Two New 'Bottletail Squids' (Cephalopoda: Sepiadariidae) from New Zealand, with New Observations on *Sepioloidea pacifica* (Kirk, 1882)

Jaever Marcel Santos

Department of Applied Ecology

2020

A thesis submitted to Auckland University of Technology in partial fulfilment of the requirements for the degree of Master of Science (Research)

supervised by Dr Kathrin Bolstad[1], Dr Heather Braid[1], and Dr Amanda Reid[2]

1: AUT Lab for Cephalopod Ecology & Systematics, Auckland University of Technology, Auckland, New Zealand.

2: Australian Museum Research Institute, Sydney, Australia.

ABSTRACT

Members of the cephalopod family Sepiadariidae, sometimes called 'bottletail squids', are known exclusively from the Indo-Pacific and southwest Pacific. To date, only one nominal species has been described from New Zealand waters: *Sepioloidea pacifica* (Kirk, 1882). However, researchers have long suspected the presence of additional *Sepioloidea* species. Herein, the majority of known *Sepioloidea* material from New Zealand national collections was examined; both morphological, and, where available, molecular characters were compared.

As a result, this thesis describes two new species (*Sepioloidea* n. sp. 1, and *Sepioloidea* n. sp. 2) using this integrative taxonomic approach, with relevant features of *Sepioloidea pacifica* redescribed and illustrated for comparison. *Sepioloidea* n. sp. 1 is distinguished from its congeners by its tentacular club sucker arrangement (transverse rows of ten suckers), hectocotylus structure, and relatively large size at maturity (to ~56 mm mantle length). The distal ~25% of the hectocotylus is modified with ~15 pairs of distinct spire- and tongue-shaped lappets. In *Sepioloidea* n. sp. 2 the tentacular club suckers are in transverse rows of six or seven suckers and females possess ruffled buccal membrane. The hectocotylised arm is modified distally along 50% of its length with ~16 pairs of globular-tipped spire-shaped lappets.

Molecular data support these morphological differences, with the minimum interspecific distance (11.09 %) being far greater than the maximum intraspecific distance (1.57 %) for COI (cyctochrome *c* oxidase subunit I). Some differences in collection depth are also apparent, with *S.* n. sp. 1 collected at depths of 73–911 m, while *S.* n. sp. 2 has been collected at depths of 0–440 m, and present data support *S. pacifica* being a shallow-dwelling species, known from depths of 0–55 m.

These findings triple the known diversity of *Sepioloidea* in New Zealand waters and nearly double the number of known species in the genus.

KEYWORDS: Cephalopoda, Sepiadariidae, *Sepioloidea*, bottletail squid, taxonomy, southwest Pacific

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ATTESTATION OF AUTHORSHIP

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

Jaever Marcel Santos

DEDICATION

I dedicate this thesis to my parents, Virgilio & Jael Santos.

Thank you for supporting me to follow my squid-filled dreams.

Papa, mum, I love you both very much.

ACKNOWLEDGEMENTS

This thesis was written with the help of countless hands. Those listed below and many more have selflessly reached out to teach me, support me, and hold me up in the most difficult of times.

To Kat Bolstad, thank you for welcoming me into the ALCES family. More than a supervisor, you are a leader and an invaluable friend to us all. You gave me a balance between instruction, freedom to explore, and moral support. Before I walked into your office, I didn't even know dorsal from ventral on a squid, but now here I am with a solid goal of becoming a taxon authority. I will always be grateful for the knowledge, experience, and crazy that you have imparted with me. Thank you.

To Heather Braid, I would have never pulled through this year without your unwavering support. From the post-it notes to the sand, I'm thankful for it all. It goes without saying that the molecular work in this thesis only exists thanks to your patience in teaching me, and your incredible expertise. Thank you for giving these squids the genetic evidence they needed to be recognised. Who knew that this thesis would end one day, and that I'd be okay?

To Mandy Reid, thank you for bringing me into your world of sepiolids. With always my best interests at heart, you have pushed me to be more critical, curious, and meticulous than I could have ever imagined. Thank you for helping to open doors that only existed in my dreams. From one ratbag to another, I look forward to all the science and mischief that lies ahead.

Thank you once again to my supervisors. I am so honoured to have my name alongside yours.

I acknowledge all the collections staff, and curators from the following institutions that have facilitated the research in this thesis: The Museum of New Zealand Te Papa Tongarewa, NIWA Taihoro Nukurangi, the Auckland War Memorial Museum Tāmaki Paenga Hira, and the Australian Museum. Thank you for your custodial care of these cephalopods and all other treasures in your collections.

An extra special thank-you to Severine Hannam at the Auckland War Memorial Museum Tāmaki Paenga Hira. Thank you for giving me the privilege of volunteering and working with you. My love and respect for collections started with you. I truly hope I can make you proud.

I am surrounded by friends who have supported me through the many years it has taken me to reach this point. I am lucky in saying that this list is too long to write in full. The presence or absence of names do not reflect the immense love I have for them all.

Grace Lee, Dayeon Nam, Amy Huang, John Haines-Brand, thank you for always being there, for feeding me, for drying my tears, and for making me laugh. I couldn't be where I am today without you all.

Catherine Meyer, Devina Shetty, thank you for always either putting a smile on my face, or joining me in my worries. I am so grateful for every step in our lives that has led us together. Along with Nick and Jade, you have made my last moments in New Zealand some of the best.

Yiming Xu, Scott Moo, Clemson Campos, and Ken Neth Yeoh, thank you for always having my back. Danny Kwok and Kenji Kamimura, thank you for the music we've made together. Grey Pham, thank you for turning some of the hardest moments of this thesis into the happiest.

One final big thank-you to the cephalopods of the world. I look forward to many more frustrating years of trying to unlock your secrets.

ABBREVIATIONS

AWMM — Auckland War Memorial Museum, New Zealand

Coll. — collector

FV — fishing vessel

MFish — (formerly) New Zealand Ministry of Fisheries (now Ministry of Primary Industries)

MPI — New Zealand Ministry of Primary Industries

NIWA — National Institute of Water and Atmospheric Research, Ltd

NMNZ — Museum of New Zealand Te Papa Tongarewa

NTM — Museum and Art Gallery Northern Territory (formerly Norther Territory Museum), Darin, Australia

RV — research vessel

SD — standard deviation

SOP — Scientific Observer Programme

Stn — station

INTRODUCTION

General introduction. The cephalopod order Sepiolida contains small animals commonly referred to as 'bobtail' and 'bottletail squids' although they are not true squids (orders Myopsida and Oegopsida). Sepiolids are characterised by their short, broad, bell-shaped mantle; adults range from ~20–80 mm in mantle length (ML), possess a ventral eyelid pore, have broad fins and their gladius is either reduced or absent. Sepiolids occur in tropical, temperate, and even subpolar oceans (Reid & Jereb, 2005). Most are benthic animals that inhabit the neritic zone, while some are known to be largely pelagic.

Humans have relatively little interest in the consumption of sepiolids compared to the consumption of octopuses and true squids. While not yet commercially exploited by fisheries, sepiolids are reported to be of use in local cuisines, sometimes as a delicacy (Reid & Jereb, 2005).

To date, only three nominal sepiolids have been recorded from within the New Zealand Exclusive Economic Zone (EEZ) (Spencer *et al.*, 2016; Vecchione *et al.*, 2013): *Sepioloidea pacifica* (Kirk, 1882) from the family Sepiadariidae Fischer, 1882, and *Heteroteuthis dagamensis* Robson 1924 and *Stoloteuthis maoria* (Dell, 1959), both in the family Sepiolidae Leach, 1817. Out of these two families, the Sepiolidae family is currently better represented in scientific literature. Recent research includes investigations into animal-bacteria symbioses and the viability of sepiolids as model organisms to study cephalopod development (Lee *et al.*, 2009). The present research focuses on the relatively understudied sepiadariids. Excluding species descriptions, published research on this group consists of proteome analyses of defensive slimes which point to a novel basis for gel formation (Caruana *et al.*, 2016, 2019, 2020) and the identification of novel parasitic dicyemid species (Catalano & Furuya, 2013).

Sepiadariidae presently contains eight nominal species across two genera (WoRMS Editorial Board, 2020) and are widely distributed across the benthos of the Indo-Pacific and southwest Pacific (Reid & Jereb, 2005). This thesis focuses on *Sepioloidea* d'Orbigny, 1845, which is currently known only from Australasian waters, with one nominal species reported from New Zealand: *Sepioloidea pacifica*. However, local cephalopod researchers and curators have long suspected the presence of additional species, represented by material in national collection facilities including the Museum of New Zealand Te Papa Tongarewa (NMNZ), the National Institute of Water and Atmospheric Research, Ltd (NIWA), and the Auckland War Memorial Museum (AWMM). These additional species are superficially similar in their gross morphology which is a reflection of their sharing of a genus but have been mis-identified largely due to the lack of specialist examination prior to this study. One potentially novel taxon was initially recognised as a subject of taxonomic interest due to the relatively

large size of mature specimens (up to three times the average mantle length of mature *S. pacifica*), while the other came to notice through peculiarities of its tentacle club morphology and opportunistic genetic sequencing. These specimens have often been informally designated within collections conservatively as '*Sepioloidea* sp. nov.', or 'Sepiolida' until detailed study and comparison with other described sepiadariids could be undertaken.

Preliminary examination revealed additional morphological characters that were consistently different from the other known *Sepioloidea* species — *S. lineolata* (Quoy & Gaimard, 1832), *S. pacifica*, and *S. magna* Reid, 2009 — indicating that more detailed investigation was, indeed, warranted. An integrative taxonomic approach was adopted for this investigation, combining molecular (cytochrome *c* oxidase subunit I [COI]) and morphological evidence to review the true diversity represented by *Sepioloidea* material collected to date within New Zealand waters.

Historical taxonomy. The taxon that would become the type species of *Sepioloidea* was first described as *Sepiola lineolata* Quoy & Gaimard, 1832, from a specimen found in Jervis Bay, New South Wales, Australia. Subsequent recognition that it lacked the distinct characters of true *Sepiola* (diagnosis at the time: hectocotylised left Arms I, ventral mantle indentation and projections to accommodate the funnel, kidney-shaped visceral photophores, and a rudimental gladius; diagnosis revised by Bello [2020]) led d'Orbigny (1842) to erect the new subgenus *Sepioloidea*, with *Sepiola lineolata* as its type species by monotypy, remaining within the family Sepiolidae. Later, another sepiolid genus, *Sepiadarium* Steenstrup, 1881, was defined and immediately placed alongside *Sepioloidea* as a sister taxon. Fischer (1882) acknowledged the characters shared by *Sepioloidea* and *Sepiadarium* and accordingly grouped these genera within his new family Sepiadariidae. This systematic arrangement is accepted in current taxonomic accounts (e.g. Reid, 2016; Young, 2010), and the sister-group relationship between Sepiolidae + Sepiadariidae, and *Sepiadarium* + *Sepioloidea* within the Sepiadariidae, have also been recovered as part of a recent broader phylogenetic analysis of decapodiform cephalopods (Anderson & Lindgren, 2020).

Since its description, *S. lineolata* has been reported from north Queensland to southern Australia and Western Australia in nearshore waters (Atlas of Living Australia, 2020). However, populations from each of these three broad locations appear geographically disjunct leading to questions regarding whether these records do, in fact, represent a single species (Reid, 2009). This requires further investigation.

Like *S. lineolata, Sepioloidea pacifica* was originally placed within *Sepiola* by its author (Kirk, 1882), who briefly and vaguely described its body shape and colour. Suter (1913) briefly mentioned *Sepiola pacifica* in his manual of New Zealand molluscs, but simply

repeated Kirk's notes on body shape and colour. Following the regrettable loss of Kirk's holotype (collected from Wellington Harbour, New Zealand), Dell (1952) redescribed the species based on 56 males and one female from Lyttelton Harbour, New Zealand and moved it into *Sepioloidea* based on shared characters with *S. lineolata*. These shared characters were outlined in his updated generic diagnosis for *Sepioloidea* which include a small, bell-shaped body, a dorsal mantle continuous with the head, mantle and funnel locking cartilage, a hectocotylised left ventral arm, and a lack of gladius. This redescription was far more thorough than the original description, adding important details about morphological proportions, funnel and hectocotylus structures, sucker formation, chromatophore distribution, and internal anatomy; he also provided images of the whole animal, hectocotylus, beaks, and the reproductive and digestive systems. However, Dell was only able to establish a neotype seven years later upon obtaining a specimen from the original type locality, Wellington Harbour (Dell, 1959). Through his establishment of a neotype and his thoroughly documented observations, Dell's redescription stands as a robust basis for identifying *S. pacifica*. Reports from surveys conducted since then have supported Dell's list of records and added new ones. *Sepioloidea pacifica* is now known to occur over a wide geographic range from Manukau Harbour (37° 1' 48" S, 174° 31' 48" E) in the North Island of New Zealand (Morrison *et al.*, 2002) to the Otago Peninsula (45° 50' S, 170° 55' E) in the South Island (Probert *et al.*, 1979). *Sepioloidea pacifica* is presently reported to occur in high numbers in inshore sand and muddy sand habitats (Probert *et al.*, 1979), and has a reported depth range of 15–550 m (Powell, 1979).

The third nominal *Sepioloidea* species, *S. magna*, was described based on nine specimens from the Arafura Sea, between northern Australia and Kep, Tanimbar (Indonesia) collected at 225–300 m depth (Reid, 2009). Since then, additional *S. magna* specimens have been identified among museum collections, extending the known distribution of *S. magna* farther across the Northwest Shelf, Scott Reef, and the Timor Sea (Reid, personal communication).

Based on our current understanding of the genus *Sepioloidea* and its three nominal species (*S. lineolata*, *S. pacifica* and *S. magna*) as outlined above, this thesis reviews *Sepioloidea* material from the New Zealand Exclusive Economic Zone, aiming to clarify the identities of the resident *Sepioloidea* fauna.

MATERIALS AND METHODS

Systematics. To facilitate direct comparisons among taxa, a revised diagnosis for *S. pacifica* is provided based on the results of this study, along with supplementary information reporting traits not included in the existing taxonomic literature (Dell, 1952, 1959; Kirk, 1882).

Specimens. Preserved *Sepioloidea* specimens were loaned from the Museum of New Zealand Te Papa Tongarewa (NMNZ) and the National Institute for Water and Atmospheric Research, Ltd (NIWA) both in Wellington, New Zealand; the Auckland War Memorial Museum (AWMM) in Auckland, New Zealand; and the Australian Museum (AM) in Sydney, Australia. Depths for each specimen lot are given when available. When a depth range is given, specimens may have been collected at any depth covered within the range. Single depths will only refer to an accurate collection depth if an opening-closing net was used and this information is not always available. In total, 610 fixed specimens were examined; an additional 61 frozen specimens were sequenced (with those of suitable condition also morphologically examined and identified to species) representing most coastal areas of the New Zealand land mass and some offshore locations (Fig. 1). Specimens previously identified as *Sepioloidea pacifica* were compared with the neotype and earlier descriptions. Specimens that appeared to belong to the family Sepiadariidae were selected for examination, those in good condition were examined in detail in order to write species descriptions and develop reliable characters that could be used for differentiating species.

Collection dates are given as the format dd/mm/yyyy (e.g. 31/01/2000), or mm/yyyy when day of collection was not recorded. Illustrations and schematic drawings were drawn either by hand or created using the 'GNU Image Manipulation Program (GIMP)' version 2.10.12 software. All image editing was processed in GIMP. Distribution maps were created with ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, CA).

Morphological examination. Morphological examinations focused primarily on external anatomy, with some internal characters assessed where possible. Terminology for anatomical structures followed Roper & Voss (1983) with notes on any additions and alterations listed in Table 1. Following Reid (2009), this study adopted the measurement of 'Fin Insertion anterior' (FIa) and the definition of the 'Arm Sucker Count' (ASC) (Fig. 2). Due to the unreliable nature of finding a halfway measure, ASC in this paper refers to the total number of suckers along an arm rather than along the basal half as in Roper & Voss (1983). Measurements were based on 10 mature specimens of each sex where possible; where damaged specimens have been excluded from a measurement, the new sample size is given as (n = x). Ranges of indices are given in the format x–y–z where x and z are the lowest and highest observed values respectively, and y is the mean. All intact mature

specimens were sexed while those that were too damaged to be determined are instead labelled ‘sex indet.’ All measurements are given in millimetres (mm).

DNA barcoding. Tissue samples were obtained from 61 frozen or ethanol-fixed specimens. (Formalin-fixed specimens were not used for the genetic analysis because DNA is extremely difficult or impossible to recover from such material.) Small tissue samples of mantle or fin tissue were subsampled (~1–3 mm^3). These tissue snips were kept frozen at –20°C until DNA extraction, or fixed in either 100% or 80% ethanol, and stored at room temperature. These specimens were examined to determine congruence with morphological patterns observed among preserved material.

DNA extraction used EconoSpin (Epoch Life Science) spin columns with QIAGEN reagents following the protocols for the DNeasy Blood & Tissue Kit (QIAGEN). The DNA barcode region (648 bp region from the 5' end of the mitochondrial gene region of COI) was amplified using Folmer *et al.* (1994) primers LCO1490/HCO2198. Polymerase chain reaction (PCR) was carried out in 12.5 µL reaction volumes with: 6.25 µL 10% trehalose, 2 µL double distilled H_2O, 1.25 µL 10X buffer, 0.625 µL $MgCl_2$ (50 mM), 0.1 µL LCO1490 (10 µm), 0.1 µL HCO2198 (10 µm), 0.0625 µL 10 mM deoxynucleoside triphosphate (dNTP), 0.06 µL Platinum Taq polymerase (5 U/µL), and 2 µL of DNA. The thermocycle reaction profile was as follows: hot start of 94°C for 1 min; 5 cycles of 94°C for 40 s, 45°C for 40 s, 72°C for 1 min; 35 cycles of 94°C for 40 s, 51°C for 40 s, 72°C for 1 min; extension at 72°C for 5 min, hold 4°C indefinitely.

The amplification success of PCR products was ascertained visually using a 1% agarose gel stained with GelRed (Biotium). A single, clear band on the gel indicated successful amplification. Samples were sequenced by Macrogen (Korea) using the same primers used for PCR. Bidirectional sequences were assembled into contigs and edited in CodonCode Aligner v.9.0.1 software (CodonCode Corporation). Sequences were aligned using Multiple Alignment using Fast Fourier Transform (MAFFT) (https://www.ebi.ac.uk/Tools/msa/mafft/) and uploaded to the Barcode of Life Data System (BOLD) (Ratnasingham & Herbert, 2007) in a project titled ‘New Zealand Sepiolids’ (project code: NZSEP). Sequences were screened for contamination using the Basic Local Alignment Search Tool (BLAST) through GenBank.

Sequences were combined with those from *Sepioloidea lineolata*, the only other sequenced nominal *Sepioloidea* species (sequences for *Sepioloidea magna* are not currently available). The outgroup species, *Rossia pacifica* Berry 1911, was chosen because the family to which it belongs (Sepiolidae) has a sister relationship with Sepiadariidae (Groenenberg *et al.*, 2009).

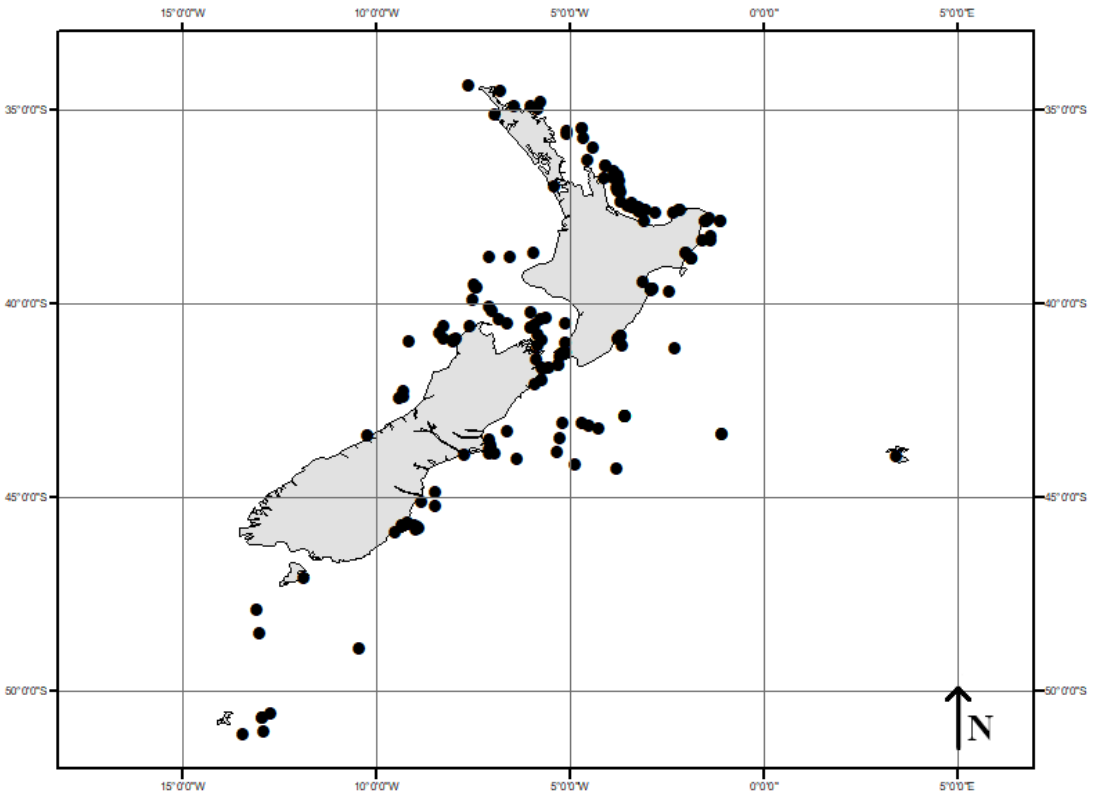

Fig. 1 Collection locations for New Zealand *Sepioloidea* specimens examined in this study.

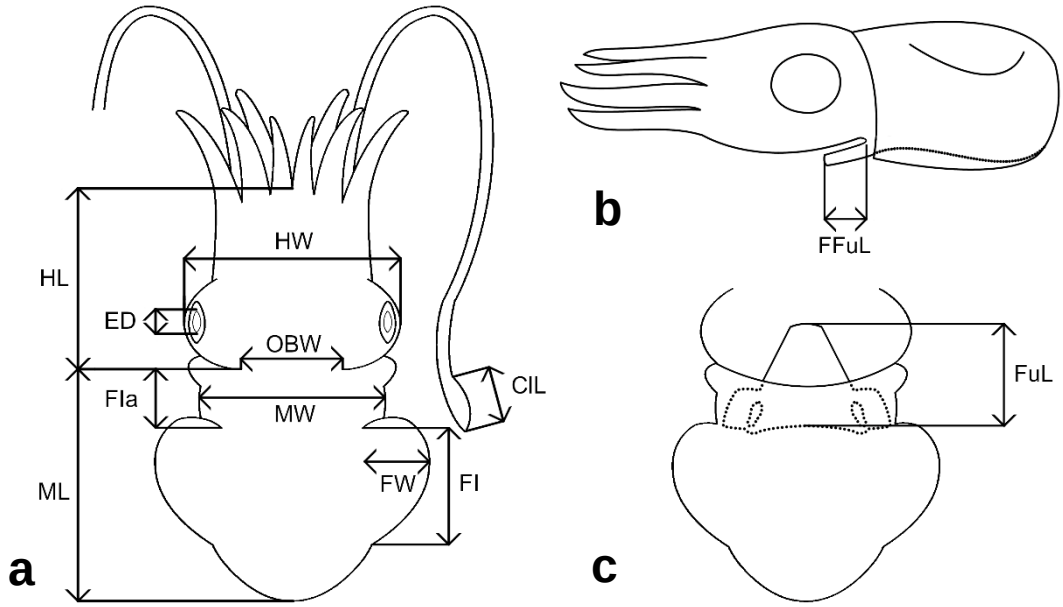

Fig. 2 Sepiolid measurements and acronyms: **a** dorsal view showing measurements; **b** lateral view showing free funnel length (FFuL); **c** ventral view showing funnel length (FuL).

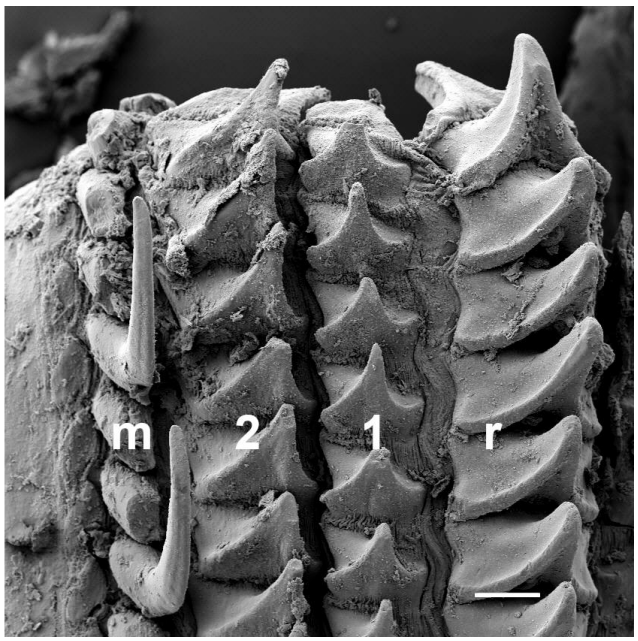

Fig. 3 SEM of lateral half of *Sepioloidea* n. sp. 1 radula: **r**, rachidian tooth; **1**, first lateral tooth; **2**, second lateral tooth; **m**, marginal tooth. Scale bar = 200 µm.

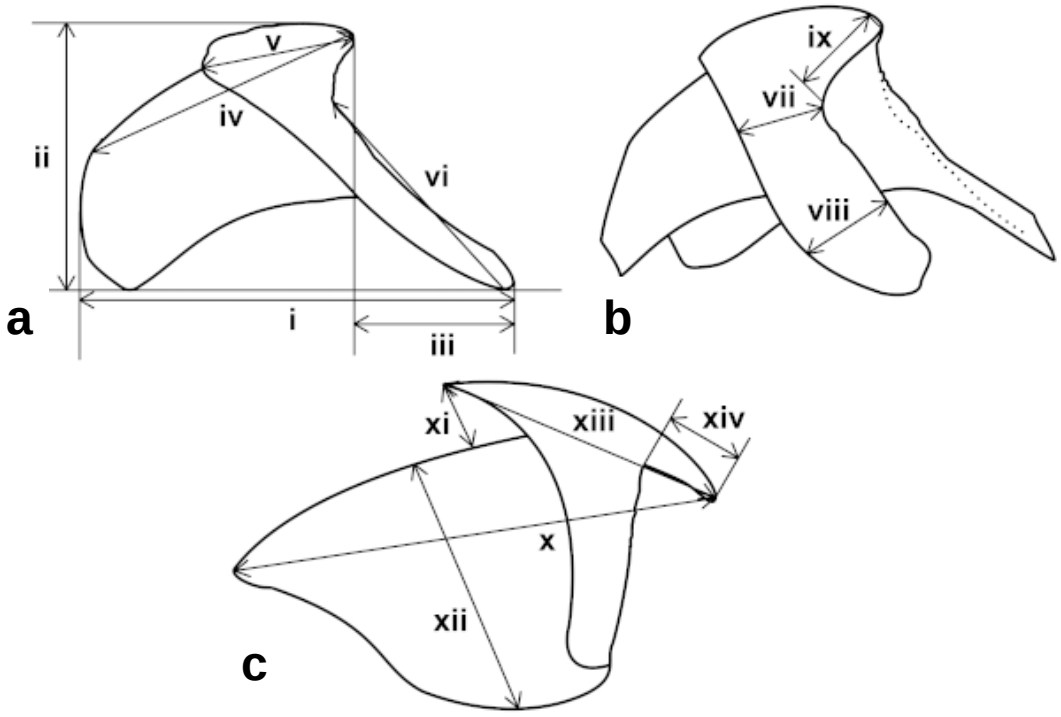

Fig. 4 Sepiolid beak measurements: **a** lower beak, lateral view (**i,** baseline; **ii**, beak height; **iii**, rostral tip behind leading edge of wing; **iv**, crest length; **v**, hood length; **vi**, wing length); **b** lower beak, oblique view (**vii**, minimum wing width; **viii**, maximum wing width; **ix**, lower rostral length); **c** upper beak, lateral view (**x**, beak length; **xi**, hood height; **xii**, beak height; **xiii**, hood length; **xiv**, upper rostral length).

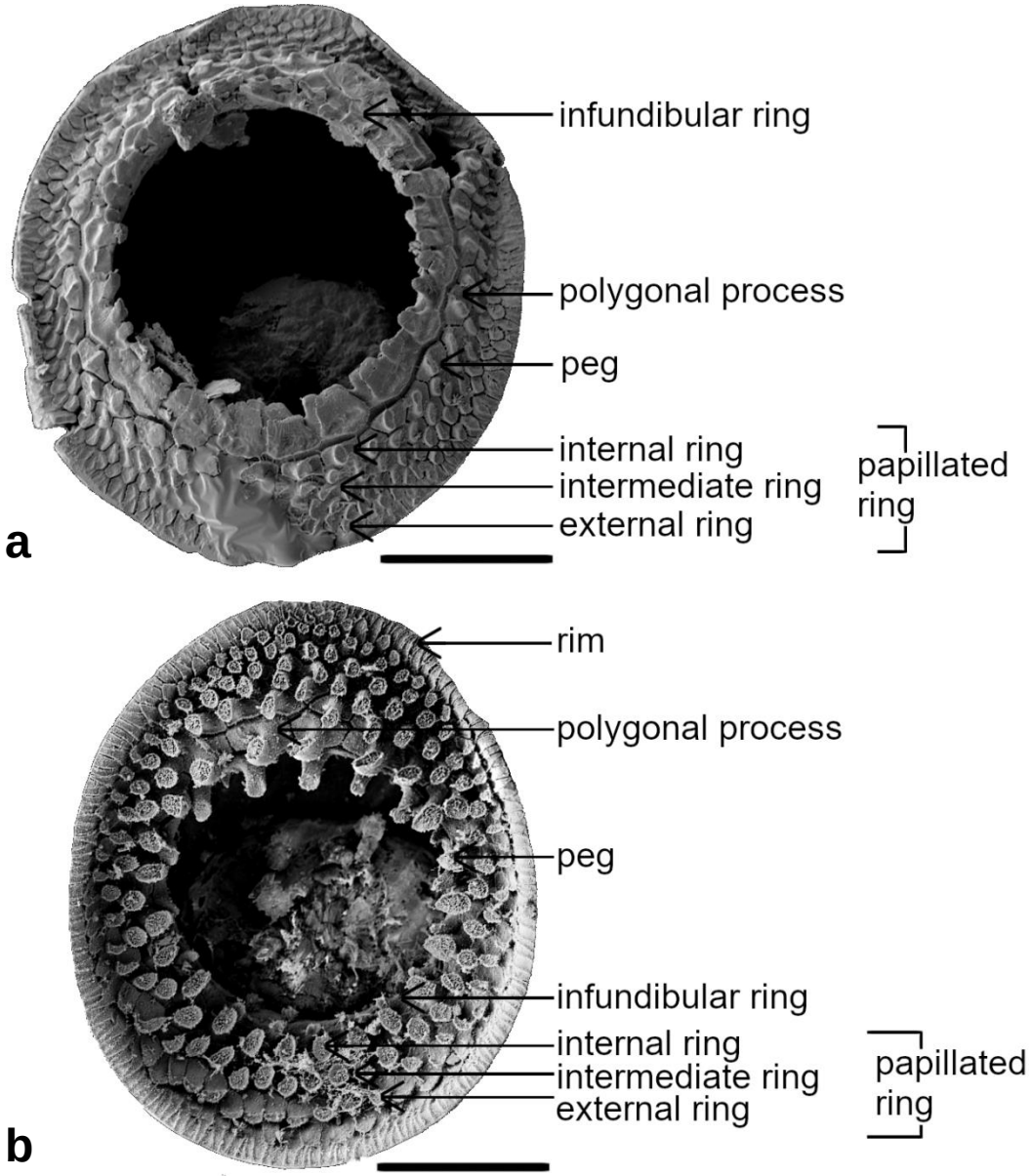

Fig. 5 SEM of *Sepioloidea pacifica* suckers showing terminology: **a** arm sucker; **b** club sucker. Scale bars = 100 μm.

Table 1 Description of measurements and counts, following Roper & Voss (1983). Metrics used in Reid (2009) indicated by single asterisks (*), new metrics indicated by double asterisks (**). Indices are shown in square brackets and are calculated as a percentage of mantle length. An exception is HcModLI, which is calculated as a percentage of hectocotylus length.

