the lateral series contain eight photophores and the medial series seven. The orientation and size of the photophores are the same as the description of *C. spoeli*.

The ink sac photophores on NMNZ M.172949 are unlike those of other species in the genus *Chiroteuthis*, with the possible exception of *C. calyx* (for which illustrations or photographs of this organ are wanting); they are too damaged on NMNZ M.286109 to determine if they are comparable, and NMNZ M.152619 was not dissected. The large size and seemingly glandular nature of these photophores agrees with the description of these structures provided by Salcedo-Vargas (1996). As tentacle clubs are lacking on all available material, none of these specimens can be definitively attributed to *C. spoeli*, but they are more similar to it in other respects than any other recognised taxon (the only other species recognised to have large, globular suckers is *C. calyx*, but this latter species has eye photophores in three series, two of which are stripes).

This species has not been reported from stomach contents of any recently stranded pygmy sperm whale or sperm whale that has stranded on New Zealand beaches. It is known from a single specimen only from north-easternmost New Zealand waters, and two specimens from north of New Zealand but not within our waters (Fig. 57). Its beaks are rather distinctive, and unlikely to be confused with any other locally occurring taxon.

On the basis of limited distributional records of this species thus far, this species is limited to tropical waters, or the nearby waters of the tropical convergence zones in the Pacific and Indian Oceans.

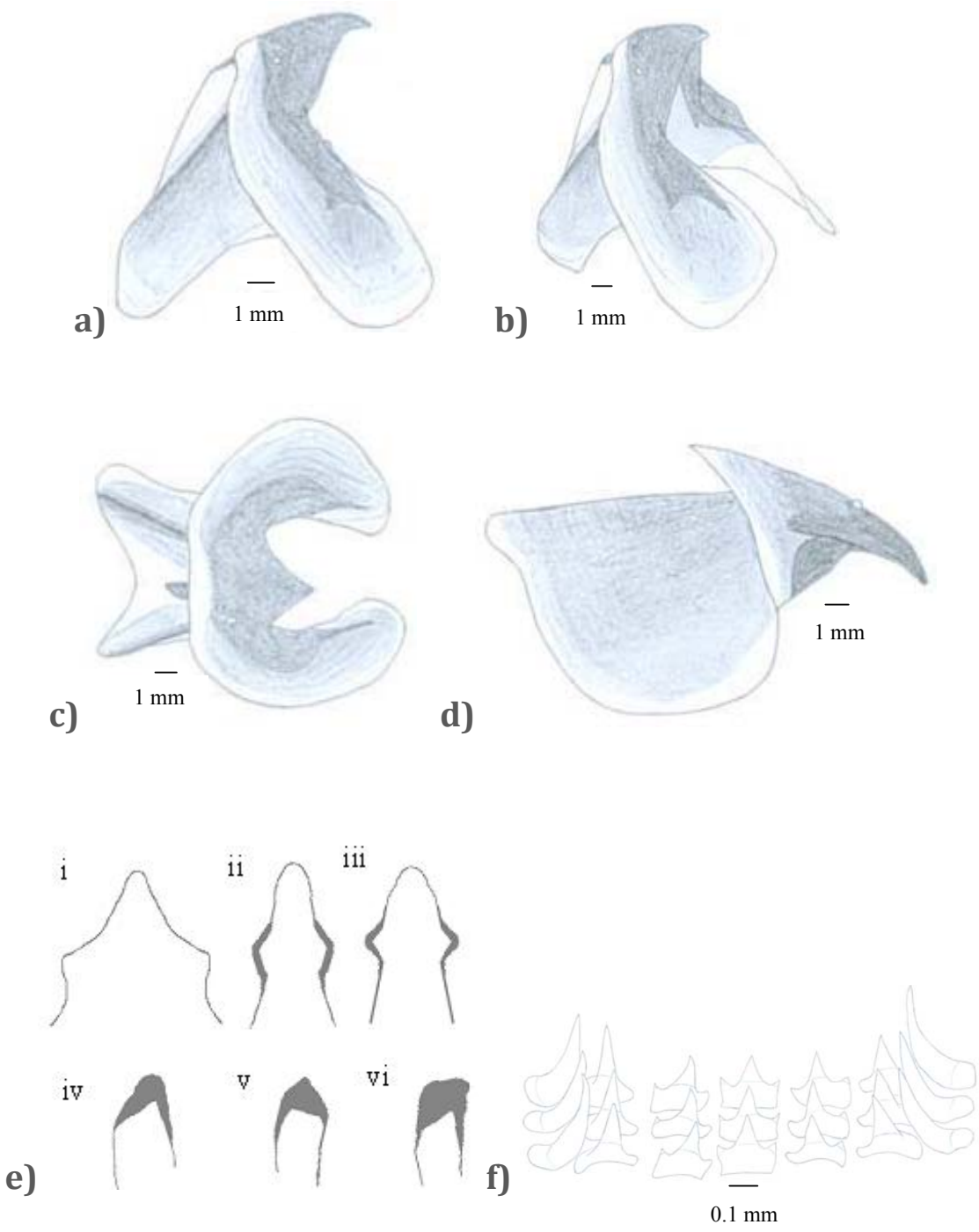

Figure 27. *Chiroteuthis spoeli* mouth parts drawings: a) lower beak lateral, b) lower beak oblique, c) lower beak aboral, d) upper beak lateral, e) lower beak cuts f) radula; a–d,f) NMNZ M.286109; e) NMNZ M.152619 lower beak, i) cut A, ii) cut B, iii) cut C, iv) cut D, v) cut E, vi) cut F

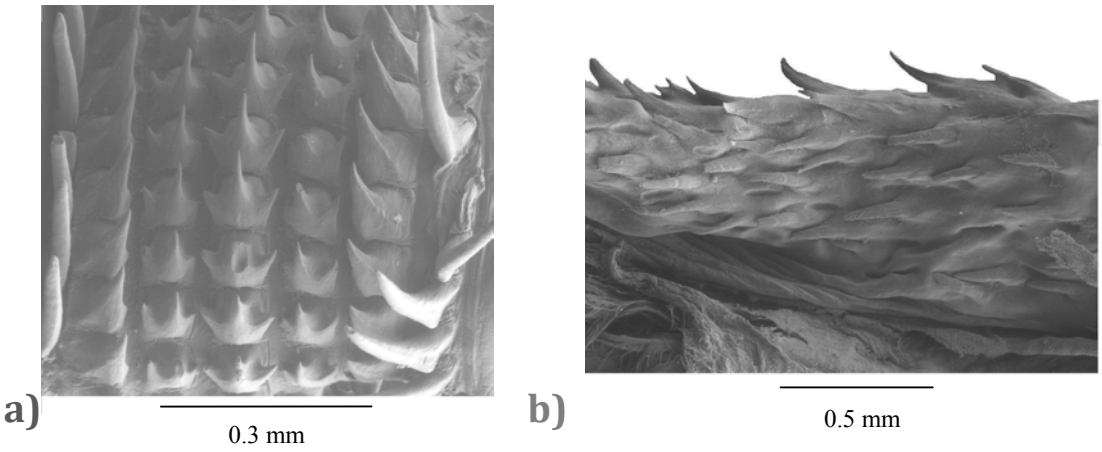

Figure 28. *Chiroteuthis spoeli* (NMNZ M.286109): a) radula, b) palatine palp oral

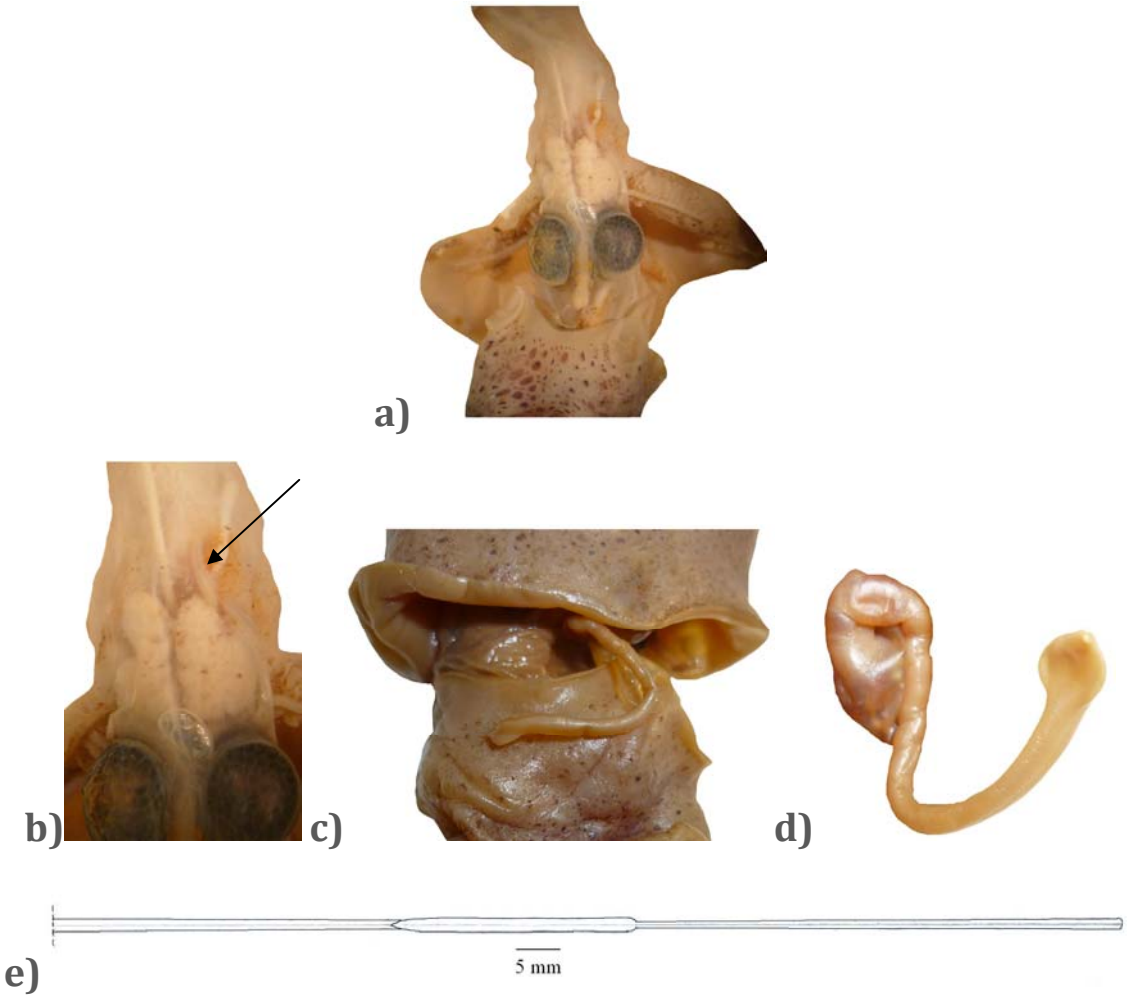

Figure 29. *Chiroteuthis spoeli* internal anatomy: a) NMNZ M.172949, b) NMNZ M.172949 immature nidamental glands, c) NMNZ M.152619 penis, d) NMNZ M.152619 penis, e) NMNZ M.172949 gladius

Table 2. Measurements of *Chiroteuthis spoeli* (mm)

	M.172949	M.286109	M.152619
ML	82	165	144
MW	16	32*	30
TL	NA	NA	NA
FL	38	73	62
FW	33	61	63
AL I	37	120	104
II	59	160	162
III	80	202	215
IV	172	315	282
ASC I	13	44	26
II	15	22	20
III	20*	26	20
IV	30*	27	30
CL	NA	NA	NA
Carpus L	NA	NA	NA
manus L	NA	NA	NA
dactylus L	NA	NA	NA
CRC	NA	NA	NA
T Stalk L	NA	NA	NA
HL	47	75	72
HW	15	24*	25
ED	11	14	21
LD	3	5	7
Gill lam in	23	26	NA
Gill lam out	25	28	NA
free lobe	Yes	No	Y & N
sex	♀	♀	♂

* = Damaged. NA = Not Applicable, either too damaged or absent.

Table 3. Indices of *Chiroteuthis spoeli*

	M.172949	M.286109	M.152619
ML	82	165	144
MWI	0.2	0.19	0.28
FLI	0.46	0.44	0.43
FWI	0.4	0.37	0.43
ALI I	0.45	0.73	0.72
II	0.72	0.97	1.12
III	0.98	1.22	1.49
IV	2.1	1.91	1.95
CLI	NA	NA	NA
Carpus LI	NA	NA	NA
Manus LI	NA	NA	NA
Dact. LI	NA	NA	NA
CRC	NA	NA	NA
T stalk LI	NA	NA	NA
HLI	0.57	0.45	0.5
HWI	0.18	0.15	0.17
EDI	0.13	0.08	0.14
LDI	0.04	0.03	0.04

* = Damaged. NA = Not Applicable, either too damaged or absent.

Chiroteuthis veranyi (Férussac, 1835)

Figures 30–57, Tables 4 & 5

New Zealand synonymy:

Chiroteuthis sp. C Clarke & MacLeod, 1982: 28, 34 (*fide* Clarke 1986: 168, 169).

Chiroteuthis sp. Spencer & Willan, 1995: 142.

Chiroteuthis sp. 1 Beatson, 2007: 142.

Chiroteuthis veranyi (Férussac) — Gomez-Villota 2007: 110.

Material Examined: 54 specimens, 9 ♂, 27 ♀, 18 sex indeterminate: NMNZ M.262499, ♀, ML 194 mm, 31°44.7'S, 178°54.8'W, NZ, 25/09/1992, RV *Kariqua*; NMNZ M.74414, sex indet., ML NA, 37°18.0'S, 176°26.0'E, 709 m, 01/08/1976, RV *James Cook* Stn J11/63/76; NMNZ M.52029, ♂, ML 50 mm, 37°34'S, 177°15'E, NZ, 420 m over 840 m, 08/05/1975, RV *James Cook* Stn J07/50/75, MWT; NIWA 48822, ♀, ML 47 mm, 38°0'S, 179°40'E, 100 m, 1999; NIWA 48819, ♀, ML 61 mm, 38°0.0'S, 179°20.0'E, 100 m, 1998; NMNZ M.286120, sex indet., ML NA, 38°59.26'S, 169°42.23'W, 23–1000 m over 4500 m, 21/03/1995, RV *Tangaroa* Stn TAN9503/16; NMNZ M.286113, sex indet., ML 46 mm, 38°59.71'S, 169°29'W, 15–103 over 4500 m, 22/03/1995, RV *Tangaroa* Stn TAN9503/17; NMNZ M.286121, sex indet., ML 51 mm, 38°58.93'S, 165°15.22'W, 20–95 over 5000 m, 22/03/1995, RV *Tangaroa* Stn TAN9503/21; NMNZ M.286122, ♀, ML 57 mm, 39°0.76'S, 175°9.7'W, NZ, 15–93 m over 4805 m, RV *Tangaroa* Stn TAN9503/06; NMNZ M.286119, ♀, ML 59 mm, 39°2.21'S, 179°6.10'E, NZ, 17–93 m over 3502 m, 27/03/1995, RV *Tangaroa* Stn TAN9503/42; NMNZ M.91569, ♀, ML 58 mm, 39°15'S, 179°51.3'E, 30 m over 3600 m, 14/09/1987, RV *James Cook* Stn J12/18/87; NMNZ M.286118, ♀, ML 40 mm, 39°21.1'S, 178°52.88'W, NZ, 27–103 m over 3400 m, 20/03/1995, RV *Tangaroa* Stn TAN9503/33; NIWA 48826, sex indet., ML NA, 39°29.4'S, 179°24.0'E, 100 m, date TBD; NIWA 48816, ♀, ML 72 mm, 39°38'S, 179°0'E, 100 m, 01/02/1998; NIWA 48816, ♀, ML 65 mm, 39°38'S, 179°0'E, 100 m, 01/02/1998; NIWA 48816, ♀, ML 43 mm, 39°38'S, 179°0'E, 100 m, 01/02/1998; NMNZ M.286114, sex indet., ML 46 mm, 39°53.50'S, 178°50.30'E, NZ, 16–107 m over 3300 m, 28/03/1995, RV *Tangaroa* Stn TAN9503/51; NMNZ M.102106, sex indet., ML NA, 40°2.4'S, 167°58.4'E, NZ, 888–903 m, 30/07/1989, RV *Amaltal Explorer* Stn EXX1/173/89; NMNZ M.286111, sex indet., ML 51 mm, 40°16.6'S, 178°29.48'E, NZ, 16–98 over 2873 m, 29/03/1995, RV *Tangaroa* Stn TAN9503/57; NMNZ M.268117, ♀, ML 58 mm, 40°30.64'S, 169°53.89'W, 17–

103 m over 4350 m, 24/03/1995, RV *Tangaroa* Stn TAN9503/33; NMNZ M.286124, ♀, ML 51 mm, 40°31.27'S, 169°16.28'E, 24/03/1995, RV *Tangaroa* Stn TAN9503/32; M.286123, ♀, ML 57 mm, 40°39.22'S, 165°34.61'W, 17–19 m over 1957 m, 23/03/1995, RV *Tangaroa* Stn TAN9503/27; NMNZ M.286123**,** sex indet., ML 46 mm, 40°39.22'S, 165°34.61'W, 17–19 m over 1957 m, 23/03/1995, RV *Tangaroa* Stn TAN9503/27; NMNZ M.286115, ♀, ML 62 mm, 40°43.16'S, 165°13.75'W, 15–98 m over 1407 m, 23/03/1995, RV *Tangaroa* Stn TAN9503/25; NMNZ M.285799, ♂, ML 54 mm, 40°59.95'S, 177°35.9'E, NZ, 15–100 m over 2424 m, 31/03/1995, RV *Tangaroa* Stn TAN9503/66; NMNZ M.144085, ♀, ML 95 mm, 41°26.0'S, 169°40.0'E, NZ, 08/06/2004, FV *Daniel Solander*; NMNZ M.74221, ♀, ML 56 mm, 41°49'S, 174°59.5'E, 10/12/1958, FV *Admiral* Stn 1958112; NIWA Z8858, ♂, ML 74 mm, 41°52'S, 174°42'E, 500 m, 22/06/1997, FV *Nan Hai;* NIWA 48825, ♂, ML 64 mm, 42°21.08'S, 176°11.68'E, 30 m, 21/02/2001; NIWA 48824, sex indet., ML NA, 42°21.05'S, 176°11.41'E, 30 m, 20/02/2001; NIWA 48823, sex indet., ML 46 mm, 42°31.85'S, 176°28.07'E, 20 m, 18/04/2001, RV *Tangaroa* Stn TAN0104/194; NIWA 48823, sex indet., ML NA, 42°34.85'S, 176°28.07'E, 20 m 18/02/2001; NIWA 48821, ♀, ML 47 mm, 42°33.08'S, 176°27.7'E, 20 m, 18/02/2001; NMNZ M.67230, ♀, ML 65 mm, 42°45.5'S, 177°59'W, NZ, 18/09/1979, FV *Mys Babuskina* Stn B01/105/79; NIWA 48890, ♀, ML 51 mm, 42°47.27'S–42°46.95'S, 179°59.82'E–179°59.92'W, 1042–880 m, 18/04/2001, RV *Tangaroa* Stn TAN0104/194; NIWA 48818, ♂, ML 67 mm, 42°50.12'S, 176°54.37'W, FV *San Waitaki*; NIWA 48815, ♂, ML 83 mm, 43°01.72'S–43°01.23'S, 174°20.65'E–174°23.32'E, 1042–880 m, 18/04/2001, RV *Tangaroa* Stn TAN0104/194; NIWA 48814, sex indet., ML NA, 44°35.38'S–44°36.48'S, 177°45.18'W–176°14.83'W, 1031–1091 m, RV *Tangaroa* Stn TAN0011/38; NMNZ M.91646, ♂, ML 94 mm, 45°27.7'S, 163°29.3'E, NZ, 480–150 m over 4640 m, 28/07/1985, RV *Kaiyo Maru* Stn KM/110A/85N.

Presently unlocalised material examined: 100320, ♀, ML 155 mm, WIL/095/89; TAZCCAP04, ♀, ML 135 mm; NIWA 48894, ♀, ML 111 mm; NIWA 48820, ♀, ML 56 mm; NIWA 48817, ♀, ML 54 mm, Stn Z11014; NIWA 48828, ♀, ML 54 mm, Stn Z11017; NIWA 48827, ♀, ML 53 mm, Stn Z11016; NIWA 48888, sex indet., ML 52 mm; NIWA 48888, ♀, ML 50 mm; NIWA 48893, ♂, ML 50 mm, Stn TAN9802/154; NIWA 48891, ♀, ML 48 mm, Stn TAN9802 102 or 107; NIWA 48829, ♀, ML 48 mm, Stn Z11021; NIWA 48828, ♀, ML 45 mm, Stn Z11017; NIWA 48830**,** sex indet., ML 43 mm, Stn Z9919; NIWA 48887, sex indet., ML NA, Stn Z11020; NIWA 48889, sex indet., ML NA; NIWA 48892, sex indet.. ML NA; NMNZ M.286110, sex indet. ML NA, RV *Tangaroa* Stn TAN0401/32; TAZCAP02, sex indet., ML NA.

Recognised distribution (New Zealand): 31°44.7–45°27.7'S, 163°29.3'E–165°13.75'W, 0–2000 m (Fig. 57).

DIAGNOSIS

With paired photophores on ink sac. Tentacle club protective membrane divided into two almost equal parts, proximal wide with narrow trabeculae, distal portion narrower with wider triangular trabeculae. Club sucker stalks in two portions, with well-defined 'pleated skirt'; medial and marginal sucker stalks with narrow keels; club suckers with 7–9 pointed teeth, the central enlarged. Eye photophores in three series: lateral and medial series with stripe; intermediate series with one large anterior photophore, one large posterior photophore, and one small photophore off-centre towards posterior. Arms without globular suckers; sucker rings variably dentate, with 12–16 pointed teeth distal and laterally, with smooth or scalloped proximal portion.

DESCRIPTION

Colour (Figs 30–34)

Ontogenetically variable. For smaller specimens entire (preserved) animal white coloured (Fig. 30). Chromatophores (Figs 32–34) especially dense around and between eyes dorsally and ventrally; laterally elongated, dark chromatophores along dorsal midline of posterior half of head. Large, oval, unfilled chromatophores along entire dorsal midline of mantle and entire anterior portion of ventral mantle. Oval, unfilled chromatophores on mid-dorsal surface and ventral edges of fins; laterally compressed chromatophores along ventral midline of fins. Chromatophores on funnel. For larger specimens entire animal purple coloured (Fig. 31). Small, dark purple chromatophores evenly and densely spaced over entire animal except buccal membrane, arm sucker

stalks, and tentacle stalks. All arms with maroon-coloured chromatophores on oral and aboral surfaces.

Photophores (Figs 35, 36)

Eye photophores (Fig. 35a–e) pink to gold coloured, in three series: lateral and medial series with stripe; intermediate series with one large anterior photophore, one large posterior photophore and one small photophore off-centre towards the posterior. Arm IV photophores (Fig. 35f, g) gold-coloured in transparency along oral surface of arms in smaller specimens, extending arm length, between sucker pairs; on larger specimens photophores not immediately obvious (Fig. 35g), buried beneath dark-coloured epithelium. Aboral photophore at base of tentacle stalk present (Fig. 36a, b), large, pad-like. Large, superficial pad to sucker-like organs (Fig. 36c–g), presumed to be photophores, extend to distal quarter of stalk, thereafter becoming more embedded and regularly spaced, damaged in all specimens; most pristine specimen (NIWA 48890) with 40 or 41 photophores on each stalk. Tip of club with tear-drop shaped 'bud'; white stripe photophore (Fig. 36h) running medially on centre of aboral surface, rest of 'bud' maroon coloured. Two large, white, round to elliptical photophores on ink sac (Fig. 36i).

Mantle (Figs 30–34, 37)

Conical, attaining greatest diameter at level of mantle aperture, broadening rapidly anterior to points of fin insertion; musculature thickens with increased mantle length.

Figure 30. *Chiroteuthis veranyi* dorsal external NIWA 48890

Figure 31. *Chiroteuthis veranyi* 100320

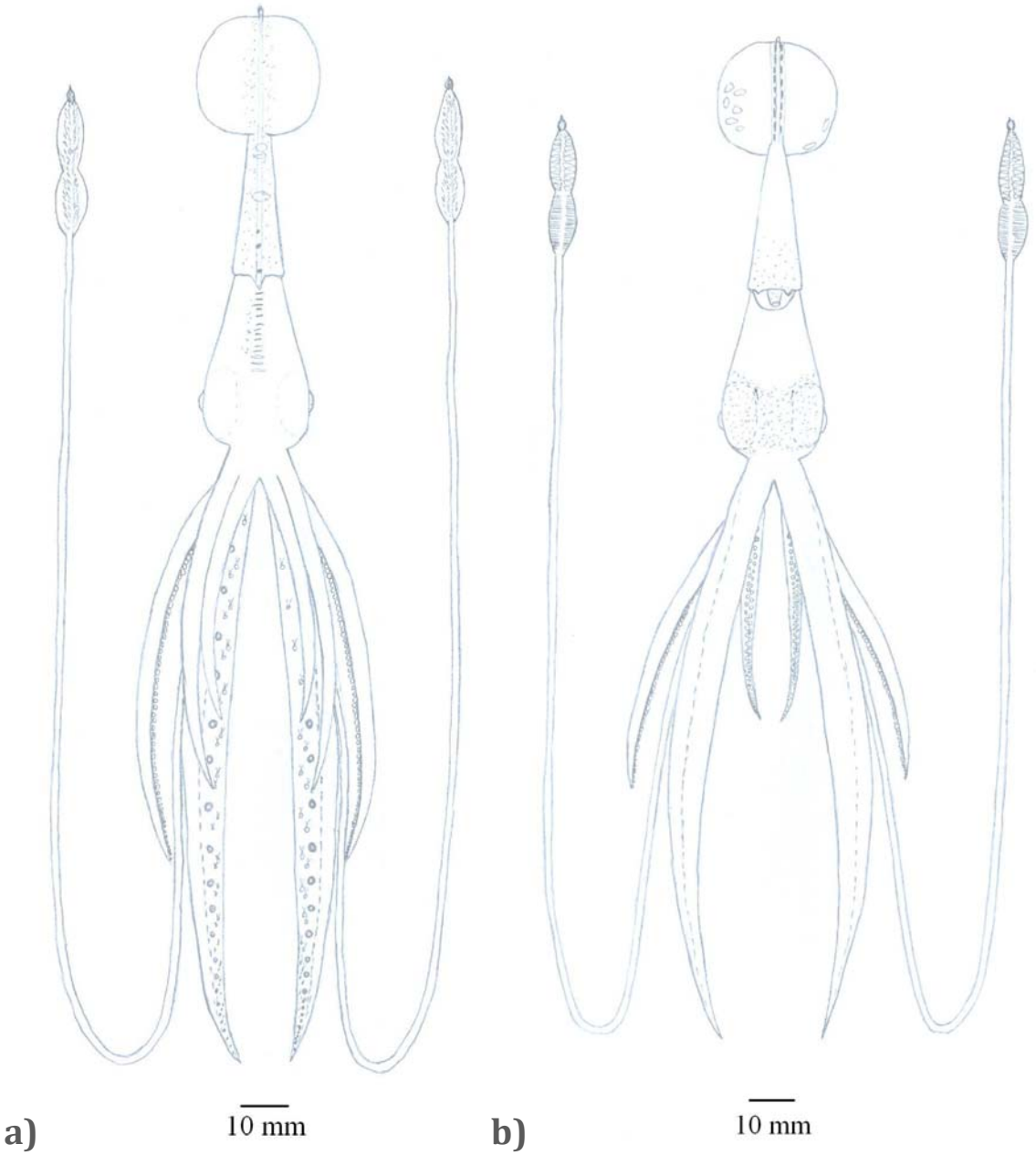

Figure 32. *Chiroteuthis veranyi* (NMNZ M.91569), schematic: a) dorsal, b) ventral

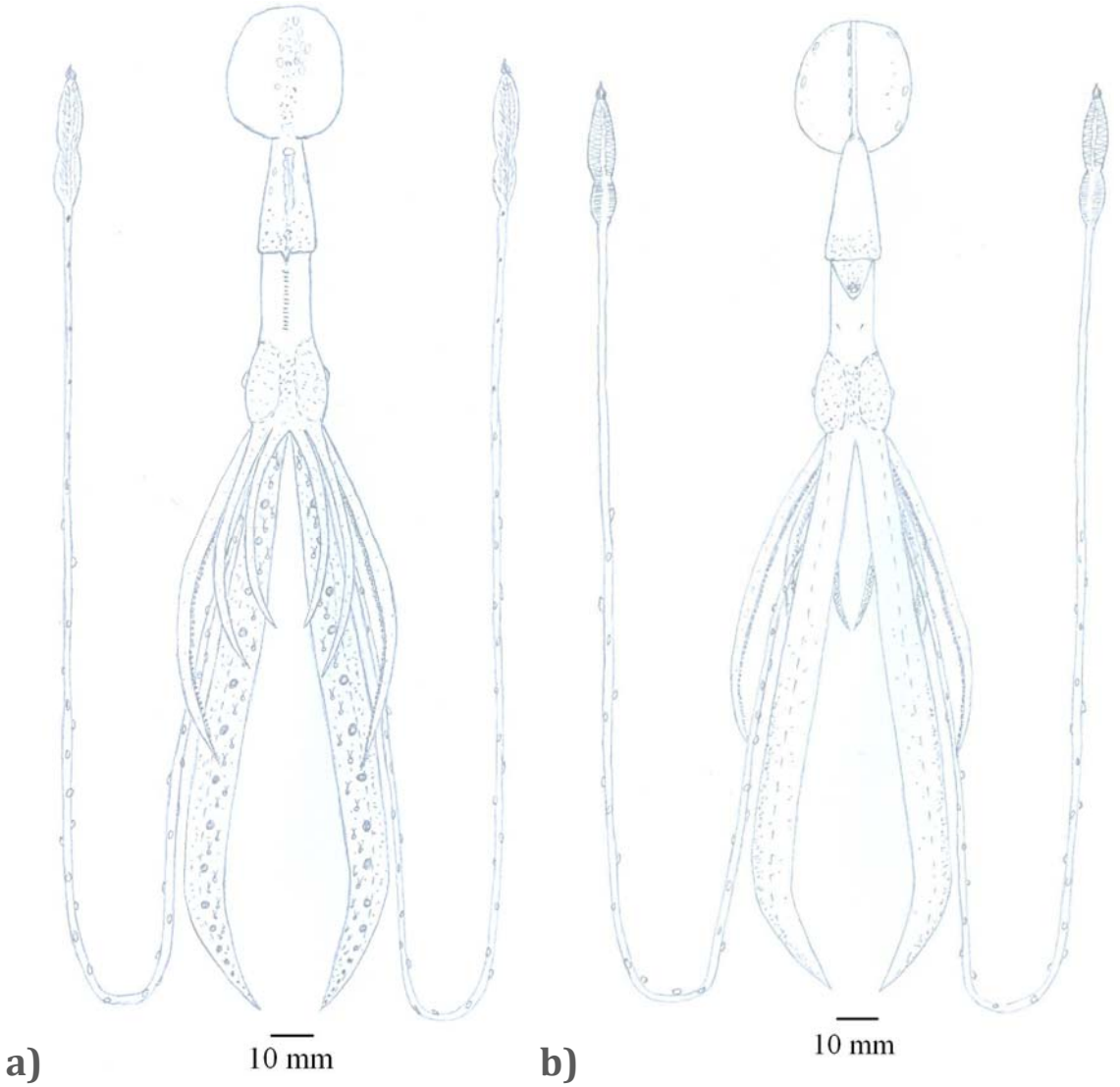

Figure 33. *Chiroteuthis veranyi* (NMNZ M.286120), schematic: a) dorsal, b) ventral

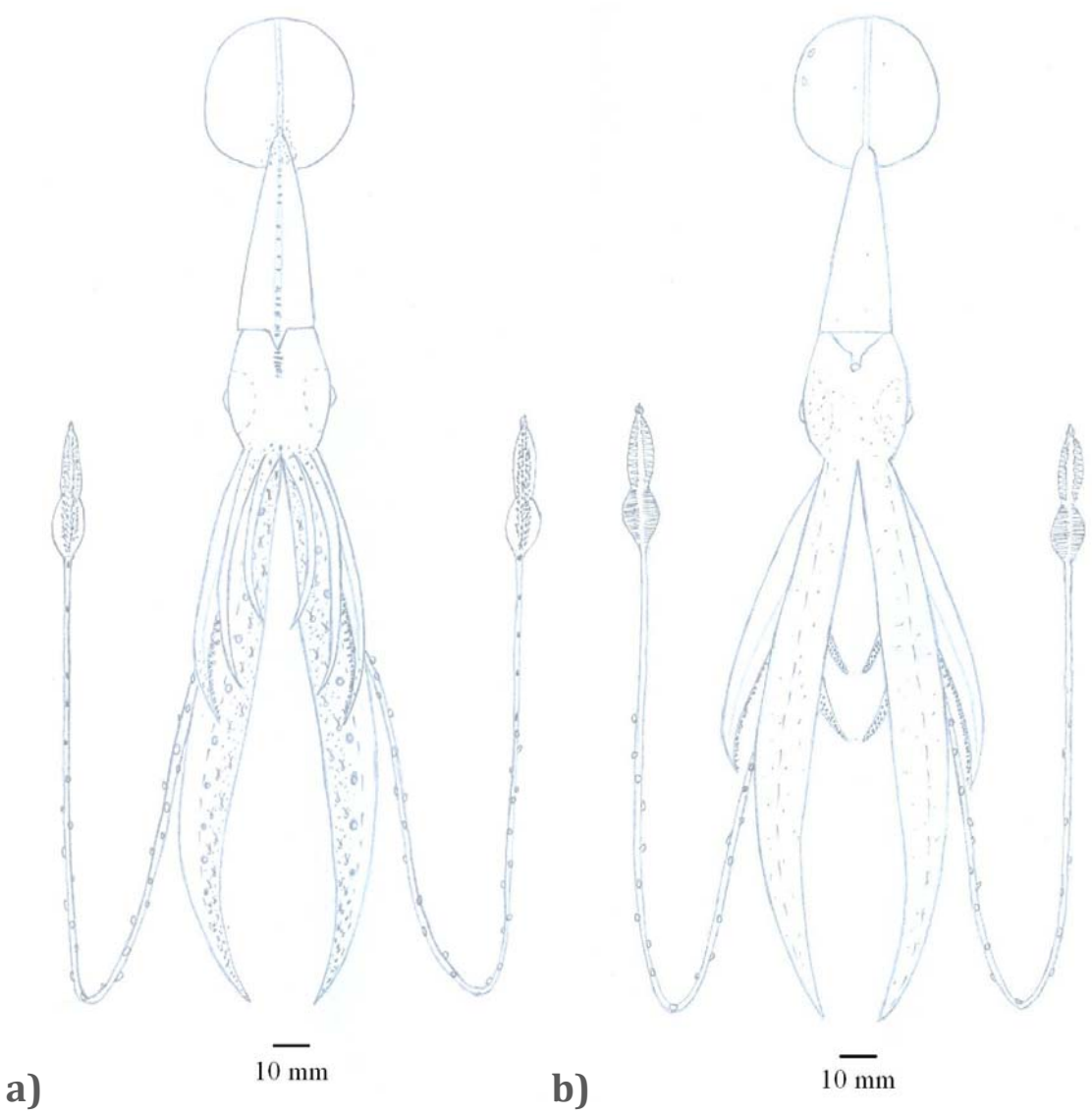

Figure 34. *Chiroteuthis veranyi* (NIWA 48890), schematic: a) dorsal, b) ventral

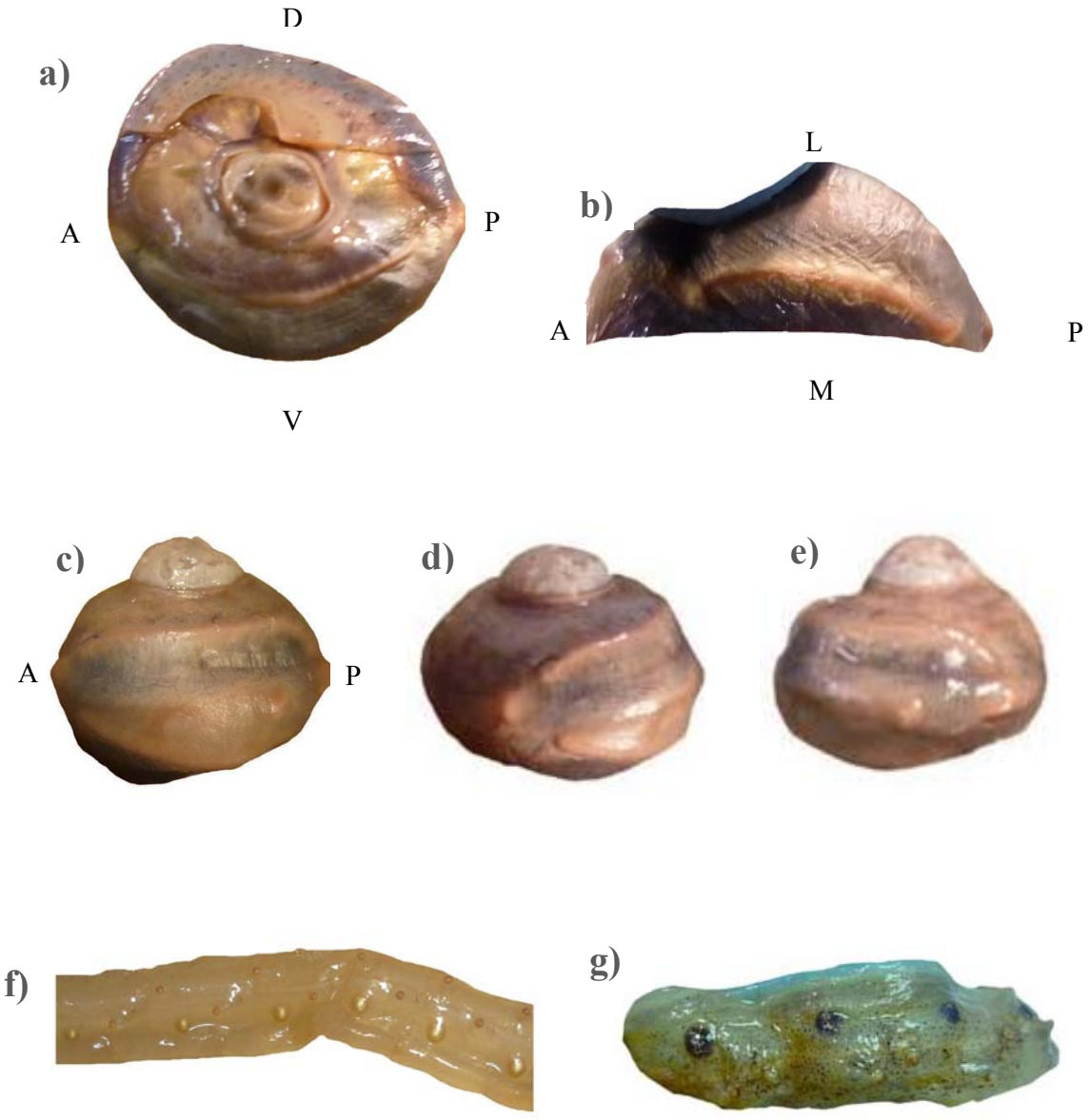

Figure 35. *Chiroteuthis veranyi* eye and IV arm photophores: a) NMNZ M.285799 lateral, b) NMNZ M.285799 cephalic, c) NIWA 48826 ventral, d) NIWA 48826 posterior, e) NIWA 48826 anterior, f) NIWA 48823, g) NMNZ M.286102