Feature	Abbreviation	Description
Arm length	**AL**	Length of each designated arm (i.e. I, II, III, IV) measured from most basal sucker to distal tip of arm (Arms I, dorsal; II, dorso-lateral; III, dorso-ventral; IV, ventral). [**ALI**].
Arm sucker count*	**ASC**	Total number of suckers on each designated arm (e.g., ASC1 for the total count on Arms 1).
Arm sucker diameter	**AS**	Diameter of largest normal sucker on each designated arm. [**ASIn**].
Club length	**ClL**	Length of tentacular club measured from proximal-most basal suckers to distal tip of club. [**ClLI**].
Club row count	**ClRC**	Number of longitudinal rows of suckers across the width of the club.
Club sucker diameter	**ClS**	Diameter of largest sucker on tentacular club. [**ClSI**].
Egg diameter	**EgD**	Diameter of largest egg in ovary. [**EgDI**]
Eye diameter	**ED**	Diameter of eye opening. [**EDI**].
Fin insertion	**FI**	Length of fin as joined to mantle. [**FII**].
Fin insertion anterior*	**FIa**	Anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle. [**FIIa**]
Fin width	**FW**	Greatest width of one fin. [**FWI**].
Free funnel length	**FFu**	Length of funnel from anterior funnel opening to point of dorsal attachment to head. [**FFuI**].
Funnel length	**FuL**	Length of funnel from anterior funnel opening to posterior margin measured along ventral midline. [**FuLI**].
Head length	**HL**	Dorsal length of head from point of fusion of dorsal arms to anterior midpoint of junction between head and mantle [**HLI**].
Head width	**HW**	Greatest width of head at level of eyes. [**HWI**].
Hectocotylus lappet pair count**	**HcLPC**	Number of lappet pairs on hectocotylised arm.
Hectocotylus length	**HcL**	Length of hectocotylus measured from basalmost sucker to distal tip. [**HcLI**].
Hectocotylus modification length**	**HcModL**	Length of modified section of hectocotylus. [**HcModLI**] (as a percentage of hectocotylus length).
Hectocotylus sucker count**	**HcSC**	Total number of suckers on hectocotylus.
Hectocotylus sucker diameter	**HcS**	Diameter of largest sucker on hectocotylus [**HcSI].**
Mantle length	**ML**	Dorsal mantle length measured from anterior-most point of mantle to posterior apex of mantle.
Occipital band width	**OBW**	Minimum width of band of skin that joins head to mantle [**OBWI**]
Spermatophore length	**SL**	Longest developed spermatophore in Needham's Sac. [**SLI**]

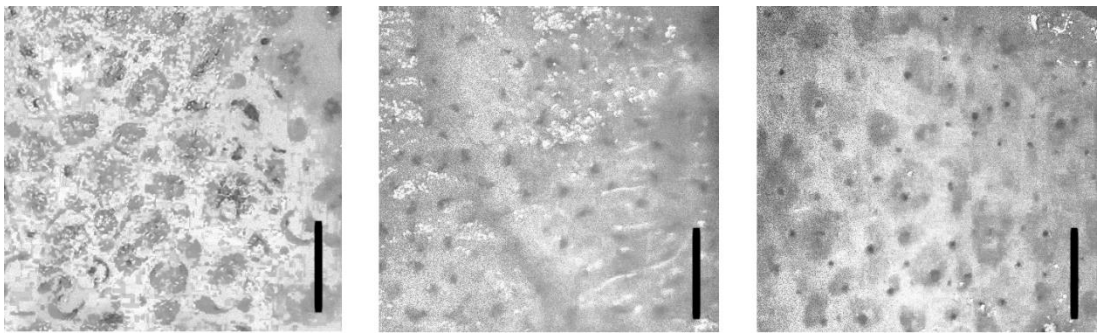

Fig. 6 Compound microscope image of dorsal mantle chromatophore patterns in preserved New Zealand *Sepioloidea*: **a** *S. pacifica* chromatophores with larger, lighter, irregular-shaped spots and smaller, darker spots; **b** *S.* n. sp. 1 chromatophores with tiny, evenly distributed dots; **c** *S.* n. sp. 2 chromatophores with light, large spots, and tiny, dark dots. Scale bar = 1 mm.

In preparation for scanning electron microscopy (SEM) tentacle clubs and radulae were critical-point dried at the University of Auckland and the Auckland University of Technology. Radular teeth descriptions (Fig. 3) follow Reid (2009). Arm suckers were air dried for at least 24 hours in a lightly sealed box containing desiccating beads. All specimens were mounted, plated with platinum, and imaged at the Auckland University of Technology with a Hitachi SU-70 SEM operated at 5kV. Beaks (Fig. 4) were described following Clarke (1986) and drawn from photographs. Arm and tentacular sucker descriptions and terminology were based on Salcedo-Vargas (1995) (Fig. 5). Chromatophore patterns and terminology are described according to patterns shown in Fig. 6.

Spermatophores were obtained from mature male specimens. Those closest to the genital opening were extracted and mounted on microscope slides in glycerine.

None of the specimens available for this study were in pristine condition. This is due to several factors including sample age, preservation, and collection method. Cephalopods trawled from depth tend to be damaged to varying degrees and the fixation of specimens sometimes causes tissues to contract. Measurements taken may not precisely reflect those of live or fresh individuals.

SYSTEMATICS

Family **Sepiadariidae Fischer, 1882**

Genus ***Sepioloidea* d'Orbigny [in Férussac & d'Orbigny], 1842**

Diagnosis [modified from Reid, 2009]. Body short and broad (MWI ~85% ML) with round posterior mantle. Fins narrow (FWI ~22% ML), positioned medially on sides of body, attachment long (FI ~80% Fin Length). Head and mantle fused at occipital band. Mantle and funnel-locking cartilage with two separate components. Arms joined by web with sheath at tentacle base between Arms III and IV. Hectocotylus present, left ventral arm distally modified with lappets. Gladius absent. Light organs absent.

Remarks. Indices in the diagnosis above exclude *S. lineolata* due to lack of available data on *S. lineolata* measurements and indices.

Type species: *Sepiola lineolata* Quoy & Gaimard, 1832.

Sepioloidea pacifica (Kirk, 1882)

(Figs 7–11, 37, 38; Tables 7, 8)

Sepiola pacifica Kirk, 1882: 283–284.

Sepioloidea pacifica (Kirk, 1882): Dell, 1952: 82–87, tables 21–23, fig. 5, pl. 33–35. Dell, 1959: 2–3 (in part); Hurst, 1969: 8–10, fig. 3 (in part); Powell, 1979: 440 (in part).

Type material examined. NMNZ M.12954 (Neotype, Dell [1959]), 1♀, ML 21 mm, 41° 15′ 30″ S, 174° 55′ 0″ E, 24/05/1953, Coll. J. Moreland.

Comparative material examined. (*) indicates specimens that have been sequenced. (^) indicates specimen lots with GPS coordinates estimated from locality descriptors. **NIWA 142282**, 4♂, ML 11–14 mm, 3♀, ML 20–21 mm, 35° 7′ 12″ S, 173° 5′ 35″ E, 24 m, 05/02/1977, Coll. NZOI, Stn P58; **NMNZ M.012960**, 1♀, ML 12 mm, 36° 19′ 27″ S, 175° 27′ 55″ E, 30 m, 14/05/1954, Coll. W. Sampson on FV *Zyder Zee*; **NMNZ M.074121**, 1♂, ML 14 mm, 36° 45′ 0″ S, 175° 4′ 0″ E, 26–31 m, 10/10/1965, RV *Ikatere*; **NMNZ M.287469**, 2♀, ML 21–22 mm, 37° 0′ 0″ S, 174° 36′ 30″ E, 3 m, 27/04/1994, Coll. S. J. O'Shea on RV *Tangaroa*; **NMNZ M.287397**, 1♀, ML 20 mm, 37° 51′ 24″ S, 178° 54′ 36″ E, 30 m over 904 m, 18/04/1980, RV *James Cook*, Stn J08/05/80; **NMNZ M.074214**, 5♂, ML 8–16 mm, 10♀, ML 9–17 mm, 37° 51′ 48″ S, 176° 56′ 48″ E, 34–39 m, 21/01/1979, RV *Tangaroa*, Stn 1979728; **NMNZ M.067236**, 11♂, ML 9–14 mm, 11♀, ML 9–20 mm, 38° 42′ 10″ S, 178° 0′ 41″ E, 18–26 m, 09/01/1980, RV *James Cook*, Stn J01/01/80; **NMNZ M.067308**, 2♂, ML 8–14 mm, 3♀, ML 10–16 mm, 38° 42′ 10″ S, 178° 0′ 41″ E, 18–26 m, 09/01/1980, RV *James Cook*, Stn J01/01/80; **NMNZ M.287491**, 1♀, ML 17 mm, 38° 43′ 18″ S, 178° 1′ 42″ E, 20 m over 21 m, 19/02/1984, RV *James Cook*, Stn J04/12/84; **NMNZ**

M.067316, 1♂, ML 10 mm, 1♀, ML 12 mm, 38° 49′ 35″ S, 178° 8′ 29″ E, 29 m over 47–89 m, 09/01/1980–10/01/1980, RV *James Cook*, Stn J01/02/80; **NMNZ M.067297**, 1♂, ML 12 mm, 38° 50′ 12″ S, 178° 9′ 12″ E, 30 m, 18/11/1979, RV *James Cook*, Stn J16/02/79; **NMNZ M.006297**, 1♂, ML 12 mm, 39° 27′ 30″ S, 176° 54′ 0″ E, 15 m, 21/05/1952, MV *Kotuku*, Stn 1952155; **NMNZ M.287488**, 12♂, ML 15–17 mm, 4♀, ML 14–21 mm, 39° 38′ 37″ S, 177° 7′ 35″ E, 51–52 m, 22/06/1983, FV *Kalinovo*, Stn K11/001/83; **NMNZ M.287492**, 7♂, ML 11–15 mm, 4♀, ML 10–14 mm, 39° 39′ 33″ S, 177° 5′ 58″ E, 12 m, 22/06/1983, FV *Kalinovo*, Stn K11/004/83; **NMNZ M.074124**, 1♀, ML 18 mm, 40° 54′ 0″ S, 172° 4′ 0″ E, 55 m, 10/03/1976, RV *Acheron*, Stn 1976530; **NMNZ M.074223**, 10♂, ML 15–19 mm, 1♀, ML 25 mm, 41° 2′ 0″ S, 174° 54′ 0″ E, 50 m, 25/05/1970, Coll. E. K. Saul; **NMNZ M.012955**, 2♀, ML 15–17 mm, 41° 15′ 30″ S, 174° 54′ 0″ E, 24/05/1953, Coll. J. M. Moreland; **NMNZ M.012956**, 1♀, ML 25 mm, 41° 15′ 30″ S, 174° 55′ 0″ E, 0 m, 14/07/1954, Coll. J. C. Yaldwyn; **NMNZ M.287498^**, 3♂, ML 15–17 mm, 6♀, ML 11–26 mm, 41° 16′ 21″ S, 174° 51′ 26″ E; **NMNZ M.287504**, 1♂, ML 19 mm, 41° 17′ 53″ S, 174° 50′ 04″ E, 5 m, 14/06/1983, Coll. A. L. Stewart, G. S. Hardy; **NMNZ M.074215**, 2♂, ML 15–17 mm, 4♀, ML 14–23 mm, 41° 27′ 0″ S, 174° 8′ 36″ E, 27–28 m, 28/01/1979, RV *Tangaroa*, Stn 1979775; **NIWA 142703***, 1 indet., 42° 49′ 31″ S, 170° 29′ 43″ E, 43–47 m, 09/04/2019, RV *Kaharoa*, Stn KAH1902/63; **NIWA 142704***, 8 indet., 42° 56′ 34″ S, 170° 26′ 19″ E, 31–32 m, 09/04/2019, RV *Kaharoa*, Stn KAH1902/64; **NIWA 142705***, 7♀, 43° 27′ 4″ S, 169° 36′ 32″ E, 45–48 m, 12/04/2019, RV *Kaharoa*, Stn KAH1902/69; **NIWA 142283**, 1♂, ML 19 mm, 2♀, ML 20–24 mm, 43° 31′ 52″ S, 172° 56′ 46″ E, 25–26 m, 12/12/1996, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9618/1; **NMNZ M.005631** (Vouchers, Dell [1952]), 10♂, ML 14–16 mm, 1♀, ML 20 mm, 43° 38′ 26″ S, 172° 57′ 57″ E, 0 m, 1949, Coll. E. Percival, G. A. Knox; **NMNZ M.287511**, 1♂, ML 15 mm, 43° 47′ 0″ S, 172° 56′ 0″ E, 5 m, 27/09/1976, RV *Acheron*, Stn 1976552; **NMNZ M.074131**, 2♀, ML 16–18 mm, 43° 51′ 30″ S, 172° 55′ 30″ E, 15 m, 27/09/1976, RV *Acheron*, Stn 1976553; **NMNZ M.090341**, 1♀, ML 20 mm, 43° 52′ 0″ S, 173° 6′ 0″ E, 44 m, 27/09/1976, RV *Acheron*, Stn 1976556; **NIWA 84786**, 1♀, ML 24 mm, 43° 53′ 35″ S, 172° 17′ 24″ E, 13 m, 17/12/1999, Stn Z9964; **NMNZ M.013470**, 1♀, ML 15 mm, 43° 56′ 49″ S, 176° 33′ 03″ E, 0 m, 29/01/1954, MV *Alert*; **NMNZ M.011032**, 2♂, ML 16–17 mm, 6♀, ML 18–24 mm, 45° 40′ 0″ S, 170° 51′ 0″ E, 37 m, 13/01/1957, MV *Alert*, Stn 1957198; **NMNZ M.074092**, 1♂, ML 11 mm, 45° 41′ 41″ S, 170° 48′ 56″ E, 33 m, 04/03/1930, Coll. D. H. Graham; **NMNZ M.287406**, 1♀, ML 16 mm, 45° 43′ 0″ S, 170° 42′ 0″ E, 27 m, 04/1975, RV *Acheron*; **NMNZ M.008859**, 3♀, ML 7–14 mm, 45° 43′ 47″ S, 170° 41′ 31″ E, 22 m, 27/06/1954, MV *Alert*; **NMNZ M.011039**, 3♂, ML 6–15 mm, 1♀, ML 15 mm, 1 indet., ML 4 mm, 45° 53′ 08″ S, 170° 30′ 57″ E, 0 m, 21/01/1979, Coll. R. K. Dell, J. M. Moreland; **NMNZ M.074222**, 4♂, ML 9–15 mm, 47° 3′ 54″ S, 168° 10′ 0″ E, 0 m, 02/03/1972, Coll. J. M. Moreland; **NMNZ M.287505**, 1♀, ML 15 mm, 1982, RV *James Cook*, Stn J16/94/82.

Revised diagnosis. Mantle length up to ~20 mm in mature males and ~25 mm in mature females (specimens examined range in size from 6–26 mm ML). Anterior mantle margin without fringing projections. Chromatophores as larger, light, irregular-shaped spots, and smaller, darker spots; no stripes. All arm suckers biserial throughout. Male and female suckers decrease in size from base to distal tip; minor enlargement in mid Arms I male suckers. Ventral left arm hectocotylised: distal ~50% of arm modified; basal unmodified section with ~6 sucker pairs; modified section curved, without suckers but with sucker pedicels joined basally and modified forming ~20 lappets; each lappet consists of two shape patterns: wedge-like ventrally, bilobed dorsally. Tentacular club suckers set in transverse rows of approximately five, noticeably largest midway along dorsal club margin.

Supplementary information. Eyes large in both sexes, occupying large portion of head; aperture covered by transparent membrane. Arm sucker-size arrangement similar in males and females: largest basally, uniformly decreasing in size distally. Males Arms I an exception, slightly enlarged mid-arm. Arm sucker ring sizes similar between sexes; infundibulum primarily smooth in males (Fig. 7), slightly crenulated in females (Fig. 8). Papillated ring with about four concentric rings of polygonal processes. Internal ring consists of ~21–32 pentagonal polygonal processes; inner margin flat, outer margin pointed, each process with ridge-like peg running medially from inner to outer margins, either straight or crescentric. Intermediate rings with ~35–70 flat, scale-like, polygonal processes that decrease in size and increase in number towards external ring. Intermediate ring polygonal processes with pegs in females; smooth in males. Hectocotylus sucker rims do not differ from those on opposite right arm IV (Fig. 7). Sucker rim ultrastructure does not differ along the length of the arm.

Left ventral arm of males hectocotylised (Fig. 9a): unmodified proximal section with ~6 normal sucker pairs; distal ~50% modified. Modified section devoid of suckers, modified sucker pair pedicels form fused lappets; lappets wedge-like ventrally, bilobed dorsally.

Tentacle stalks long, slender, semi-circular in cross-section, without suckers. Clubs (Fig. 9b) expanded, tapering to a blunt tip. About five suckers per transverse row, set on short pedicels. Suckers usually largest along medial 25–50% of club dorsal margin. Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacular suckers (Fig. 10) with irregular ovoid pegs. Pegs widely spaced; underlying polygonal processes visible between pegs; peg surfaces pitted. Proximal suckers asymmetrical; rim with lip on aboral margin; pegs in up to seven intermediate rings. Distal suckers symmetrical; rim lip absent; pegs in about four intermediate rings. Inner ring consists of ~13 pegs, external ring with ~40–60 pegs.

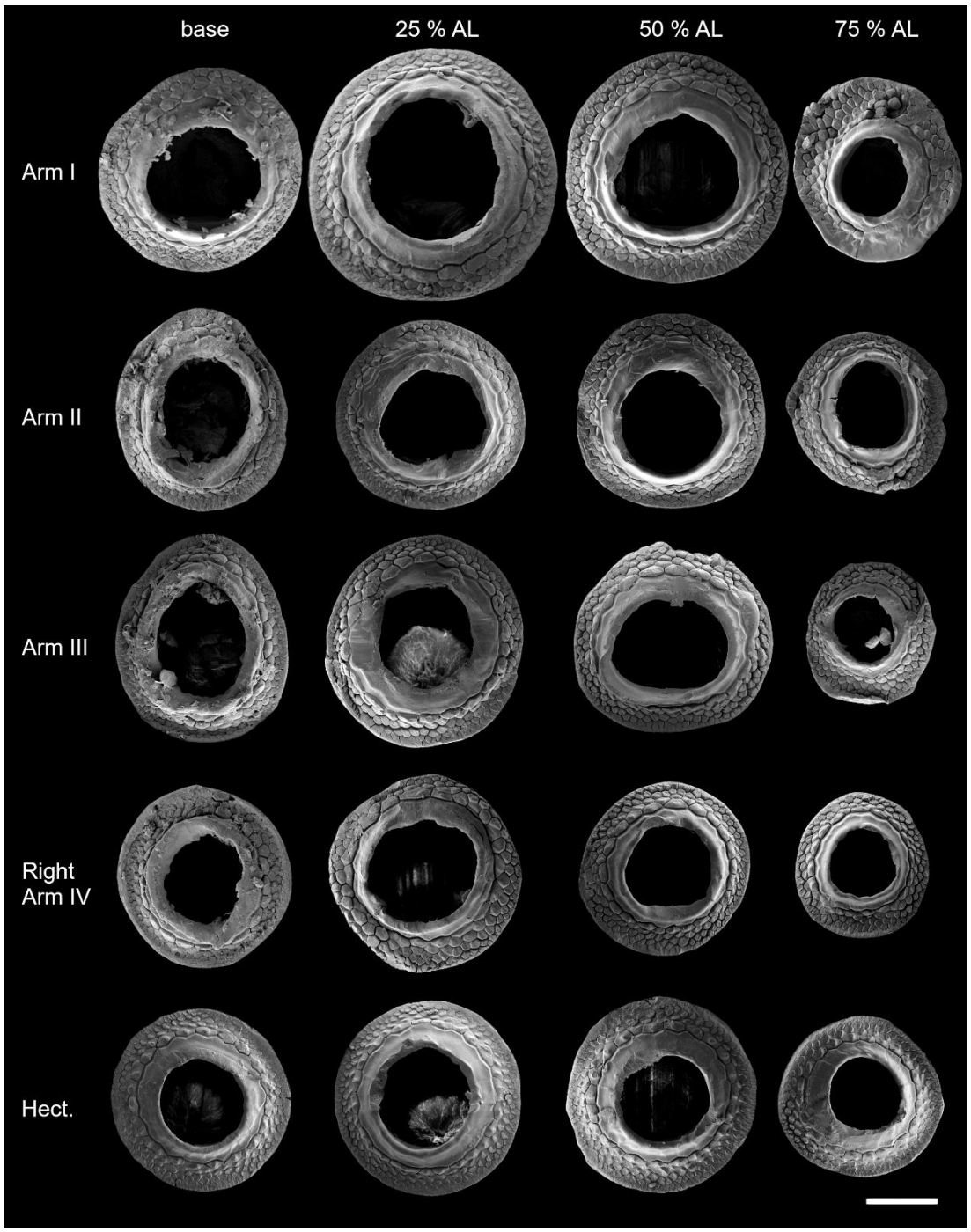

Fig. 7 SEM of *Sepioloidea pacifica*: male arm suckers (hect, hectocotylus; NMNZ M.074214, ♂, 14 mm ML). Scale bar = 100 µm.

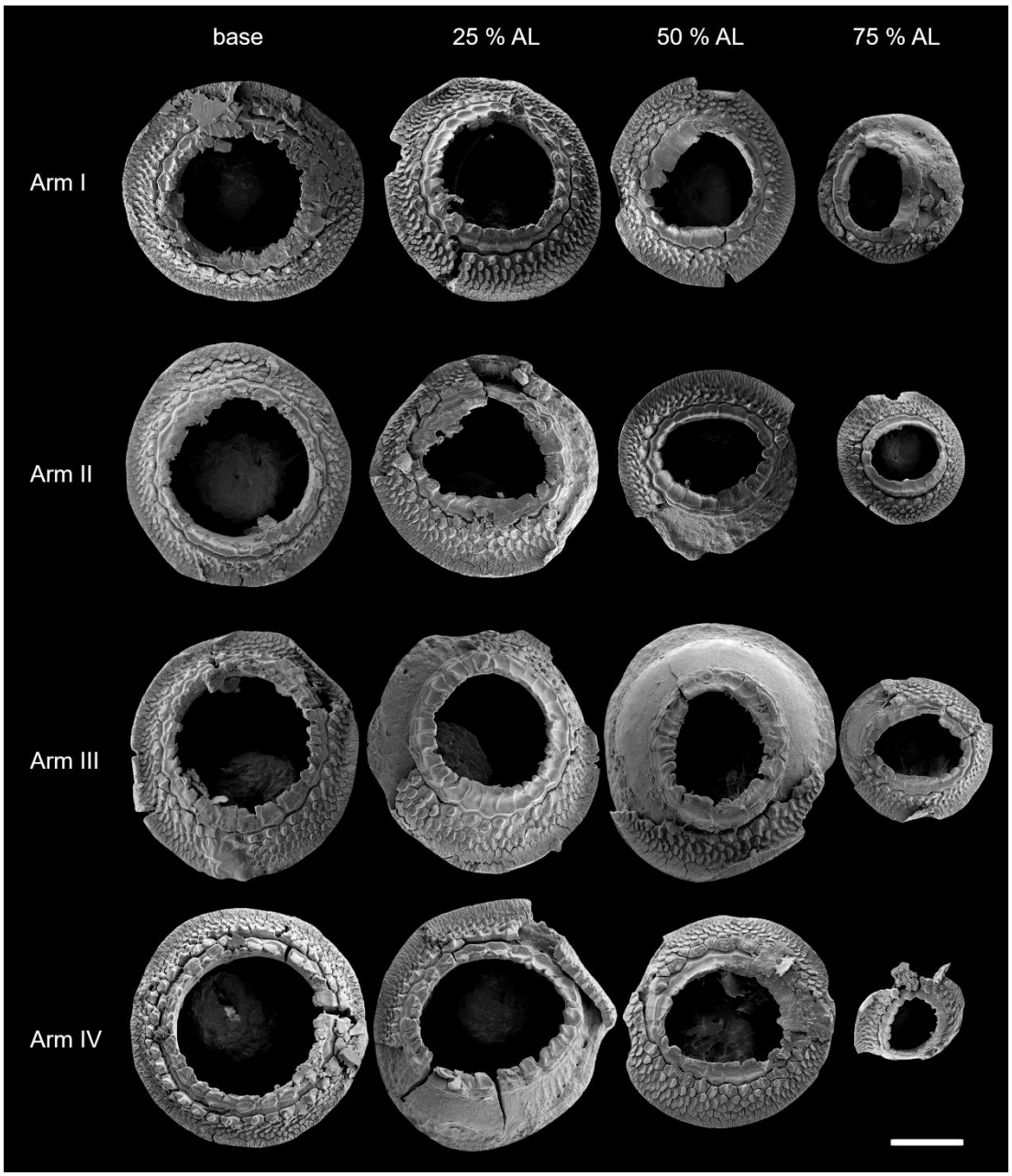

Fig. 8 SEM of *Sepioloidea pacifica*: female arm suckers (NMNZ M.12955, ♀, 17 mm ML). Scale bar = 100 µm.

Preserved specimen colouration varies from pale cream to dark brown. Chromatophores (Fig. 6a) visible as both tiny dots and larger spots, dark brown/purple, evenly distributed across dorsal surface of mantle, fins, head, and along Arms I–III; sparsely concentrated on ventral surfaces of the mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club, small and densely set near tip, proximally larger and very sparse, continuing along stalk for 150% club length.

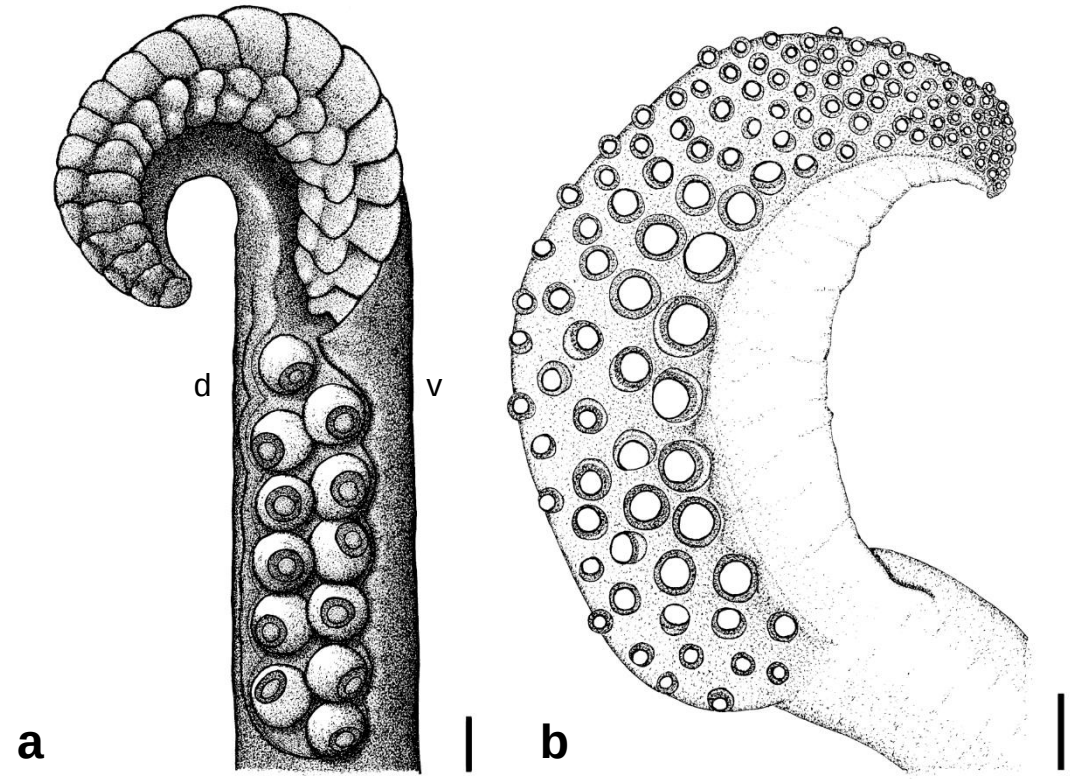

Fig. 9 *Sepioloidea pacifica*: **a** hectocotylised left arm IV, oral view (d, dorsal; v, ventral; NMNZ M.005361, ♂, 16 mm ML); **b** tentacular club (NMNZ M.012955, ♂, 17 mm ML). Scale bars = 500 µm.

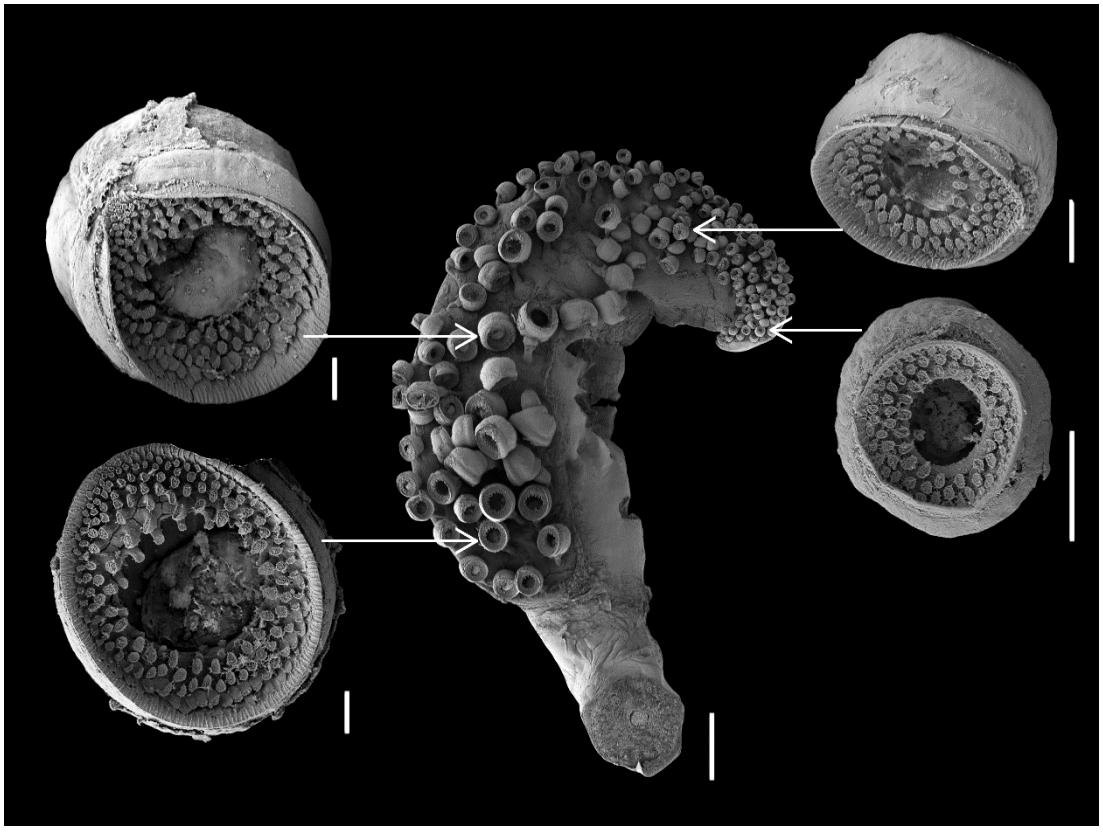

Fig. 10 SEM of *Sepioloidea pacifica*: tentacular club and suckers (NMNZ M.012955, ♀, 17 mm ML). Scale bars = suckers 50 µm, club 500 µm.

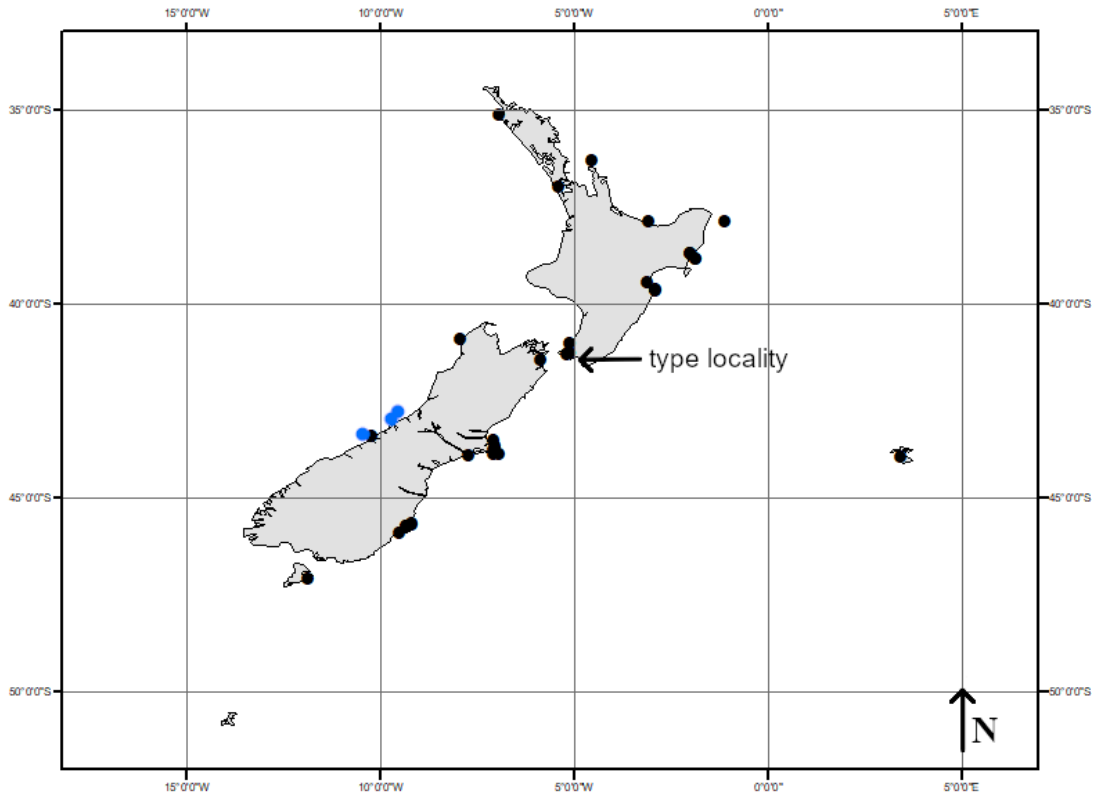

Fig. 11 Distribution of *Sepioloidea pacifica* specimens examined in this study including sequenced (blue) and non-sequenced (black) specimens.