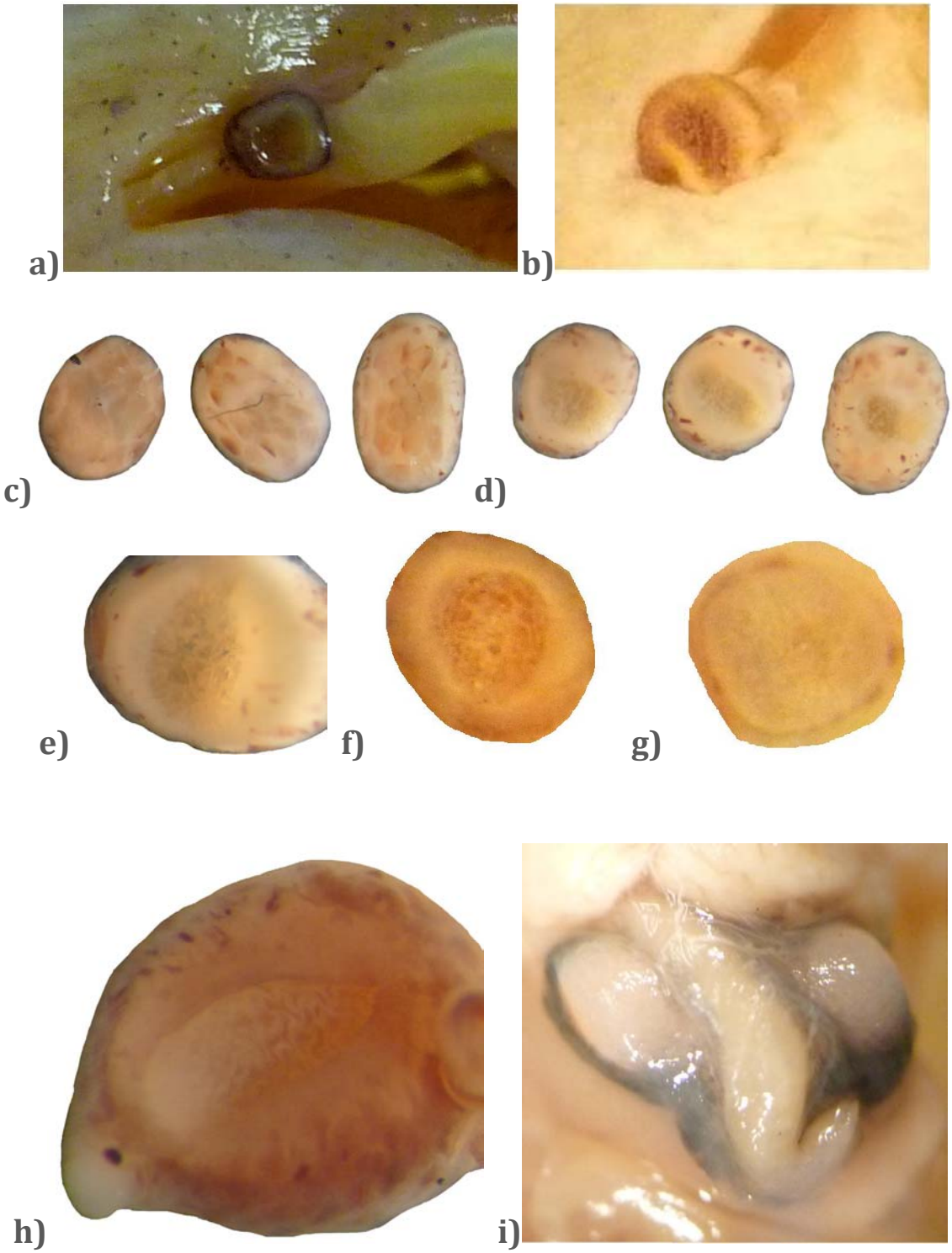

Figure 36. *Chiroteuthis veranyi* tentacle and ink sac photophores: a) NMNZ M.286120, b) NMNZ M.74221, c–e) NIWA 48890, f & g) NMZM M.74221, h) NIWA 48890, i) NMNZ M.286120 ; a–b) stalk base, c–g) stalk, d) club tip, i) ink sac

Head (Figs 30–34, 37)

Round, length variable, 29–*53.6*–100% ML, widest at eyes (18–*31.7*–50% ML), narrowing at brachial pillar. Funnel conical; olfactory papillae narrow, with rounded tip, positioned on inside margin of posterior-most point of eye. Eyes relatively large (10–*23.4*–32% ML).

Fins (Fig. 38)

Nearly circular, length 35–*43.6*–50% ML, width 31–*47.5*–68%; with anterior lobe absent or free for small portion only; with no apparent tail.

Arms (Fig. 39)

Formula IV>>III>II>I. Arm I narrow. Arm II narrow, with keel on aboral side of distal half. Arm III much less robust than IV; with narrow membrane extending along aboral, proximal half. Arm IV very long 128–*216*–419% ML and robust, with well-developed, wide membrane along entire dorso-lateral side of arm to sheathe of tentacle stalk.

Suckers (Figs 40–44)

With variable tooth count. All suckers, except those at arm tips, with narrow and acutely pointed distal teeth, becoming curved and saw-like laterally, then irregular or with scallops proximally. Arm tip suckers with teeth around circumference; distal and lateral teeth as in other suckers, but proximal teeth are low and squared. Arm I (Figs 40a, b; 41) basal sucker (Fig. 41a–c) with 16–25 distal and lateral teeth and 5–10 proximal

scallops; largest sucker (Figs 40a, b; 41d) between basal and mid-arm portions, with about 18 distal and lateral teeth, proximal portion with about five scallops; mid-arm sucker (Fig. 41e) with 18–22 distal and lateral teeth, and 4–6 proximal scallops; arm tip suckers (Fig. 41f) with 20–27 teeth extending around circumference of ring. Arm II (Figs 40c, d; 42) basal sucker (Fig. 42a) with 16–22 distal and lateral teeth, and 5–10 proximal scallops; largest sucker (Figs 40c, d; 42b) between basal and mid-arm portions, with about 16 distal and lateral teeth, and 4 proximal scallops; mid-arm suckers (Fig. 42c–e) with 16–19 distal and lateral teeth, and 4–10 proximal scallops; arm tip suckers (Fig. 42f–h) with 24 or 25 teeth extending around circumference of ring. Arm III (Figs 40e, f; 43) basal suckers (Fig 43a, b) with 16–26 distal and lateral teeth, and 3–9 proximal scallops; largest sucker (Figs 40e, f; 43d) between basal and mid-arm portions, with 19 or 20 distal and lateral teeth and 3–7 proximal scallops; mid-arm suckers (Fig. 43c) with 19 or 20 distal and lateral teeth and 5–9 proximal scallops; arm tip suckers (Fig. 43e, f) with 22–24 teeth extending around circumference of ring. Arm IV (Figs 40g, h; 44) basal suckers (Fig. 44a–d) with 18–22 distal and lateral teeth, and 4–10 proximal scallops; largest sucker (Figs 40g, h; 44f) between base and mid-arm, with 19–23 distal and lateral teeth, and 2–5 proximal scallops; mid-arm sucker (Fig. 44e) with 15–19 distal and lateral teeth and 2–6 proximal scallops; arm tip suckers (Fig. 44g, h) with about 19 teeth extending around circumference of ring.

Figure 37. *Chiroteuthis veranyi* NMNZ M.74221 (Brown due to preservation)

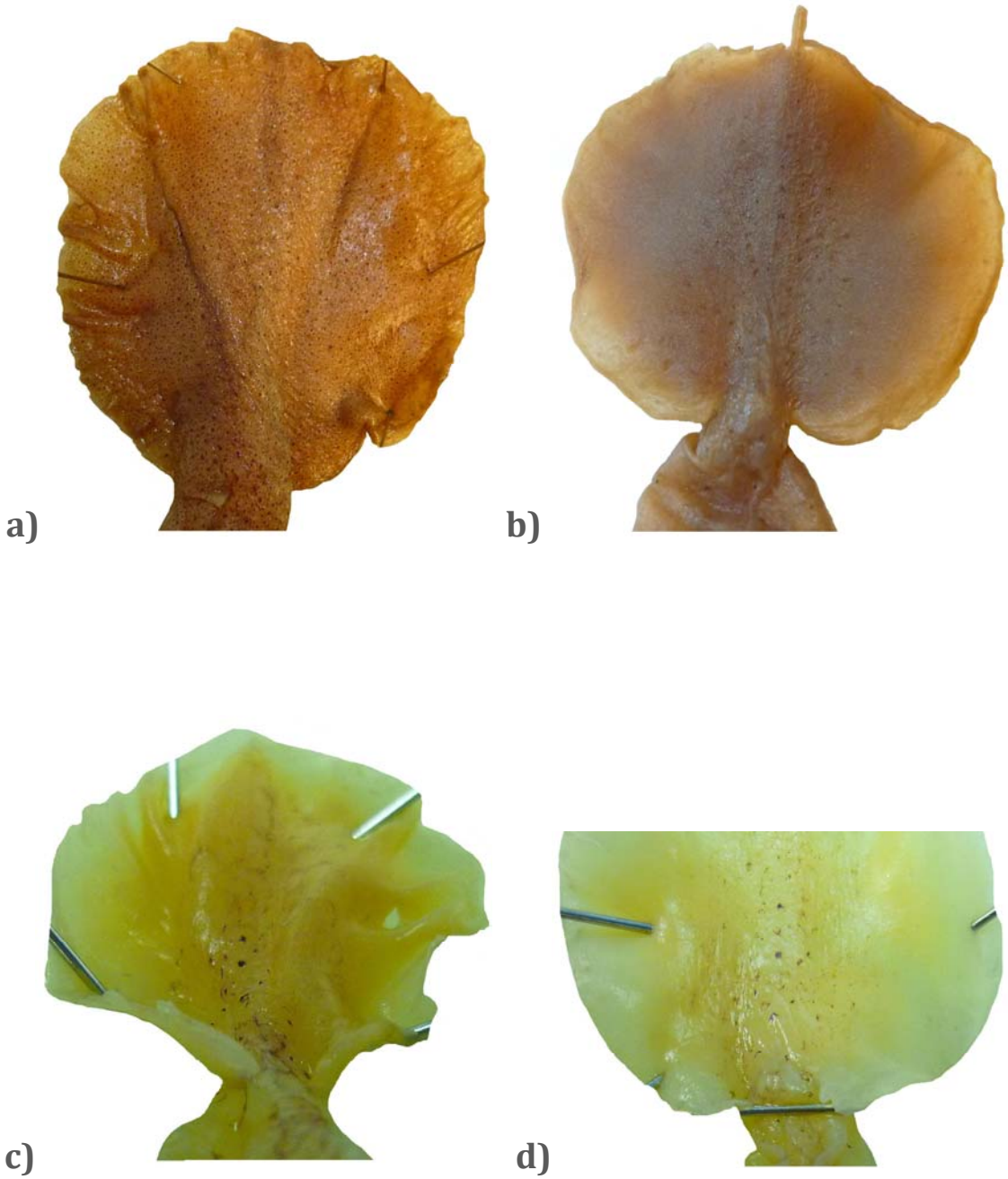

Figure 38. *Chiroteuthis veranyi* fins: a) NMNZ M.262499, b) NMNZ M. 74221, c) NMNZ M.286120, d) NMNZ M.91569

Tentacles (Figs 45–49)

Narrow and long (230–*625*–1462% ML). Club (Fig. 45) long, well developed (36–*60*–143% ML) with protective membrane (Fig. 46) extending its length, differentiated into two sections: proximal 2/5th of club with 39–42 narrow, closely spaced trabeculae; distal 3/5th with 23 or 24 wider, triangular trabeculae. Carpus (Fig. 45) with 5–9 unpaired suckers; manus (Fig. 45) with 10 or 11 rows of alternating, paired suckers; dactylus (Fig. 45) with 23 or 24 rows of alternating, paired suckers; total sucker counts on clubs 139–144. Sucker stalks (Figs 47, 48) differentiated into long and thick, and short and narrow basal and distal sections; distal portion of basal stalk with maroon-coloured 'pleated skirt'. Lateral stalks about ¼ longer than medial stalks. Lateral keels on medial and lateral stalks. Club sucker ring dentition (Figs 48, 49) with 7–9 distal and lateral teeth, with distal central tooth enlarged; proximal portion smooth.

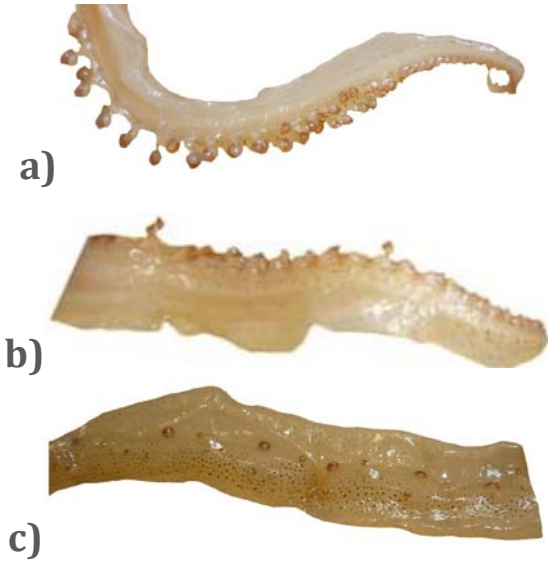

Figure 39. *Chiroteuthis veranyi* (NIWA 48890): a) arm II, b) arm III, c) arm IV

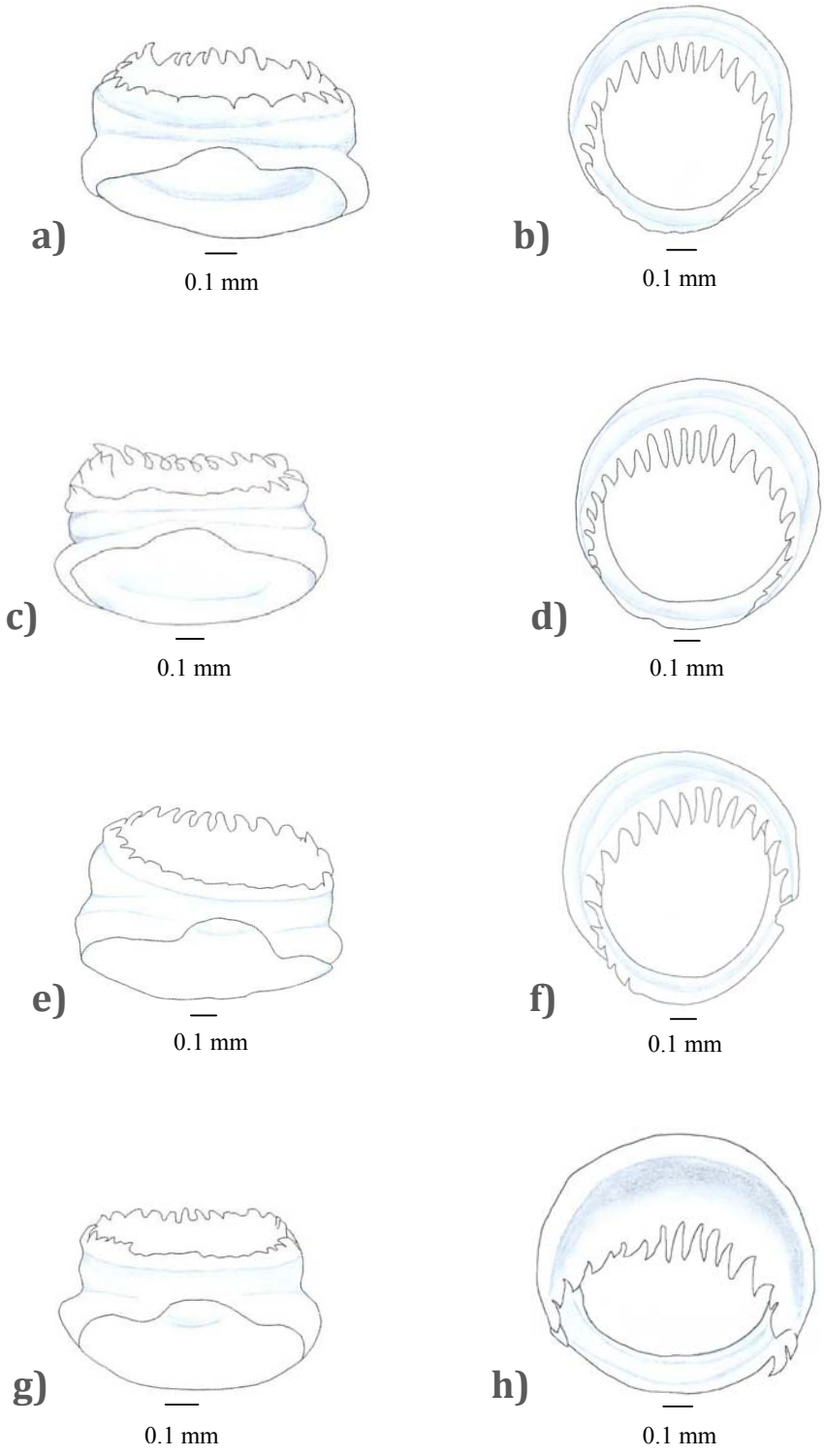

Figure 40. *Chiroteuthis veranyi* largest arm sucker drawings: a) NMNZ M.286120, b, d–g) NIWA 48890, c & h) NMNZ M.091569; a & b) I, c & d) II, e & f) III, g & h) IV

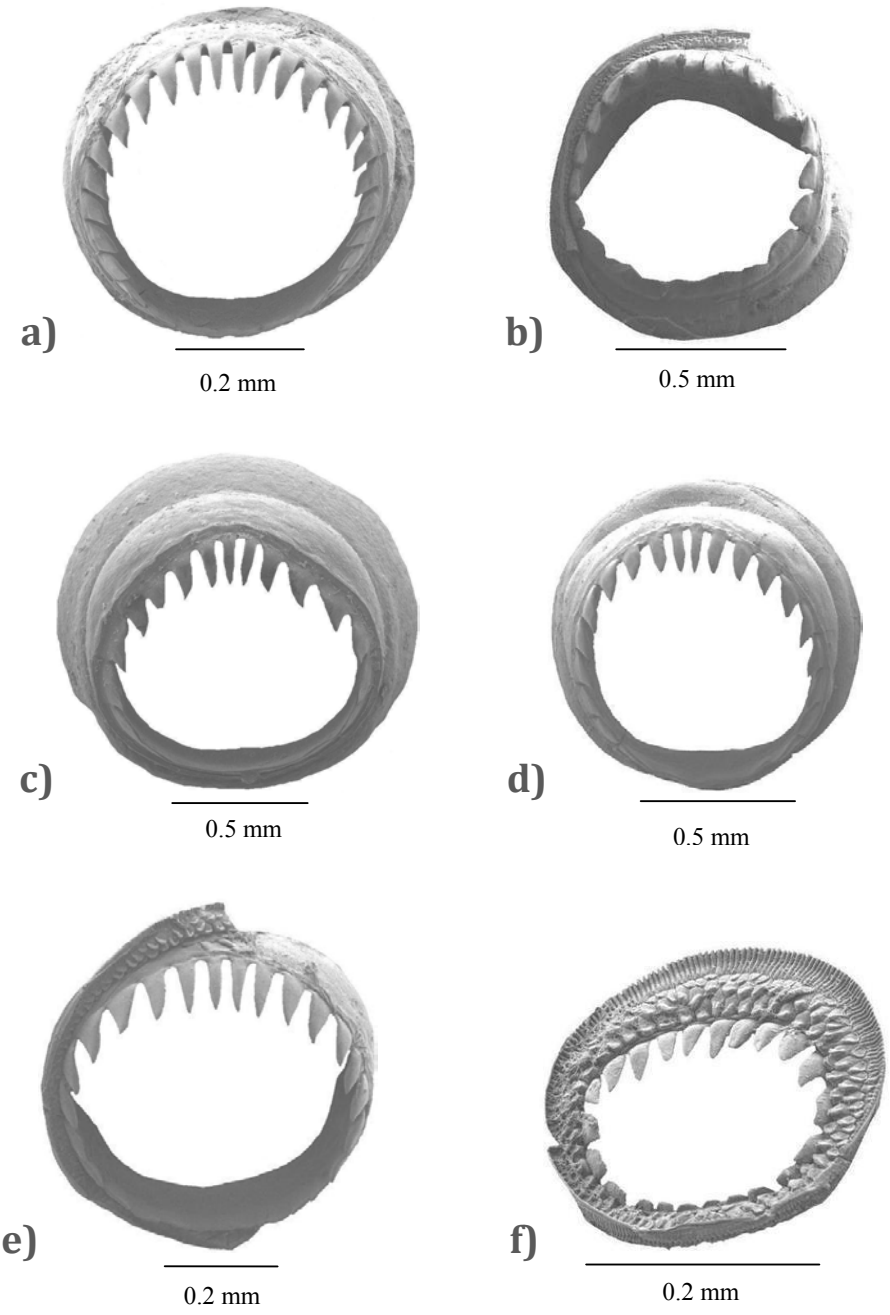

Figure 41. *Chiroteuthis veranyi* arm I suckers: a) NMNZ M.286120, b) NMNZ M.91646, c) NMNZ M.102106, d) NMNZ M. 91646, e) NMNZ M.091646, f) NMNZ M.91646; a–c) basal, d) largest, e) middle, f) tip

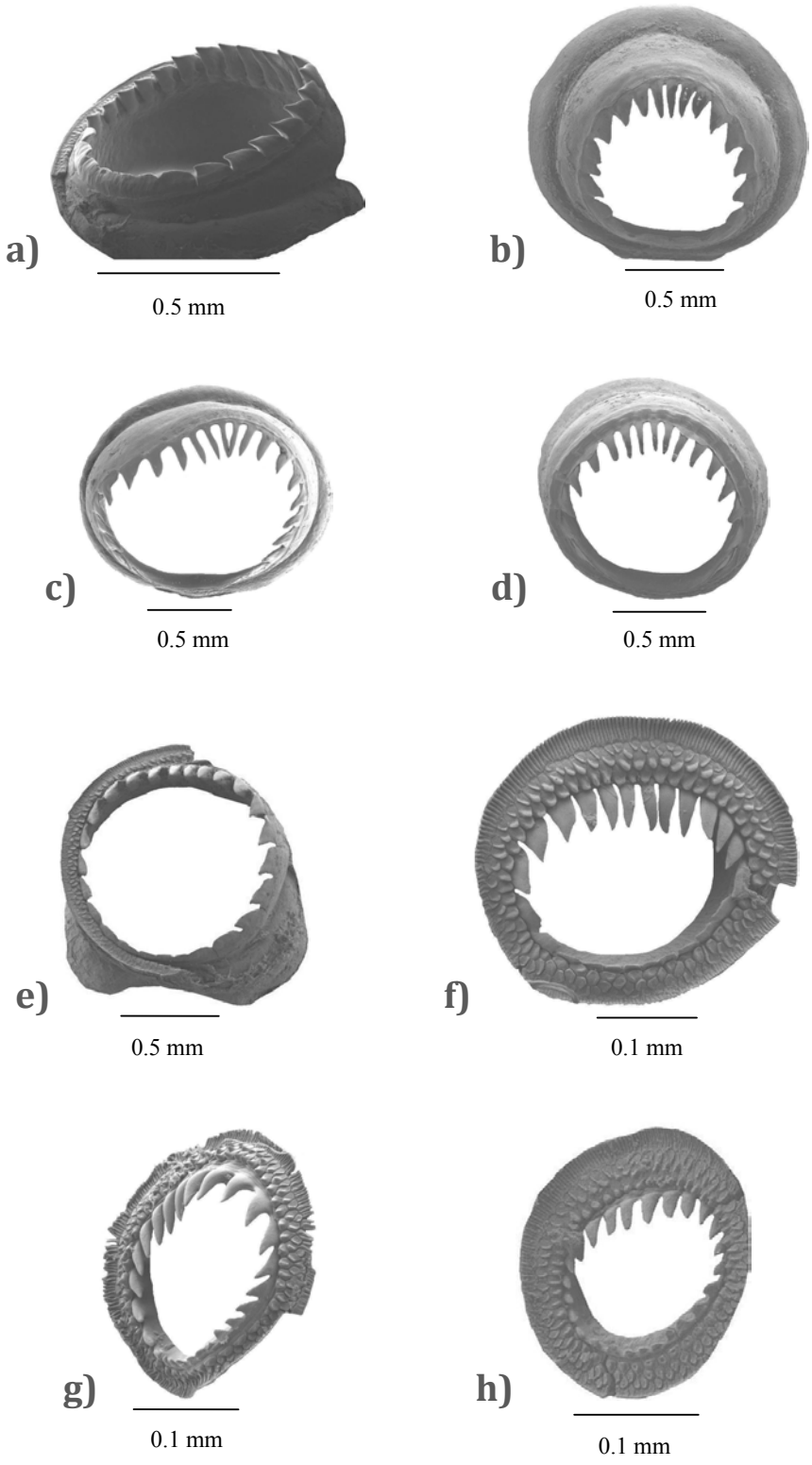

Figure 42. *Chiroteuthis veranyi* arm II suckers: a) NMNZ M.91646, b) NMNZ M.102106, c) NIWA 48814, d) NMNZ M.102106, e) NMNZ M.91646, f) NMNZ M.91646, g) NMNZ M. 91569, h) NIWA 48820; a) basal, b) largest, c–e) middle, f–h) tip

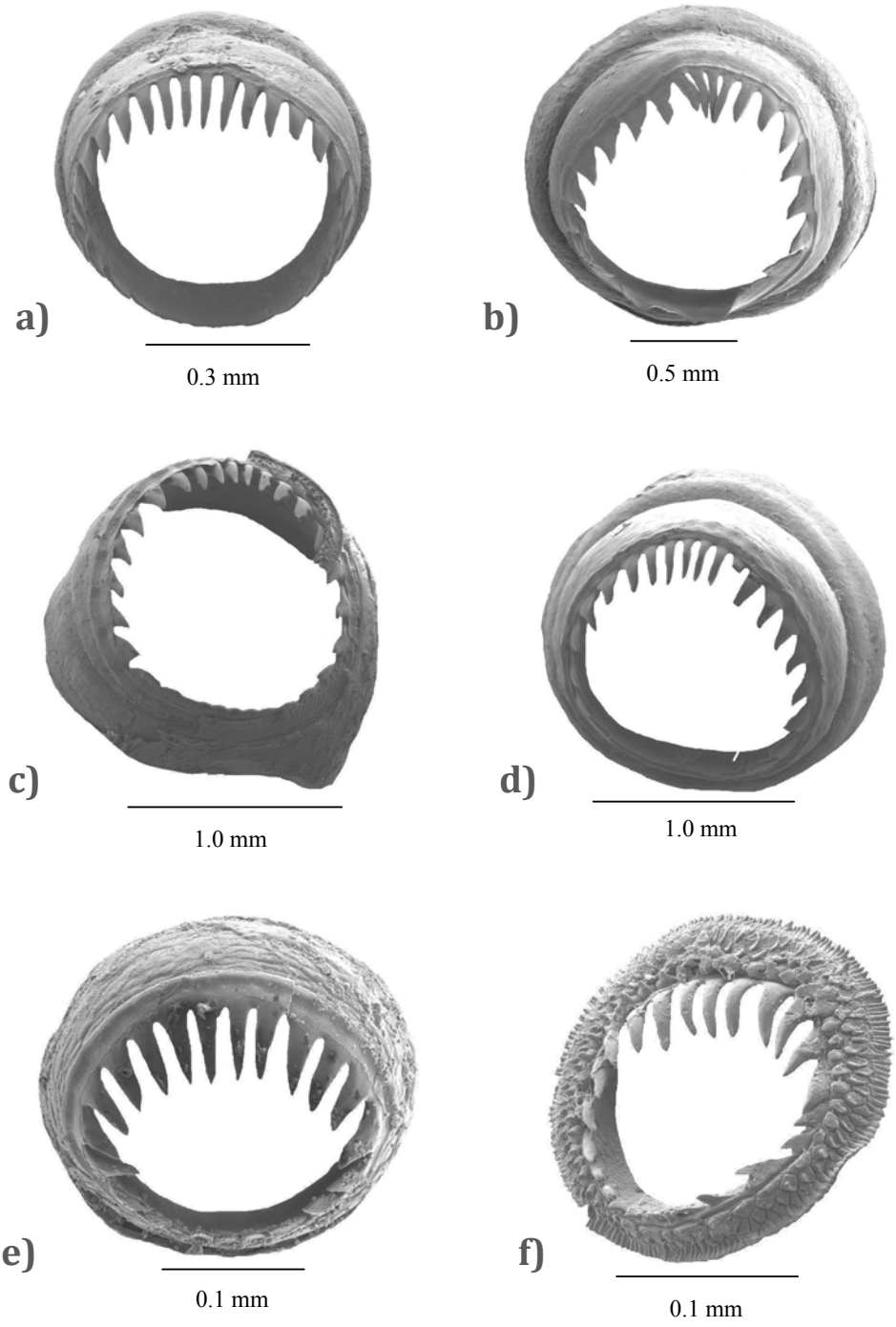

Figure 43. *Chiroteuthis veranyi* arm III suckers: a) NMNM M.91569, b) NIWA 48814, c) NMNZ M.102106, d) NMNZ M.102106, e) NIWA 48814, f) NMNZ M.91569; a & b) basal, c) middle, d) largest, e & f) tip

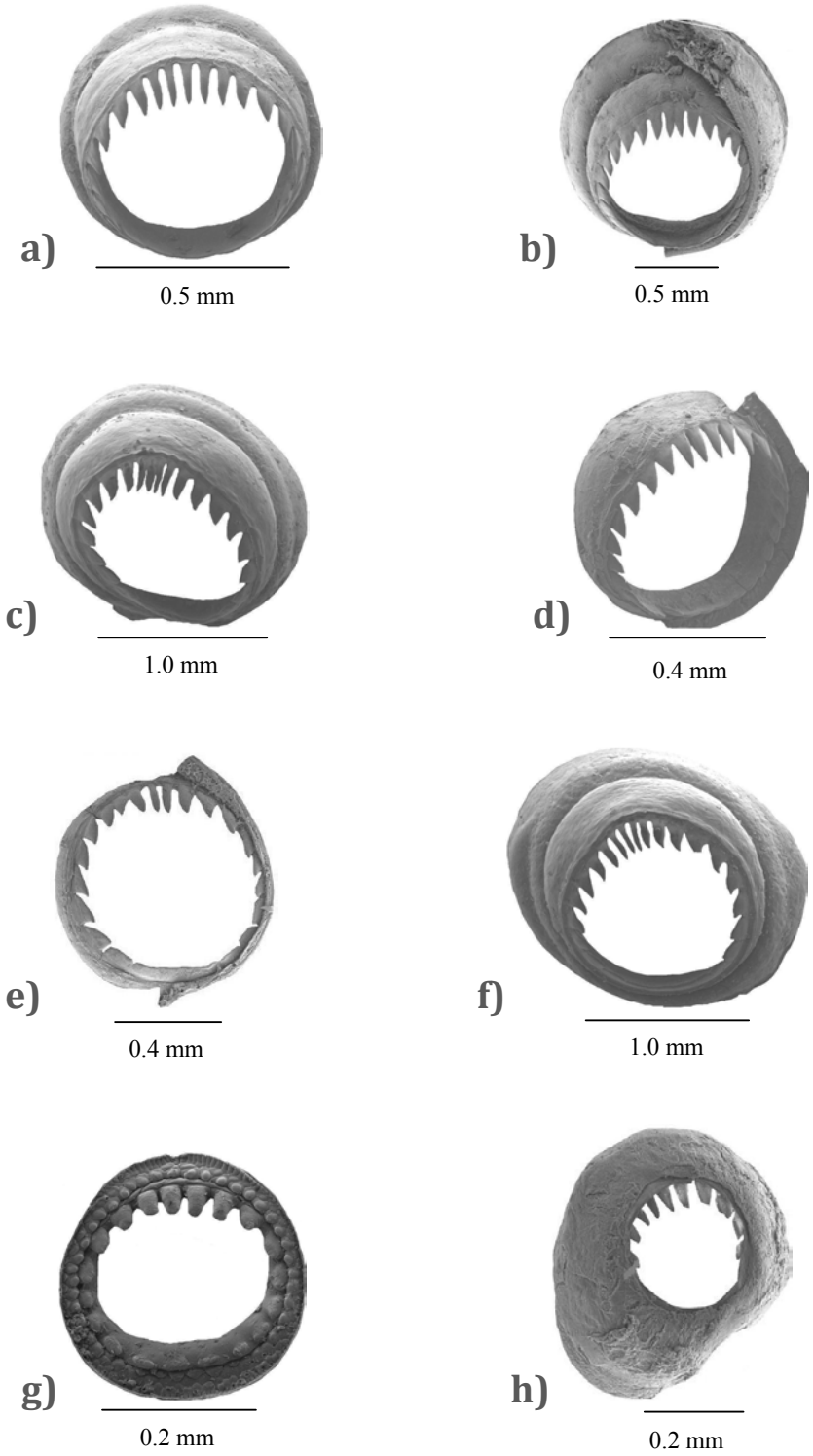

Figure 44. *Chiroteuthis veranyi* arm IV suckers: a) NMNZ M.91569, b) NMNZ M.91646, c) NMNZ M.102106, d) NIWA 48820, e) NMNZ M.91646, f) NMNZ M.102106, g) NMNZ M.286120, h) NMNZ M.91646; a–d) basal, e) middle, f) largest, g & h) tip

Figure 45. *Chiroteuthis veranyi* oral tentacle club: a) NIWA 48890, b) NMNZ M.74221