Type locality. Lowry Bay, Wellington Harbour, Wellington, New Zealand, 41º 15′ 30″ S, 174º 54′ 30″ E, 0 m [otter trawl].

Known distribution (Fig. 11). Southwest Pacific, New Zealand including Chatham Islands; 0–110 m.

Remarks. Morphological differences between *S. pacifica* and all other recognised *Sepioloidea* are highlighted in the Remarks after each species description below and summarised in Table 7. Previous authors have referred to relatively deep-water representatives of this species (e.g. Dell, 1959: 2: "large specimens … from depths greater than 75 fathoms [137 m]"; Hurst, 1969: 3: "deep-water specimen … collected from depths of 140 and 210 meters"; Powell, (1979): 440: "*Sepioloidea pacifica* … Dunedin Harbour. Off eastern Otago, 75–300 fathoms [137–550 m]."). It is now known that these references likely refer to other *Sepioloidea* species. Further details of the "in part" entries in the *S. pacifica* synonymy above are provided in the Remarks sections for *S.* n. sp. 1 and *S.* n. sp. 2 below.

This study provides the first known genetic sequences for *S. pacifica* (see Molecular Results below). Specimens morphologically identified as *S. pacifica* showed a low intraspecific distance and a high interspecific distance, which strongly supports the morphological characters found herein to define *S. pacifica sensu stricto*.

A single specimen has also been reported from the Sala y Gómez submarine ridge of the eastern Pacific (Parin *et al.*, 1997) but could not be examined in this study to confirm its identity. The outlying specimen collected from the Chatham Islands has been thoroughly examined and conforms in all traits with *S. pacifica* from the North and South Islands.

Sepioloidea n. sp. 1

(Figs 12–24, 37, 38; Tables 2, 3, 7, 8)

Sepioloidea pacifica (not Kirk, 1882): Dell (1959) (in part): "large specimens…from depths greater than 75 fathoms" [p. 2]; Hurst (1969) (in part): "deep-water specimen … collected from depths of 140 and 210 meters" [p. 3]; Powell, (1979): "*Sepioloidea pacifica* … Dunedin Harbour. Off eastern Otago, 75–300 fathoms [p. 440].

Type material examined. (*) indicates specimens that have been sequenced. *Holotype:* **NMNZ M.118323**, 1♂ ML 28 mm, 50º 40′ S, 167º 06′ E, 367–528 m, 02/1994, FV *Peterson*. *Paratypes:* **NMNZ M.330520**, 5♂ ML 30–33 mm, 50º 40′ S, 167º 06′ E, 367–528 m, 02/1994, FV *Peterson*; **NMNZ M.330521**, 4♂ ML 26–30 mm, 50º 40′ S, 167º 06′ E, 367–528 m, 02/1994, FV *Peterson*; **NMNZ M.330522**, 4♀ ML 50–56 mm, 50º 40′ S, 167º 06′ E, 367–528 m, 02/1994, FV *Peterson*; **NMNZ M.330523**, 3♀ ML 40–55 mm, 50º 40′ S, 167º 06′ E, 367–528 m, 02/1994, FV *Peterson*; **NIWA 95297***, 1♀ ML 54 mm, 50º 30′ S, 167º 18′ E, 160–228 m, 15/04/2016, SOP Trip 4669/23**; NIWA 128471***, 2♀ ML 36–47 mm, 51º 2′ 31″ S, 167º 7′ 33″ E–51º 1′ 26″ S, 167º 9′ 7″ E, 492 m, 09/03/2007, Stn TON0701/55.

Additional material examined. (*) indicates specimens that have been sequenced. (^) indicates specimen lots with GPS coordinates estimated from locality descriptors. **NMNZ M.074144**, 1♀, ML 39 mm, 34° 49′ 0″ S, 174° 17′ 0″ E, 468–475 m, 24/02/1974, RV *Acheron*; **NMNZ M.015785**, 1♀, ML 49 mm, 35° 28′ 0″ S, 175° 19′ 0″ E, 512 m, 11/11/1962, RV *Ikatere*, Stn 1962075; **NMNZ M.015786**^, 1♂, ML 29 mm, 35° 28′ 0″ S, 175° 19′ 0″ E, 366 m, 28/09/1962, RV *Ikatere*; **NMNZ M.287476**, 1♀, ML 51 mm, 36° 35′ 22″ S, 176° 10′ 29″ E, 355 m, 08/01/1995, RV *Kaharoa*, Stn KAH9501/18; **NIWA 142285***, 1♂, ML 19 mm, 36° 40′ 55″ S, 176° 14′ 46″ E, 470–468 m, 24/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/37; **NIWA 84776**, 1♀, ML 46 mm, 37° 0′ 25″ S, 176° 16′ 41″ E, 425 m, 21/10/1996, Coll. NIWA, MFish, Z8579; **NIWA 84774**, 1♀, ML 51 mm, 37° 5′ 36″ S, 176° 15′ 12″ E, 393 m, 22/01/1998, Coll. MFish, NIWA, Z9011; **NIWA 84775**, 1♀, ML 46 mm, 37° 5′ 36″ S, 176° 15′ 12″ E, 393 m, 22/01/1998, Coll. MFish, NIWA, Z9011; **NIWA 142297***, 1♀, ML 22 mm, 37° 8′ 38″ S, 176° 19′ 37″ E, 472–473 m, 21/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/23; **NIWA 142299***, 1♀, ML 26 mm, 1 indet., ML 15 mm, 37° 25′ 12″ S, 176° 36′ 29″ E, 557–537 m,

19/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/13; **NMNZ M.118390**, 1♀, ML 47 mm, 37° 31′ 38″ S, 176° 37′ 1″ E, 310–345 m, 10/01/1994, RV *Kaharoa*, Stn KAH9401/25; **NIWA 84785**, 1♀, ML 51 mm, 37° 37′ 0″ S, 176° 48′ 30″ E, 360 m, 21/01/1998, Z9005; **NIWA 84777**, 1♂, ML 23 mm, 3♀, ML 27–35 mm, 41° 4′ 10″ S, 176° 21′ 47″ E, 309 m, 08/05/1999, Coll. NIWA, MFish, Z9827; **NMNZ M.012959**, 1♀, ML 38 mm, 41° 34′ 18″ S, 174° 43′ 18″ E, 274 m, 29/08/1957, FV *Admiral*, Stn 1957099; **NMNZ M.015782^**, 1♀, ML 36 mm, 41° 34′ 18″ S, 174° 43′ 18″ E, 373 m, 25/09/1962, RV *Ikatere*; **NMNZ M.074103**, 1♀, ML 34 mm, 42° 26′ 30″ S, 170° 36′ 30″ E, 366 m, 23/11/1970, RV *James Cook*, Stn J22/59/70; **NMNZ M.119118**, 17♀, ML 45–59 mm, 42º 54′ 0″ S, 176º 26′ 0″ E, 368–411 m, 27/12/1994–18/01/1995, Coll. M. Marinovich on FV *Petersen*; **NMNZ M.119118/1**, 13♀, ML 47–54 mm, 42º 54′ 0″ S, 176º 26′ 0″ E, 368–411 m, 27/12/1994–18/01/1995, Coll. M. Marinovich on FV *Petersen*; **NMNZ M.119118/2**, 13♀, ML 29–54 mm, 42º 54′ 0″ S, 176º 26′ 0″ E, 368–411 m, 27/12/1994–18/01/1995, Coll. M. Marinovich on FV *Petersen*; **NMNZ M.119118/4**, 2♀, ML 52–53 mm, 42º 54′ 0″ S, 176º 26′ 0″ E, 368–411 m, 27/12/1994–18/01/1995, Coll. M. Marinovich on FV *Petersen*; **NIWA 106127***, 2 indet., 42º 54′ 23″ S, 177º 26′ 35″ E, 406–409 m, 16/08/2015, RV *Tangaroa*, Stn 1511/95; **NIWA 92514***, 1 indet., 42º 55′ 14″ S, 174º 36′ 57″ E, 911 m, 25/01/2014, RV *Tangaroa*, Stn 1401/131; **NIWA 106088***, 4 indet., 43º 4′ 25″ S, 175º 1′ 0″ E, 357–367 m, 14/08/2015, RV *Tangaroa*, Stn 1511/71; **NIWA 105547***, 1♀ ML 32 mm, 43° 6′ 0″ S, 174° 50′ 24″ E, 450–480 m, 22/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/98; **NIWA 126973***, 1 indet., 43° 8′ 48″ S, 175° 32′ 29″ E, 414–422 m, 28/01/2018, RV *Tangaroa*, Stn TAN1801/112; **NIWA 105544***, 1 indet., ML 29 mm, 43° 12′ 36″ S, 175° 45′ 0″ E, 425–442 m, 25/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/112; **NIWA 92512***, 1 indet., 43° 15′ 3″ S, 174° 46′ 1″ E, 429 m, 25/01/2014, RV *Tangaroa*, Stn TAN1601/112; **"109DS"*** (material not yet registered), 1 indet., 43° 16′ 34″ S, 177° 5′ 51″ E, 250–275 m, 27/01/2018, RV *Tangaroa*, Stn TAN1801/109; **NIWA 128493***, 2♀ ML 38–44 mm, 43° 22′ 1″ S, 178° 54′ 58″ E, 400–404 m, 19/12/2015, Coll. NIWA on RV *Tangaroa*, Stn TAN1516/155; **NIWA 106212***, 1♂, ML 16 mm, 1♀, ML 22 mm, 43° 22′ 12″ S, 178° 56′ 24″ E, 394–395 m, 20/08/2015, Coll. NIWA on RV *Tangaroa*, Stn TAN1511/134; **NIWA 131078***, 1 indet., 43° 25′ 44″ S, 177° 33′ 4″ E, 306 m, 06/06/2018, RV *Tangaroa*, Stn TAN1805/253; **NIWA 1055457***, 1♀ ML 33 mm, 43° 28′ 12″ S, 174° 45′ 36″ E, 349–372 m, 23/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/102; **NIWA 106078***, 1 indet., 43° 31′ 21″ S, 174° 34′ 53″ E, 487–491 m, 13/08/2015, RV *Tangaroa*, Stn TAN1511/56; **NIWA 106082***, 1 indet., 43° 31′ 43″ S, 174° 35′ 22″ E, 482–487 m, 13/08/2015, RV *Tangaroa*, Stn TAN1511/65; **NIWA 106067***, 1♀, ML 33 mm, 43° 31′ 44″ S, 174° 34′ 28″ E, 497–500 m, 11/08/2015, RV *Tangaroa*, Stn TAN1511/48; **NIWA 106059***, 1 indet., 43° 32′ 23″ S, 174° 35′ 2″ E, 496 m, 11/08/2015, RV *Tangaroa*, Stn TAN1511/50; **NIWA 92513***, 1 indet., 43° 39′ 44″ S, 175° 27′ 46″ E, 304 m, 22/01/2014,

RV *Tangaroa*, Stn TAN1401/116; **NIWA 106117***, 1♀, ML 23 mm, 43° 48′ 16″ S, 176° 35′ 52″ E, 465 m, 15/08/2015, RV *Tangaroa*, Stn TAN1511/89; **NIWA 106070***, 2 indet., 43° 54′ 50″ S, 175° 55′ 36″ E, 528–544 m, 08/08/2015, RV *Tangaroa*, Stn TAN1511/29; **NIWA 106244***, 1♀, 44° 2′ 11″ S, 179° 2′ 44″ E, 305–316 m, 23/08/2015, RV *Tangaroa*, Stn TAN1511/164; **NIWA 128485***, 1♀ ML 33 mm, 44° 5′ 49″ S, 174° 43′ 56″ E, 510–516 m, 11/12/2015, RV *Tangaroa*, Stn TAN1516/59; **NIWA 106095***, 1♂, 1♀, ML 28 mm, 44° 11′ 1″ S, 175° 52′ 14″ E, 444 m, 15/08/2015, RV *Tangaroa*, Stn TAN1511/75; **NIWA 128489***, 3♀, ML 42–50 mm, 44° 15′ 36″ S, 176° 13′ 44″ E, 357–331 m, 10/12/2015, RV *Tangaroa*, TAN1516/65; **NIWA 106104***, 1♀, ML 24 mm, 44° 15′ 44″ S, 176° 13′ 8″ E, 315–328 m, 16/08/2015, RV *Tangaroa*, TAN1511/87; **NMNZ M.011047**, 1♀, ML 37 mm, 45° 44′ 0″ S, 171° 2′ 0″ E, 137 m, 23/01/1957, MV *Alert*, Stn 1957202; **NMNZ M.008944**, 1♂, ML 24 mm, 9 sex indet., ML 6–14 mm, 45° 45′ 24″ S, 171° 5′ 0″ E, 549 m, 16/08/1955, MV *Alert*, Stn 1955190; **NMNZ M.008959**, 2♂, ML20–26 mm, 4♀, ML 29–33 mm, 2 sex indet., ML14–17 mm, 45° 47′ 0″ S, 171° 7′ 0″ E, 457–549 m, 16/08/1955, Stn 1955191; **NIWA 84771**, 2♂, ML 23–24 mm, 48° 54′ 26″ S, 169° 34′ 55″ E, 800 m, 26/04/1998, Z9203; **NMNZ M.330527**, ~260 specimens comprising both sexes, ML 20–37 mm, 12♀, ML 37–43 mm, 50º 40′ 0″ S, 167º 06′ 0″ E, 367–528 m, 02/1994, FV *Peterson*; **NMNZ M.118323/1**, 14♂, ML 20–37 mm, 12♀, ML 37–43 mm, 50º 40′ 0″ S, 167º 06′ 0″ E, 367–528 m, 02/1994, FV *Peterson*; **NMNZ M.287613**, 1♀, ML 37 mm, 51° 7′ 36″ S, 166° 35′ 54″ E, 515 m, 22/04/1997, Coll. C. Morrish on FV *Venture K*, Stn 991/17; **NIWA 84772**, 2♂, ML30–35 mm, 3♀, ML 40–55 mm; **NIWA 84783**, 1♂, ML 29 mm, 2♀, ML 37–41 mm; **NMNZ M.287770**, 1♀, ML 46 mm, FV *Drysdale*, Stn DRY9602/01.

Diagnosis. Mantle length up to ~33 mm in mature males and ~56 mm in mature females. Anterior mantle margin without fringing projections. Chromatophores small and dot-like; no stripes or spots. All arm suckers biserial throughout. Median arm suckers of males enlarged, most prominently in sucker pairs 4–8 on Arms I–III. Modified section of hectocotylus short, slightly curved (distal ~25% of arm); basal unmodified section with ~14 sucker pairs, modified section without suckers but with sucker pedicels joined basally forming ~15 lappets; each lappet comprises a dorsal spire-shaped structure with globular tip and ventral tongue-shaped structure with lobed apex; from proximal to distal end of modified portion of arm, tips of lappets become pointed, rather than rounded. Tentacular club suckers in transverse rows of approximately ten suckers; suckers tiny and uniform in size.

Description. Species sexually dimorphic at maturity. Males smaller than females: ML mature males 26.0–*30.3*–33.0 mm (SD 2.3), mature females 36.0–*49.2*–56.0 mm (SD 6.7). Mantle short, broad; maximum length and width subequal; posterior margin rounded (Figs 12, 13a, 13b). MWI males 72.7–*97.6*–121.4 (SD 12.4), females 66.1–*89.0*–108.3 (SD 13.4). Fins small, narrow, often lobed anteriorly. Fin length approximately 60% ML. FII males

45.5–*52.1*–61.3 (*n* = 9, SD 5.4), females 46.2–*58.4*–65.0 (SD 5.3). FIIa males 20.0–*26.4*–36.7 (*n* = 9, SD 5.4), females 14.5–*20.2*–30.0 (SD 4.4). FWI males 13.3–*19.8*–27.3 (*n* = 9, SD 4.6), females 17.3–*25.1*–34.0 (SD 5.1). Fin tapers to attachment point posteriorly, rarely with tiny convex lobe. Anterior fin convex often with larger lobes projecting slightly beyond anterior attachment point. Anterior fin margin does not reach anterior mantle margin.

Head length and width proportions similar in both sexes: HLI males 66.7–*82.3*–100.0 (SD 10.4), females 67.9–*76.0*–81.5 (SD 4.9); HWI males 63.3–*87.9*–100.0 (SD 10.6), females 58.9–*75.4*–87.5 (SD 9.2). Occipital band width approximately half mantle length in both sexes. OBWI males 33.3–*45.0*–67.9 (SD 10.0), females 33.9–*43.0*–52.5 (SD 5.4). Two pores present on each side of head: one posterolateral to eye, one anteroventral to eye. Eyes large in both sexes, occupying large portion of head; aperture covered by transparent membrane. EDI males 16.7–*21.5*–26.9 (SD 3.3), females 13.0–*16.8*–22.5 (SD 3.2).

Funnel long, muscular; broad basally, tapering to nearly cylindrical anteriorly; extends almost to anterior margin of eye. FuLI males 40.0–*56.1*–65.5 (SD 8.5), females 37.0–*51.1*–61.1 (SD 8.0). FFuI males 16.1–*24.8*–33.3 (SD 6.2), females 16.7–*22.4*–30.0 (SD 5.1). Funnel valve small, semi-circular flap with extended apex inside dorsal rim of funnel aperture. Funnel organ (Fig. 14a) with broad, rounded wedge-shaped ventral components, broadest medially; dorsal component triangular, apex almost meeting ventral component anterior margin.

Funnel component of locking cartilage (Fig. 14c) comprises two pockets: anterior pocket deep, ovular (concavity deepest posteriorly) and posterior pocket shallow narrow groove. Mantle component (Fig. 14b) complements funnel component. Anterior lobe prominent and nose-like in shape, posterior protuberance shallow.

Arms robust, broad basally, tapered distally (Figs 15a, 15b). Arm formula variable; typically, as follows: males, IV > III = II > I; females, IV > III = I > II. ALI4 males 66.7–*89.0*–106.9 (SD 11.3), females 62.5–*77.0*–88.9 (SD 7.5). ALI1 males 53.3–*68.3*–82.1 (SD 9.2). ALI2 females 51.9–*61.4*–70.8 (n = 9, SD 7.2). All arms similar in shape, subtriangular in cross section along whole arm. Arm suckers biserial along whole arm; suckers spherical with chitinous rims; rim always narrower than sucker diameter. Arms connected by membranous web; in males, web depth varies, shallowest at Arms I (one quarter arm length), deepest at Arms III (one third arm length); in females web extends to approximately half of arm length on all arms; arm web absent between Arms IV of males and females. Females with protective membrane bordering lateral margins of arm suckers.

Table 2 Counts, measurements (mm) and indices of mature male *Sepioloidea* n. sp. 1.

Collection	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ
Reg. No.	M.118323	M.330521 (part)	M.330521 (part)	M.330520 (part)	M.330521 (part)	M.330521 (part)	M.330520 (part)	M.330520 (part)	M.330520 (part)	M.330520 (part)
Type	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
ML	28.0	26.0	29.0	30.0	30.0	30.0	31.0	33.0	33.0	33.0
MWI	121.4	107.7	96.6	96.7	103.3	96.7	93.5	97.0	90.9	72.7
FWI	21.4	na	24.1	20.0	13.3	13.3	19.4	18.2	21.2	27.3
FIIa	21.4	na	31.0	20.0	26.7	36.7	22.6	24.2	30.3	24.2
FII	53.6	na	58.6	46.7	50.0	50.0	61.3	48.5	45.5	54.5
FuLI	60.7	57.7	65.5	63.3	40.0	43.3	58.1	60.6	51.5	60.6
FFuI	21.4	26.9	31.0	30.0	16.7	26.7	16.1	27.3	18.2	33.3
HLI	100.0	92.3	79.3	70.0	86.7	86.7	87.1	66.7	72.7	81.8
HWI	100.0	100.0	86.2	83.3	83.3	63.3	87.1	93.9	93.9	87.9
EDI	21.4	26.9	20.7	20.0	16.7	20.0	25.8	24.2	18.2	21.2
OBWI	67.9	42.3	34.5	43.3	33.3	46.7	48.4	48.5	48.5	36.4
AL1I	82.1	65.4	58.6	66.7	53.3	66.7	80.6	75.8	63.6	69.7
AL2I	89.3	84.6	96.6	70.0	70.0	70.0	87.1	87.9	66.7	69.7
AL3I	107.1	76.9	96.6	90.0	70.0	70.0	83.9	81.8	75.8	87.9
AL4I	85.7	100.0	106.9	96.7	66.7	90.0	83.9	90.9	78.8	90.9
ASIn1	7.3	7.4	7.1	5.9	5.3	6.5	6.8	5.9	5.8	6.8
ASIn2	8.0	8.2	7.6	6.1	6.2	7.6	7.7	6.6	5.7	6.9
ASIn3	8.1	7.7	7.2	6.5	6.2	6.4	7.3	6.7	6.1	6.7
ASIn4	8.2	6.4	5.9	5.2	4.7	5.5	6.5	4.9	4.6	6.7
ASC1	48	48	37	47	41	43	40	45	50	46
ASC2	51	47	48	51	45	46	45	48	51	50
ASC3	55	45	53	49	48	50	39	54	54	52
ASC4	43	55	57	49	49	57	55	64	55	53
ClLI	42.9	38.5	na	40.0	36.7	33.3	54.8	42.4	42.4	45.5
ClRC	9	8	na	8	8	8	9	8	6	8
TIRC	50	40	na	40	35	40	40	40	50	50
ClSI	0.7	0.7	na	0.8	0.8	0.9	0.8	0.7	0.8	0.7
HcLI	92.9	84.6	93.1	80.0	63.3	76.7	87.1	87.9	60.6	72.7
HcModLI	34.6	22.7	22.2	20.8	26.3	30.4	25.9	27.6	30.0	33.3
HcLapC	15	15	13	15	14	14	16	14	15	15
HcSC	28.0	28.0	28.0	26.0	27.0	28.0	28.0	29.0	28.0	27.0
HcSI	5.75	4.81	5.17	4.47	4.13	4.33	5.48	4.12	4.45	6.73
SLI	17.9	34.6	27.6	20.0	23.3	23.3	22.6	18.2	21.2	27.3

Table 3 Counts, measurements (mm) and indices of mature female *Sepioloidea* n. sp. 1.

Collection	NIWA	NMNZ	NIWA	NMNZ	NMNZ	NMNZ	NMNZ	NIWA	NMNZ	NMNZ
Reg. No.	128471	M.330523 (part)	128471	M.330522 (part)	M.330522 (part)	M.330522 (part)	M.330523 (part)	95297	M.330523 (part)	M.330522 (part)
Type	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
ML	36.0	40.0	47.0	48.0	50.0	52.0	54.0	54.0	55.0	56.0
MWI	108.3	105.0	97.9	89.6	76.0	76.9	96.3	87.0	87.3	66.1
FWI	27.8	30.0	34.0	25.0	20.0	17.3	22.2	24.1	29.1	21.4
FIIa	19.4	30.0	14.9	22.9	22.0	19.2	20.4	18.5	14.5	19.6
FII	61.1	65.0	59.6	60.4	56.0	46.2	61.1	61.1	60.0	53.6
FuLI	61.1	57.5	55.3	60.4	46.0	48.1	50.0	37.0	41.8	53.6
FFuI	27.8	30.0	19.1	22.9	30.0	19.2	16.7	16.7	20.0	21.4
HLI	77.8	77.5	72.3	79.2	74.0	80.8	79.6	81.5	69.1	67.9
HWI	83.3	87.5	83.0	83.3	70.0	69.2	68.5	70.4	80.0	58.9
EDI	19.4	22.5	17.0	20.8	16.0	13.5	13.0	14.8	16.4	14.3
OBWI	47.2	52.5	44.7	43.8	46.0	42.3	37.0	44.4	38.2	33.9
AL1I	69.4	65.0	61.7	62.5	64.0	53.8	63.0	70.4	74.5	48.2
AL2I	69.4	64.3	57.4	70.8	60.0	51.9	61.1	70.4	58.2	53.6
AL3I	80.6	87.5	72.3	79.2	76.0	57.7	68.5	77.8	70.9	64.3
AL4I	88.9	85.0	76.6	81.3	76.0	69.2	79.6	75.9	74.5	62.5
ASIn1	3.0	3.0	2.5	2.5	2.5	2.4	2.2	2.1	2.0	2.1
ASIn2	3.1	3.1	2.6	2.2	2.3	2.3	2.2	2.0	2.3	2.1
ASIn3	3.2	3.3	2.7	2.6	2.3	2.3	2.2	2.2	2.2	2.4
ASIn4	2.8	3.0	2.3	2.6	2.5	2.3	2.3	2.1	2.0	2.3
ASC1	65	61	59	64	56	64	62	60	64	60
ASC2	70	34	63	64	56	64	64	56	75	60
ASC3	72	80	69	66	66	67	72	65	75	69
ASC4	74	71	76	69	70	63	70	65	70	69
ClLI	47.2	47.5	38.3	41.7	38.0	26.9	37.0	35.2	36.4	30.4
ClRC	10	10	9	10	9	9	9	11	11	11
TIRC	56	53	60	50	56	55	52	57	53	55
ClSI	0.7	0.7	0.8	0.8	0.7	0.5	0.7	0.6	0.7	0.5
EgDI	na	15.0	12.8	20.8	16.0	11.5	13.0	13.0	14.5	12.5

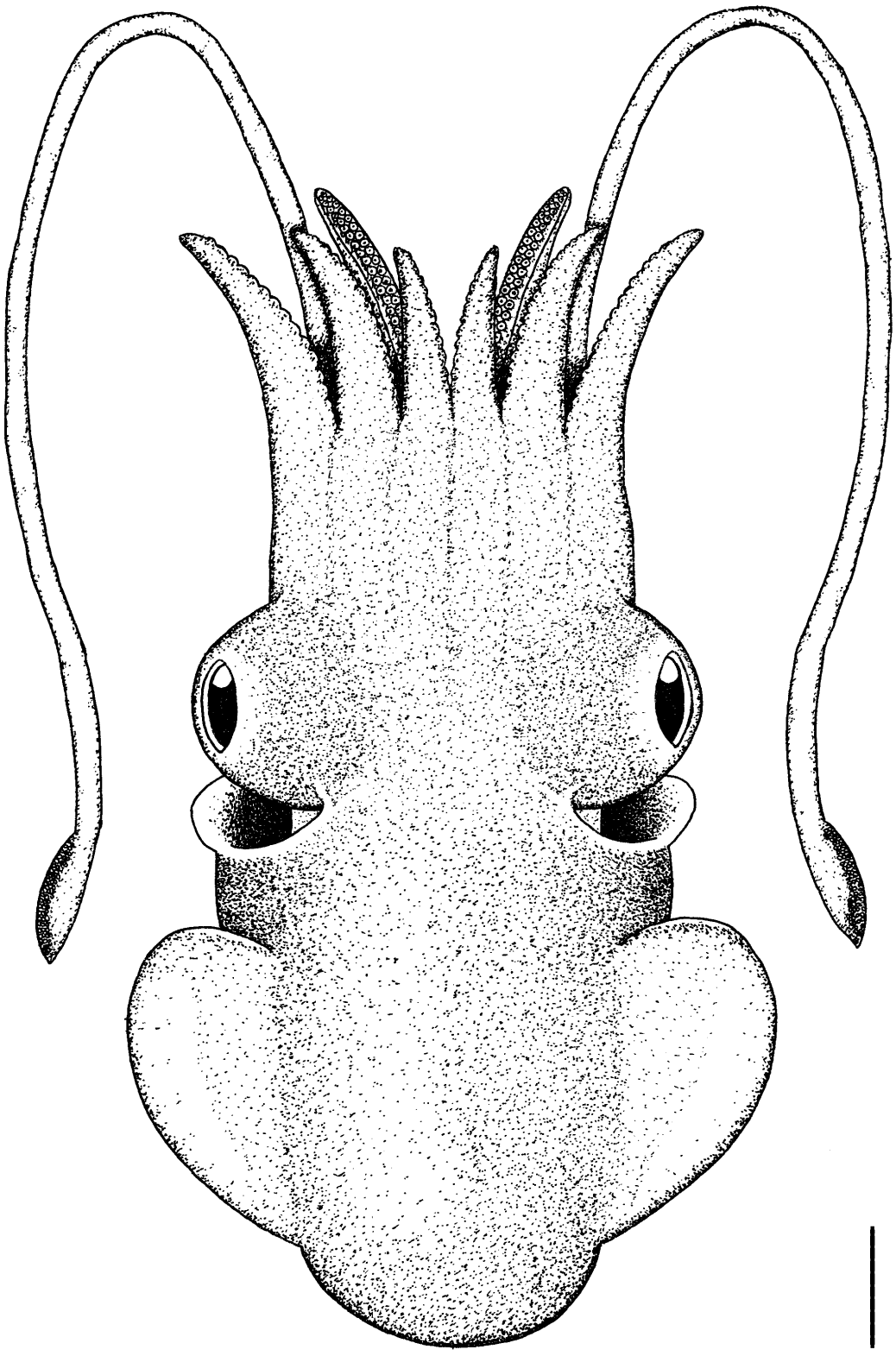

Fig. 12 *Sepioloidea* n. sp. 1: dorsal schematic illustration (NIWA 84775, ♀, 46 mm ML). Scale bar = 10 mm.

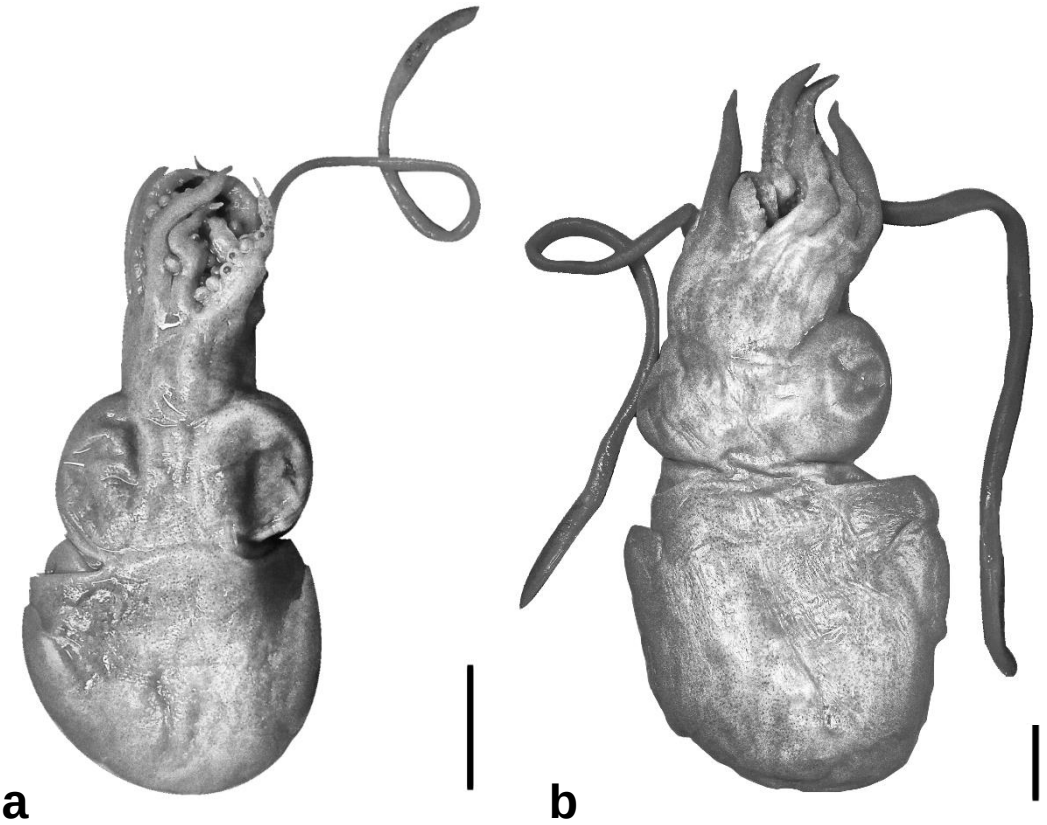

Fig. 13 Photographs of *Sepioloidea* n. sp. 1: **a** holotype (NMNZ M.118323, ♂, 28 mm ML); **b** female paratype (NMNZ M.330522, ♀, 50 mm ML). Scale bars = 10 mm.