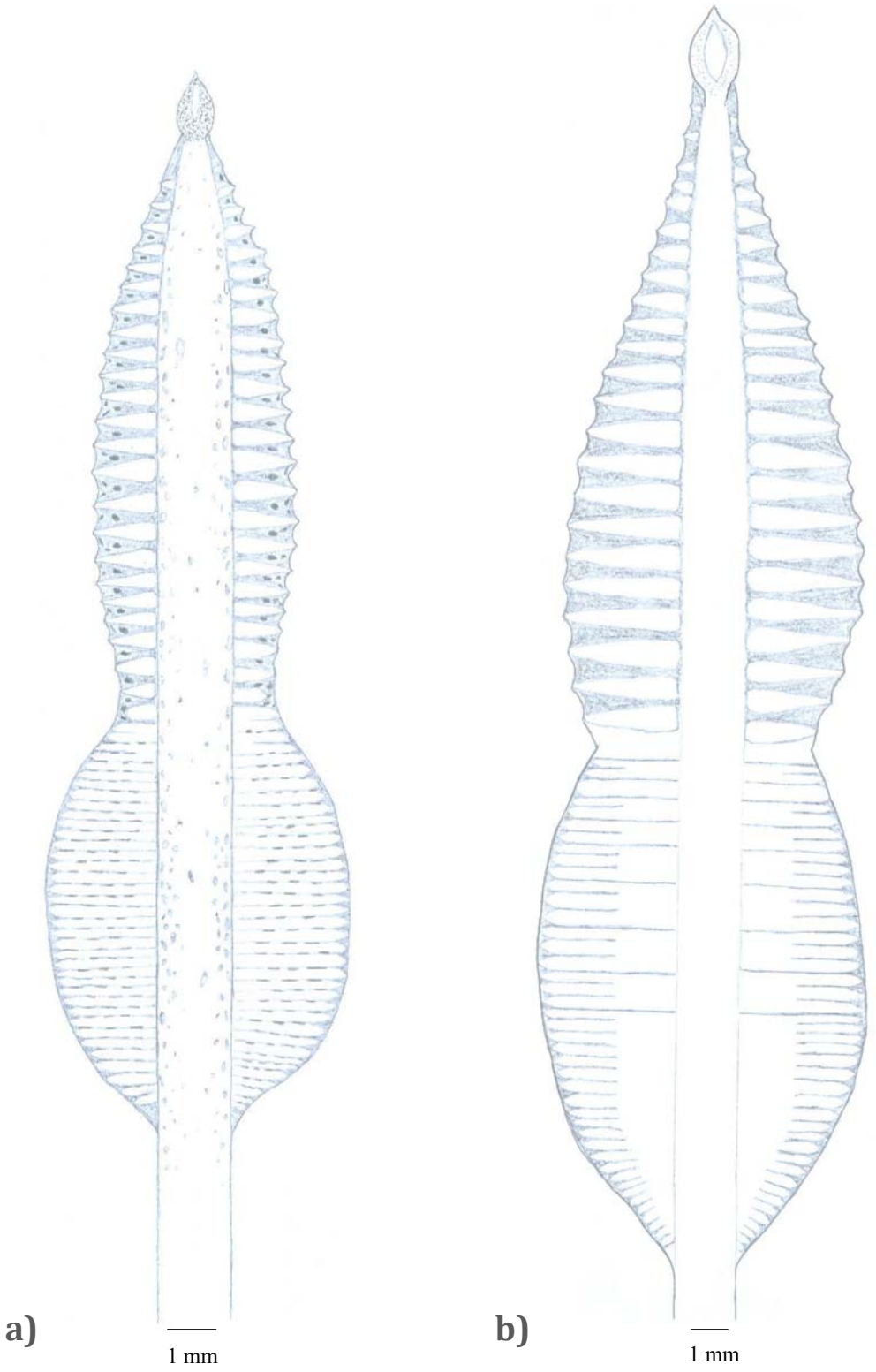

Figure 46. *Chiroteuthis veranyi* aboral tentacle club: a) NIWA 48890, b) NMNZ M. 74221

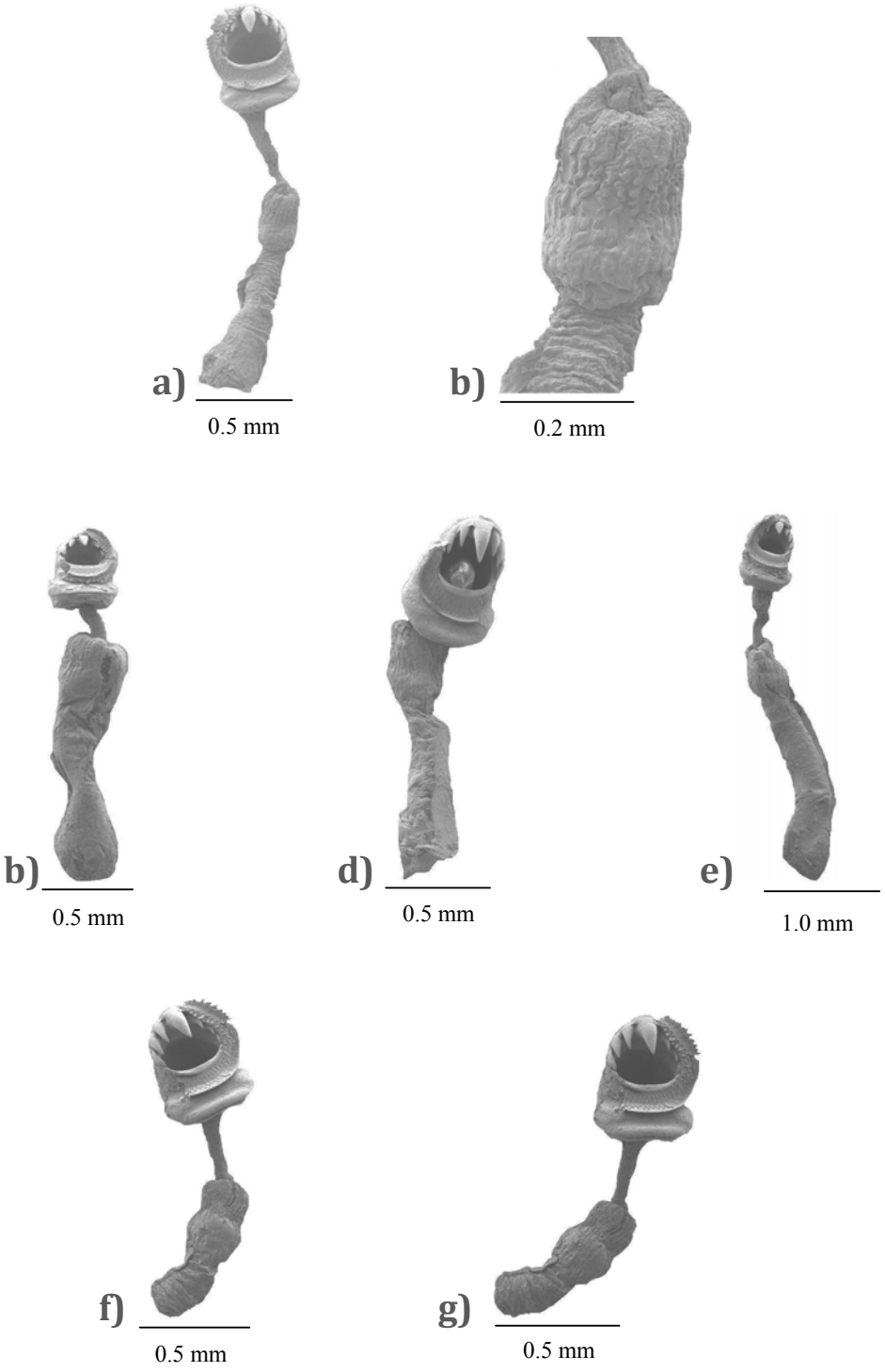

Figure 47. *Chiroteuthis veranyi* tentacle club sucker stalks: a & b) carpus NMNZ M.91569, c) manus NMNZ M.286120, d & e) manus NMNZ M.91569, f & g) dactylus NMNZ M.91569; e, & g) lateral, c, d & f) medial

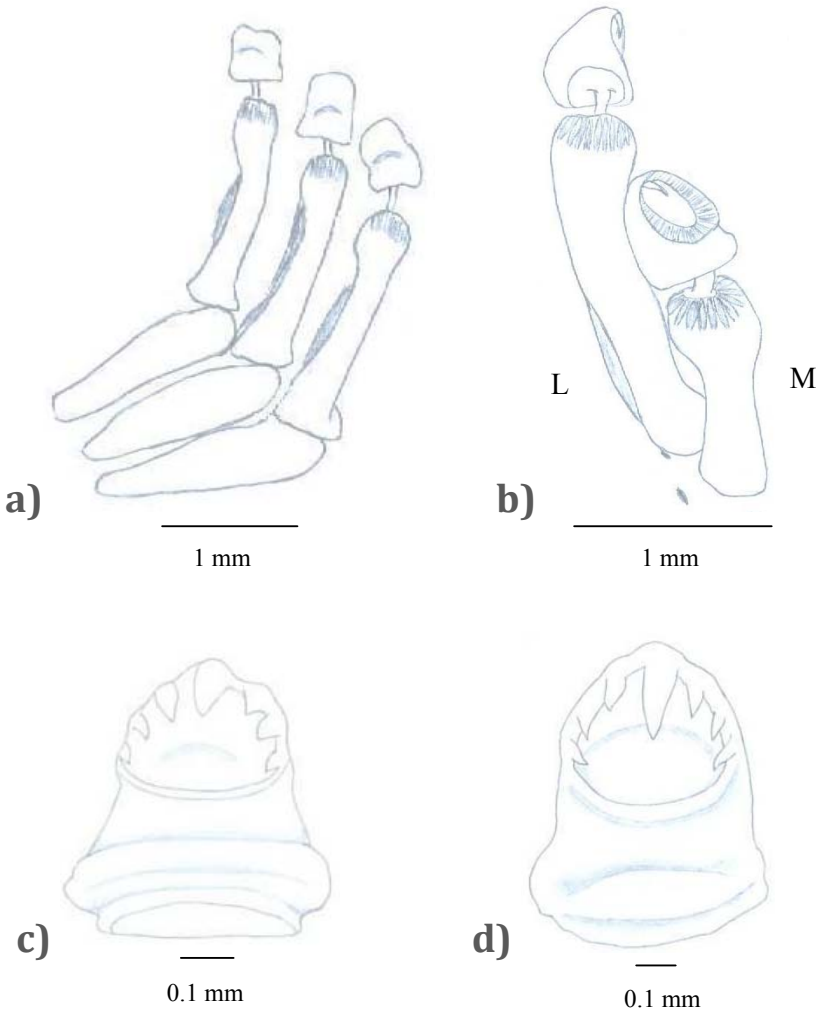

Figure 48. *Chiroteuthis veranyi* tentacle club sucker stalks and suckers: a–c) NIWA 48890, d) NMNZ M.91569; a, c, & d) lateral, b) lateral and medial

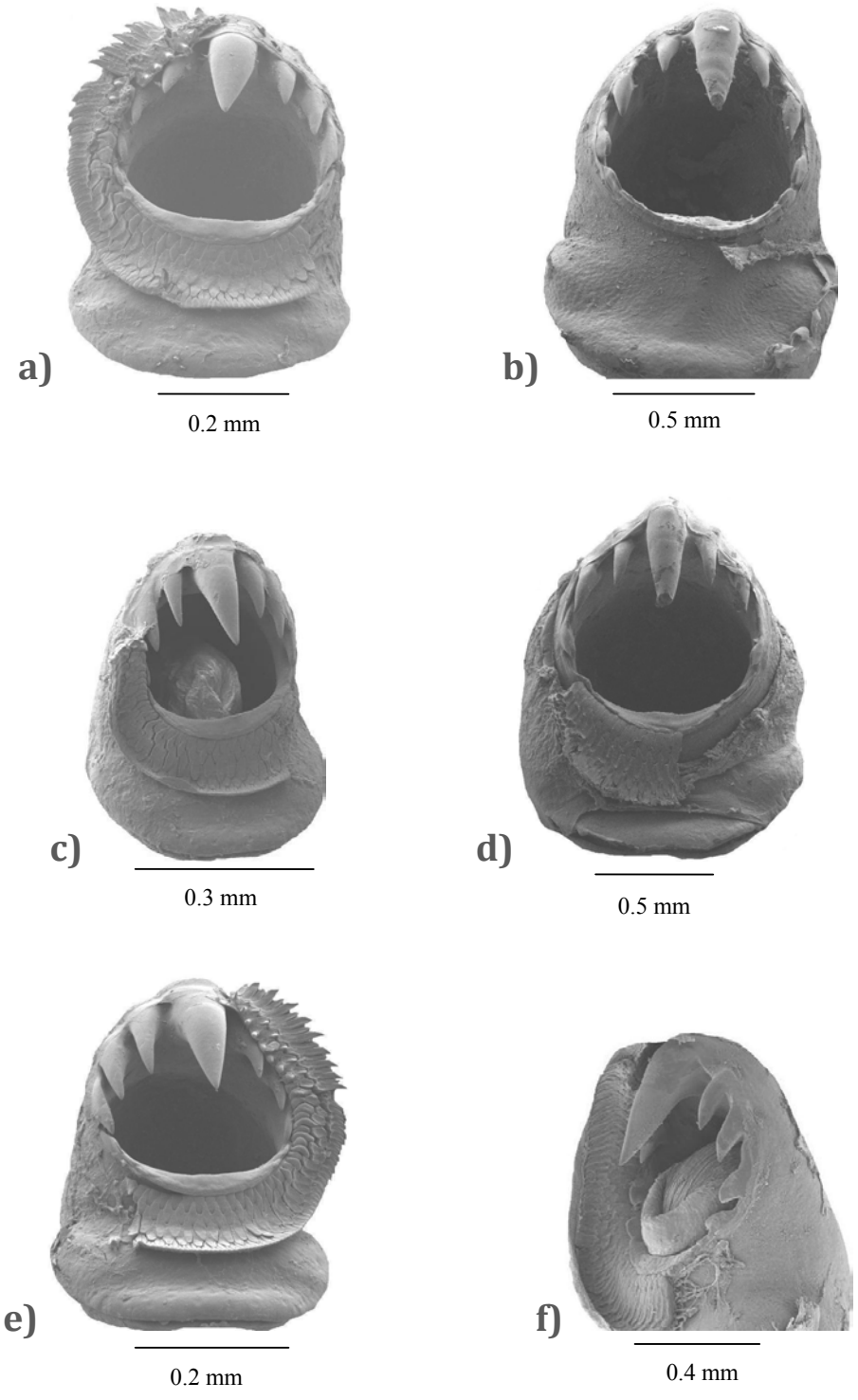

Figure 49. *Chiroteuthis veranyi* tentacle club sucker rings: a) NMNZ M.91569 carpus, b) NMNZ M.102106 carpus, c) NMNZ M.91569 manus, d) NMNZ M.102106 manus, e) NMNZ M.91569 dactylus, f) NMNZ M.91646 dactylus; c & e) medial, d & f) lateral

Lower beak (Figs 50–52)

Width slightly less to greater than height; wing fold obscures jaw angle and shoulder in lateral profile. Hood closely adpressed to crest; visible crest shorter than hood. Wall fold extends to posterior edge of lateral wall at angle of 33–55˚ from baseline; ratio of A to B variable; jaw angle obtuse (110–150˚); shoulder without tooth. Oral surface of jaw darkened past jaw angle, extends past shoulder and down wing with increasing size; hood darkened out from rostrum tip, not extending to edge of hood in smaller specimens. Edge of posterior lateral wall translucent in smaller specimens, darkening with increased mantle length, never as dark as hood. Rostrum (Fig. 50i iv–vi) thickened with small keel. Lateral wall (Fig. 50i i–iii) with thickened fold, but without keel.

Upper beak (Fig. 53)

With pointed rostrum; jaw angle poorly defined; obtuse (135–142˚) when present; shoulder concave or straight. Hood length 65–76% crest length. Hood and crest darken out from rostral tip with increasing mantle length; larger specimens have only a small portion around edges that remain translucent.

Radula (Fig. 54) **and palatine palp** (Fig. 55)

Rachidian with three cusps, the central the largest, with pronounced groove between central and lateral cusps. First lateral with large central tooth and slightly smaller lateral tooth; medial area may have shoulder or small tooth. Second lateral with large central tooth, medial area may have shoulder or small tooth. Marginal blocks sabre-like, long, narrow.

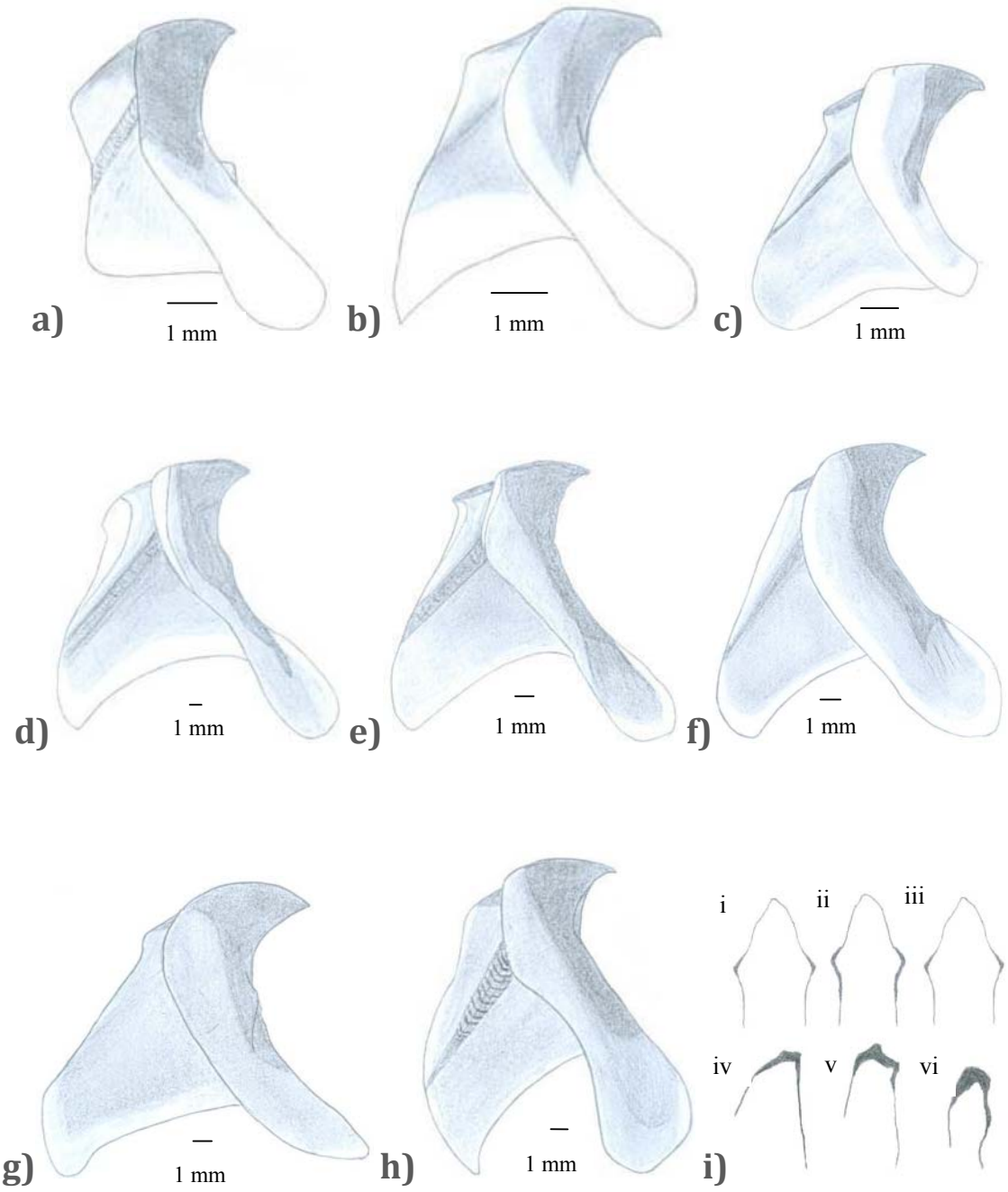

Figure 50. *Chiroteuthis veranyi* lower beak a–h) lateral, i) cuts: a) NMNZ M.286120, b) NIWA 48890, c) NMNZ M.74221, d) NIWA 48814, e) NMNZ M.102106, f) CAP04, g) 100320, h) NMNZ M.262499, i) 100320 i) cut A, ii) cut B, iii) cut C, iv) cut D, v) cut E, vi) cut F