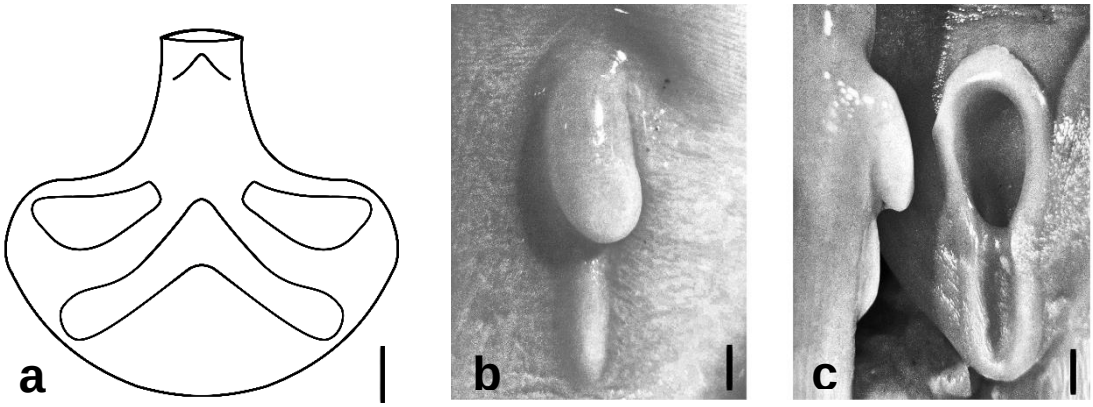

Fig. 14 *Sepioloidea* n. sp. 1: **a** funnel organ (NIWA 142281, ♀, 50 mm ML); **b** photograph of right locking cartilage, mantle component, dorsal view; **c** photograph of right locking cartilage, mantle component, lateral view and funnel component, ventral view; NMNZ M. 330522 (part), ♀ paratype, 48 mm ML). Scale bars = a, 10 mm; b–c, 1 mm.

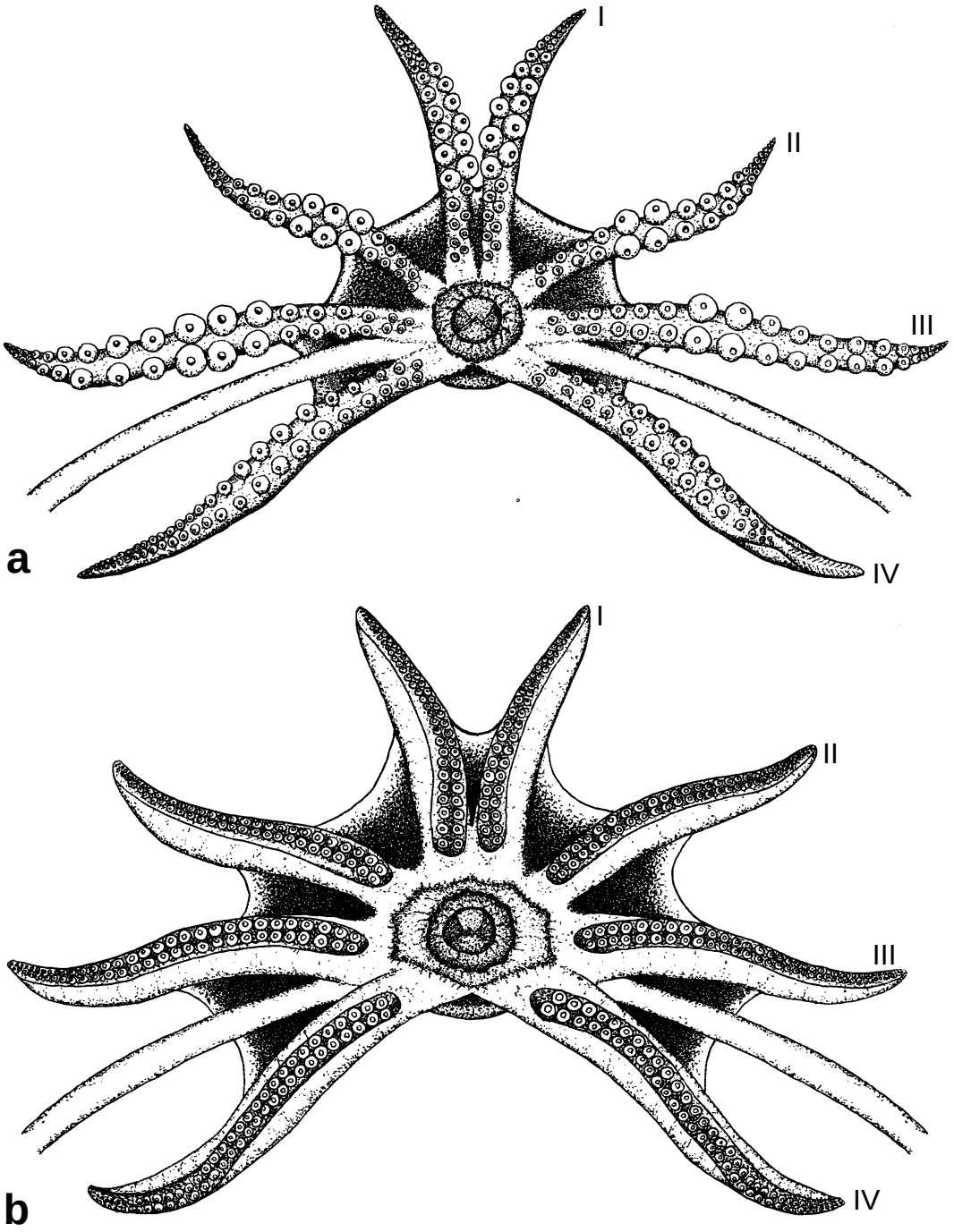

Fig. 15 *Sepioloidea* n. sp. 1 arm crowns: **a** male arm crown composite schematic (NMNZ M.118323 holotype, NMNZ M.330520 ♂ paratypes, NMNZ M.330521 ♂ paratypes); **b** female arm crown composite schematic (NMNZ M.330522 ♀ paratypes, M.330523, ♀ paratypes); I–IV, arm numbers.

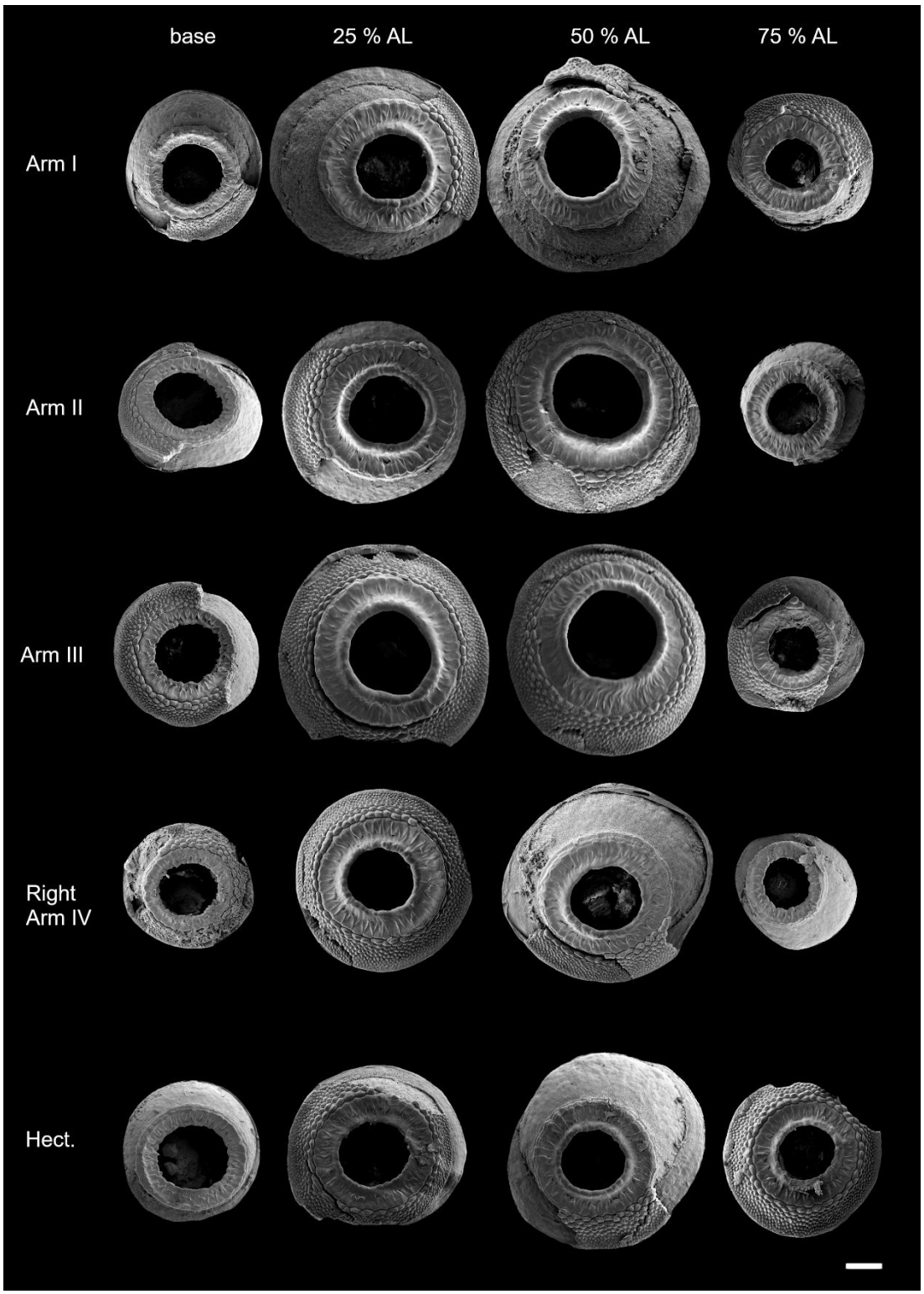

Fig. 16 SEM of *Sepioloidea* n. sp. 1: male arm suckers (hect, hectocotylus; NMNZ M.330520 (part), ♂ paratype, 30 mm ML). Scale bar = 100 µm.

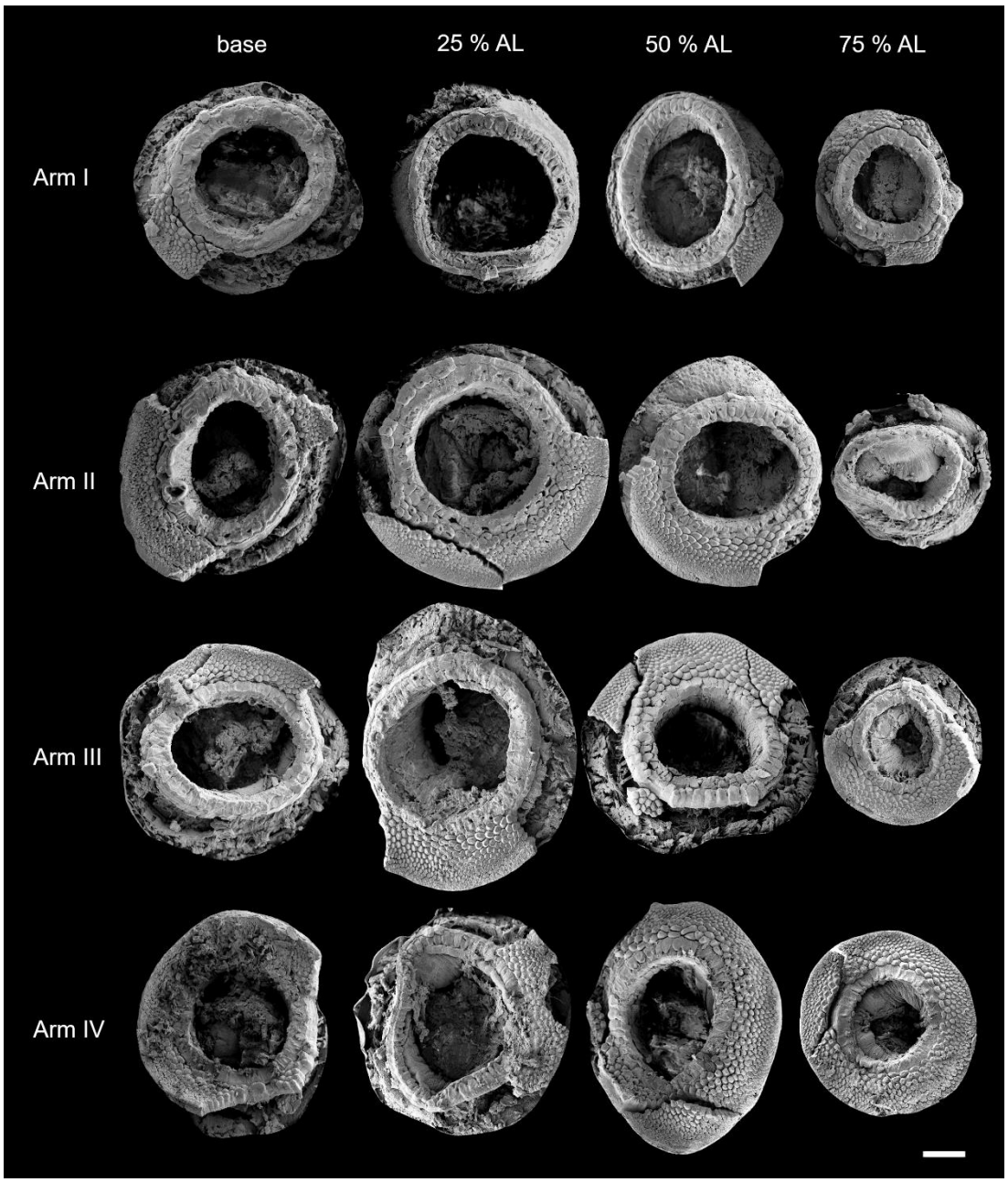

Fig. 17 SEM of *Sepioloidea* n. sp. 1: female arm suckers (NMNZ M.330522 (part), ♀ paratype, 52 mm ML). Scale bar = 100 µm.

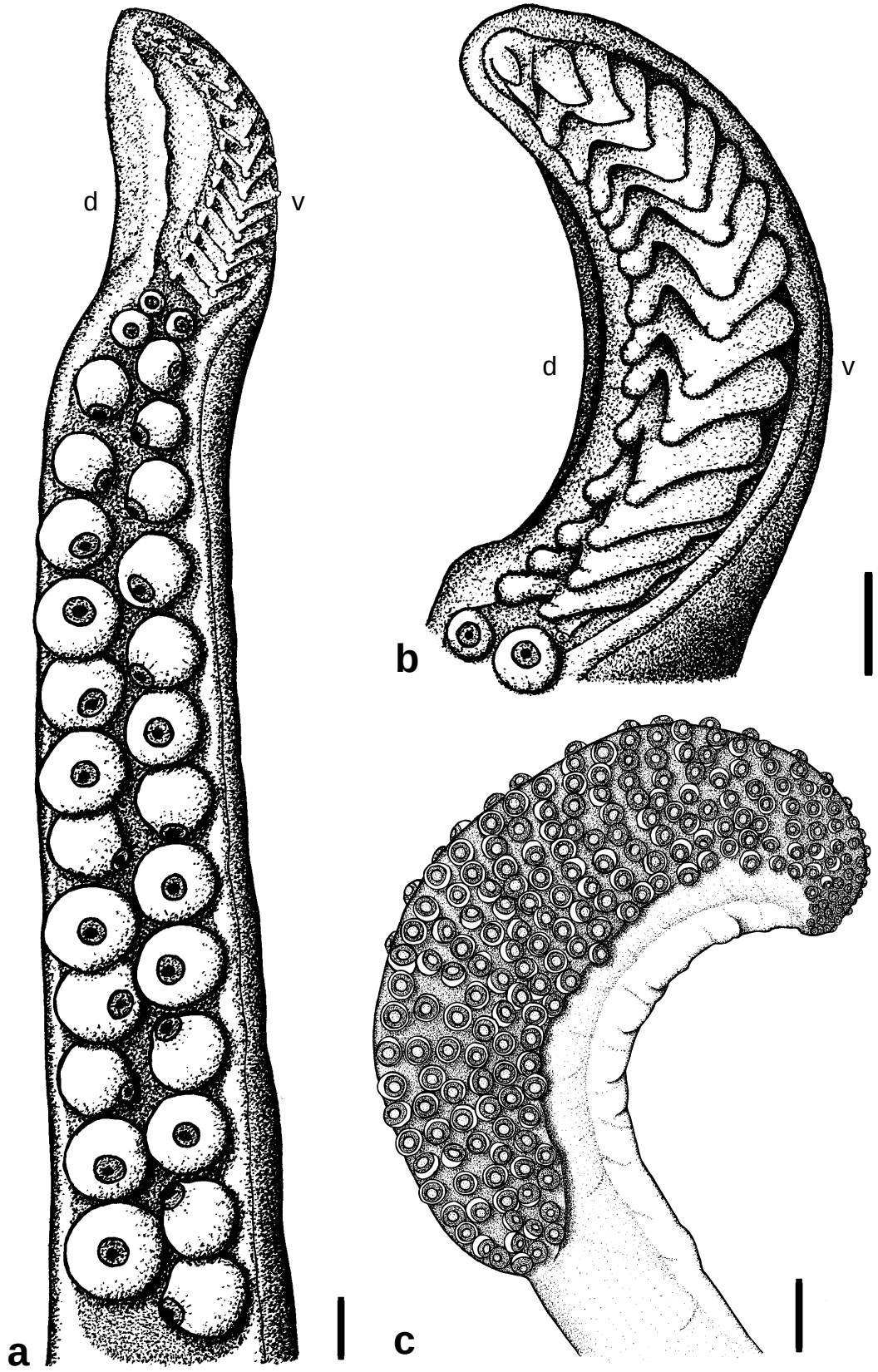

Fig. 18 *Sepioloidea* n. sp. 1: **a** hectocotylised left arm IV, oral view; **b** modified distal left arm IV tip (d, dorsal; v, ventral; NMNZ M.015786, ♂, 29 mm ML); **c** tentacular club (drawn from preserved specimen, M.84771, ♂, 21mm ML). Scale bars = 1 mm.

Arm sucker counts and measurements differ between sexes; females with higher sucker counts on all arms. ASC1–4 in males 37–*45*–50 (SD 4.1), 45–*48*–51 (SD 2.4), 39–*50*–55 (SD 5.0), 43–*54*–64 (SD 5.7) respectively; females 56–*62*–65 (SD 2.8), 56–*64*–75 (SD 6.1), 65–*70*–80 (SD 4.7), 63–*70*–76 (SD 3.8) respectively. Male arm suckers noticeably enlarged about halfway along each arm length, most prominent in sucker pairs 4–8 on Arms I–III (Fig. 15a); suckers increase in size from basal-most suckers to about sucker pairs 5 or 6, then decreases gradually towards distal arm tips, often with prominent decrease in size around distal 25% of arms; Arms IV suckers show less pronounced form of this size arrangement with median suckers reaching only ~twice basal sucker size at most. All female arm suckers similar in size, taper gradually to tip of arm; no markedly enlarged suckers (Fig. 15b). Sucker diameters relatively larger in males than females for all arms. ASIn1–4 and HcSI males 5.3–*6.5*–7.4 (SD 0.7), 5.7–*7.0*–8.2 (SD 0.9), 6.1–*6.9*–8.1 (SD 0.7), 4.6–*5.9*–8.2 (SD 1.1), 4.1–*5.0*–6.7 (SD 0.8) respectively; ASIn1–4 females 2.0–*2.4*–3.0 (SD 0.4), 2.0–*2.4*–3.1 (0.4), 2.2–*2.6*–3.3 (SD 0.4), 2.0–*2.4*–3.0 (SD 0.3) respectively.

Arm-sucker infundibular rings (Figs 16, 17) mostly smooth but shallow grooves create appearance of ~35–50 rectangular/tongue-shaped blocks. Papillated ring with 6–9 concentric rings of polygonal processes. Innermost ring with ~30–55 laterally elongated, mound-like polygonal processes. Intermediate rings with ~50–170 scale-like polygonal processes, becoming flatter, smaller, and greater in number towards external ring.

Left ventral arm of males hectocotylised (Fig. 18a): HcLI 60.6–*79.9*–93.1; unmodified proximal section with 14–15 normal sucker pairs; distal tip modified (Figs 18a, 18b), HcModLI 20.0–*27.4*–34.6 (SD 4.7). Modified section devoid of suckers; sucker pedicels fused basally to form lappets; HcLPC 13.0–*14.6*–16.0 (SD 0.8). Each lappet comprises dorsal spire-shaped structure with globular tip and ventral tongue-shaped structure with lobed apex; components joined basally in deep median crease; lappets well defined proximally, less defined and decreasing in size distally.

Tentacle stalks approximately 3–4× mantle length, slender, ovular in cross-section, without suckers. Clubs (Fig. 18c) expanded, tapering to blunt tips. ClLI males 33.3–*41.8*–54.8 (n = 9, SD 6.1), females 26.9–*37.9*–47.5 (SD 6.5). Clubs with tiny, uniform-sized suckers arranged with ~10 in a transverse row. Largest club sucker diameters similar in both sexes. ClSI males 0.65–*0.75*–0.87 (n = 9, SD 0.06); females 0.46–*0.66*–0.81 (SD 0.11). Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacular club (Fig. 19) sucker ultrastructure symmetrical. Inner ring with ~15–20 polygonal processes. Four to six intermediate rings with processes decreasing in size but increasing in number towards external ring. External ring with ~70 processes. Processes flat without pegs; surface pitted. Inner surface of rim processes similar in shape to papillate ring processes.

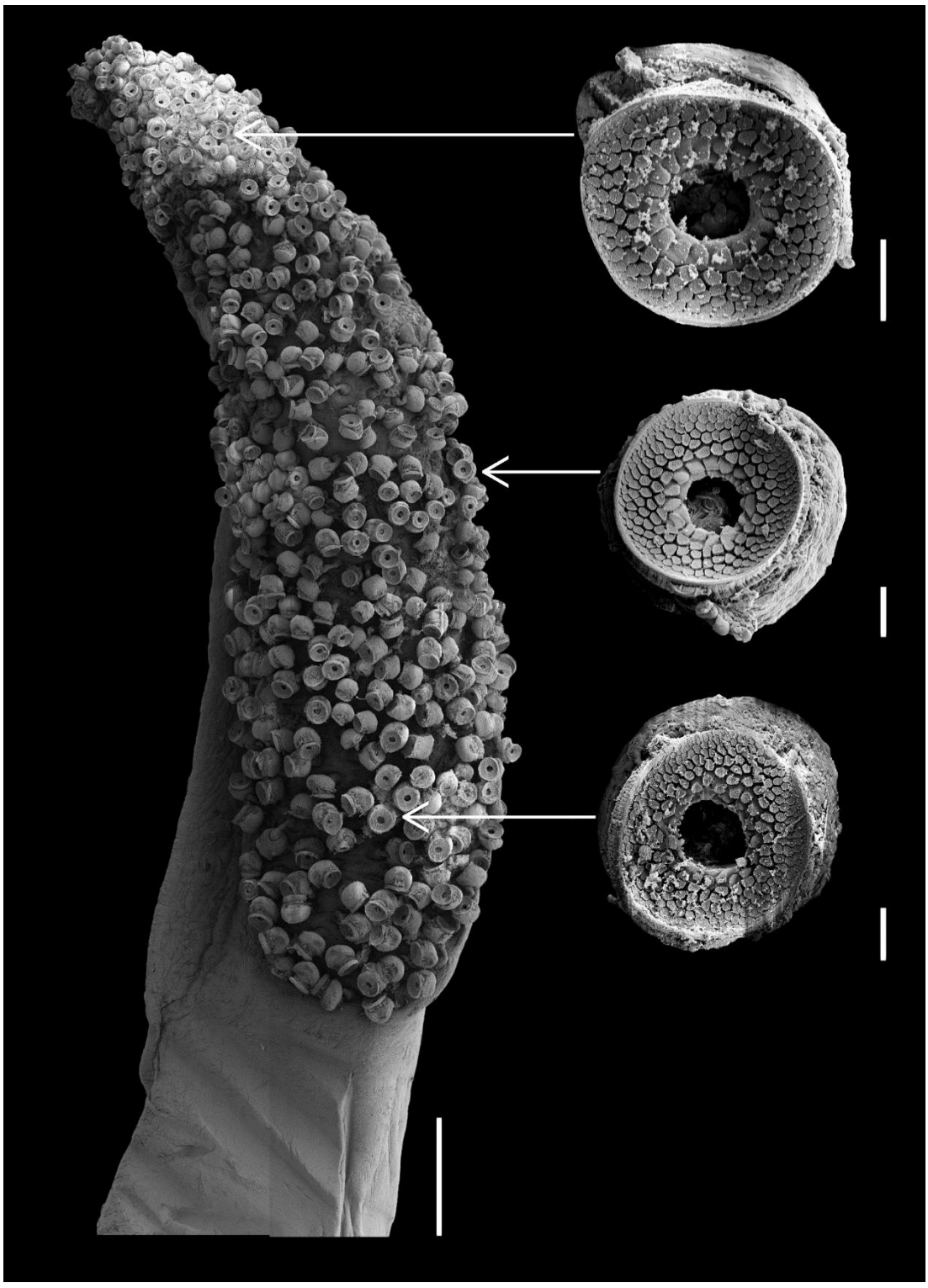

Fig. 19 SEM of *Sepioloidea* n. sp. 1: tentacular club and suckers (NMNZ M.330522 (part), ♀ paratype, 52 mm ML). Scale bars = club 1 mm, suckers 50 µm.

Gills with 22–24 lamellae per demibranch.

Male reproductive system typical of the family (Fig. 20), with testis occupying large portion of posterior mantle cavity. Spermatophores (Fig. 21) with bipartite cement body, posteriorly barrel-shaped, with slight median constriction, connecting to sperm reservoir via narrow duct. Cement body anterior part narrower than posterior part, cylindrical, approximately same length as posterior part, connecting to posterior part via a narrow ridged 'neck'. Ejaculatory apparatus coiled, extending into anterior dilation of spermatophore. SPlI 17.9–*23.6*–34.6 (SD 5.1).

Eggs approximately spherical in shape. EgDI 11.5–*14.3*–20.8 (*n* = 9, SD 2.8).

Upper and lower beaks (Fig. 22a–c) clear at posterior margin, darkening to brown then black towards beak tips. Lower beak (Figs 22a, 22b) with beak height just under half baseline length. Leading edge of wing roughly one third of baseline ahead of rostral tip. Hood length half crest length. Hood closely adherent to crest. Jaw angle obtuse. Wing length subequal to beak height. Minimum wing width slightly shorter than maximum wing width. Lower rostral length just over a quarter of beak height. Upper beak (Fig. 22c) height roughly half beak length. Hood clear of crest posteriorly, with hood height a quarter of beak height. Upper rostral length over one third crest length. Rostral tip blunt. Jaw angle near right angle.

Radula (Fig. 22d) with seven rows of teeth. Rachidian teeth approximately twice the length of lateral teeth, triangular, with base width equal to mesocone height; proximal and lateral margins concave; underside strongly indented medially. First lateral teeth weakly bicuspid; mesocone narrow, shorter than rachidian teeth; outer lateral cusp broad; lateral cusp about a quarter mesocone height. Second lateral teeth unicuspid, similar in height to rachidian teeth; broad basally, directed medially; outer margin nearly straight between base and mesocone tip; inner margin near vertical from tip; outer margin near 45 degrees from tip to base. Marginal teeth simple, curved proximally, straight distally, longer than rachidian teeth.

Preserved specimen colouration varies from pale cream through to dark brown. Chromatophores (Fig. 6b) tiny dots, dark brown/purple, evenly distributed across dorsal surface of mantle, fins, head, and along Arms I, II, and III; chromatophores more sparsely set on ventral surfaces of mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club, small and densely set near tip, larger and very sparse proximally, extending along stalk for 150% club length.

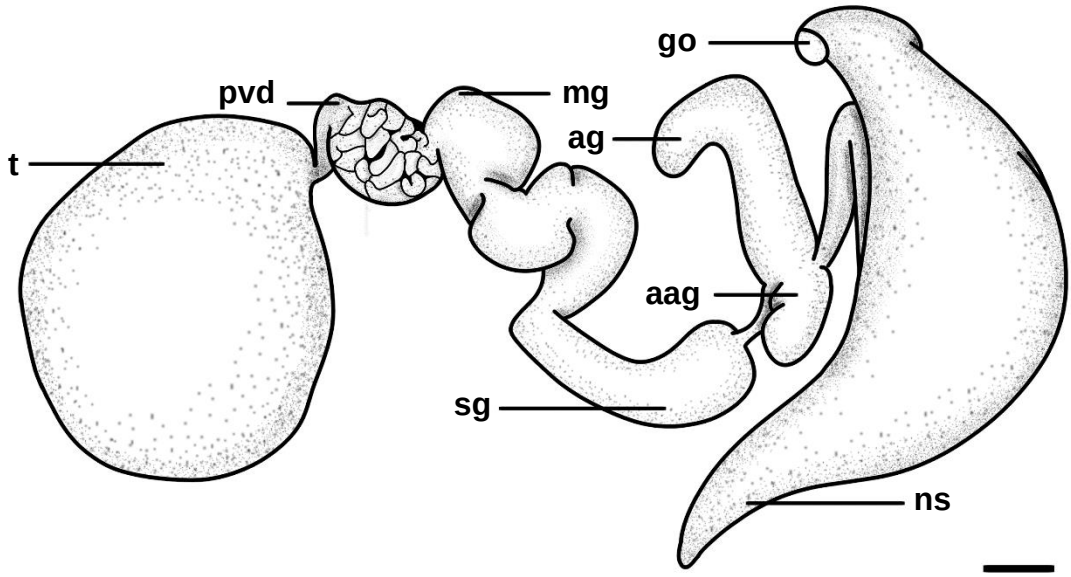

Fig. 20 *Sepioloidea* n. sp. 1: male reproductive system (**aag**, appendix of accessory gland; **ag**, accessory gland; **go**, genital opening; **mg**, mucilaginous gland; **ns**, Needham's sac; **pvd**, posterior vas deferens; **sg**, spermatophoric gland; **t**, testis; NMNZ M.330520 (part), ♂ paratype, 31 mm ML). Scale bar = 2 mm.

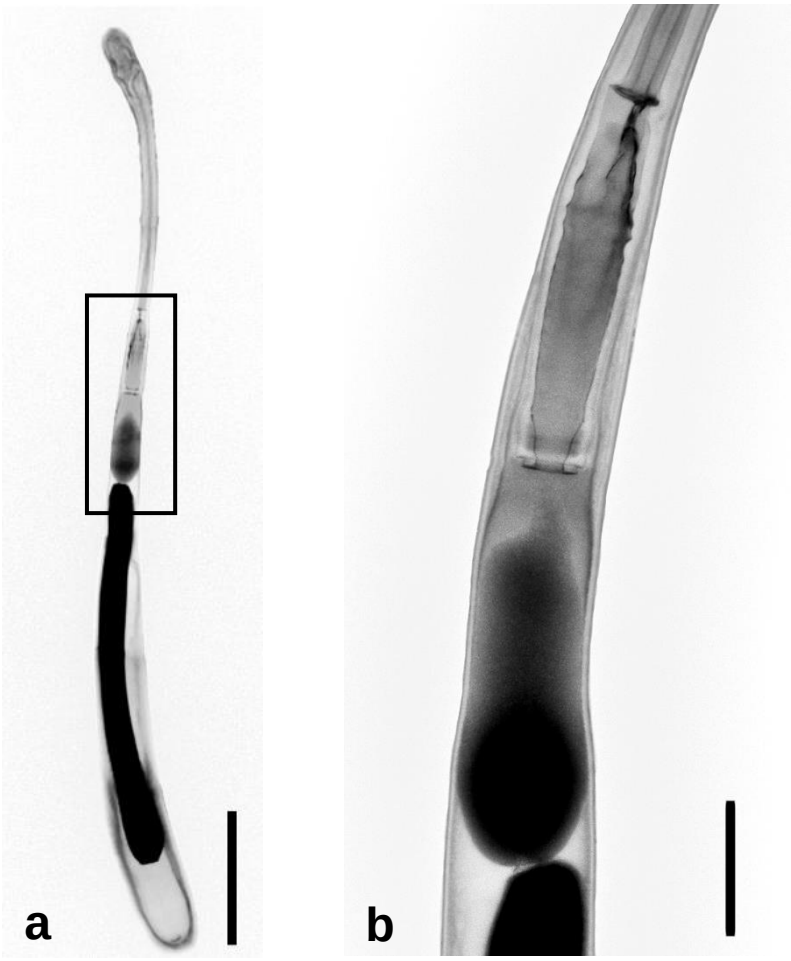

Fig. 21 Stereo microscope image of *Sepioloidea* n. sp. 1: spermatophore (NMNZ M.330520 (part), ♂ paratype, 31 mm ML); **a** whole spermatophore, cement body outlined; **b** close-up of cement body. Scale bars = a, 1 mm; b, 500 µm.

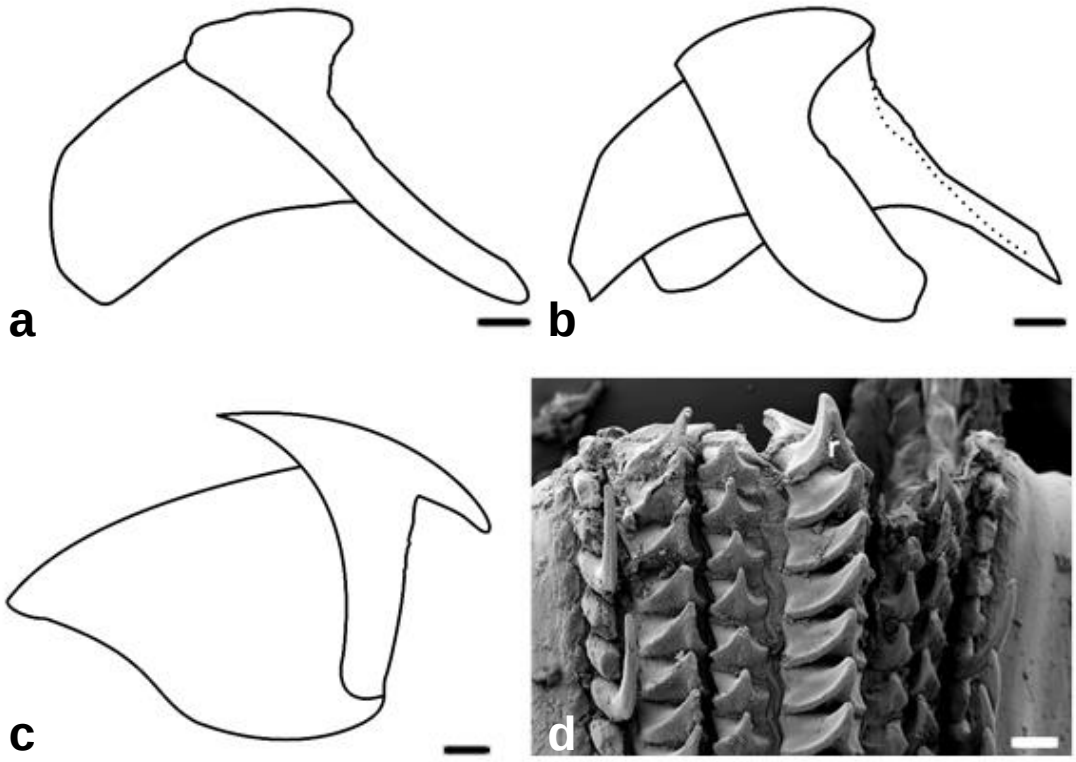

Fig. 22 *Sepioloidea* n. sp. 1: **a** lower beak, profile view; **b** lower beak, oblique view; **c** upper beak, profile view (NIWA 106067, ♀ 33 mm ML); **d** SEM of radula (r, rachidian tooth; NMNZ M.330527, ♀, 48 mm ML). Scale bars = a–c, 1 mm; d, 100 µm.

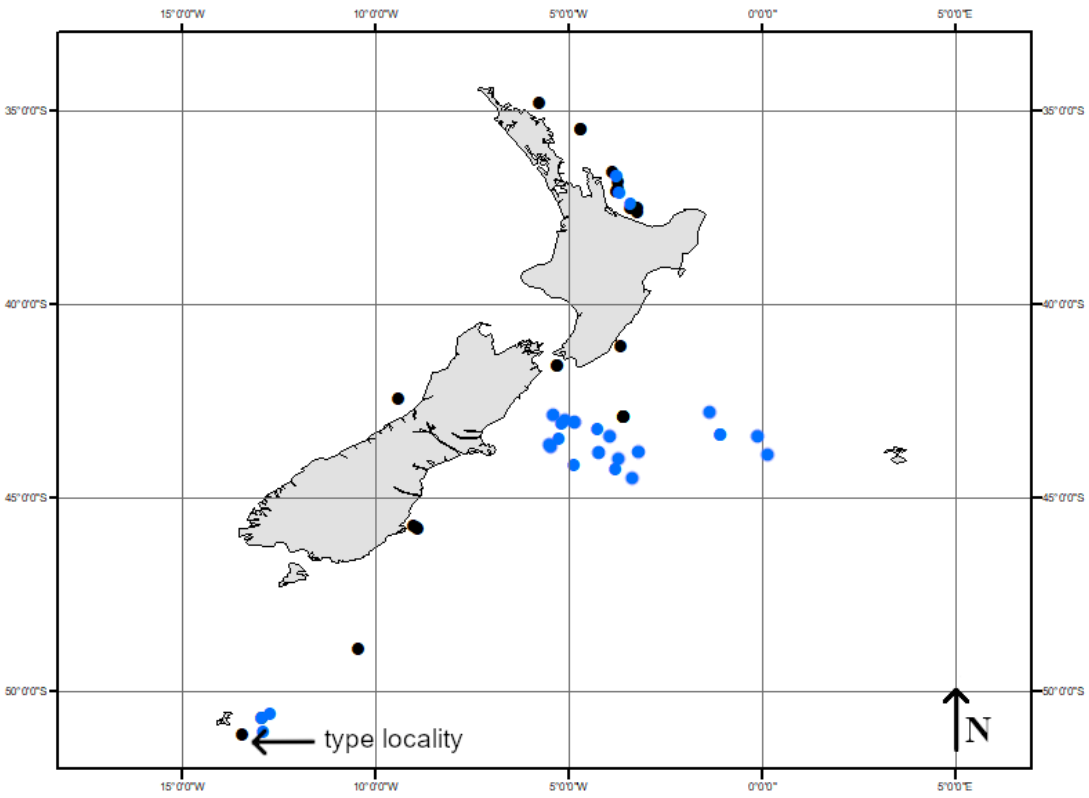

Fig. 23 Distribution of *Sepioloidea* n. sp. 1 specimens examined in this study including sequenced (blue) and non-sequenced (black) specimens.

Type locality. Auckland Islands, New Zealand, 50º 40′ S, 167º 06′ E, 367–528 m.

Known distribution (Fig. 23). Southwest Pacific, New Zealand, including Auckland Islands and Chatham Rise; 73–911 m.

Remarks. Of the known sepiadariids, *Sepioloidea* n. sp. 1 is superficially most similar to *S. magna*. Table 4 below compares the quantitative characters between these species. It should be noted that due to material availability at the time of its description, the *S. magna* male data are based on a single specimen (Reid, 2009). At maturity, *S.* n. sp. 1 is only slightly smaller than *S. magna* (♂ *S.* n. sp. 1 ~37 mm ML, ♂ *S. magna* ~46 mm ML; ♀ *S.* n. sp. 1 ~59 mm ML, ♀ *S. magna* ~62 mm ML). The chromatophore arrangement is also similar, with both species pale in colour, and only displaying tiny, sparsely distributed chromatophores (Fig. 6b). The two species differ, however, in arm and tentacle club morphology, and hectocotylus structure.

All arm suckers in *S.* n. sp. 1 are biserial, and the club suckers are arranged with ~10 per transverse row (Fig. 18c). In *S. magna,* arm suckers are biserial basally, tetraserial distally, and club suckers are arranged with ~40 per transverse row (Reid, 2009; confirmed by examination of AM C.476096). Males of both species exhibit enlarged arm suckers. In *S.* n. sp. 1, the suckers are enlarged midway along all arms (although to a lesser extent on Arms IV), with sucker pairs 5 and 6 often largest (Fig. 15a); in *S. magna* the suckers are enlarged

on Arms II and III (and to a lesser extent on Arms IV), from the basal 2 or 3 sucker pairs. The collection and examination of more mature male *S. magna* specimens will be important for determining the reliability of the patterns seen here.

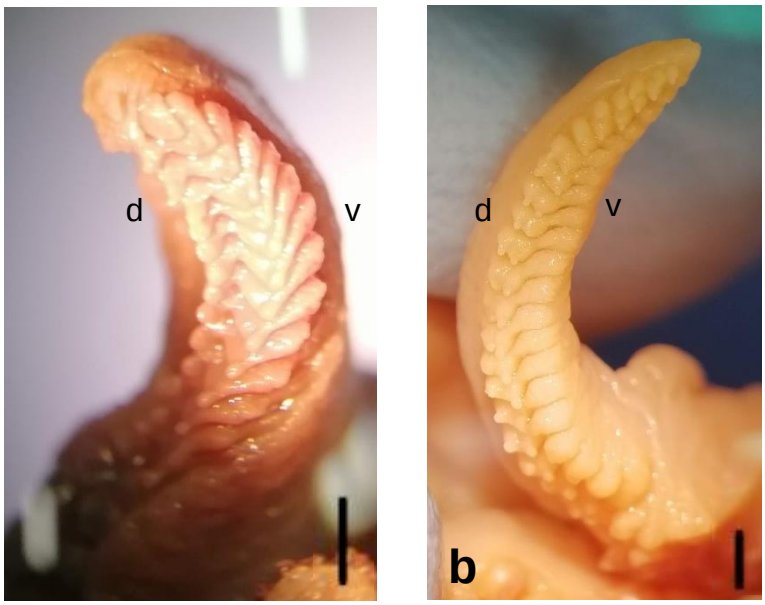

Fig. 24 Photographs of *Sepioloidea* n. sp. 1 and *Sepioloidea magna* hectocotyli (d, dorsal; v, ventral): **a** *S.* n. sp. 1 hectocotylus (NIWA 015786 ♂, 29 mm ML); **b** *S. magna*, AM C.476096, ♂, 62 mm ML). Scale bars = 1 mm.

The hectocotylus morphology also differs between the two species. The hectocotylus of *S.* n. sp. 1 is modified only on the distal quarter of the arm; its two-structure lappet consists of a spire-like dorsal component and a tongue-shaped ventral component (Figs 18b, 24a). In *S. magna* (Fig. 24b), the modified portion of the hectocotylus begins approximately halfway along the arm, and its two-structure lappet consists of a bilobed dorsal component, each lobe with pronounced tip, and a simple, ridge-like ventral component.

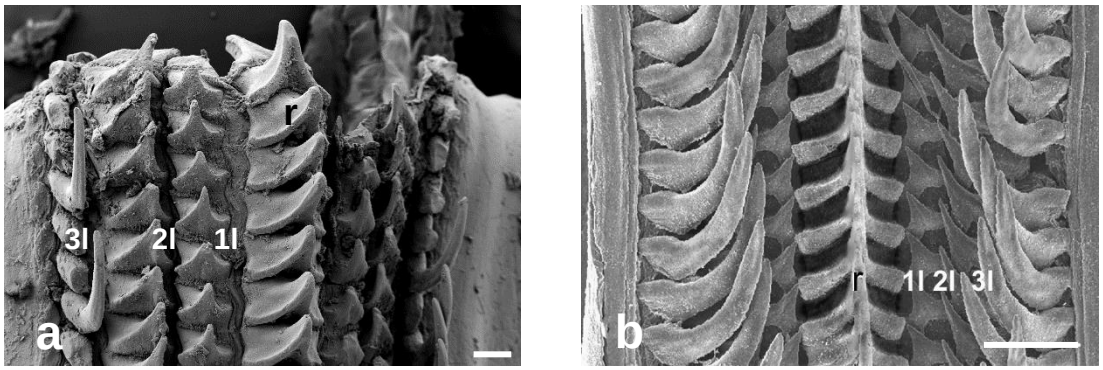

Fig. 25 SEM of *Sepioloidea* radulae: **a** *S.* n. sp. 1 radula (NMNZ M.330527, ♀, 48 mm ML); **b** *S. magna* radula (NTM P.1387, ♀, 56 mm ML). Abbreviations: r, rachidian tooth; 1l, first lateral tooth; 2l, second lateral tooth; 3l, third (marginal) tooth. Scale bars = a, 100 µm; b, 200 µm.

Both species have similar arm sucker, club sucker, and radula dentition. However, the rachidian tooth differs greatly in these species. In *S.* n. sp. 1 (Fig. 25a), the rachidian is more robust and has a distinct concave underside, while in *S. magna* (Fig. 25b) the rachidian teeth have very wide, narrow, rectangular bases.

Further differences between *S.* n. sp. 1 and the other recognised *Sepioloidea* are provided below in Remarks for *S.* n. sp. 2 and are summarised in Table 7 to facilitate identification.

It is possible that many early records of 'deep-water' *S. pacifica* may have been *S.* n. sp. 1. While establishing the *S. pacifica* neotype, Dell (1959: 2) reported finding these 'larger' specimens (up to 40 mm ML compared to the 'typical' 20 mm ML) from depths greater than 75 fathoms (137 m). He hypothesised that this may be an indicator of size classes with older individuals living in deeper water. In the only *S. pacifica*-focused research to date, Hurst (1969: 8–10, fig. 3) described a clear separation in size class between smaller shallow-water specimens (<140 m) and larger deep-water specimens (140–210 m), which were approximately double the mantle width and length of the shallow-water group. Powell (1979) may not have been aware of any differences according to depth when he listed the *S. pacifica* depth as 75–300 fathoms. Unfortunately, none of these larger, deep-water specimens were lodged in museum collections for further examination. The depths at which confirmed *S. pacifica* specimens have been captured are all shallower than those of *S.* n. sp. 1 (all collected between 73 and 911 m). For example, the type locality of Kirk's holotype (and subsequently, Dell's neotype) is Wellington Harbour, New Zealand, which has a maximum depth of 21 m. Dell's voucher specimens from 1952 were from Lyttelton Harbour (maximum depth is 12 m). All 30+ confirmed *S. pacifica* lots loaned for this study were collected at <55 m depth. Reid (2009: 108) quoted a 15–550 m depth range for *S. pacifica* based on the data cited by Powell (1979). It is possible that the deeper end of this depth range may correspond to collection records for *S.* n. sp. 1 and/or the other new species described below rather than *S. pacifica.* The present results suggest that *S. pacifica* is a smaller-bodied, shallow-dwelling species and *S.* n. sp. 1 is a larger-bodied, deep-dwelling species.

The morphological traits distinguishing *S.* n. sp. 1 from the other *Sepioloidea* species are supported by DNA barcoding. Thirty-two specimens of *S.* n. sp. 1 (sourced throughout its known range) were sequenced and compared with 22 specimens of *S. pacifica. Sepioloidea* n. sp. 1 showed a minimum interspecific distance of 12.20 % from *S. pacifica* while the maximum intraspecific distance of *S.* n. sp. 1 was only 0.18 %. (Unfortunately, no COI sequences are currently available for *S. magna* for comparison, but they clearly differ based on morphology.)

Table 4 Comparison of counts and measurements of *Sepioloidea* n. sp. 1 and *Sepioloidea magna*; highlighted numbers indicate distinct differences.

Measurement / Count	*Sepioloidea* n. sp. 1 males	*Sepioloidea magna* male	*Sepioloidea* n. sp. 1 females	*Sepioloidea magna* females
ML	26.0–*30.3*–33.0	45.7	36.0–*49.2*–56.0	39.5–*30.3*–33.0
MWI	72.7–*97.6*–121.4	81.0	66.1–*89.0*–108.3	75.0–*87.5*–96.7
FWI	13.3–*19.8*–27.3	15.5	17.3–*25.1*–34.0	10.5–*18.0*–25.5
FIIa	20.0–*26.4*–36.7	20.6	14.5–*20.2*–30.0	22.5–*26.0*–29.9
FII	45.5–*52.1*–61.3	21.9	46.2–*58.4*–65.0	-
FuLI	40.0–*56.1*–65.5	53.6	37.0–*51.1*–61.1	48.5–*61.2*–72.7
FFuI	16.1–*24.8*–33.3	32.8	16.7–*22.4*–30.0	25.0–*28.4*–30.7
HLI	66.7–*82.3*–100.0	70.9	67.9–*76.0*–81.5	55.4–*71.2*–89.6
HWI	63.3–*87.9*–100.0	72.6	58.9–*75.4*–87.5	56.5–*71.0*–80.0
EDI	16.7–*21.5*–26.9	17.7	13.0–*16.8*–22.5	13.1–*15.8*–20.2
AL1I	53.3–*68.3*–82.1	65.6	48.2–*63.3*–74.5	69.8–*75.5*–80
AL2I	66.7–*79.2*–96.6	76.6	51.9–*61.4*–70.8	67.9–*81.7*–96.6
AL3I	70.0–*84.0*–107.1	78.8	57.7–*73.5*–87.5	76.7–*87.1*–101.3
AL4I	66.7–*89.0*–106.9	78.8	62.5–*77.0*–88.9	71.6–*84.6*–91.7
ASIn1	5.3–*6.5*–7.4	4.16	2.0–*2.4*–3.0	2.3–*2.7*–3.5
ASIn2	5.7–*7.0*–8.2	6.35	2.0–*2.4*–3.1	2.3–*2.7*–3.5
ASIn3	6.1–*6.9*–8.1	6.35	2.2–*2.6*–3.3	2.4–*2.9*–3.3
ASIn4	4.6–*5.9*–8.2	3.06	2.0–*2.4*–3.0	2.2–*2.6*–3.3
ASC1	37–*45*–50	76	56–*62*–65	100–*119*–134
ASC2	45–*48*–51	80	56–*64*–75	114–*128*–134
ASC3	39–*50*–55	100	65–*70*–80	130–*143*–152
ASC4	43–*54*–64	104	63–*70*–76	122–*141*–166
ClLI	33.3–*41.8*–54.8	54.7	26.9–*37.9*–47.5	58.2–*66.0*–75.1
ClRC	6–*8*–9	-	9–*10*–11	39–*41*–42
ClSI	0.7–*0.8*–0.9	-	0.5–*0.7*–0.8	0.3–*0.4*–0.5
EgDI	-	-	11.5–*14.3*–20.8	15.3–*17.3*–20.8
HcModLI^	20.8–*27.4*–34.6	~50	-	-

Sepioloidea n. sp. 2

(Figs 26–39; Tables 5–8)

Sepioloidea pacifica (not Kirk, 1882): Powell, (1979): 440.

Type material examined. *Holotype* **NMNZ M.287489**, 1♂ ML 16 mm, 40º 14.4′ S, 174º 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*. *Paratypes.* **NMNZ M.330524**, 9♂ ML 14–16 mm, 40º 14.4′ S, 174º 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*. **NMNZ M.330525**, 5♀ ML 14–16 mm, 40º 14.4′ S, 174º 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*. **NMNZ M.330526**, 5♀ ML 12–22 mm, 40º 14.4′ S, 174º 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*.

Additional material examined. (*) indicates specimens that have been sequenced. **NMNZ M.090405**, 1♀, ML 15 mm, 34° 22′ 48″ S, 172° 24′ 36″ E, 121 m, 02/02/1981, Stn 1981912;

NMNZ M.067326, 1♀, ML 16 mm, 34° 32′ 0″ S, 173° 13′ 0″ E, 40 m, 05/07/1977, RV *Ikatere*; **NIWA 55378***, 1♂, ML 13 mm, 34° 54′ 36″ S, 174° 0′ 0″ E, 143–149 m, 08/07/2009, Coll. Oceans Survey 2020, Stn TAN0906/78; **NMNZ M.074141**, 1♂, ML 12 mm, 34° 56′ 0″ S, 173° 34′ 0″ E, 47 m, 18/09/1971, Stn 1971003; **NIWA 142311**, 1♂, ML 13 mm, 35° 0′ 0″ S, 174° 12′ 0″ E, 175 m, 08/05/1975, Coll. NZOI, Stn I39; **NMNZ M.074122**, 1♂, ML 13 mm, 1♀, ML 18 mm, 35° 33′ 0″ S, 174° 57′ 0″ E, 183–201 m, 14/02/1974, RV *Acheron*, Stn 1974365/A; **NMNZ M.287497**, 3♀, ML 13–19 mm, 35° 38′ 0″ S, 174° 56′ 0″ E, 165 m, 20/11/1962, RV *Ikatere*, Stn 1962086; **NMNZ M.287503**, 2♂, ML 12–14 mm, 35° 44′ 42″ S, 175° 22′ 36″ E, 185 m, 01/06/1982, FV *Kalinovo*; **NIWA 142308**, 1♂, ML 13 mm, 36° 0′ 0″ S, 175° 37′ 12″ E, 139 m, 13/05/1975, Coll. NZOI, Stn I68; **NMNZ M.074099**, 1♂, ML 15 mm, 9♀, ML 16–20 mm, 36° 26′ 34″ S, 175° 57′ 03″ E, 159–170 m, 11/11/1964, RV *Ikatere*; **NMNZ M.074118**, 1♀, ML 18 mm, 36° 26′ 34″ S, 175° 57′ 03″ E, 154 m, 24/11/1965, RV *Ikatere*; **NMNZ M.287395**, 1♂, ML 10 mm, 36° 45′ 42″ S, 176° 9′ 24″ E, 148 m, 25/02/1981, RV *James Cook*, Stn J04/88/81; **NMNZ M.287507**, 1♂, ML 11 mm, 36° 46′ 09″ S, 175° 55′ 06″ E, 99–104 m, 24/02/1981, RV *James Cook*, Stn J04/85/81; **NMNZ M.287510**, 3♀, ML 11–13 mm, 37° 0′ 48′ S, 176° 12′ 18″ E, 178–248 m, 23/01/1979, RV *Tangaroa*, Stn 1979756; **NMNZ M.287512**, 1♂, ML 11 mm, 37° 21′ 54″ S, 176° 20′ 54″ E, 203–248 m, 22/01/1979, RV *Tangaroa*, Stn 1979743; **NIWA 142272**, 1♂, ML 13 mm, 6♀, ML 11–19 mm, 37° 29′ 24″ S, 176° 31′ 05″ E, 219–217 m, 20/02/2000, Coll. NIWA, MFish, Stn KAH0001/76; **NMNZ M.067294**, 1♀, ML 17 mm, 37° 35′ 13″ S, 177° 52′ 55″ E, 30 m over 94 m, 03/11/1979, RV *James Cook*, Stn J15/02/79; **NMNZ M.287495**, 2♂, ML 10–11 mm, 1♀, ML 9 mm, 37° 35′ 48″ S, 177° 49′ 48″ E, 82–109 m, 23/02/1981, RV *James Cook*, Stn J04/70/81; **NMNZ M.287514**, 1♂, ML 14 mm, 37° 35′ 54″ S, 176° 59′ 30″ E, 139–179 m, 20/01/1979, RV *Tangaroa*, Stn 1979723; **NMNZ M.287396**, 1♂, ML 9 mm, 37° 39′ 0″ S, 177° 14′ 36″ E, 108 m over 622–820 m, 13/12/1975, RV *James Cook*, Stn J17/51/75; **NMNZ M.067288**, 2♂, ML 11–12 mm, 1♀, ML 16 mm, 37° 39′ 12″ S, 177° 41′ 30″ E, 30 m, 20/11/1979, RV *James Cook*, Stn J16/22/79; **NMNZ M.091694**, 1♂, ML 14 mm, 37° 48′ 0″ S, 178° 36′ 0″ E, 27 m over 73 m, 18/10/1969–19/10/1969, RV *James Cook*, Stn J06/112/69; **NMNZ M.287494**, 7♂, ML 8–13 mm, 7♀, ML 7–20 mm, 37° 51′ 0″ S, 178° 35′ 0″ E, 20 m, 10/01/1980–11/01/1980, RV *James Cook*, Stn J01/15/80; **NMNZ M.067904**, 1♂, ML 11 mm, 37° 51′ 41″ S, 178° 54′ 42″ E, 30 m over 800 m, 11/01/1980, RV *James Cook*, Stn J01/17/80; **NMNZ M.067314**, 2♂, ML 7–14 mm, 1♀, ML 8 mm, 37° 51′ 42″ S, 178° 29′ 48″ E, 29–30 m, 10/01/1980, RV *James Cook*, Stn J01/14/80; **NMNZ M.067842**, 1♂, ML 14 mm, 37° 51′ 49″ S, 178° 29′ 49″ E, 30 m, 29/09/1979, RV *James Cook*, Stn J13/01/79; **NMNZ M.067838**, 8♂, ML 8–14 mm, 6♀, ML 11–17 mm, 37° 52′ 03″ S, 178° 33′ 38″ E, 30 m, 29/09/1979, RV *James Cook*, Stn J13/02/79; **NMNZ M.287410**, 2♀, ML 15–17 mm, 38° 15′ 12″ S, 178° 38′ 36″ E, 139 m, 16/01/1979, RV *Tangaroa*, Stn 1979673; **NMNZ M.067846**, 1♂, ML 12 mm, 38° 22′

09″ S, 178° 25′ 36″ E, 30 m, 30/09/1979, RV *James Cook*, Stn J13/07/79; **NMNZ M.016866**, 1♀, ML 9 mm, 38° 22′ 30″ S, 178° 40′ 0″ E, 161 m, 06/04/1963, RV *Ikatere*, Stn 1963044; **NMNZ M.102124**, 1♂, ML 13 mm, 3♀, ML 11–12 mm, 38° 41′ 30″ S, 174° 4′ 30″ E, 82–83 m, 18/08/1985, RV *Kaiyo Maru*, Stn KM/201A/85; **NMNZ M.102128**, 1♂, ML 13 mm, 2♀, ML 10–17 mm, 38° 48′ 18″ S, 172° 57′ 18″ E, 120 m over 146 m, 22/08/1985, RV *Kaiyo Maru*, Stn KM/202B/85; **NMNZ M.287430**, 2♂, ML 14–17 mm, 2♀, ML 19–22 mm, 38° 48′ 48″ S, 173° 29′ 36″ E, 146 m, 09/01/1981, RV *Tangaroa*, Stn 1981791; **NMNZ M.067831**, 1♂, ML 14 mm, 3♀, ML 12–14 mm, 38° 50′ 04″ S, 178° 8′ 56″ E, 30–45 m, 02/10/1979, RV *James Cook*, Stn J13/23/79; **NMNZ M.067841**, 1♂, ML 11 mm, 1♀, ML 10 mm, 39° 31′ 0″ S, 172° 33′ 10″ E, 60 m over 190 m, 13/04/1980, RV *James Cook*, Stn J07/62/80; **NMNZ M.067848**, 4♂, ML 8–11 mm, 3♀, ML 8–16 mm, 1 indet., ML 11 mm, 39° 34′ 26″ S, 172° 35′ 04″ E, 127 m, 13/04/1980, RV *James Cook*, Stn J07/63/80; **NMNZ M.016862**, 1♀, ML 10 mm, 39° 40′ 30″ S, 177° 35′ 0″ E, 137–143 m, 07/04/1963, RV *Ikatere*, Stn 1963048; **NMNZ M.067271**, 4♂, ML 12–19 mm, 13♀, ML 10–19 mm, 39° 55′ 16″ S, 172° 29′ 51″ E, 133–207 m, 13/12/1978, RV *James Cook*, Stn J19/24/78; **NMNZ M.067896**, 4♀, ML 17–20 mm, 40° 4′ 35″ S, 172° 57′ 35″ E, 30 m, 13/10/1979, RV *James Cook*, Stn J14/09/79; **NMNZ M.067882**, 10♀, ML 18–20 mm, 40° 12′ 21″ S, 173° 1′ 42″ E, 80 m over 92 m, 13/10/1979, RV *James Cook*, Stn J14/10/79; **NMNZ M.330528**, >30 specimens comprising both sexes, ML 14–16 mm, 40º 14.4′ S, 174º 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*; **NMNZ M.102222**, 3 indet., ML 8–9 mm, 40° 22′ 24″ S, 174° 23′ 12″ E, 111–112 m, 17/07/1985, RV *Kaiyo Maru*, Stn KM/104A/85; **NMNZ M.287500**, 3♂, ML 12–15 mm, 40° 23′ 48″ S, 173° 12′ 12″ E, 70–73 m, 02/05/1981, RV *James Cook*, Stn J07/04/81; **NMNZ M.074125**, 1♀, ML 16 mm, 40° 24′ 0″ S, 174° 17′ 0″ E, 110 m, 04/03/1976, RV *Acheron*, Stn 1976508; **NMNZ M.074123**, 1♀, ML 18 mm, 40° 30′ 30″ S, 174° 53′ 30″ E, 101 m, 01/03/1976, RV *Acheron*, Stn 1976484; **NMNZ M.067883**, 3♂, ML 6–16 mm, 2♀, ML 19–20 mm, 40° 31′ 24″ S, 173° 23′ 54″ E, 45 m, 14/10/1979, RV *James Cook*, Stn J14/14/79; **NMNZ M.074120**, 1♂, ML 9 mm, 1 indet., ML 8 mm, 40° 33′ 0″ S, 174° 7′ 0″ E, 132 m, 04/03/1976, RV *Acheron*, Stn 1976509; **NMNZ M.287427**, 1♂, ML 12 mm, 40° 34′ 30″ S, 172° 26′ 12″ E, 51–63 m over 53–64 m, 07/05/1981, RV *James Cook*, Stn J07/60/81; **NMNZ M.067890**, 1♂, ML 12 mm, 40° 35′ 33″ S, 171° 46′ 54″ E, 60 m over 182 m, 12/10/1979, RV *James Cook*, Stn J14/02/79; **NMNZ M.074127**, 5♂, ML 11–12 mm, 6♀, ML 16–19 mm, 40° 38′ 30″ S, 174° 1′ 0″ E, 183–187 m, 04/03/1976, RV *Acheron*, Stn 1976510; **NMNZ M.287429**, 1♂, ML 9 mm, 5♀, ML 14–17 mm, 40° 38′ 30″ S, 174° 1′ 0″ E, 183–187 m, 04/03/1976, RV *Acheron*, Stn 1976510; **NMNZ M.067897**, 2♂, ML 12–13 mm, 40° 45′ 15″ S, 171° 40′ 12″ E, 10 m, 12/10/1979, RV *James Cook*, Stn J14/04/79; **NMNZ M.010933**, 1♀, ML 18 mm, 40° 48′ 0″ S, 174° 11′ 0″ E, 71 m, 03/01/1957, MV *Alert*, Stn 1957196; **NMNZ M.067315**, 1♂, ML 11 mm, 2♀, ML 16–17 mm, 40° 50′ 21″ S, 176° 20′ 18″ E, 130 m, 13/01/1980, RV *James*

Cook, Stn J01/60/80; **NMNZ M.287408**, 2♀, ML 11–17 mm, 40° 54′ 24″ S, 176° 16′ 12″ E, 52 m, 25/04/1980, RV *James Cook*, Stn J08/85/80; **NMNZ M.287409**, 2♂, ML 12–13 mm, 2♀, ML 9–20 mm, 40° 54′ 24″ S, 176° 16′ 12″ E, 52 m, 25/04/1980, RV *James Cook*, Stn J08/85/80; **NMNZ M.067891**, 1♀, ML 22 mm, 40° 55′ 36″ S, 172° 1′ 12″ E, 30 m, 13/10/1979, RV *James Cook*, Stn J14/05/79; **NMNZ M.074119**, 2♀, ML 14–15 mm, 40° 57′ 30″ S, 174° 18′ 0″ E, 139–144 m, 03/03/1976, RV *Acheron*, Stn 1976500; **NMNZ M.067875**, 2♂, ML 16–17 mm, 2♀, ML 20–23 mm, 40° 58′ 18″ S, 172° 0′ 48″ E, 60 m, 13/10/1979, RV *James Cook*, Stn J14/06/79; **NMNZ M.102257**, 1♂, ML 11 mm, 1♀, ML 11 mm, 40° 59′ 30″ S, 170° 52′ 54″ E, 440 m over 500 m, 22/07/1985, RV *Kaiyo Maru*, Stn KM/105B/85; **NMNZ M.021303**, 2♂, ML 12–13 mm, 1♀, ML 10 mm, 41° 5′ 0″ S, 174° 10′ 58″ E, 10/05/1967, Coll. M. van Dooren; **NMNZ M.287508**, 1♂, ML 13 mm, 41° 10′ 0″ S, 177° 43′ 0″ E, 37 m over 53 m, 21/10/1969, RV *James Cook*, Stn J06/125/69; **NMNZ M.074091**, 1♀, ML 15 mm, 41° 14′ 48″ S, 174° 51′ 30″ E, 15 m, 16/01/1956, Stn VUZ32; **NMNZ M.074097**, 2♂, ML 9–11 mm, 4♀, ML 8–12 mm, 2 indet., ML 7–10 mm, 41° 16′ 42″ S, 174° 54′ 06″ E, 15–17 m, 20/01/1956, Stn VUZ47; **NMNZ M.074095**, 1♂, ML 8 mm, 1♀, ML 12 mm, 41° 18′ 24″ S, 174° 52′ 18″ E, 4–7 m, 18/01/1956, Stn VUZ40; **NMNZ M.074096**, 1♂, ML 12 mm, 1♀, ML 18 mm, 41° 18′ 24″ S, 174° 48′ 24″ E, 15–18 m, 18/01/1956, Stn VUZ38; **NMNZ M.067285**, 1♀, ML 17 mm, 41° 22′ 24″ S, 174° 46′ 54″ E, 30 m, 20/04/1979, RV *James Cook*, Stn J05/11/79; **NMNZ M.012962**, 1♀, ML 17 mm, 41° 40′ 0″ S, 174° 18′ 0″ E, 73 m, 05/12/1956, Coll. F. Abernethy, Stn 1956030; **NMNZ M.067888**, 8♂, ML 11–14 mm, 2♀, ML 12–13 mm, 41° 59′ 03″ S, 174° 18′ 48″ E, 57 m over 164 m, 16/12/1978, RV *James Cook*, Stn J19/36/78; **NIWA 121888***, 1 indet., 42° 15′ 40″ S, 170° 44′ 29″ E, 213–221 m, 13/08/2017, RV *Tangaroa*, Stn 1609/41; **NMNZ M.067884**, 1♂, ML 14 mm, 4♀, ML 15–19 mm, 42° 23′ 14″ S, 170° 43′ 05″ E, 158 m over 216–224 m, 10/12/1978, RV *James Cook*, Stn J19/05/78; **NIWA 106088***, 4 indet., 43º 4′ 25″ S, 175º 1′ 0″ E, 357–367 m, 14/08/2015, RV *Tangaroa*, Stn 1511/71; **NMNZ M.287513**, 4♂, ML 9–10 mm, 2♀, ML 8–9 mm, 43° 6′ 06″ S, 175° 20′ 30″ E, 153 m, 12/01/1979, RV *Tangaroa*, Stn 1979656; **NMNZ M.074093**, 1♀, ML 9 mm, 43° 9′ 0″ S, 175° 30′ 30″ E, 112 m, 23/01/1954, MV *Alert*, Stn 1954002; **NMNZ M.091663**, 6♂, ML 9–13 mm, 2♀, ML 12–13 mm, 43° 17′ 48″ S, 173° 23′ 12″ E, 65 m over 78–86 m, 16/08/1985, RV *Kaiyo Maru*, Stn KM/119C/85; **142705***, 5 indet., 43° 27′ 4″ S, 169° 36′ 32″ E, 45–48 m, 12/04/2019, RV *Kaharoa*, Stn KAH1902/69; **NIWA 95247***, 1 indet., 43° 30′ 0″ S, 177° 18′ 0″ W, 170–187 m, 27/10/2020, SOP TRIP4567/80; **NMNZ M.067269**, 1♂, ML 12 mm, 2♀, ML 16–17 mm, 43° 50′ 35″ S, 174° 42′ 10″ E, 400 m, 01/06/1979, RV *James Cook*, Stn J07/01/79; **NIWA 142310**, 3♂, ML 12–13 mm, 4♀, ML 12–18 mm, 44° 0′ 29″ S, 173° 38′ 35″ E, 123 m, 30/10/1979, Coll. NZOI, Stn S176; **NMNZ M.091662**, 3♂, ML 13–14 mm, 5♀, ML 12–21 mm, 44° 51′ 54″ S, 171° 33′ 0″ E, 40–46 m over 67–69 m, 12/08/1985, RV *Kaiyo Maru*, Stn KM/116A/85; **NMNZ M.013473**, 6♂, ML 16–17 mm, 2♀, ML 23–24 mm,

45° 7′ 30″ S, 171° 10′ 36″ E, 44–55 m, 11/1960, Coll. J. Graham; **NMNZ M.102260**, 2♂, ML 9–14 mm, 1♀, ML 8 mm, 47° 53′ 06″ S, 166° 57′ 0″ E, 120–151 m over 120–153 m, 01/08/1985, RV *Kaiyo Maru*, Stn KM/113A/85; **NIWA 95127** 1♀, ML 19 mm, 49° 12′ S, 167° 20′ E, 90 m, 21/03/2015, Coll. SOP; **NMNZ M.102261**, 3♂, ML 11–12 mm, 48° 30′ 12″ S, 167° 0′ 42″ E, 50–110 m over 142–144 m, 02/08/1985, RV *Kaiyo Maru*, Stn KM/113B/85; **NIWA 95297***, 1 indet., 50° 30′ 0″ S, 167° 18′ 0″ E, 160–228 m, 15/04/2016, Stn 466923.