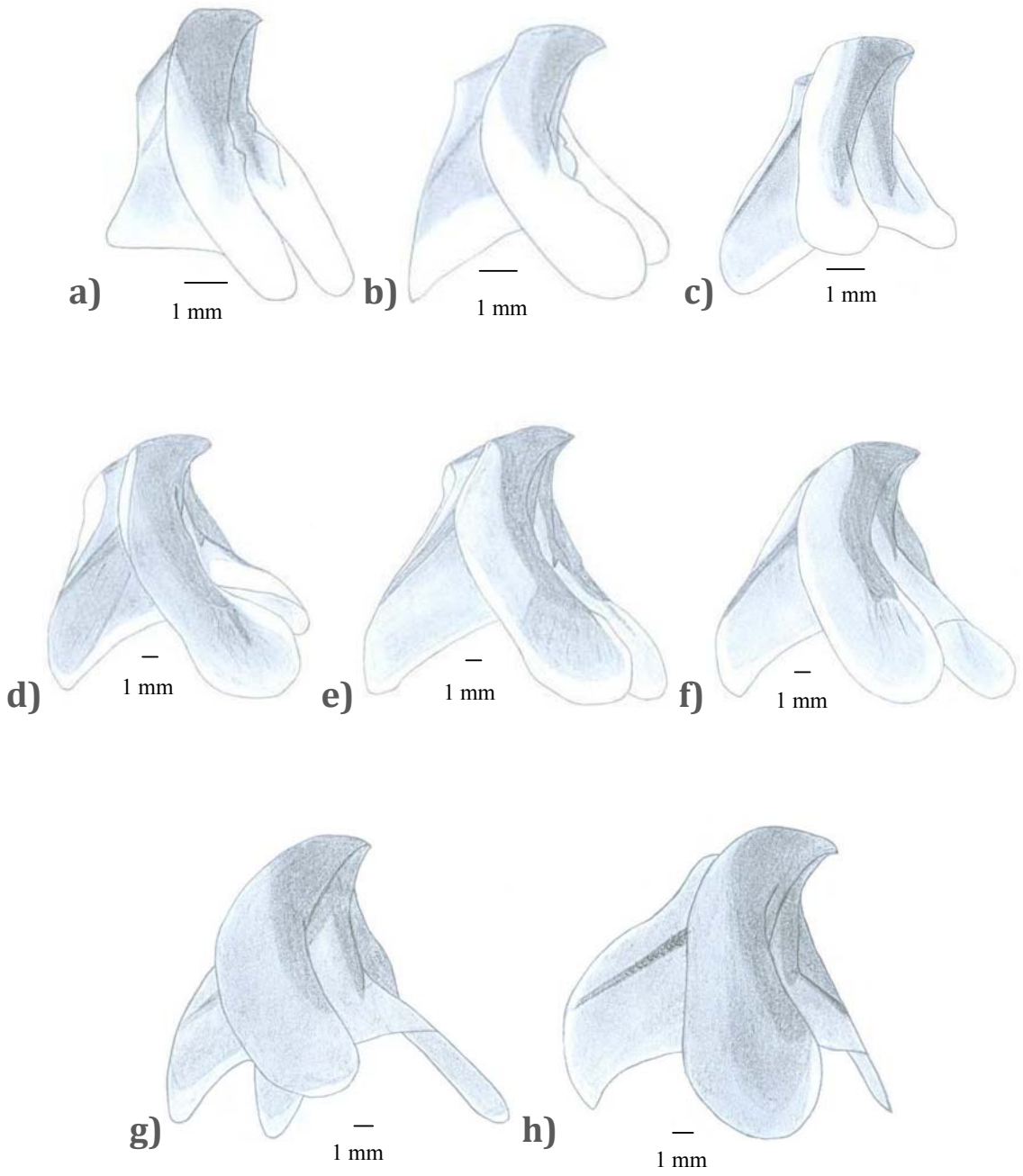

Figure 51. *Chiroteuthis veranyi* lower beak oblique: a) NMNZ M.286120, b) NIWA 48890, c) NMNZ M.74221, d) NIWA 48814, e) NMNZ M.102106, f) CAP04, g) 100320, h) NMNZ M.262499

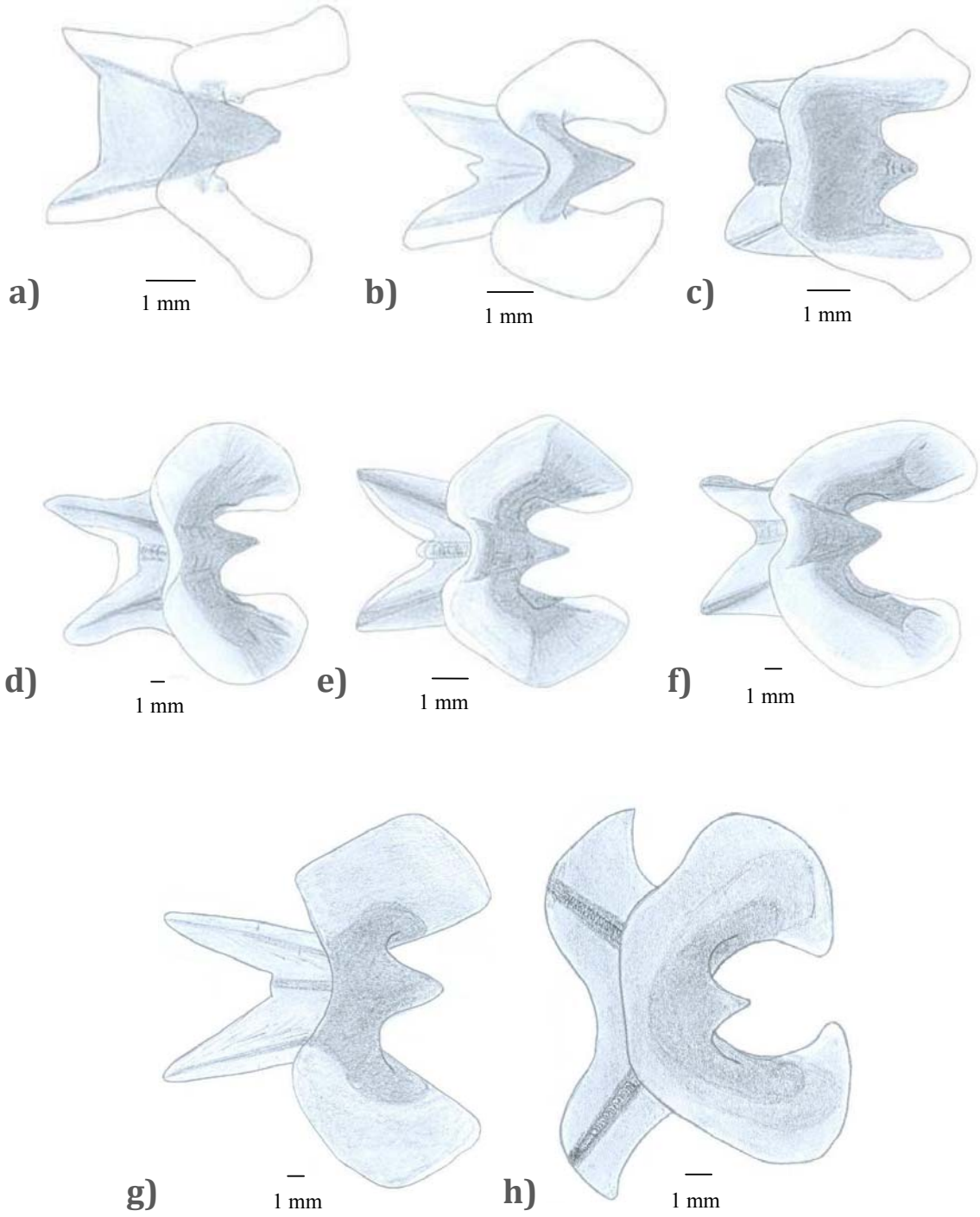

Figure 52. *Chiroteuthis veranyi* lower beak aboral: a) NMNZ M.286120, b) NIWA 48890, c) NMNZ M.74221, d) NIWA 48814, e) NMNZ M.102106, f) CAP04, g) 100320, h) NMNZ M.262499

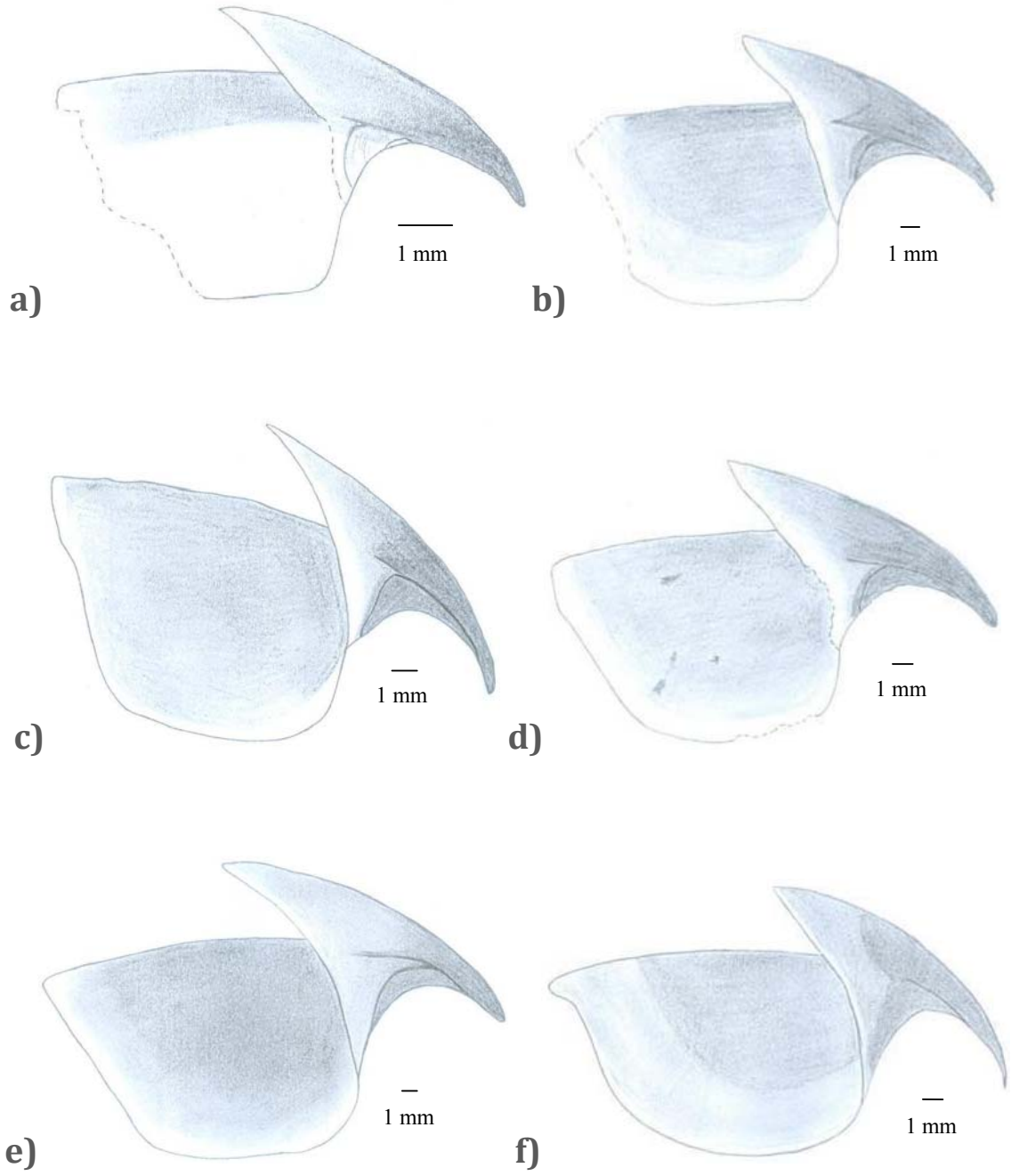

Figure 53. *Chiroteuthis veranyi* upper beaks: a) NIWA 48890, b) NIWA 48814, c) NMNZ M.102106, d) CAP04, e) 100320, f) NMNZ M.262499

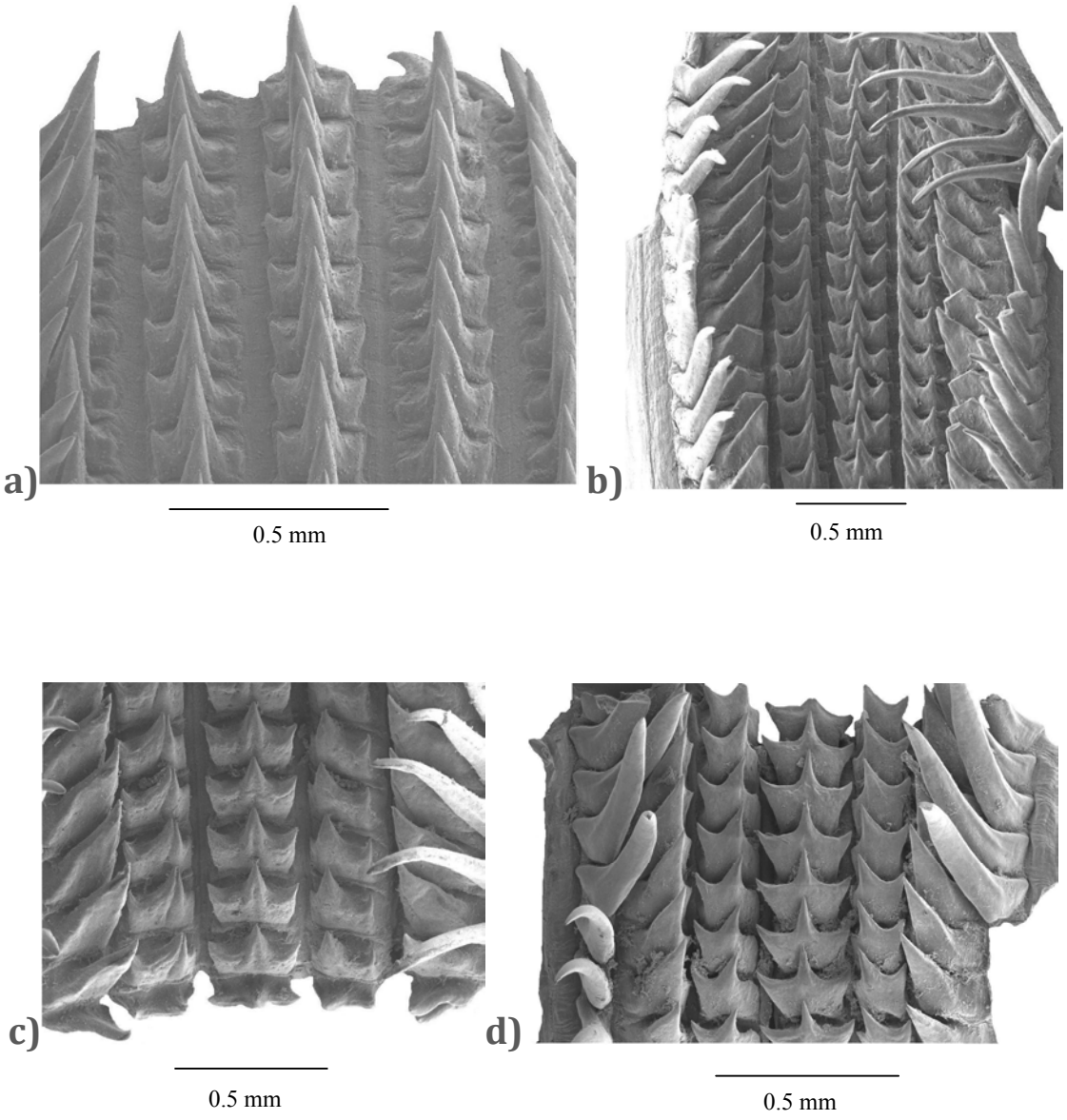

Figure 54. *Chiroteuthis veranyi* radula: a) NIWA 48820, b) NMNZ M.102106, c) NMNZ M.102106, d) NIWA 48814

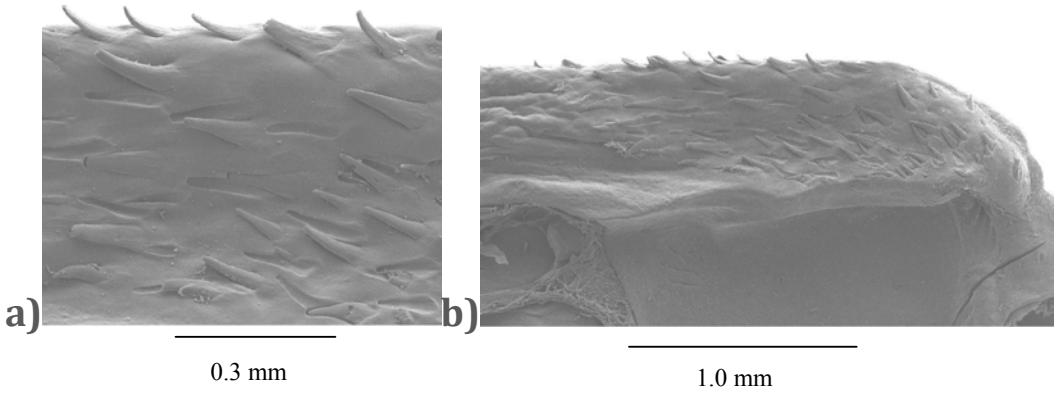

Figure 55. *Chiroteuthis veranyi* (NIWA 48820) palatine palp: a & b) oral surface

Internal anatomy (Fig. 56)

Outer demibranch of gill with 19–24 lamellae, inner demibranch with 17–23 lamellae. Immature nidamental glands (Fig. 56a) clear or white, become larger and darker (Fig. 56b, c) with increasing mantle length. Penis (Fig. 56d) prominent, beige-coloured, with terminal spade-like modification.

Gladius (Fig. 56e)

Long, narrow, translucent, protruding slightly from posterior edge of fins. Long free rachis (54–62% present GL), widest anteriorly, tapers posteriorly, narrowest at vane insertion (FRWantIr: 2.4–4%, FRWpostIr: 1.0–1.6%). Conus long (Ir 48–71.3%), always broken. Vane length variable (Ir 4–19.4%).