Diagnosis. Mantle length up to ~19 mm in mature males and ~24 mm in mature females. Anterior mantle margin without fringing projections. Chromatophores small and dot-like; dorsal surface sometimes with minute spots; no stripes. All arm suckers biserial throughout. Male and female arm suckers uniformly decrease in size from base to distal tip. Females often with thick, ruffled buccal membrane visible ventrally between Arms IV. Modified section of hectocotylus long (~50% of arm), slightly curved; basal unmodified section with about six sucker pairs; modified section without suckers, but with sucker pedicels joined basally and modified forming ~16 lappets; each lappet consists of two laterally positioned spire-like projections with globular tips, decreasing in size to distal tip. Tentacular club with transverse rows of approximately seven suckers; suckers small and uniform in size.

Description. Males slightly smaller than females: ML mature males 14.0–*15.0*–16.0 mm (SD 0.8), mature females 12.0–*18.9*–22.0 mm (SD 3.1). Mantle short, broad; maximum length and width subequal; posterior margin rounded (Figs 25, 26a, 26b). MWI males 73.3–*83.4*–93.3 (SD 6.1), females 66.7–*78.5*–100.0 (SD 9.6). Fins small, narrow, often lobed anteriorly. Fin length approximately 45% ML. FII males 31.3–*40.7*–50.0 (SD 5.7), females 42.1–*50.8*–66.7 (SD 6.4). FIIa males 25.0–*28.8*–40.0 (SD 5.1), females 17.6–*24.2*–33.3 (SD 5.2). FWI males 18.8–*22.0*–31.3 (SD 4.3), females 22.7–*27.6*–41.7 (SD 5.7). Posterior fin tapers to attachment point. Anterior fin convex often with larger lobes projecting slightly beyond anterior attachment point. Anterior fin margin does not reach anterior mantle margin.

Head wider than long in both sexes. HLI males 50.0–*60.2*–66.7 (SD 5.4), females 45.5–*55.5*–75.0 (SD 8.5). HWI males 68.8–*76.1*–92.9 (SD 8.1), females 45.0–*68.7*–100.0 (SD 14.2). Occipital band width approximately 25% mantle length in both sexes. OBWI males 18.8–*26.8*–37.5 (SD 6.5); females 20.0–*24.5*–30.0 (SD 3.4). Two pores present on each side of head: one posterolateral to eye, one anteroventral to eye. Eyes large in both sexes, occupying large portion of head; aperture covered by transparent membrane. EDI males 14.3–*19.3*–25.0 (SD 3.2), females 12.5–*15.7*–25.0 (SD 3.5).

Table 5 Counts, measurements (mm) and indices of mature male *Sepioloidea* n. sp. 2.

Collection	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ
Reg. No.	M.287489 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)	M.330524 (part)
Type	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
ML	16.0	14.0	14.0	14.0	15.0	15.0	15.0	15.0	16.0	16.0
MWI	87.5	85.7	85.7	85.7	73.3	86.7	80.0	93.3	81.3	75.0
FWI	31.3	21.4	28.6	21.4	20.0	20.0	20.0	20.0	18.8	18.8
FIIa	25.0	28.6	35.7	28.6	26.7	26.7	26.7	40.0	25.0	25.0
FII	50.0	42.9	42.9	42.9	40.0	40.0	33.3	46.7	31.3	37.5
FuLI	50.0	50.0	64.3	57.1	53.3	60.0	53.3	53.3	50.0	50.0
FFuI	18.8	21.4	28.6	21.4	20.0	26.7	20.0	26.7	18.8	18.8
HLI	62.5	64.3	64.3	64.3	60.0	60.0	53.3	66.7	56.3	50.0
HWI	81.3	71.4	92.9	71.4	73.3	73.3	73.3	86.7	68.8	68.8
EDI	18.8	14.3	14.3	21.4	20.0	20.0	20.0	20.0	18.8	25.0
OBWI	67.9	48.4	48.5	36.4	48.5	46.7	34.5	42.3	33.3	43.3
AL1I	75.0	71.4	64.3	71.4	73.3	66.7	66.7	66.7	62.5	68.8
AL2I	81.3	64.3	71.4	85.7	80.0	73.3	66.7	73.3	62.5	75.0
AL3I	75.0	71.4	78.6	85.7	80.0	66.7	73.3	73.3	68.8	75.0
AL4I	75.0	71.4	78.6	85.7	73.3	73.3	73.3	73.3	75.0	75.0
ASIn1	5.1	5.2	5.1	5.4	4.5	4.3	4.3	5.1	4.6	4.3
ASIn2	5.2	5.6	6.1	5.6	5.4	5.0	4.6	4.8	4.7	4.9
ASIn3	5.9	6.0	5.9	5.9	5.8	5.1	5.1	5.0	5.1	4.8
ASIn4	6.1	5.8	5.5	5.9	5.1	5.2	4.9	5.0	4.8	4.4
ASC1	32.0	28.0	30.0	30.0	26.0	30.0	27.0	24.0	28.0	32.0
ASC2	31.0	24.0	28.0	30.0	27.0	28.0	24.0	28.0	30.0	30.0
ASC3	31.0	30.0	32.0	34.0	34.0	30.0	26.0	30.0	32.0	38.0
ASC4	31.0	29.0	24.0	32.0	32.0	35.0	26.0	34.0	32.0	32.0
ClLI	25.0	28.6	28.6	28.6	20.0	26.7	20.0	20.0	25.0	25.0
ClRC	5	5	6	6	6	6	6	7	5	6
TIRC	24	23	27	26	26	26	22	22	26	24
ClSI	1.3	1.2	1.4	0.9	1.3	1.1	1.2	0.8	0.9	1.3
HcLI	81.3	71.4	85.7	78.6	73.3	73.3	66.7	73.3	68.8	62.5
HcModLI	46.2	50.0	50.0	45.5	45.5	54.6	50.0	54.6	54.6	50.0
HcLapC	18	16	17	16	17	15	14	15	17	18
HcSC	11	12	12	11	12	12	12	12	11	12
HcSI	4.8	6.1	4.6	4.8	5.5	5.3	4.7	4.8	5.0	4.1
SLI	37.5	28.6	28.6	28.6	26.7	26.7	20.0	26.7	25.0	25.0

Table 6 Counts, measurements (mm) and indices of female *Sepioloidea* n. sp. 2.

Collection	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ	NMNZ
Reg. No.	M.330526 (part)	M.330526 (part)	M.330526 (part)	M.330525 (part)	M.330525 (part)	M.330525 (part)	M.330526 (part)	M.330525 (part)	M.330525 (part)	M.330526 (part)
Type	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
ML	12.0	16.0	17.0	19.0	20.0	20.0	20.0	21.0	22.0	22.0
MWI	100.0	81.3	82.4	79.0	85.0	75.0	75.0	66.7	68.2	72.7
FWI	41.7	25.0	23.5	31.6	30.0	25.0	25.0	23.8	27.3	22.7
FIIa	33.3	25.0	17.7	31.6	25.0	20.0	25.0	23.8	22.7	18.2
FII	66.7	50.0	47.1	42.1	55.0	50.0	50.0	47.6	50.0	50.0
FuLI	83.3	68.8	58.8	63.2	60.0	55.0	55.0	47.6	45.5	50.0
FFuI	33.3	25.0	23.5	26.3	30.0	20.0	25.0	14.3	18.2	18.2
HLI	75.0	50.0	58.8	63.2	55.0	50.0	55.0	52.4	50.0	45.5
HWI	100.0	68.8	70.6	68.4	45.0	80.0	60.0	66.7	63.6	63.6
EDI	25.0	12.5	17.7	15.8	15.0	15.0	15.0	14.3	13.6	13.6
OBWI	52.5	37.0	44.4	46.0	43.8	38.2	47.2	42.3	33.9	44.7
AL1I	83.3	56.3	47.1	57.9	55.0	60.0	50.0	57.1	54.6	50.0
AL2I	83.3	56.3	52.9	63.2	60.0	55.0	50.0	57.1	50.0	50.0
AL3I	91.7	62.5	52.9	63.2	60.0	65.0	60.0	57.1	54.6	50.0
AL4I	83.3	62.5	52.9	63.2	65.0	60.0	60.0	57.1	50.0	50.0
ASIn1	4.3	2.9	3.1	3.5	2.4	2.8	2.7	2.5	2.77	2.7
ASIn2	4.1	3.4	3.4	3.2	2.8	3.0	2.9	2.9	2.9	2.6
ASIn3	4.3	3.5	3.3	4.0	2.5	3.4	3.0	2.8	3.0	2.7
ASIn4	4.2	3.3	3.2	3.6	2.5	2.9	2.9	2.9	2.6	2.8
ASC1	39	38	35	42	40	42	36	45	42	41
ASC2	42	38	41	42	41	44	40	45	40	43
ASC3	44	39	38	41	43	44	41	48	44	49
ASC4	44	41	44	46	36	44	42	49	46	46
ClLI	33.3	25.0	23.5	26.3	20.0	25.0	20.0	23.8	22.7	18.2
ClRC	7	6	6	7	7	6	7	7	7	6
TIRC	31	34	28	35	30	37	32	32	32	38
ClSI	1.3	1.1	0.9	0.8	0.8	1.1	1.2	1.1	1.1	1.1
EgDI	-	12.5	-	10.5	15.0	15.0	10.0	14.3	13.6	13.6

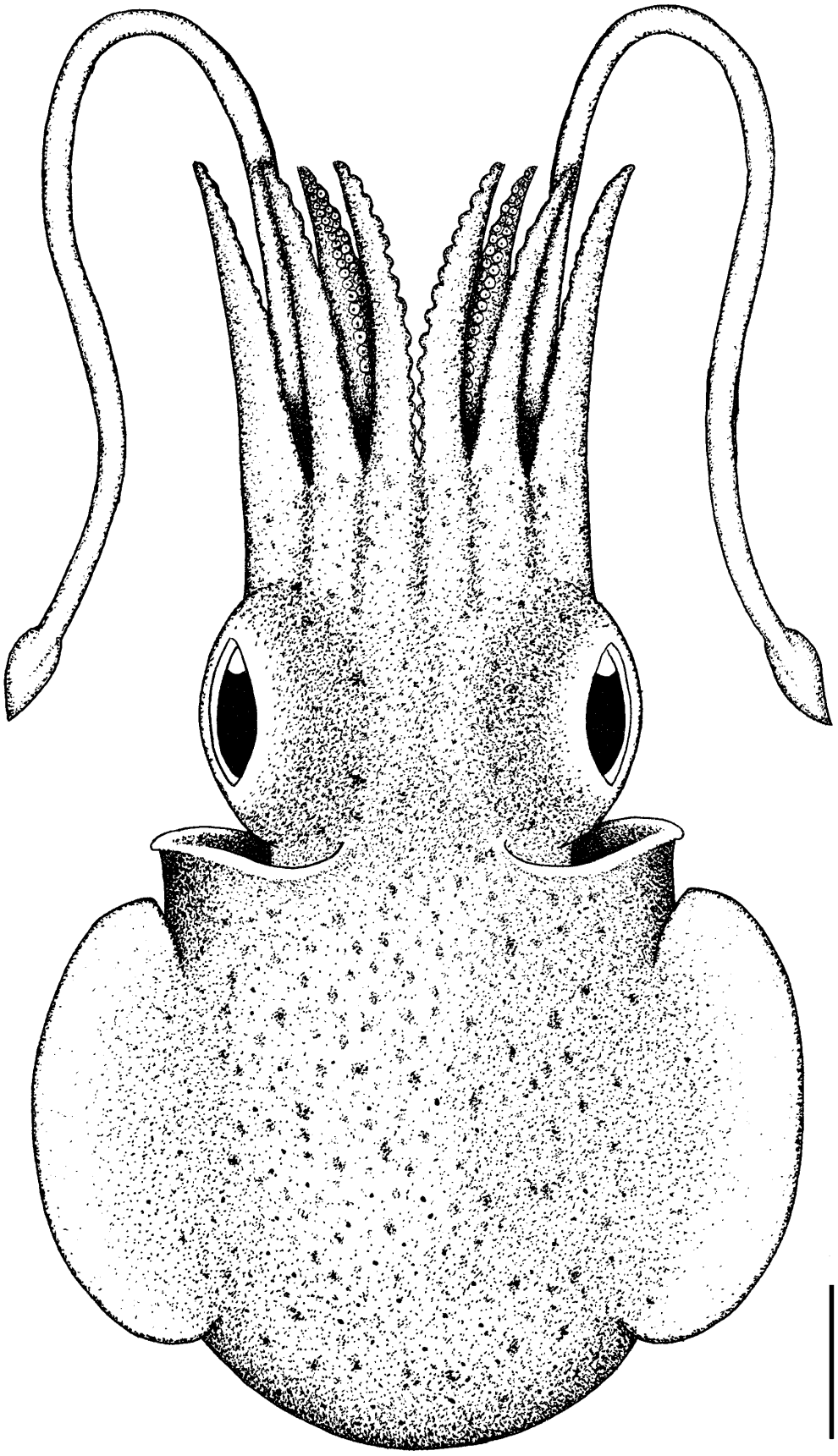

Fig. 26 *Sepioloidea* n. sp. 2: dorsal schematic (NMNZ M.330525, ♀ paratype , 20 mm ML). Scale bar = 5 mm.

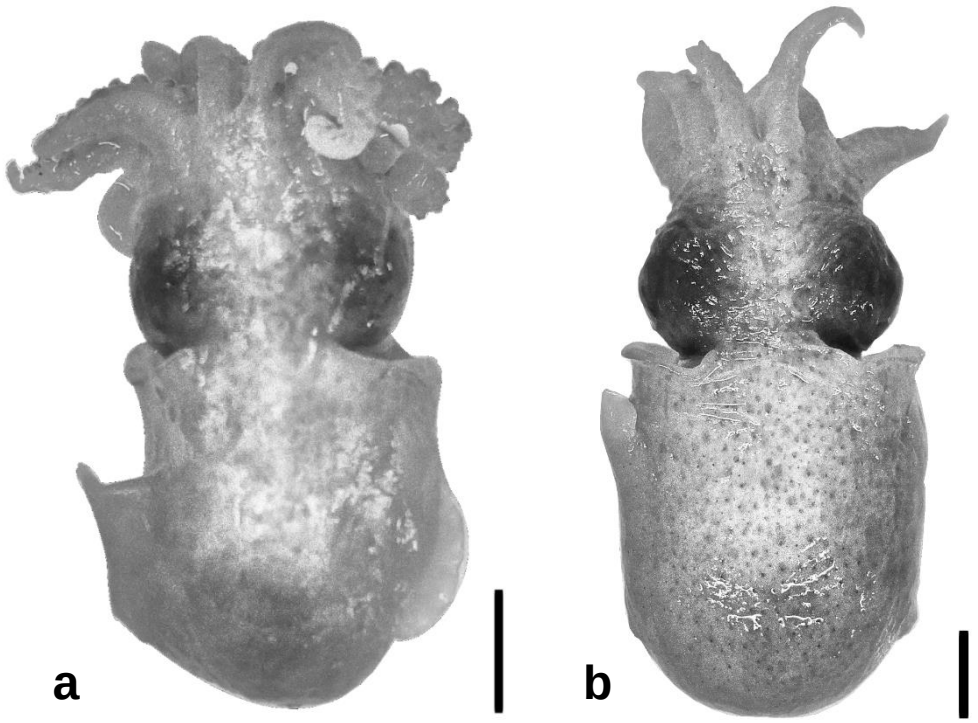

Fig. 27 Photographs of *Sepioloidea* n. sp. 2: **a** holotype (NMNZ M.287489, ♂, 16 mm ML); **b** female paratype (NMNZ M.330525, ♀, 20 mm ML). Scale bars = 5 mm.

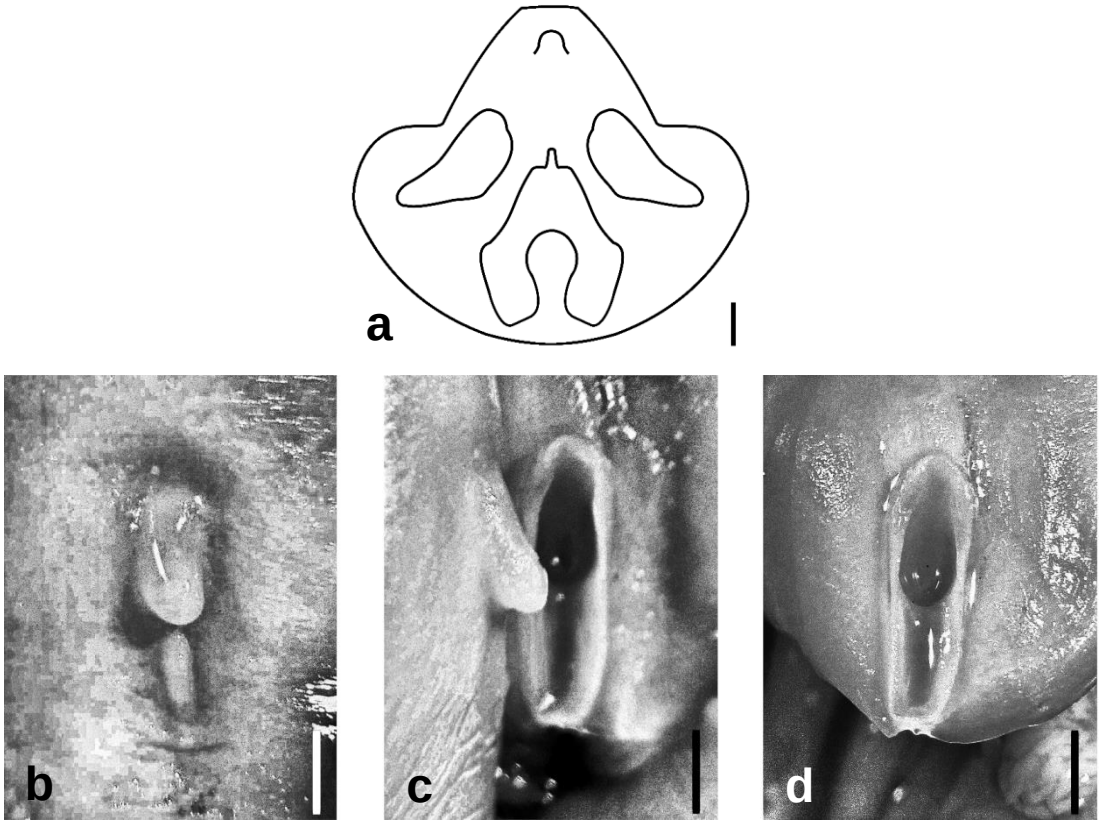

Fig. 28 *Sepioloidea* n. sp. 2: **a** funnel organ (NMNZ.067882, ♀, 20 mm ML) ; **b** photograph of right locking cartilage, mantle component, dorsal; **c** photograph of right locking cartilage, mantle component, lateral and funnel component, ventral; **d** photograph of right locking cartilage, funnel component, ventral (NMNZ M.330525 (part), ♀ paratype, 20 mm ML). Scale bars = a, 2 mm; b–d, 1 mm.

Funnel long, muscular; broad at base, tapering anteriorly to nearly cylindrical; aperture located approximately at anterior margin of eye. FuLI males 50.0–*54.1*–64.3 (SD 4.9), females 45.5–*58.7*–83.3 (SD 11.2). FFuI males 18.8–*22.1*–28.6 (SD 3.8), females 14.3–*23.4*–33.3 (SD 5.8). Funnel valve small, semi-circular flap inside dorsal rim of funnel aperture. Funnel organ (Fig. 28a) with broad, rounded wedge-shaped ventral components, broadest anteriorly; dorsal component roughly diamond in outline, apex almost meeting ventral component anterior margin, with small protrusion.

Funnel component of locking cartilage (Fig. 28c, 28d) with deep, ovular anterior pocket (concavity deepest posteriorly) and shallower narrow anterior groove. Mantle component (Fig. 28a) complements funnel component. Anterior lobe prominent and nose-like in shape, posterior protuberance shallow.

Arms broadest basally, slender distally, more robust in females (Figs 28a, 28b). Arm formula variable; typically, as follows: males, IV > III = II > I; females, III > IV > II = I. ALI4 males 71.4–*75.4*–85.7 (SD 4.1). ALI3 females 50.0–*61.7*–91.7 (SD 11.6). ALI1 males 62.5–*68.7*–75.0 (SD 4.0), females 47.1–*57.1*–83.3 (SD 10.1). All arms similar in shape, subtriangular in cross section along whole arm. Arm suckers biserial throughout, with chitinous rims. Arms connected by membranous web, shallowest at Arms I (~10% arm length), deepest at Arms IV (~20% arm length); depths similar in both sexes. Females often with thick, ruffled buccal membrane (Fig. 29b) visible ventrally between Arms IV.

Arm-sucker counts and sizes differ between sexes. ASC1–4 in males 24–*29*–32 (SD 2.6), 24–*28*–31 (SD 2.4), 26–*32*–38 (SD 3.2), 24–*31*–35 (SD 3.4) respectively; females 35–*40*–45 (SD 3.1), 38–*42*–45 (SD 2.1), 38–*43*–49 (SD 3.5), 41–*45*–49 (SD 2.4) respectively. Sucker size pattern similar in males and females, tapering gradually to tip of arm without markedly enlarged suckers. Male suckers relatively larger than those of females, distinctly globular in shape, not sitting in arm or with surrounding tissue. Female suckers often inset within arm with protective membrane bordering lateral sucker margins. ASIn1–4 and HcSI males 4.3–*4.8*–5.4 (SD 0.4), 4.6–*5.2*–6.1 (SD 0.5), 4.8–*5.5*–6.0 (SD 0.5) , 4.4–*5.3*–6.1 (SD 0.5), 4.1–*5.0*–6.1 (SD 0.5) respectively; mean ASIn1–4 females 2.4–*3.0*–4.3 (SD 0.6), 2.6–*3.1*–4.1 (SD 0.4), 2.5–*3.2*–4.3 (SD 0.6), 2.5–*3.1*–4.2 (SD 0.5) respectively.

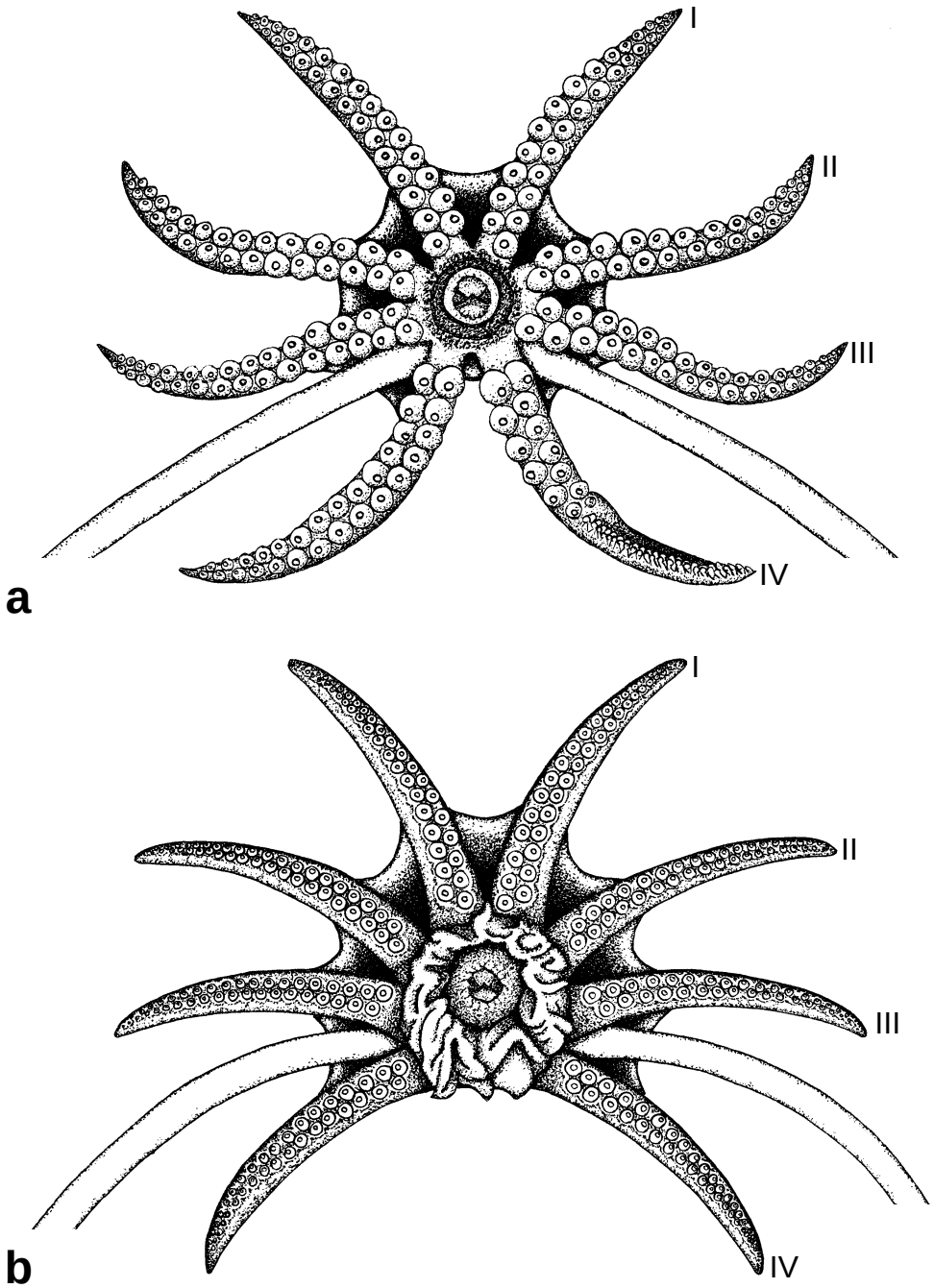

Fig. 29 *Sepioloidea* n. sp. 2 arm crowns: **a** male arm crown composite schematic (NMNZ M.287489 holotype, NMNZ M.330524, ♂ paratypes); **b** female arm crown composite schematic (NMNZ M.330525, ♀ paratypes); I–IV, arm numbers.

Arm-sucker rings without teeth; usually relatively larger in males (Fig. 30) than females (Fig. 31). Infundibular ring mostly smooth, with shallow grooves creating appearance of ~16–23 blocks with flat inner margins and triangular, pointed outer margins. Papillated ring with 3 or 4 concentric rings of polygonal processes. Internal ring consists of ~15–20 pentagonal polygonal processes; inner margin flat, outer margin pointed; each process with subtle ridge-like peg running medially from inner to outer margins. Intermediate rings with

~55–90 flat, scale-like polygonal processes. External ring with slightly smaller and more numerous processes.

Left ventral arm of males hectocotylised (Fig. 32a): HcLI 62.5–*73.5*–85.7; unmodified proximal section with 5 or 6 normal sucker pairs; distal tip modified, HcModLI 45.5–*50.1*–54.5 (SD 3.6). Modified section devoid of suckers; modified sucker pair pedicels form fused lappets; HcLPC 14.0–*16.0*–18.0 (SD 1.3); each lappet consists of two laterally positioned spire-like projections with globular tips, decreasing in size to distal tip.

Tentacle stalks long, slender, ovular in cross-section, without suckers; length approximately equal to mantle length. Clubs (Fig. 32b) expanded, tapering to blunt tips. ClLI males 20.0–*24.7*–28.6 (SD 3.6), females 18.2–*23.8*–33.3 (SD 4.2). Clubs with uniformly sized small suckers set in transverse rows of about seven; mean TIRC male 25; females 33. ClSI similar between sexes. ClSI males 0.8–*1.1*–1.4 (SD 0.2); females 0.8–*1.1*–1.3 (SD 0.2). Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacular club suckers (Fig. 33) with symmetrical papillated ring. Internal ring with ~10–13 pegs. Three to four intermediate rings present. External ring with ~40 pegs. Pegs irregular ovoid in shape; surface pitted. Internal surface of rim processes elongated and concave.

Gills with approximately 20 lamellae per demibranch.

Male reproductive system (Fig. 34) typical for the family with testis occupying large portion of the posterior mantle cavity. Spermatophore (Fig. 35) cement body bipartite. Cement body posterior part barrel-shaped, with slight median constriction, connecting to sperm reservoir via a narrow duct. Cement body anterior part narrower than posterior part, cylindrical, approximately 150% length of posterior part, connecting to posterior part via narrow ridged ‘neck’. Ejaculatory apparatus coiled, extending into anterior dilation of spermatophore. SPlI 20.0–*27.3*–37.5 (SD 4.4).

Eggs approximately spherical in shape. EgDI 10.0–*13.1*–15.0 (*n* = 8, SD 1.9).

Upper and lower beaks (Fig. 36a–c) clear at posterior margin, darkening to brown then black towards beak tips. Lower beak (Fig. 36a, 36b) with beak height roughly equal to baseline length. Leading edge of wing roughly one tenth of baseline ahead of rostral tip. Hood length slightly over half crest length. Hood closely adherent to crest. Jaw angle obtuse. Wing length around two thirds beak height. Maximum wing width close to jaw angle; marginally wider than minimum wing width. Lower rostral length roughly one third of beak height. Upper beak (Fig.35c) height roughly equal to beak length. Hood clear of crest posteriorly, with hood height around one fifth of beak height. Upper rostral length over one third crest length. Rostral tip pointed. Jaw angle near right angle.

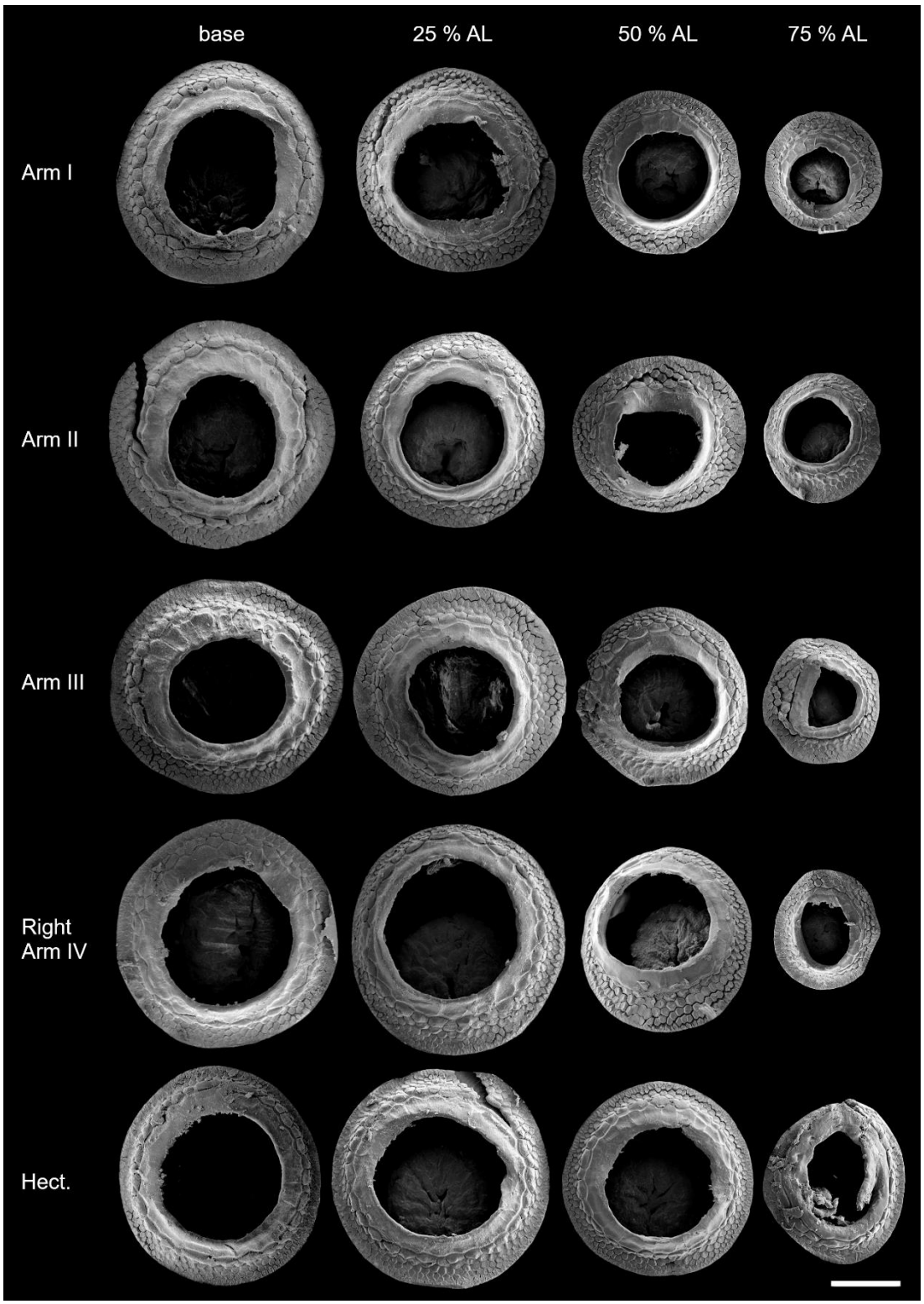

Fig. 30 SEM of *Sepioloidea* n. sp. 2: male arm suckers (hect, hectocotylus; NMNZ M.330528, ♂, 16 mm ML). Scale bar = 100 µm.

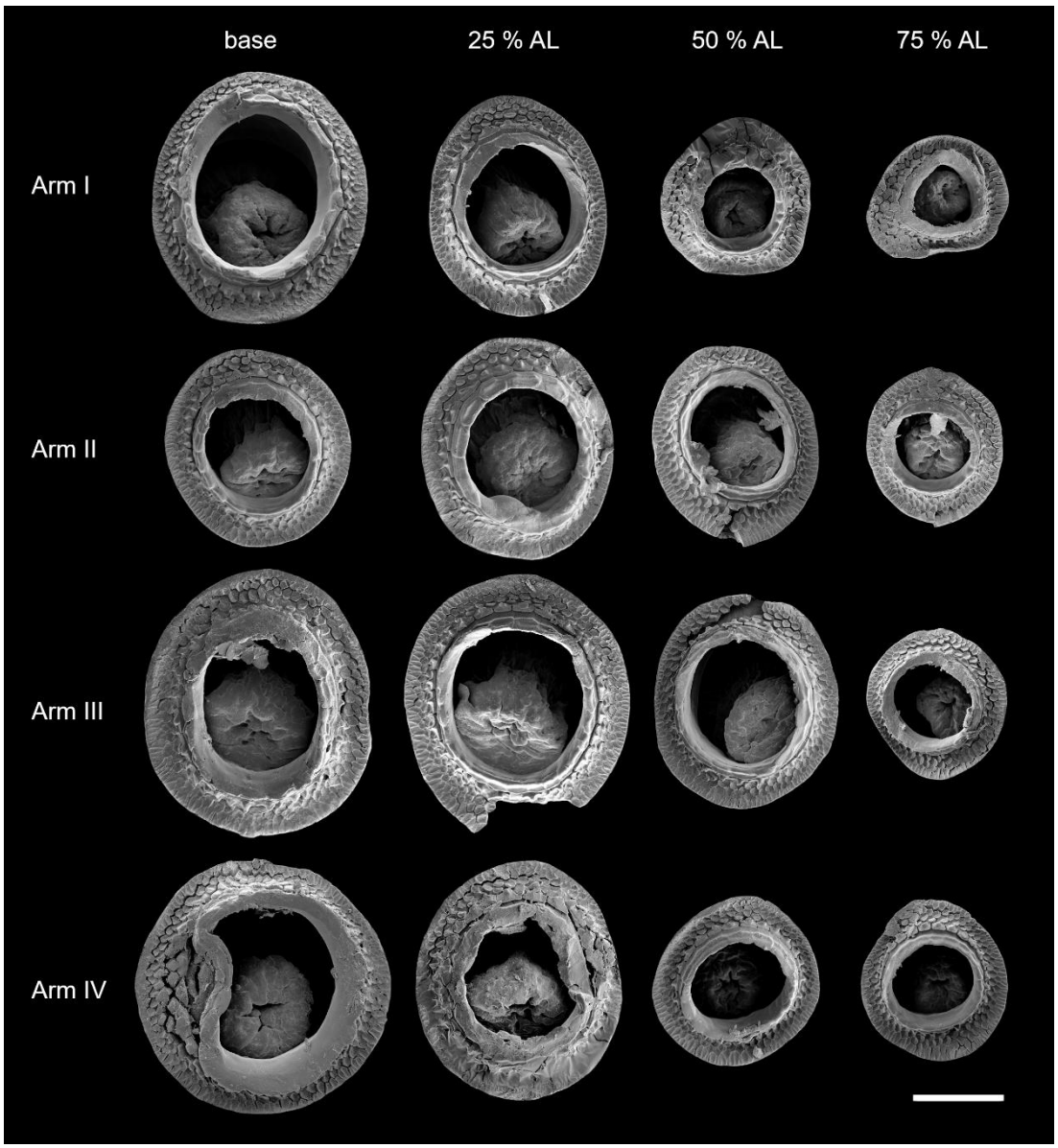

Fig. 31 SEM of *Sepioloidea* n. sp. 2: female arm suckers (NMNZ M.330528, ♀, 23 mm ML). Scale bar = 100 µm.

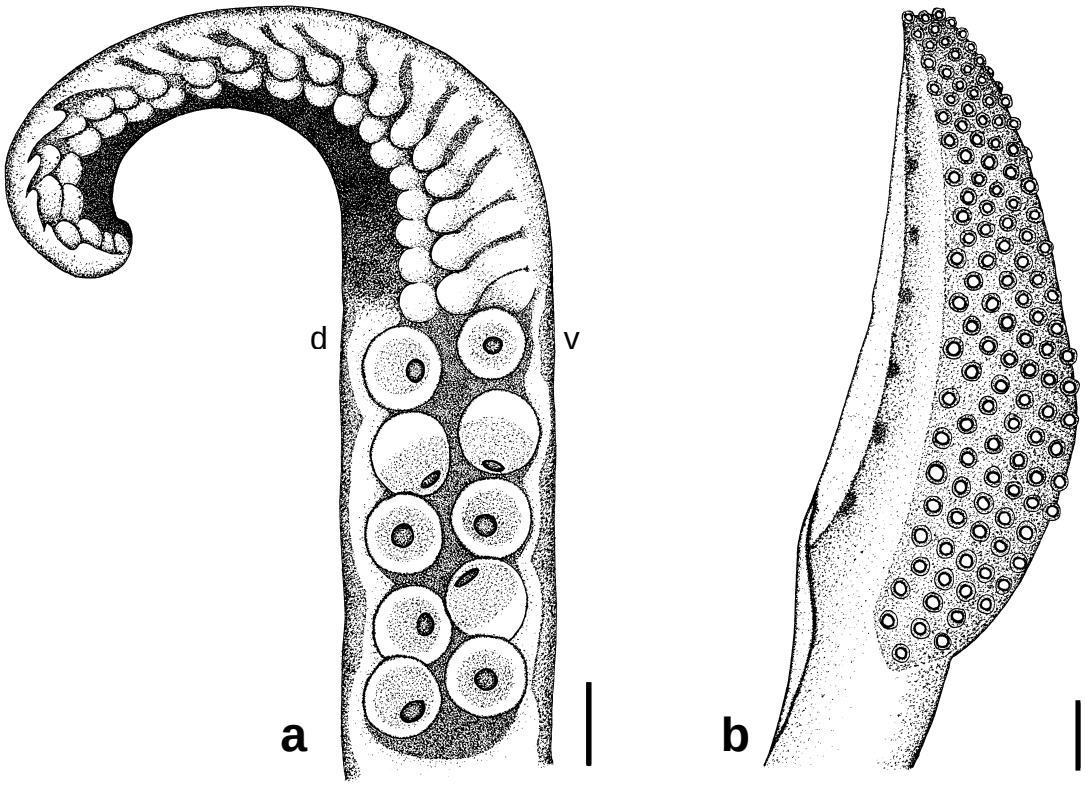

Fig. 32 *Sepioloidea* n. sp. 2: **a** hectocotylised left arm IV, oral view (d, dorsal; v, ventral; NMNZ M.330528, ♂, 15 mm ML); **b** tentacular club (drawn from fresh specimen, M.287502, ♂, 14 mm ML). Scale bars = a, 1mm; b, 300 µm.

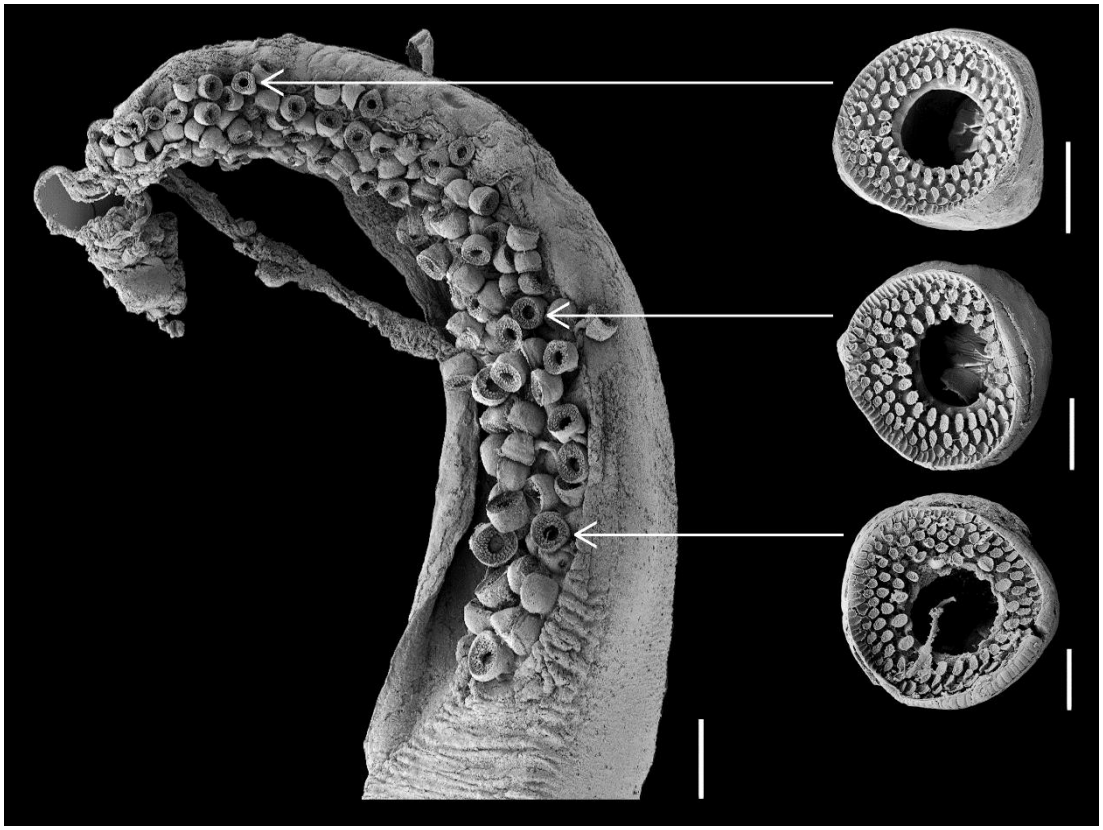

Fig. 33 SEM of *Sepioloidea* n. sp. 2: tentacular club and suckers (NMNZ M.330528, ♀, 20 mm ML). Scale bars = club 300 µm, suckers 50 µm.

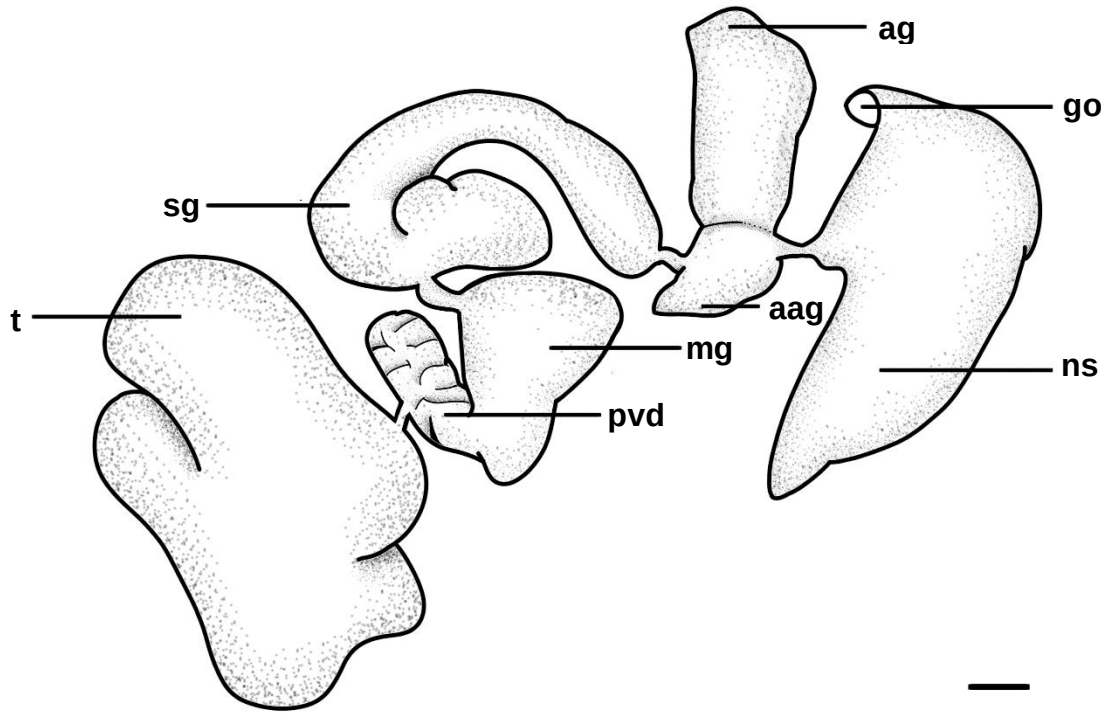

Fig. 34 *Sepioloidea* n. sp. 2: male reproductive system (**aag**, appendix of accessory gland; **ag**, accessory gland; **go**, genital opening; **mg**, mucilaginous gland; **ns**, Needham's sac; **pvd**, posterior vas deferens; **sg**, spermatophoric gland; **t**, testis; NMNZ M.330524 (part), ♂ paratype, 14 mm ML). Scale bar = 2 mm.

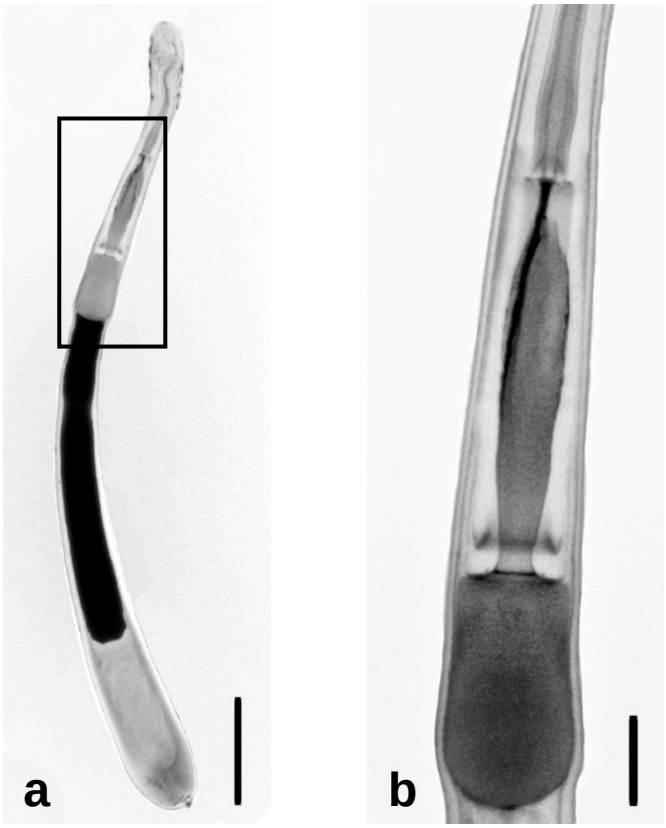

Fig. 35 Stereo microscope image of *Sepioloidea* n. sp. 2: spermatophore (NMNZ M.330524 (part), ♂ paratype, 31 mm ML); **a** whole spermatophore, cement body outlined; **b** close-up of cement body. Scale bars = a, 500; b, 100 µm.

Radula (Fig. 36d) with seven rows of teeth. Rachidian teeth unicuspid, with long, narrow mesocone; base width approximately two thirds mesocone height; proximal margin concave; underside with longitudinal indent. First lateral teeth bicuspid with asymmetrical lateral margins; mesocone robust, its height about one third rachidian teeth height, angled weakly towards rachidian teeth; inner margin concave from tip to base; outer cusp around two thirds mesocone height. Second lateral teeth simple, unicuspid, approaching rachidian height, leaning weakly towards rachidian teeth. Marginal teeth simple, curved proximally, straight distally, longer than rachidian teeth.

Preserved specimen colouration varies from pale cream through to dark brown. Chromatophores (Fig. 6c) tiny dots and larger spots, dark brown/purple, evenly distributed across dorsal surface of the mantle, fins, head, and along Arms I, II, and III; fewer on ventral surfaces of the mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club, small and densely set near tip, larger and very sparse towards the stalk for 150% club length.

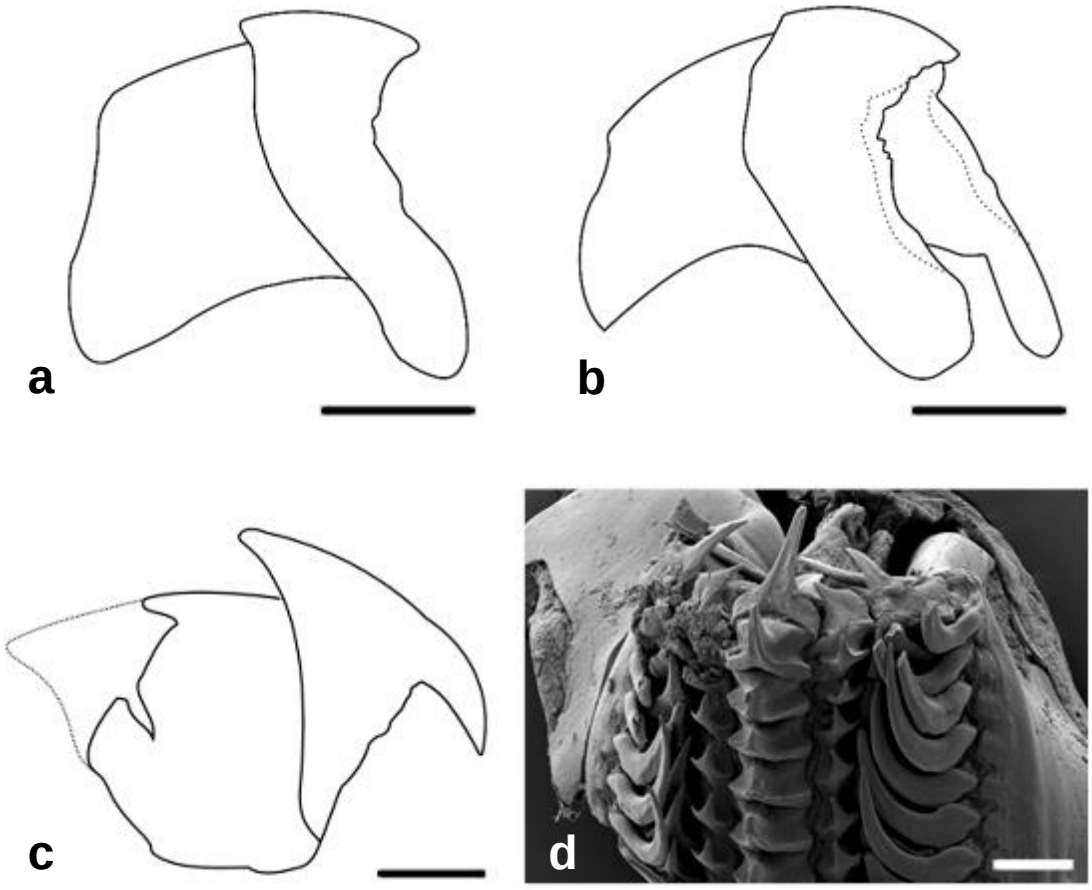

Fig. 36 *Sepioloidea* n. sp. 2: **a** lower beak, profile view; **b** lower beak, oblique view; **c** upper beak, profile view (NMNZ M.95127, ♀, 19 mm ML); **d** SEM of radula (r, rachidian tooth; NMNZ M.330528, ♀, 20 mm ML). Scale bars = a–c, 1 mm; d, 100 µm.

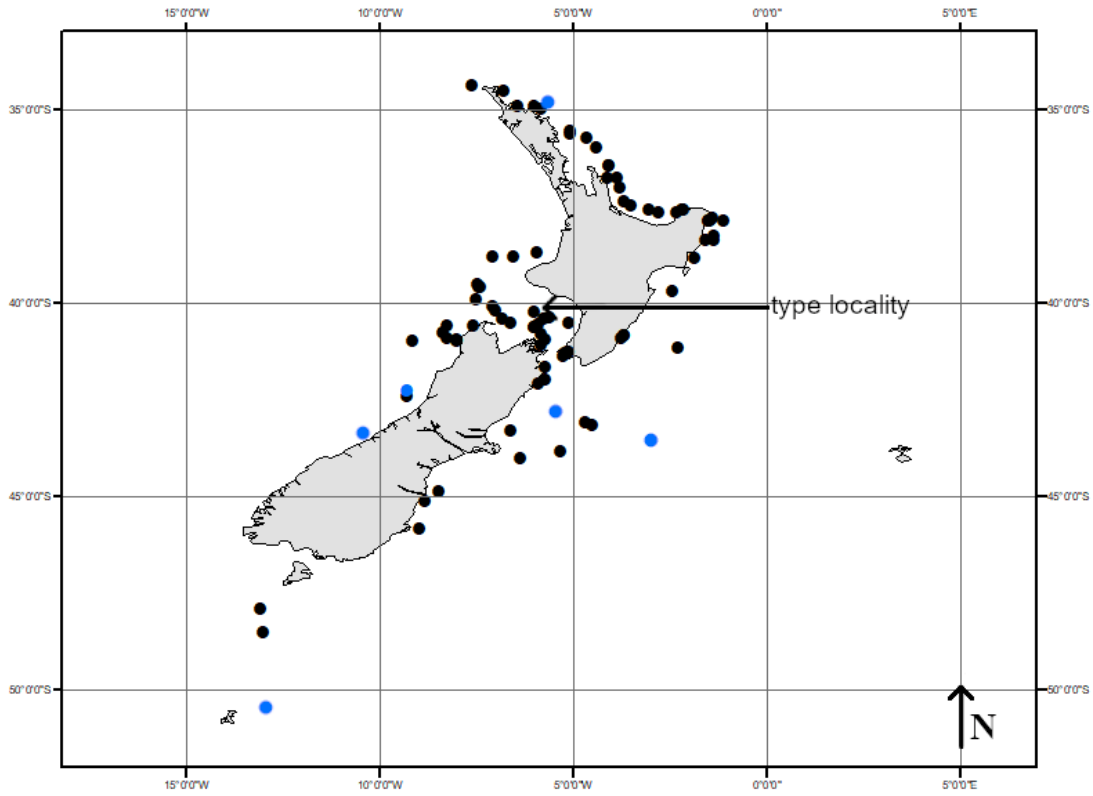

Fig. 37 Distribution of *Sepioloidea* n. sp. 2 specimens examined in this study including sequenced (blue) and non-sequenced (black) specimens.

Type locality. Southern Taranaki Basin, New Zealand, 40º 14′ 24″ S, 174º 0′ 6″ E, 96–101 m.

Known Distribution (Fig. 37). Southwest Pacific, New Zealand; 0–440 m.

Remarks. At maturity *Sepioloidea* n. sp. 2 is unlikely to be mistaken for any other *Sepioloidea* species apart from *S. pacifica*. At all specimen sizes observed to date, it has clear morphological differences from all other congeners (summarised in Table 7) and additionally does not appear to reach sizes greater than ML 20 mm, further separating it from *S. magna* and *Sepioloidea* n. sp. 1 (maximum size for males ML ~45 and ~37 mm, respectively; for females: ~62 and ~59 mm ML). While the similar maximum size, overall morphological similarities, and geographic co-occurrence of *Sepioloidea* n. sp. 2 and *S. pacifica* could potentially lead to confusion, these taxa can be reliably distinguished due to the differences in club morphology, and hectocotylus structure.

In *Sepioloidea* n. sp. 2, the tentacle club suckers are more numerous (set in transverse rows of about six or seven, compared to about five in *S. pacifica*), are uniform in size (Fig. 32b), with very short pedicels, often resulting in near-identical sucker aperture orientation. In contrast, *S. pacifica* tentacle club suckers sit on pedicels long enough to result in a variety of sucker aperture orientations and are markedly enlarged midway along the dorsal club margin (Fig. 9b). While the modified portion of the hectocotylus in both species spans the distal

Table 7 Summary of diagnostic characters across *Sepioloidea* including novel species.

Species	Diagnostic Structure		
	Hectocotylus	**Tentacle club suckers**	**Arm suckers**
***Sepioloidea pacifica* (Kirk, 1882)**	Modified for ~50% of arm length. Lappets (~20) asymmetrical. Lappets bilobed ventrally, wedge-shaped dorsally.	~5 suckers per transverse row. Suckers largest midway along dorsal club margin.	Biserial.
***Sepioloidea* n. sp. 1**	Modified for ~25% of arm length. Lappets (~15) asymmetrical; spire-shaped ventrally, tongue-shaped dorsally.	~10 suckers per transverse row. No sucker enlargement.	Biserial.
***Sepioloidea* n. sp. 2**	Modified for ~50% of arm length. Lappets (~16) symmetrical; each with paired globular tips.	~6 suckers per transverse row. No sucker enlargement.	Biserial.
***S. magna* Reid, 2009**	Modified for ~50% of arm length. Lappets (~22) asymmetrical; bilobed ventrally, lobe tips pronounced, ridge-shaped dorsally.	~40 suckers per transverse row. No sucker enlargement.	Biserial proximally; tetraserial distally.
***S. lineolata* (Quoy & Gaimard, 1832)**	Details unknown. Requires full redescription. Species unique. Only species in genus to have longitudinal lines along mantle and head, and fringed anterior margin of dorsal mantle.		

half of the arm's length, the lappet structures are vastly different. In *Sepioloidea* n. sp. 2*,* the dorsal and ventral lappet components are identical, globular, spire-like structures (Fig. 32a). However, in *S. pacifica,* the dorsal lappet component is asymmetrically bilobed (like the capital letter 'B') and the ventral lappet component is a simple flap (Fig. 9b).

Arm sucker and tentacle club sucker ring dentition also differ clearly between *Sepioloidea* n. sp. 2 and *S. pacifica.* Arm suckers of both species have a papillated ring consisting of ~4 concentric rings with the internal ring consisting of medially ridged polygonal processes. In *S. pacifica* these ridges continue in the intermediate ring of polygonal processes as straight or crescent-shaped pegs (Figs 7, 8), the pegs more prominent in females; pegs are absent in *Sepioloidea* n. sp. 2.

A large majority of female *Sepioloidea* n. sp. 2 specimens also exhibit thick, ruffled buccal membrane around the entire oral aperture (Fig. 29b), usually thickest ventrally, often clearly visible in ventral view within the space between both Arms IV. All spermatangia observed in female specimens of *Sepioloidea* n. sp. 2 in this study were embedded in the inner parts of this buccal area. This buccal membrane morphology was also occasionally observed in

Sepioloidea pacifica or *Sepioloidea* n. sp. 1. Its potential presence and frequency in the Australian congeners are currently unknown.

In published literature, there is only one potential instance of *Sepioloidea* n. sp. 2 having been reported under the name *S. pacifica*. Reid (2009:108) cited the depth range reported by Powell (1979) for *S. pacifica* as 15–550 m; observations made in the present study suggest that encountering true *S. pacifica* in waters at the deeper end of this estimate would be unlikely (but of course not impossible). It is probable that collection data for specimens previously identified by default as *S. pacifica*, but which would now be recognised as *Sepioloidea* n. spp. 1 and 2, were factored into this estimated depth range. These apparent depth associations may be an artefact of sampling bias but could also be an accurate representation of habitat differences or physiological limitations.

In addition to the morphological differences discussed above, molecular results (Fig. 38, Table 8) show that *S.* n. sp. 2 can also be reliably distinguished from other *Sepioloidea* species by DNA barcoding. This may be particularly useful for distinguishing between the sister species *S. pacifica* and *S.* n. sp. 2, if small specimens in poor condition are encountered (e.g., from predator gut contents).

MOLECULAR RESULTS

Cytochrome *c* oxidase subunit I (COI) sequences were obtained for 61 New Zealand *Sepioloidea* specimens. The aligned 658 bp sequences showed no insertions, deletions, or stop codons. Five separate clades were identified in the phylogeny, representing five sepioloids: *S. pacifica*, *S. lineolata*, *S.* n. sp. 1, *S.* n. sp. 2, and the outgroup species, *Rossia pacifica* (Fig. 38).

Sepioloidea n. sp. 1 was represented by the most numerous (n = 32) and most geographically widespread samples. Even with such wide coverage, *S.* n. sp. 1 showed the lowest intraspecific distances (Table 8). The fewest specimens from New Zealand waters were available for *S.* n. sp. 2 (n = 7). Both *S.* n. sp. 2 and *S. pacifica* had relatively high maximum intraspecific distances (*S.* n. sp. 2: 1.42 %; *S. pacifica*: 1.57 %) compared with *S.* n. sp. 1 and *S. lineolata* (*S.* n. sp. 1: 0.18 %; *S. lineolata*: 0.31 %). High interspecific distances were found within the New Zealand *Sepioloidea*, with a minimum of 11.09 % between *S. pacifica* and *S.* n. sp. 2 and a maximum of 14.29 % between *S. pacifica* and *S.* n. sp. 1. All New Zealand *Sepioloidea* species showed high interspecific distances with the Australian *S. lineolata* (mean ~25 %).