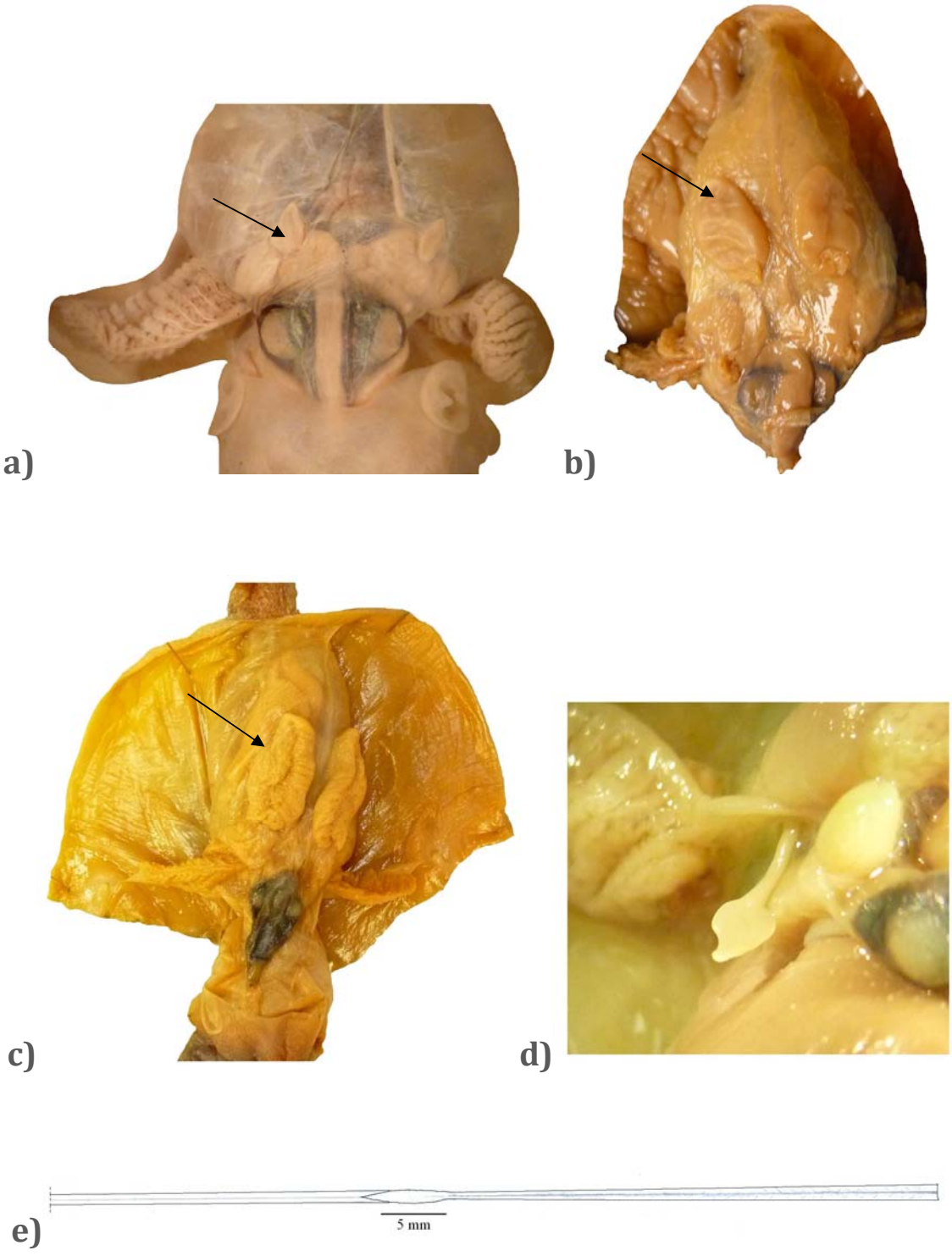

Figure 56. *Chiroteuthis veranyi* mantle cavity: a) NMNZ M.74221 immature nidamental glands, b) NIWA 48894 developing nidamental glands, c) NMNZ M.262499 nidamental glands, d) Z8858 penis e) NMNM M.74221 gladius

REMARKS

The type species of this genus, *Chiroteuthis veranyi*, was originally penned as "*veranii*" (Férussac 1835). Having been named for M. Verany, ICZN rules require amendment of the spelling to "*veranyi*", a correction made by d'Orbigny (1845) (as cited in Berry 1963), although the original specific spelling is still occasionally used (Jereb 1996; Sweeney & Roper 1998).

Based on representation within museum collections, this species would appear to be the most abundant and widely distributed chiroteuthid taxon occurring within New Zealand waters (Fig. 57). Perhaps not remarkably it also appeared to be the most frequently preyed upon species of *Chiroteuthis* in the diets of the seemingly locally foraging pygmy sperm whale (*fide* Beatson 2007), and the more extensively migratory sperm whale (*fide* Gomez-Villota 2007), accounting for the greatest biomass of chiroteuthid species preyed upon by these whales also. Elsewhere this species has an extensive distribution, from the northern subtropics to the southern subtropical zone throughout the Atlantic and eastern Pacific Oceans, in addition to the southern subtropical zone of Indian Ocean (Roper & Young 1999b).

Arm sucker ring dentition is quite variable, ranging from 16 to 27 teeth. This variation is greater than that earlier reported for this taxon, 12 to 16 teeth (Roper & Young 1999b), but could represent regional variation (as described for tentacle club sucker ring dentition on specimens attributed to this species by Rodhouse and Lu (1998)).

Unfortunately the gladius was broken on all available specimens, protruding slightly from the fins, with a small tail present on nearly every specimen. This indicates the presence of a larger tail, or possibly even secondary fins. Reproductive organs are

visible on specimens from 46 mm ML in both sexes. No female was encountered with spermatophores implanted into any part of her body.

Table 4a. Measurements of *Chiroteuthis veranyi* (mm)

	M.286120	M.091569	M.074221	M.262499	48890	48815	48820	M.091646	48816	Z8858
ML	50	58	56	194	51	83	56	94	72	47
MW	12	12	17	50*	13	22	12	30	25	20
TL	403	405	464	NA	288	846	NA	730	680	875
FL	23	24	25	68	25	33	24	47	34	22
FW	24	28	28	60	23	36	26	46	34	32
AL I	36	49	50	180	33	115	35	127	64	98
II	45	64	55	233	42	146	48	142	88	125
III	60	74	60	270	48	165	64	173	118	144
IV	102	116	129	365	90	246	92	242	165	197
ASC I	15	21*	20	20	14	31	18	40	NA	28
II	27	20*	22	22	18	32	22	32	NA	28
III	18	23*	22	22	18	34	24	31	NA	30
IV	9	16	18	15	12	17	14	17	NA	17
CL	26	34.5	32	NA	23	63	NA	76	53	67
Carpus L	5	7	6	NA	4	7	NA	12	11	7
manus L	5.5	10	8.5	NA	5	20	NA	22	14	25
dactylus L	15.5	17.5	17.5	NA	14	36	NA	42	28	35
CRC	38	37	36	NA	32	33	NA	32	35	37
T Stalk L	290	312	335	NA	195	703	NA	465	560	687
HL	35	40	25	56	19	63	23	51	38	47
HW	16	22	28	35	17	28*	18	25*	15*	18*
ED	15	14	15	20*	13	21*	17	23	NA	15*
LD	5	5	6	7	4	9*	5	10	NA	7*
Gill lam in	18	19	20	20	20	20	19	17	NA	20
Gill lam out	20	21	22	22	22	22	21	19	NA	22
free lobe	Yes	Yes	No	No	Yes	No	Yes	Yes	Yes	No
sex	♀	♀	♀	♀	♀	♂	♀	♂	♀	♂

* = Damaged. NA = Not Applicable, either too damaged or absent.

Table 4b. Measurements of *Chiroteuthis veranyi* (mm), continued

	48893	48821	M.286123	48823	M.286121	M.286114	M.286111	M.285799	48826	48888
ML	50	47	57	46	51	46	51	54	50	52
MW	10	10	12	10	11	13	15	12	15	16
TL	378	191	371	203	371	438	NA	526	352	532
FL	21	20	25	20	23	20	22	23	22	23
FW	25	23	25	22	25	21	22	23	25	27
AL I	30	17	28	20	27	27	37	43	28	31
II	38	24	38	32	41	43	53	54	39	45
III	55	30	51	44	58	52	62	68	46	74
IV	95	60	94	65	110	107	122	125	97	101
ASC I	18	14*	18*	18	NA	NA	NA	NA	NA	NA
II	20	28	24*	20	NA	NA	NA	NA	NA	NA
III	24	17	28	22	NA	NA	NA	NA	NA	NA
IV	17	15	15	15	NA	NA	NA	NA	NA	NA
CL	26	17	24	19	25	26	NA	26	28	31
Carpus L	3	2	4	3	3	4	NA	4	6	5
manus L	7	6	8	5	7	7	NA	8	6	9
dactylus L	16	9	12	11	15	15	NA	14	16	17
CRC	36	36	33	35	35	40*	NA	36	31	38
T Stalk L	275	108	265	116	271	342	NA	418	248	420
HL	27	19	25	22	24	23	29	28	26	29
HW	13	11	12	16	15	17	15	18*	19*	15*
ED	13	9	13	11	13	13	16	16	11	13*
LD	5	3	4	3	4	4	5	4	4	4
Gill lam in	22	18	18	18	18	18	20	18	17	18
Gill lam out	24	20	20	20	20	20	22	20	19	20
free lobe	Yes	Yes	Yes	No	No	Yes	No	Yes	Yes	Yes
sex	♂	♀	♀	Indt	Indt	Indt	Indt	♂	Indt	Indt

* = Damaged. NA = Not Applicable, either too damaged or absent. Indt = indeterminate.

Table 5a. Indices of *Chiroteuthis veranyi*

	M.286120	M.091569	M.074221	M.262499	48890	48815	48820	M.091646	Z8858	48893
ML	50	58	56	194	51	83	56	94	47	50
MWI	0.24	0.21	0.31	0.26	0.25	0.27	0.21	0.32	0.43	0.2
FLI	0.46	0.41	0.45	0.35	0.49	0.4	0.43	0.5	0.47	0.42
FWI	0.48	0.48	0.5	0.31	0.45	0.43	0.46	0.49	0.68	0.5
ALI I	0.72	0.84	0.89	0.93	0.65	1.39	0.63	1.35	2.09	0.6
II	0.9	1.1	0.98	1.2	0.82	1.76	0.86	1.51	2.66	0.76
III	1.2	1.28	1.07	1.39	0.94	1.99	1.14	1.84	3.06	1.1
IV	2.04	2	2.3	1.88	1.76	2.96	1.64	2.57	4.19	1.9
CLI	0.52	0.59	0.57	NA	0.45	0.76	NA	0.81	1.43	0.52
Carpus LI	0.1	0.12	0.1	NA	0.08	0.08	NA	0.13	0.15	0.04
Manus LI	0.11	0.17	0.15	NA	0.1	0.24	NA	0.23	0.51	0.14
Dact. LI	0.31	0.3	0.31	NA	0.27	0.43	NA	0.45	0.74	0.32
T stalk LI	5.8	5.38	5.98	NA	3.82	8.47	NA	4.95	14.62	5.5
HLI	0.7	0.69	0.45	0.29	0.37	0.76	0.41	0.54	1	0.54
HWI	0.32	0.38	0.5	0.18	0.33	0.34	0.32	0.27	0.38	0.26
EDI	0.3	0.24	0.27	0.1	0.25	0.25	0.3	0.24	0.32	0.26
LDI	0.1	0.09	0.1	0.04	0.08	0.11	0.09	0.11	0.15	0.1

* = Damaged. NA = Not Applicable, either too damaged or absent.

Table 5b. Indices of *Chiroteuthis veranyi*, continued

	48821	48829	M.286123	48823	M.286121	M.286114	M.286111	M.285799	48826	48888
ML	47	48	57	46	51	46	51	54	50	52
MWI	0.21	0.27	0.21	0.22	0.22	0.28	0.29	0.22	0.3	0.31
FLI	0.43	0.42	0.44	0.43	0.45	0.43	0.43	0.43	0.44	0.44
FWI	0.49	0.48	0.44	0.48	0.49	0.46	0.43	0.43	0.5	0.52
ALI I	0.36	0.69	0.49	0.43	0.53	0.59	0.73	0.8	0.56	0.6
II	0.51	0.85	0.67	0.7	0.8	0.93	1.04	1	0.78	0.87
III	0.64	1.15	0.89	0.97	1.14	1.13	1.22	1.26	0.92	1.42
IV	1.28	2.29	1.65	1.41	2.16	2.65	2.39	2.31	1.94	1.94
CLI	0.36	0.67	0.42	0.41	0.49	0.57	NA	0.48	0.56	0.6
Carpus LI	0.04	0.1	0.07	0.07	0.06	0.09	NA	0.07	0.12	0.1
Manus LI	0.13	0.21	0.17	0.11	0.14	0.15	NA	0.15	0.12	0.17
Dact. LI	0.19	0.35	0.21	0.24	0.29	0.33	NA	0.16	0.32	0.33
T stalk LI	2.3	8.75	4.65	2.52	5.31	7.43	NA	7.74	4.96	8.08
HLI	0.4	0.5	0.44	0.48	0.47	0.5	0.57	0.52	0.52	0.56
HWI	0.23	0.31	0.21	0.35	0.29	0.37	0.29	0.33	0.38	0.29
EDI	0.19	0.27	0.23	0.24	0.25	0.28	0.31	0.3	0.22	0.25
LDI	0.06	0.1	0.07	0.07	0.08	0.09	0.1	0.07	0.08	0.08

* = Damaged. NA = Not Applicable, either too damaged or absent.

ADDITIONAL CHIROTEUTHID TAXA

As this is the first revision of the New Zealand *Chiroteuthis* fauna, and two of the three species herein reported are represented in collections by three or less specimens, it is possible that additional taxa occur within New Zealand waters. Of the six species for which general consensus maintains their validity (Roper & Young 1998, Sweeney & Roper 1998, Okutani 2005), three not yet recognised from New Zealand waters, *C. calyx*, *C. joubini*, *C. picteti*, are briefly diagnosed to facilitate identification, should a species that disagree with descriptions furnished herein.

Chiroteuthis calyx

The tentacle club of *C. calyx* has a protective membrane divided into two approximately equal parts. The proximal part is slightly wider than the distal. The trabeculae on the proximal portion are very wide, close together, and divided into two or three parts. The trabeculae on the distal portion are triangular and much more widely spaced. The club sucker stalks are in two portions with a widened 'pleated skirt' in between the two portions. Lateral stalks posses a lateral keel. The sucker rings have 11–13 pointed teeth, the central one on the distal portion being enlarged. Eye photophores are in three series: lateral and medial series are both one stripe; intermediate series with three round photophores, a large one at each of the posterior and anterior portions and a small one slightly off centre towards the anterior portion. Arms I–III have large globular suckers in their middle portions. These large suckers have nearly smooth rings. All other suckers have 18–20 short, squared teeth (Roper & Young 1999c, Young 1972).

Chiroteuthis joubini

The protective membrane on the tentacle club of *C. joubini* is divided into three parts: the proximal section is very short with only about 10 trabeculae, the middle portion has

no trabeculae and is about ⅓ of the total club length, the distal portion is about ½ of the total club length and has triangular trabeculae. Club sucker stalks are in two parts without 'pleated skirt' and without any lateral keels. The club sucker rings have seven or eight pointed teeth, the central one on distal portion is not enlarged. Eye photophores are in two series: lateral series with five or six round photophores, posterior-most one enlarged; medial series with five round photophores. There are no globular suckers. Arm suckers have 22–26 pointed, triangular teeth (Joubin 1933b, Nesis 2003, Roper & Young 1999d, Voss 1967).

***Chiroteuthis picteti* s.spp**

Two subspecies of *C. picteti* have been recently described: *C. picteti picteti*, and *C. picteti somaliensis* (Salcedo-Vargas 1996). The characteristics of the species include a very long tentacle club with a protective membrane divided into two parts, but with the proximal portion being much shorter than the distal. The proximal trabeculae are very narrow and closely set, whereas the distal trabeculae form wide triangular structures. The club sucker stalks are in two portions and lack a 'pleated skirt'. Both medial and lateral stalks have lateral keels, with the medial being shorter. Club sucker rings have 11–15 pointed teeth, of which the central on the distal portion is enlarged. Eye photophores are round, in three series: lateral series with 6–9 photophores, intermediate series with 8–11 photophores, medial series with 8–11 photophores. Arms lack globular suckers; their suckers each with 10–20 variably shaped teeth, from pointed to blunt (Joubin 1894, Roper & Young 1999e, Salcedo-Vargas 1996).

DISTRIBUTION

Coordinates for many specimens lots are not available, so the distributions of those taxa herein reported are incomplete (Fig. 57).

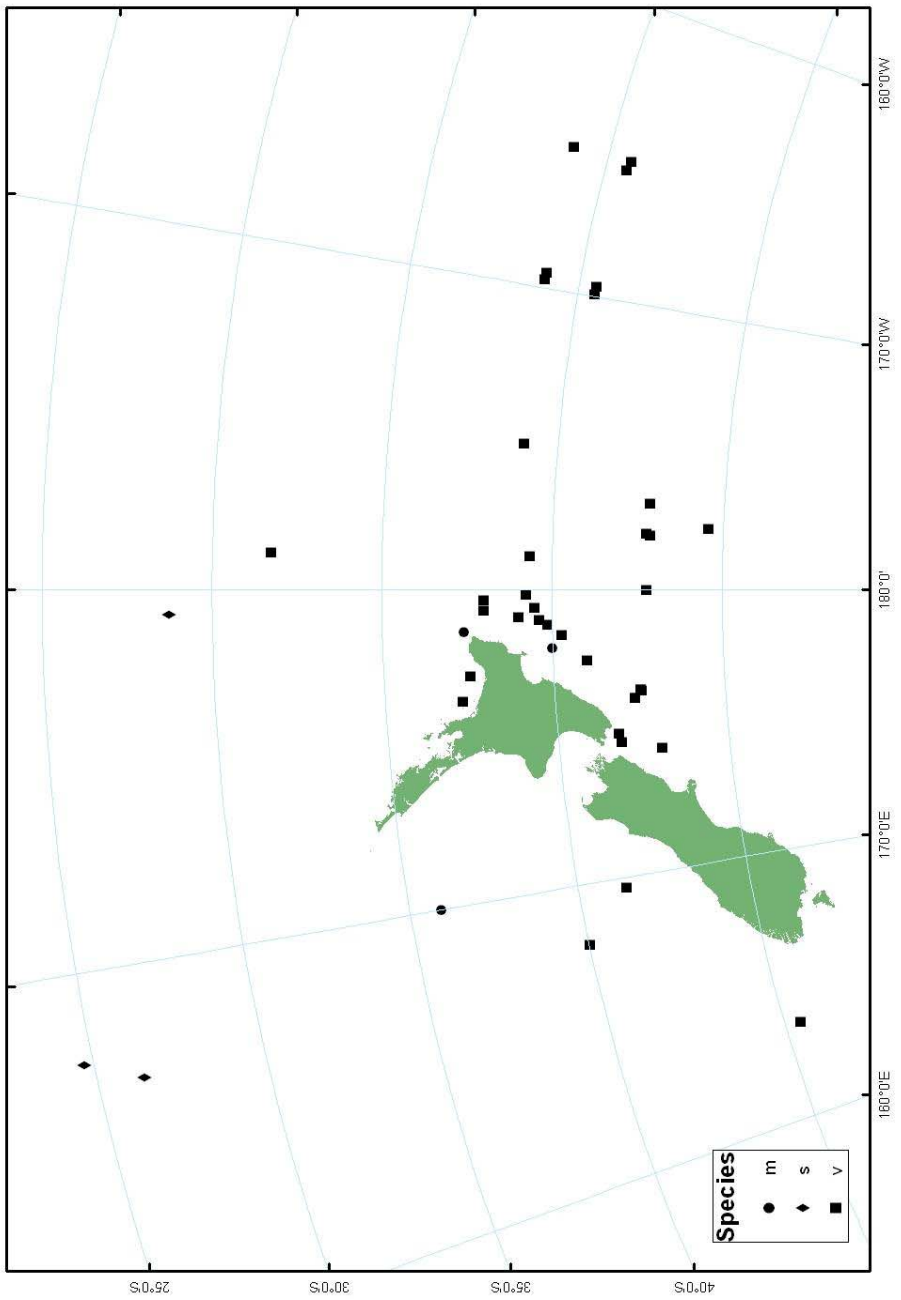

Figure 57. Distribution of *Chiroteuthis* spp. in New Zealand waters (m = *C. mega*, s = *C. spoeli*, v = *C. veranyi*)

DISCUSSION

Colour

Colour can be affected by preservation, but both *C. mega* and *C. veranyi* appear to darken with age; all *C. spoeli* specimens are large (82, 144, and 165 mm ML), so it cannot be determined if the same applies for this species also. Colour does appear to be a characteristic of at least two of the three species that occur in New Zealand waters, *C. mega* and *C. veranyi*, with *C. mega* being distinctly darker than *C. veranyi* at comparable mantle length.

General condition of specimens available for study

The extensively gelatinous nature of these squids renders them prone to desiccation in high-alcohol content preservatives (such as 70% ethanol); a 40% isopropyl alcohol concentration as a preservative is preferred. Dimensions of the mantle and head are likely to be affected by preservative, and therefore indices based on their widths, diameters or thicknesses should be treated with caution for differentiating species fixed in different preservatives, and especially those frozen prior to fixation and those fixed live or narcotised aboard vessels. Having said this, indices are not the most effective way of differentiating those taxa reported herein from New Zealand waters, so this has not hampered identification of species. This may become more important in the event ontogenetic series of specimens of species are described as part of a larger, global review of *Chiroteuthis* taxa.

Chiroteuthid fins are delicate and easily damaged during capture. The delicate margins of almost all fins were damaged to some extent; the same applies also to the arms of many specimens, the integument along which was frequently stripped off over large areas, the delicate aboral keels and membranes were often missing altogether, and many suckers also were stripped from the arms. Unfortunately, some of the older specimens in collections caught using finer-meshed scientific-sampling nets, and in better overall condition that those specimens retained from commercial fisheries bycatch, have lost most of their sucker rings given inappropriate initial fixation techniques. Most every specimen had lost one or both of its tentacles (e.g., of the three *C. spoeli* specimens none retained a tentacle club, and although a single club was present in each *C. mega* specimen, unfortunately the sucker rings of the larger specimens were lost due to improper fixation). These challenges aside, sufficient characters remained for many of the specimens to unambiguously assign them to species.

Characters of systematic value

The lower beaks from the specimens of *C. veranyi* varied little in morphology, and the beaks of each of these three species can be readily differentiated (and have been, with minimal error, in previous predator dietary studies for which vouchers are available, namely Beatson (2007) and Gomez-Villota (2007)). There are no immediately obvious differences in upper beak morphology for each of these species, rendering them of more limited taxonomic value (and of very limited value in predator-prey studies at the level of species). Variation in radular and palatine palp morphology for *C. veranyi* is considerable, rendering the value of either structure of limited taxonomic value, at least

for differentiating chiroteuthid species (dentition in teeth on one radula alone is variable (Fig. 57d)).

This thesis is the first to report the presence and absence of the pad-like photophore on the extreme base of the tentacle stalk. This is of some taxonomic value, as it is present in all *C. veranyi* specimens examined, but none of the *C. mega* or *C. spoeli* specimens examined. This pad is much less vulnerable than the others further along the stalk, so it is less likely to be lost during capture.

Subgeneric Classifications

Of the two subgeneric classifications available, that recognising *Chirothauma* and *Chiroteuthis* as subgenera (*sensu* Salcedo-Vargas 1996), wherein *C. mega*, *C. picteti*, and *C. imperator* were attributed to *Chirothauma*, and *C. calyx, C. veranyi, C. spoeli*, and *C. joubini* to *Chiroteuthis* (*s.s.*); and the three 'Groups' of Roper & Young (1998), with Group 1 comprising *C. picteti* and *C. mega*, Group 2 *C. joubini*, *C. spoeli*, and an unknown species, and Group 3, *C. veranyi* and *C. calyx*, I am inclined to follow that of Roper & Young (1998). These two classifications group taxa quite differently.

Based on data presented herein, and that discerned from the literature and web (particularly the Tree of Life pages), characters of eye photophore and tentacle club morphology (summarised in Figs 58–60) group taxa in the same manner as Roper & Young (1998) (admittedly based largely on these very same characters). This grouping of taxa resulting from these two classifications is entirely different from that proposed by Salcedo-Vargas (1996). Intuitively the classification of Salcedo-Vargas should be more meaningful as it was based on many more characters, like eye photophore

distribution, tentacle club morphology (suckers, stalks, trabeculae, teeth), ink sac photophores, fin shape, and body length, but there are a number of inconsistencies in this classification that render it unworkable.

Those taxa assigned to subgenera recognised and diagnosed by Salcedo-Vargas did not necessarily agree with his diagnoses (Tables 6, 7). In particular, the subgenus *Chiroteuthis* as diagnosed by him included *C. veranyi* and *C. calyx*, both supposed to have a non-trabeculated area on the club membrane (in order to be ascribed to this subgenus), but neither *C. veranyi* nor *C. calyx* has a non-trabeculated portion on the club. Also, the series of eye photophores in members of the subgenus *Chiroteuthis* were diagnosed to be distributed in two series, but those of *C. veranyi* and *C. calyx* have theirs placed in three series. Moreover, those taxa attributed to *Chirothauma*, as re-diagnosed by Salcedo-Vargas (*ibid*) are supposed to have 60–85 trabeculae on the club membrane, however, *C. picteti* has at least 84–109; this subgenus is also diagnosed with heart-shaped fins, whereas the genus itself is diagnosed by him with nearly circular fins.

Three courses of action were therefore available to me: 1) abandon the concept of the subgenus altogether; 2) re-diagnose those subgenera recognised by Salcedo-Vargas (1996) to accommodate taxa that disagree with original diagnoses; or 3) follow that classification advocated by Roper & Young (1998). Rather than uncritically follow option 3, which in fact I favour, I have elected to abandon the concept of the subgenus herein as I have not had access to sufficient taxa to thoroughly review the genus, or evaluate the validity of any subgenera or operational taxonomic units (“groups” of Roper & Young); moreover, I do not have independent corroboration from molecular data to contrast with morphological classifications.

Were those subgenera recognised by Salcedo-Vargas to be re-diagnosed in order to correct inconsistencies and ambiguities in descriptions and diagnoses (Tables 6, 7), then the distinction between them would break down (for example, trabeculae on *C. picteti*, in *Chirothauma*, number 84–109, the subgenus was diagnosed with 60–85; *C. veranyi*, in subgenus *Chiroteuthis* has 65 (data herein), rendering this character of limited or dubious subgeneric value). The same applies to the presence of a keel on the club suckers of *Chirothauma* taxa, which is present also on some *Chiroteuthis* taxa (*C. veranyi*)).

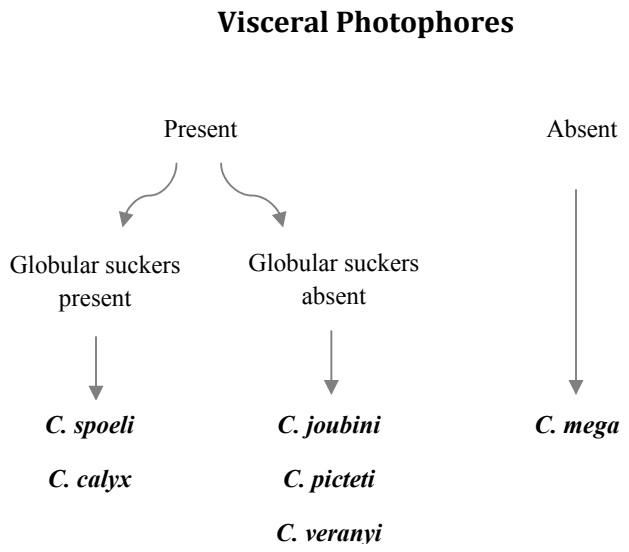

Figure 58. Schematic for species identification (visceral photophores and sucker shape)

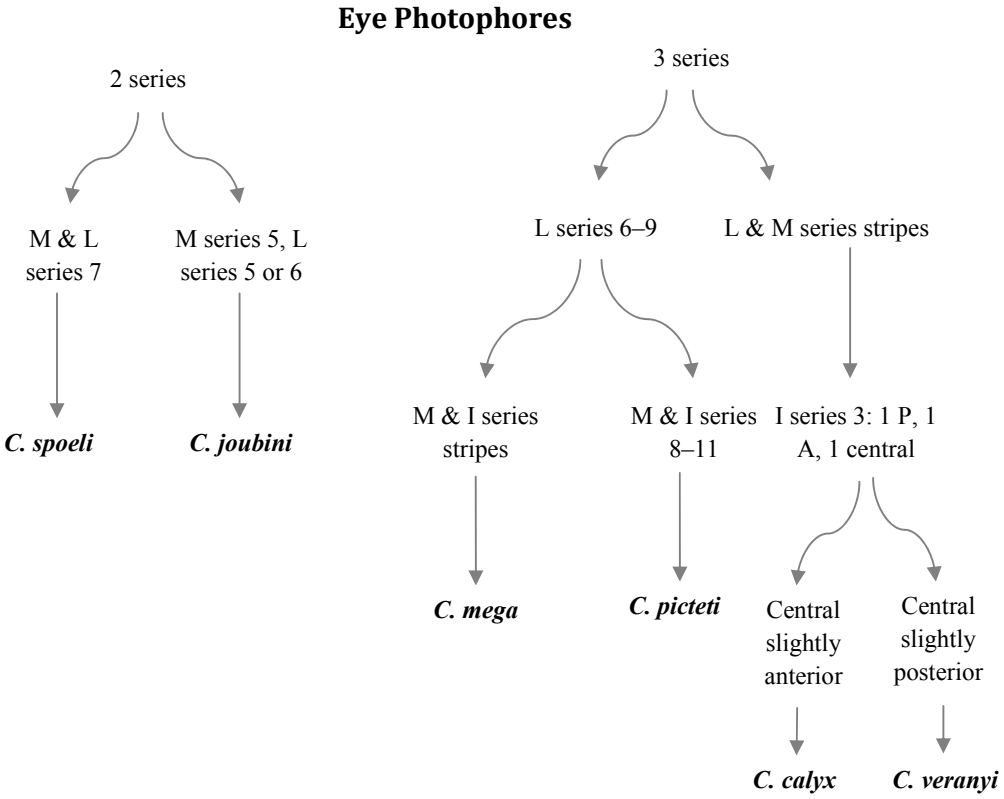

Figure 59. Schematic for species identification (eye photophores)

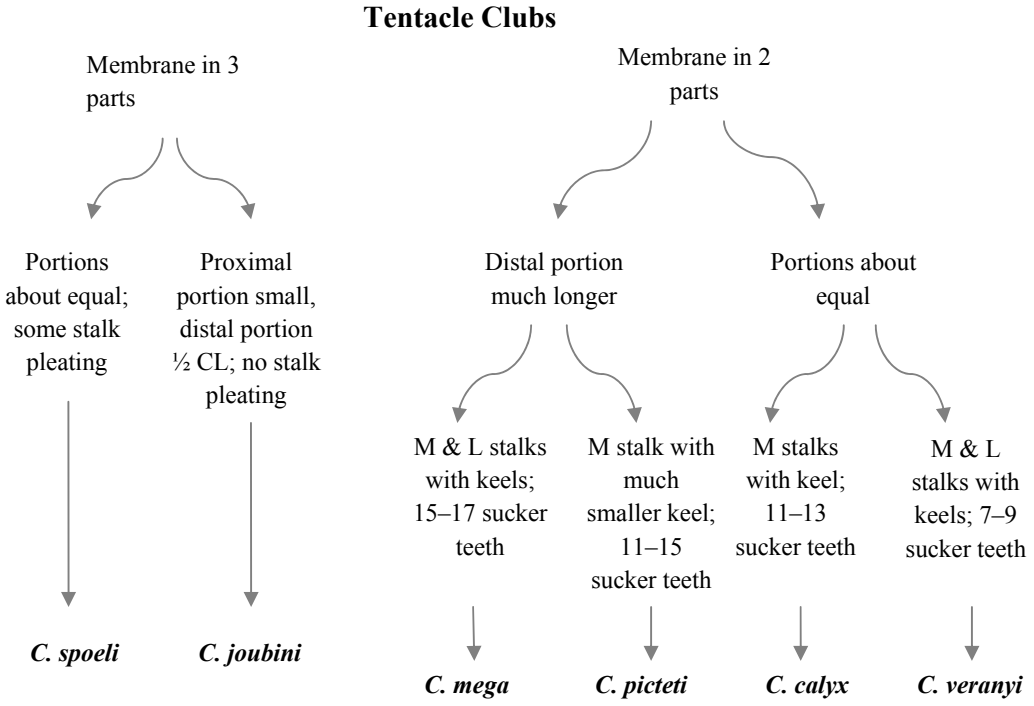

Figure 60. Schematic for species identification (tentacle club morphology)

Table 6. Characters of subgenera *Chiroteuthis* and *Chirothauma* (*sensu* Salcedo-Vargas, 1996)

	Chiroteuthis	*Chirothauma*
1	Body short to medium	Body long and slender
2	Mantle tapering gradually, without swollen part in end of fin mantle-insertion	Cylindrical anteriorly but abruptly tapered posteriorly with swollen part in posterior end of fins
3	Tail small	Not described
4	Club-area bordered symmetrically with small trabeculae	Not described
5	Wide trabeculated part or fin-like, non-trabeculated membrane present in first third of club-area	Not described
6	Sucker stalk thick and cylindrical, thinner stalk that bears suckers protrudes from skirt, cup or ring-like thickened section	Not described
7	Large sucker in arms II and III of some species	Not described
8	2 stripes or rows of photophores on eyeball	Eyeball has 22-27 photophores arranged in 3 rows of photophores
9	1 or 2 photophores on ink-sac	0 or 2 ink sac photophores round or drop-like shape
10	Not described	Fins medium to large, heart shaped
11	Not described	Anti-tragus strongly developed and usually larger than tragus
12	Not described	Club-area strongly trabeculated, with 60-85 trabeculae
13	Not described	Sucker stalk bears raised keel which ends at base
14	Not Included	9-18 sharp teeth in distal margin, but central median tooth largest
15	Not Included	Chromatophores arranged in circular pattern

Table 7. Subgenera *Chiroteuthis* (*Cs*.) and *Chirothauma* (*Cm*.) character states for species

	C. (Cs.) veranyi	*C. (Cs.) calyx*	*C. (Cs.) joubini*	*C. (Cs.) spoeli*	*C. (Cm.) mega*	*C. (Cm.) picteti*
1	√	√	√	**X**	√	√
2	√	√	√	√	√	√
3	0	0	√	√	0	0
4	√	√	√	√	0	0
5	0	0	√	√	0	0
6	√	√	√	√	0	**X**
7	0	√	0	√	0	0
8	**X**	**X**	√	√	√	√
9	√	√	—	√	√	√
10	0	0	0	0	0	0
11	0	0	0	0	0	√
12	0	0	0	0	√	0
13	**X**	**X**	**X**	0	√	√
14	0	**X**	0	0	√	√
15	—	—	—	—	—	—

√ = species state matches ascribed subgenus state. **X** = species state matches opposite subgenus state. 0 = does not match either subgeneric state OR the state is not specified for the ascribed subgenus, but it does not match the opposite subgenus. — = not described or conflicting evidence.

It transpires that characters 1 (body shape), 6 (specific details of sucker-stalk morphology), 8 (two stripes or rows of photophores on eyeball), 13 (further details of sucker-stalk morphology) and 14 (details of sucker-ring dentition) (see Table 6) are of limited value for differentiating subgenera of *Chiroteuthis*, at least in accordance with the classification proposed by Salcedo-Vargas (1996). Some of these characters may prove of value in subsequent classifications, in the event taxa are distributed amongst them appropriately (Figures 58–60). For instance, aspects of eye photophore distribution are used in that 'grouping' classification advocated by Roper & Young (1998), and employed herein also.

Although the three taxa now recognised from New Zealand waters are relatively well described, and their specific identity now known, the current knowledge of *Chiroteuthis* diversity in New Zealand is hindered by both a lack of specimens, and the quality of available specimens. For taxonomic purposes, future collections should ensure adoption of preservation techniques more appropriate for cephalopods, as low pH in poorly (if at all) buffered fixatives has resulted in loss of all sucker rings on many specimens (and accordingly loss of systematic data). Specimens should be frozen only as a last resort, as this technique results in the specimen becoming very gelatinous and deformed. It is also important that specimens be placed into appropriate-sized containers (many older museum specimens had been crammed into inappropriate-sized containers, with some specimens folded in half at the neck, with the arms packed in wherever they would fit).

There is much about this group that is unknown, but the most pressing matters which need to be resolved are the real diversity, geographic and bathymetric distribution and abundance of taxa, their ontogenetic variation, and life-history parameters, not limited to New Zealand waters. With this advanced knowledge, and with advances in molecular analysis, the validity of species and subgenera can be more appropriately appraised. The Chiroteuthidae is a family of squids that does require more intensive investigation in a world-wide review or taxa.

Perhaps the only life-history contribution made herein is the recognition that (remarkably) no single female had spermatophores embedded in any of her body tissues, whether in the mantle, arms, head, around the beaks, or physically inserted into the viscera, and very few specimens would appear to be mature. The terminal spade-like modification of the male's terminal organ ("penis") is suggestive of it being used to directly impregnate the female with spermatophores in a manner similar to that

proposed for *Pholidoteuthis massyae* (O'Shea *et al*. 2007), but the reproductive behaviour and life cycles of these species remain unknown. It is possible that larger, mature and mated *Chiroteuthis* specimens occur at depths greater than those regularly trawled in New Zealand waters for commercial fisheries (to 1300 metres), which may explain their absence from collections.

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