The maximum-likelihood phylogeny (Fig. 38) shows high support for the distinction between all New Zealand *Sepioloidea* species and the Australian *Sepioloidea lineolata* (bootstrap value of 0.999).

The maximum-likelihood bPTP analysis supported the morphological determination of the two new species in this thesis (*S.* n. sp. 1 and *S.* n. sp. 2; Fig. 39).

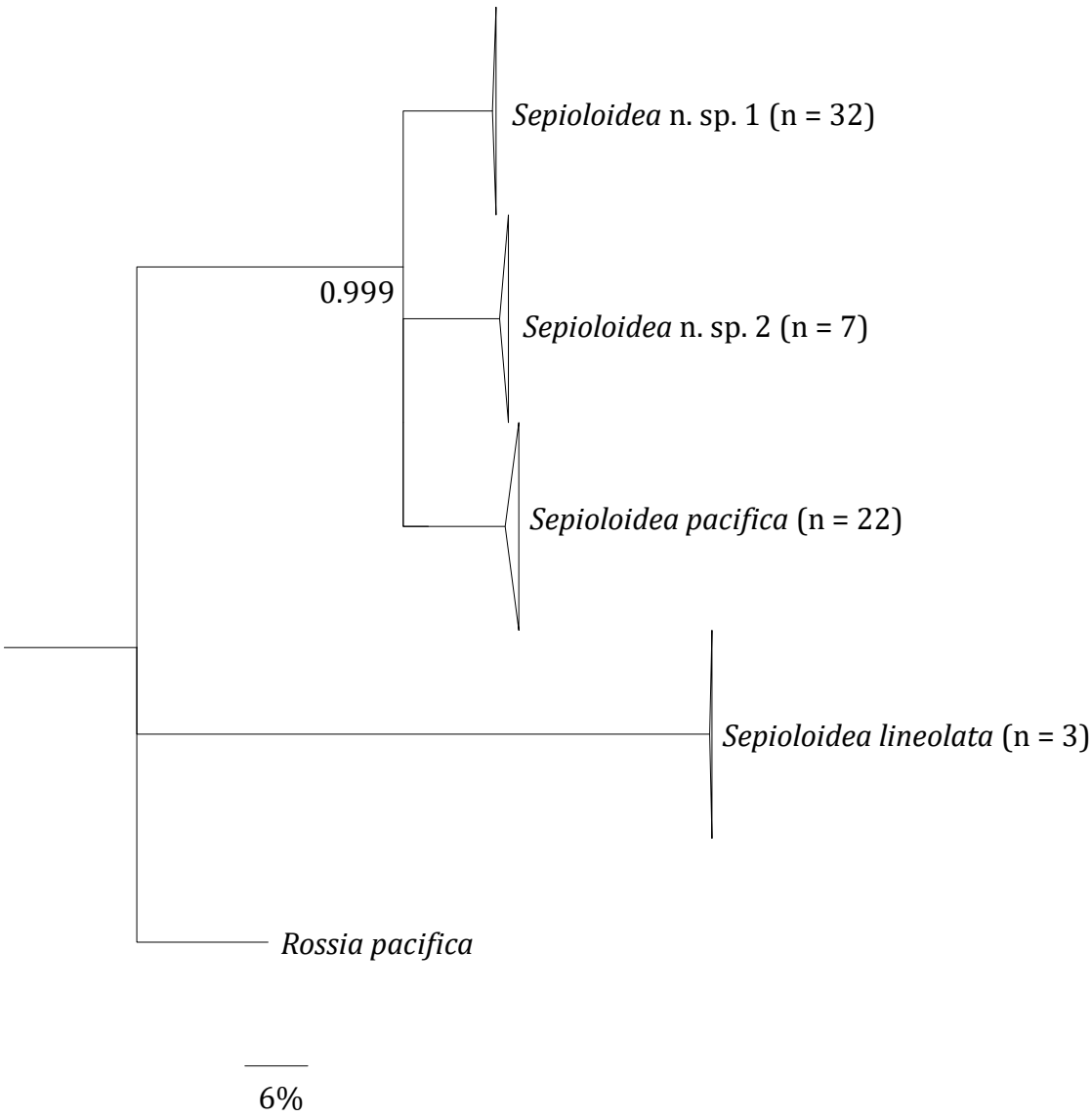

Fig. 38 Maximum-likelihood phylogeny based on cytochrome *c* oxidase subunit I (COI) for specimens of *Sepioloidea*, morphologically identified as *S. pacifica*, *S.* n. sp. 1, and *S.* n. sp. 2, with *Rossia pacifica* used as an outgroup, with 1000 bootstrap replicates.

Table 8 Percent intraspecific (in dark grey) and interspecific distances for cytochrome *c* oxidase subunit I (COI) for four species of *Sepioloidea*.

	***S.* n. sp. 2**			***S. pacifica***			***S.* n. sp. 1**			***S. lineolata***		
	min	mean	max	min	mean	max	min	mean	max	min	mean	max
***S.* n. sp. 2**	0.00	0.50	1.42	–	–	–	–	–	–	–	–	–
S. pacifica	11.09	12.37	13.12	0.00	0.34	1.57	–	–	–	–	–	–
***S.* n. sp. 1**	11.55	12.21	13.82	12.20	13.12	14.29	0.00	0.02	0.18	–	–	–
S. lineolata	23.56	25.18	26.45	24.60	26.83	27.94	24.05	25.54	26.63	0.00	0.10	0.31

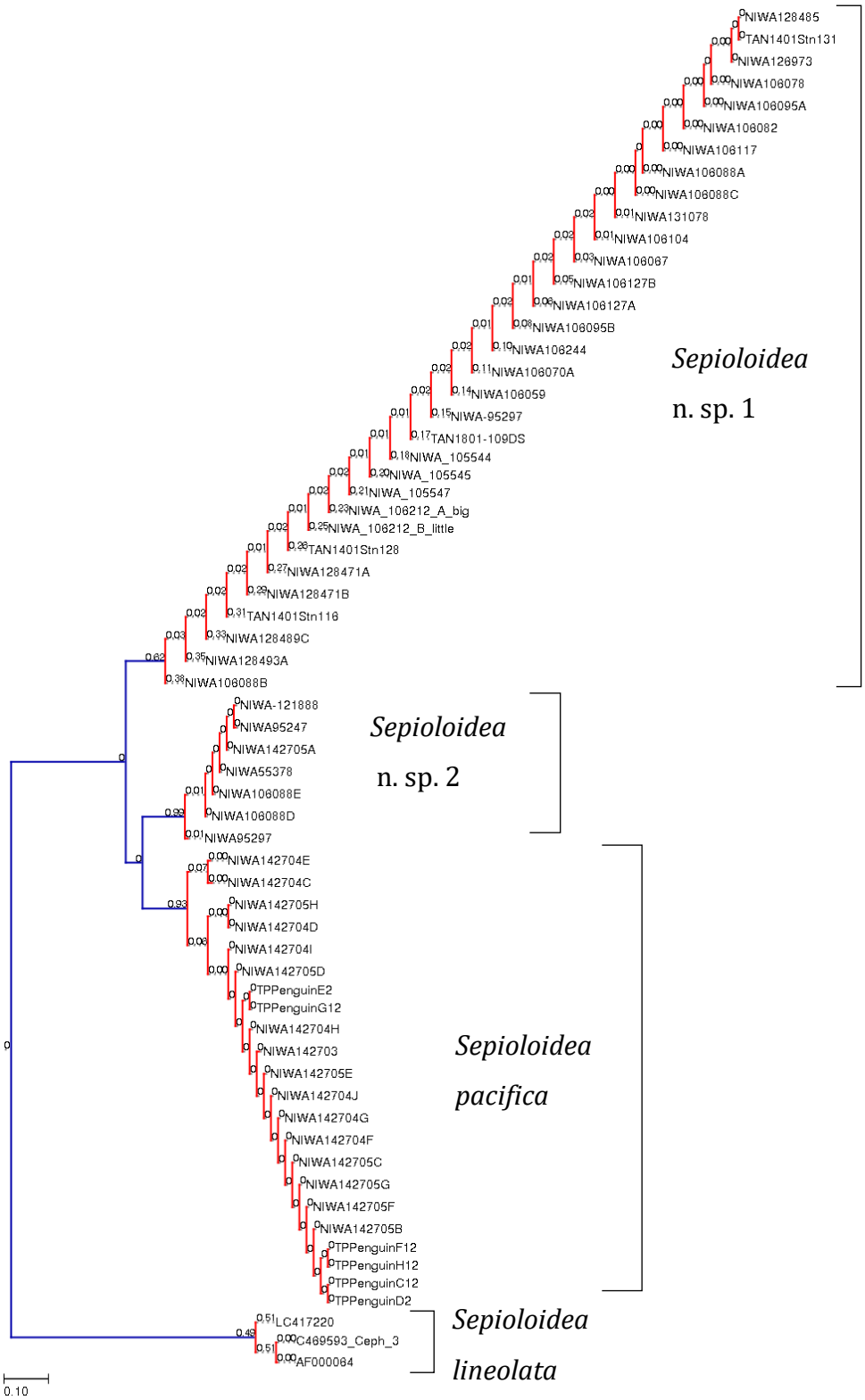

Fig. 39 Maximum-likelihood solution from the Bayesian Poisson tree processes (bPTP) analysis of cytochrome *c* oxidase subunit I (COI) sequences for *Sepioloidea*. Blue bars indicate sequences that represent separate species, while red lines indicate sequences that represent the same species. This analysis supports the morphological recognition of four distinct species in *Sepioloidea*: *S. pacifica*, *S.* n. sp. 1, and *S.* n. sp. 2, and *S. lineolata* (*S. magna* sequences are not available).

DISCUSSION

To date, all specimens of the Australasian 'bottletail squid' genus *Sepioloidea* collected in New Zealand waters have been attributed to a single nominal species, *S. pacifica* (Spencer *et al.*, 2016). Through the examination of over 600 specimens, plus the sequencing of an additional 61 specimens (with those of suitable condition also examined thoroughly), this thesis confirms the presence of two novel species in addition to *S. pacifica* in New Zealand waters. Morphological examinations of all *Sepioloidea* species (except *S. lineolata*) provided the basis for a summary of reliable diagnostic characters (Table 7). In addition, this thesis presents the first sequences of *S. pacifica* and both novel species, which support the morphological findings (Fig. 38). By taking this integrative taxonomic approach, the recognition of two novel species — *Sepioloidea* n. sp. 1 and *Sepioloidea* n. sp. 2 — is robustly supported by multiple lines of evidence. Additionally, this thesis reports on some additional morphological details for a new, fully mature male *Sepioloidea magna* specimen (AM registration number C. 476096) that has become available since the species' description in 2009. Morphological information and images obtained from this specimen provided more information upon which to build diagnostic species descriptions.

As a result of this work, *Sepioloidea* is now known to contain at least five species, with multiple representatives in both New Zealand and Australian waters, inhabiting depths from tens to hundreds of meters. These comprise both small-bodied taxa (*S. lineolata, S., pacifica*, *Sepioloidea* n. sp. 2) and relatively large-bodied taxa (*S. magna*, *Sepioloidea* n. sp. 1). While many morphological features unite these species (e.g. narrow fins, hectocotylised left Arms IV, biserial arm suckers, locking cartilage structure, mantle and head fusion) and support their grouping within *Sepioloidea*, it would be useful to undertake a thorough complementary examination of Australian material. In particular, a review of *S. lineolata* is essential because some morphological details of this species are not yet well reported, and some of its known characters do differ from those of all other now-known *Sepioloidea* species (such as the fringed anterior mantle margin and the pattern of longitudinal lines). Based on COI, the three species from New Zealand waters appear closely related, but their relationship to *S. lineolata* was not resolved (Fig. 38). Since this analysis was limited to a single mitochondrial gene, the inclusion of additional genes (including nuclear genes) will be required to fully understand the relationships between species in this family. In addition, now that more fully mature *S. magna* are available in museum collections (in particular, the Melbourne Museum, Melbourne, Reid pers. comm.) more comparative material can be examined for morphological differences.

Distribution. Both *Sepioloidea* n. spp. 1 and 2 have only been observed in New Zealand waters to date, and do not appear to overlap geographically with either *S. lineolata* or *S. magna* from Australia.

Despite the potential for bias due to sampling and collection effort, the records of the New Zealand *Sepioloidea* species appear to reflect three different depth preferences. Like *S. magna*, both *Sepioloidea.* n. spp. 1 and 2 appear to occur in deeper waters (73–911 m, and 0–440 m, respectively) than *Sepioloidea pacifica* which instead appears to occupy shallower depths like *S. lineolata* (<55 m and <100 m, respectively). Unfortunately, because it is unclear from collection data whether those specimens purportedly collected within a range including 0 m occurred intertidally or were collected at the surface (possibly at night), the suspected depth differences among the three species may actually be more discrete than is apparent from the data. The apparent depth distribution of the three New Zealand species align with different habitats: *S. pacifica* is only reported from inshore waters (Fig. 11); *Sepioloidea*. n. sp. 2 has mainly been collected offshore in deeper waters, particularly within in the Southern Taranaki Basin (Fig. 37), and *Sepioloidea* n. sp. 1 presently appears to have the widest distribution offshore, having been collected from deep waters (to 911 m) near the Auckland Islands and along the Chatham Rise (Fig. 23). Occasionally, multiple *Sepioloidea* species are collected in a single event. This, along with the overlaps in collection depth between species, show that multiple species may inhabit the same habitat at the same time. For example, the following NIWA specimen lots are yet to be split: NIWA 142705 has *S. pacifica* and *S.* n. sp. 2 individuals from 45–48 m depth; NIWA 95297 and NIWA 106088 both have *S.* n. sp 2 and *S.* n. sp 1 individuals from 160–228 m and 357–367 m depths respectively. Interestingly, one female specimen with tentacle club morphology conforming to *S. pacifica* (which is common around / under wharves) has also been collected from Waitangi Wharf in the Chatham Islands. It is possible that this specimen represents a once-connected, but now isolated population of *S. pacifica*, but the collection of additional material is needed to determine whether this is, indeed, the case. Based on a single record only, little inference should be drawn but is worthy of mention. There is also a possibility that the collection data associated with this individual may be incorrect.

The Chatham Islands are presently connected to the New Zealand mainland by the Chatham Rise, which is relatively shallow compared with the surrounding seafloor (~1000m depth compared to the ~3000m trenches along the north and south margins) but still far below the known depth range for *S. pacifica* at any life stage. As the Chatham Rise began submerging along with the Zealandia continent relatively recently at the end of the Cretaceous period (Stilwell & Consoli, 2012), the rise could have provided a habitat for ancient *S. pacifica*, thus resulting in the formation of this isolated population. Another explanation may be that a natural flow continues to exist between the two populations, but that seems highly unlikely

due to the apparent depth limits of *S. pacifica* and current depth of the Chatham Rise. These limits are suggested by the very little overlap of *S. pacifica* into the offshore habitat of *S.* n. sp. 2 and the absence of *S. pacifica* from deep water records (i.e. the depth range of *S. pacifica* is unlikely to be a simple reflection of collection effort). In future, molecular data could be compared from the mainland and Chatham Islands populations to provide insight into whether/when these populations may have diverged. The absence of deep-water *S. pacifica* specimens from collections to date — and by extension, the potential stratification of these three species by depth — could be due to specific adaptations to pressure, food availability (Summers, 1983) or biogeographic history.

DNA barcoding. Specimens were available from all three species of *Sepioloidea* in New Zealand waters for genetic analysis, which allowed for the direct comparison of both morphological characters and the DNA barcode region (COI). The DNA barcoding results support a distinct separation of all three *Sepioloidea* from New Zealand (bootstrap support 0.999), which are also distinct from the only sequenced species from this genus in Australian waters (Fig. 38). This is the first study to provide sequences for the New Zealand taxa in this genus. However, the relationships between the New Zealand *Sepioloidea,* and between these species and the Australian *Sepioloidea*, remain unresolved. In order to resolve these relationships, future research will require sequences from *S. magna*, in addition to additional gene regions (including additional mitochondrial genes and nuclear genes).

The smallest maximum intraspecific distance was identified in *Sepioloidea* n. sp. 1 (0.18 %) despite having the most numerous and geographically widespread samples (n = 32) (Fig. 38). The *Sepioloidea pacifica* and *Sepioloidea* n. sp. 2 specimens both represented smaller geographic ranges but showed larger intraspecific distances (*S. pacifica* max = 1.57 %; *S.* n. sp. 2 max = 1.42 %). These differences could suggest greater mixing of the entire population within the New Zealand region, or alternatively could indicate a recent bottleneck and/or population expansion outward from a more restricted location, as has been recently postulated for the giant squid *Architeuthis dux* Steenstrup, 1857 (Winkelmann *et al.*, 2013).

A DNA barcode gap (as discussed by Meier *et al.*, 2008) was observed within the *Sepioloidea* sequenced in this study (Table 8). The maximum intraspecific difference observed within any single New Zealand species was 1.57 % (*S. pacifica*), while the minimum interspecific difference observed was 11.09 % (also *S. pacifica*), with the mean pairwise distance between any two New Zealand *Sepioloidea* species falling in the range of 12–14 %. Interestingly, the minimum interspecific distances between the New Zealand *Sepioloidea* species and the Australian *S. lineolata* were nearly double, at a minimum of 23.56 % (mean 25–27 %). Although no conclusions about the higher taxonomy in this family can be made from a single mitochondrial gene, this discrepancy indicates that an integrative taxonomic investigation into the higher classification of these species is

warranted. In particular, the Australian *Sepioloidea* require better representation in phylogenetic analyses; despite being recorded from nearly the entire coastline of Australian (Atlas of Living Australia, 2020), only three sequences are currently available for *Sepioloidea lineolata*. In addition, future studies should include *Sepioloidea magna* if fresh specimens become available.

Ecology. Unlike species from the Sepiadariidae family, species of the Sepiolidae family have been the subject of intensive and comprehensive ecological and behavioural studies. Much of this discussion on ecology will infer findings from studies on neritic subfamilies Sepiolinae and Rossinae (not the pelagic subfamily Heteroteuthinae) to be relevant to Sepiadariidae species as well. These inferences are explored due to these taxa having relatively close evolutionary relationships (Sanchez *et al.*, 2018; Anderson & Lindgren, 2020) and similarities in morphology (Reid & Jereb, 2005; Reid, 2016). However, as the biology of these species has not been studied directly, these similarities remain speculative, but testable hypotheses only.

Very little is known about the ecology of New Zealand *Sepioloidea*. Dell (1959) stated that it is 'fairly certain' that *S. pacifica* shelters in mud or debris diurnally and is active nocturnally. This is supported by benthic sampling efforts around New Zealand, which showed *S. pacifica*'s presence throughout the continuum of sandy to muddy habitats (Knight, 1974). Sampling of different bathymetric habitats (i.e. from inshore to deep canyon) off the Otago peninsula found that *S. pacifica* only occurred in inshore sandy and inshore muddy sand habitats (Probert *et al.,* 1979). This was supported in later research that shows all taxa within the family Sepiadariidae (*Sepioloidea* and its sister taxon *Sepiadarium*) are known to bury in sand during the day and emerge at night (Reid & Jereb, 2005; Reid, 2016). The affinity of sepiolids with the benthic environment can also be seen throughout species of the sepiolid subfamilies Sepiolinae and Rossinae from the sister family Sepiolidae. The Food and Agriculture Organization of the United Nations Catalogue of Cephalopods (Reid & Jereb, 2005) contains information on the habitat and biology of 25 Sepiolinae and Rossinae species from around the world, 21 of which have noted preferences for neritic, epibenthic, benthic, or muddy/sandy substrate habitats. In terms of physiological features, none of the *Sepioloidea* species show the suite of characters typical of pelagic-dwelling sepiolids such as silver lateral sides, transparent fins, ventral luminous glands that disperse light throughout a gelatinous shield (Orsi Relini, 1991) and relatively large fins. There is little evidence to cast doubt on the assumption that *S. pacifica* and the two novel species described in this study are also benthic animals. Whether juvenile *Sepioloidea* species have a planktonic stage is a separate matter that is not yet known.

Sepiolids are frequently reported in the diets of predators. For example, globally, sepiolids have been found in the guts of marine mammals such as pinnipeds (Goodman-Lowe, 1998)

and cetaceans (dos Santos & Haimovici, 2001; Spitz *et al.*, 2006), large finfish (Romeo *et al.*, 2012), and chondrichthyans (Kousteni *et al.*, 2018). Due to the nature of the surveys, this data often represents region-specific food webs. In New Zealand waters, sepiolids are known from the gut contents of common dolphins, *Delphinus delphis*. (Meynier *et al.*, 2008); smooth skate, *Dipturus innominatus* (Garrick & Paul, 1974) (Forman & Dunn, 2012); and a variety of finfish including hoki, *Macruronus novaezelandiae* (Hector, 1871) (Connell *et al.*, 2010). The present description of two new *Sepioloidea* species has implications for the gut content analysis of predator species if the prey can be identified. Specifically, depth ranges of foraging could be inferred when prey is identified to species. An example of this link is the group of *Sepioloidea pacifica* genetic sequences labelled 'penguin' (Fig. 39) The Fiordland penguins (*Eudyptes pachyrhynchus* Gray, 1845) from which specimens were obtained were studied by Poupart *et al.* (2019) and were found to forage from early morning to afternoon at an average depth of 22 m. This infers that these penguins are able to locate and feed on the shallow-dwelling *S. pacifica* despite their strategy of hiding beneath sand during the day. A potential use of this information within fisheries is with hoki. These fish are an economically valuable species in New Zealand waters and are known to inhabit depths between 200–800 m. Hoki move to the deeper end of this range as they age and grow larger (Livingston *et al.*, 2002). Knowledge of hoki migration patterns and the ages at which certain movements occur is important to fisheries. Applying the hypotheses of *Sepioloidea* depth stratification to the gut content analyses of hoki samples around the country could prove an additional tool to further fisheries knowledge. For example, where any sepiolid prey encountered in hoki gut contents may have previously been identified by default as *S. pacifica*, insights from the present study suggest that hoki foraging within their known depth range would be far more likely to encounter *S.* n. sp. 1 or *S.* n. sp. 2. In future, if any hoki prey items were to be positively identified as *S. pacifica* (*sensu stricto*), this would suggest either a considerably shallower foraging depth for hoki than is presently understood, or else a deeper range of occurrence for *S. pacifica* than is demonstrated by the material housed presently in national collections.

Few studies have focused on the diet of sepioloids themselves. In one study, Vafidis *et al.*, (2009) analysed the gut contents of 100 individuals from six Sepiolidae species from four genera: *Rondeletiola* Naef, 1921, *Rossia* Owen, 1835, *Sepietta* Naef, 1912, and *Sepiola* Leach, 1817. This was a highly varied group of taxa, with species from a range of sizes from 24 mm ML to 84 mm ML. Most of the gut contents were made up of crustaceans, mainly decapods, followed by mysidaceans, and amphipods. Fish and polychaetes were found consistently, at lower proportions. The fact that this highly varied group of sepiolid taxa showed such similar diets indicates the possibility of similar patterns in Sepiadariidae species. Very little is known about the ecology of local sepiadariids and more research is

required in order to begin understanding the impact of their ecological roles beyond speculation.

Reproductive biology. The only research known to date that involved the rearing of live New Zealand *Sepioloidea* was a dissertation on the biology of *Sepioloidea pacifica* (Hurst, 1969). In this study, mating was reported through second-hand accounts and therefore not documented with any detail. However, egg-laying and hatchling behaviour was observed.

Mating has been observed in several species of the Sepiolidae family, for example those of the genera *Euprymna* and *Sepiola* (Nabhitabhata *et al.,* 2005; Rodrigues *et al.,* 2009). In these species the male latches onto the female's head and mantle from below usually using Arms II and Arms III, together they drop to the substrate, then the male deposits spermatangia into the female. In these genera, the mating configuration is thought to be based on 1) the dorsal location of the hectocotylus (left Arms I) in the male and 2) the presence of an internal seminal receptacle known as a bursa copulatrix in the female. In *Sepioloidea* species the hectocotylus is located ventrally (left Arms IV) in males and spermatangia are implanted in the female's buccal membrane rather than a bursa copulatrix. It is unclear if these differences result in a different mating configuration. Further research involving first-hand mating observations of *Sepioloidea* specimens will be required to confirm any differences.

Hurst (1969) described the hatchlings of *Sepioloidea pacifica* as "similar to the adult" and that they were capable of active swimming but tended to settle on the aquarium substrate. The distributions of *Sepioloidea* species may be limited by a strong association to the benthos from early life, as has been discussed by Bello (2017) regarding the endemism of large-egged *Sepiola* species in the Atlantic Ocean and Mediterranean Sea. Furthermore, this could possibly be limited further by substrate preferences, such as that of *S. pacifica* and sandy substrates (Knight, 1974; Probert *et al.*, 1979). The large eggs seen in the oviducts of preserved *S.* n. sp. 1 and *S.* n. sp. 2 suggest that the hatchlings are also relatively large and well-developed (Laptikhovsky *et al*., 2008) (14.3 EgDI average in *S.* n. sp. 1, 13.1 EgDI average in *S.* n. sp. 2). This is a common reproductive strategy in sepiolid squids; females of benthic species invest in egg size and yolk provisioning at the cost of fecundity to provide hatchlings with direct developmental advantages (Mangold, 1987). The opposite can be seen in pelagic myopsid squids where females often lay tens of thousands of eggs, which end up as planktonic hatchlings, in contrast to the hundred or so laid by benthic sepiolids (Summers, 1984). This investment into fewer, larger eggs reduces the influence of various factors on hatchlings such as a nutrient-poor and dangerous pelagic environment. In some examples this may allow hatchlings to rapidly assume an adult lifestyle; in the context of benthic sepiolids, this means direct integration into the relatively safer benthic ecosystem, foregoing the need for a potentially hazardous pelagic life stage (Laptikhovsky et al., 2008). It also

means that distributional species-ranges are likely narrower than those with widely dispersed hatchlings. However, even among benthic sepiolids there are exceptions to this reproductive strategy. Deickert (2009) put forward the case of the littoral *Sepietta obscura* Naef 1916, which lays large eggs and has benthic hatchlings, compared with the deep-sea *Sepietta oweniana* (d'Orbigny [in Férussac & d'Orbigny], 1841), which has a high mortality for its planktonic hatchlings. The marginal differences in EgDI between *Sepioloidea* n. spp. 1 and 2 indicates that they may share similar reproductive strategies. The reproductive biology of species from the sister family Sepiolidae is comparatively well studied (e.g. *Sepiettta oweniana* (Salman, 1998); *Semirossia patagonica* (Smith 1881) (Önsoy *et al.*, 2008); *Rossia macrosoma* (delle Chiaje 1830) (Salman and Önsoy, 2010); *Neorossia caroli* (Joubin, 1902) (Salman, 2010)). These studies often include specific fecundity calculations, maturation rates, and notes on seasonal spikes in reproductive activity. While the reproductive strategy of benthic sepiolids may stretch across both Sepiolidae and Sepiadariidae, observations of species-specific reproductive biology in sepiadariids remains to be studied in depth.

CONCLUSION

Until now, almost all *Sepioloidea* specimens from New Zealand (apart from those few labelled conservatively in collections facilities) were thought to comprise a single species: *Sepioloidea pacifica.* We now know that there are actually three species in this genus present in New Zealand waters. While Reid (2009), among many others, has already called for a comprehensive revision of the phylogeny of Sepioidea, a very worthwhile project of smaller scope within this broader study would be a re-investigation into the systematics of the family Sepiadariidae, its two member genera *Sepioloidea* and *Sepiadarium*, and their relationships. Additionally, the procurement of molecular data from all Sepidariidae species would be a great help to the untangling of both the global Sepiolida phylogeny and the Cephalopoda order as a whole — projects which are growing in reliance on DNA yet severely lacking in Sepiadariidae representation.

REFERENCES

Anderson, F. E., & Lindgren, A. R. (2020). Phylogenomic analyses recover a clade of large-bodied decapodiform cephalopods. *Molecular Phylogenetics and Evolution*, 107038.

Atlas of Living Australia website at https://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:de5d0313-4cd8-4daf-9611-0c6fe200d41d#overview. Accessed 20 May 2020

Bello, G. (2017). The Mediterranean Sepiolidae (Mollusca: Cephalopoda) diversity. *Bull. Entomol. Soc. Malta, 9*(128).

Bello G. (2020). Evolution of the hectocotylus in Sepiolinae (Cephalopoda: Sepiolidae) and description of four new genera. *European Journal of Taxonomy*, 655: 1-53

Berry, S.S. (1911). Preliminary notices of some new Pacific cephalopods. *Proceedings of the United States National Museum*. 40(1838):589-592.

Caruana, N, J., Cooke, I. R., Faou, P., Finn, J., Hall, N. E., Norman, M., Pineda, S. S., Strugnell, J. M. (2016). A combined proteomic and transcriptomic analysis of slime secreted by the southern bottletail squid, *Sepiadarium austrinum* (Cephalopoda). *Journal of Proteomics, 148,* 170–182. https://doi.org/10.1016/j.jprot.2016.07.026

Caruana, N. J., Strugnell, J. M., Faou, P., Finn, J., & Cooke, I. R. (2019). Comparative proteomic analysis of slime from the striped pyjama squid, *Sepioloidea lineolata*, and the southern bottletail squid, *Sepiadarium austrinum* (Cephalopoda: Sepiadariidae). *Journal of Proteome Research, 18*(3), 890–899.

Caruana, N. J., Strugnell, J. M., Finn, J., Faou, P., Plummer, K. M., & Cooke, I. R. (2020). Quantitative Proteomic Analysis of the Slime and Ventral Mantle Glands of the Striped Pyjama Squid (*Sepioloidea lineolata*). *Journal of Proteome Research, 19*(4), 1491–1501. https://doi.org/10.1021/acs.jproteome.9b00738

Catalano, S. R., & Furuya, H. (2013). Two new species of dicyemid (Dicyemida: Dicyemidae) from two Australian cephalopod species: *Sepioteuthis australis* (Mollusca: Cephalopoda) and *Sepioloidea lineolata* (Mollusca: Sepiadariidae). *Journal of Parasitology, 99*(2), 203–211. https://doi.org/10.1645/ge-3252.1

Clarke, M. R. (1986). *A Handbook for the Identification of Cephalopod Beaks*. Oxford, United Kingdom: Clarendon Press.

Connell, A. M., Dunn, M. R., & Forman, J. (2010). Diet and dietary variation of New Zealand hoki *Macruronus novaezelandiae*. *New Zealand Journal of Marine and*

Freshwater Research, 44(4), 289–308. https://doi.org/10.1080/00288330.2010.515232

Deickert, A. (2009). Reproductive mode in the genus *Sepietta* (Cephalopoda: Sepiolidae). *Bolletino Malacologico, 45,* 87–94.

Dell, R. (1952). The recent Cephalopoda of New Zealand. *Dominion Museum Bulletin 16*, 1–157.

Dell, R. (1959). Some additional New Zealand Cephalopods from Cook Strait. *Zoology Publications from Victoria Museum of Wellington*, *25,* 1–12.

delle Chiaje S., 1830. Memorie sulla storia e notomia degli animali senza vertebre del Regno di Napoli (Figure); [Società Tipografica], Napoli: plts. LXX-CIX.

Férussac, A.E.J.P.F. d'Audebard de & d'Orbigny, A. (1835-1848). *Histoire naturelle générale et particulière des Céphalopodes acétabulifères vivants et fossiles*. pp. [1-96], i-lvi, 1–361, Atlas with 144 plates. Paris, Baillière.

Fischer, P. (1882). *Manuel de Conchyliologie et de paléontologie conchyliologique on histoire naturelle des mollusques vivants et fossils*. Paris, France: J.B. Baillière.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology, 3,* 294–299.

Forman, J. S., & Dunn, M. R. (2012). Diet and scavenging habits of the smooth skate *Dipturus innominatus*. *Journal of Fish Biology*, *80*(5, SI), 1546–1562. https://doi.org/10.1111/j.1095-8649.2012.03255.x

Goodman-Lowe, G. D. (1998). Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the northwestern Hawaiian islands during 1991 to 1994. *Marine Biology*, *132*(3), 535–546. https://doi.org/10.1007/s002270050419

Groenenberg, D. S., Goud, J., De Heij, A., & Gittenberger, E. (2009). Molecular phylogeny of North Sea Sepiolinae (Cephalopoda: Sepiolidae) reveals an overlooked *Sepiola* species. *Journal of Molluscan Studies*, *75*(4), 361–369.

Hurst, H. L. (1969). *Biology of* Sepioloidea pacifica [Honour dissertation, University of Otago].

Joubin, L. (1902). Observations sur divers Céphalopodes, sixième note: sur une nouvelle espèce du genre *Rossia*. *Bulletin de la Société Zoologique de France*. 27:138-143.

Kirk, T.W. (1882). Descriptions of new Cephalopoda. *Transactions and Proceedings of the New Zealand Institute*, *14*(42), 283–286.

Knight, G. S. (1974). Benthic community structure in Lyttelton Harbour. *New Zealand Journal of Marine and Freshwater Research, 8*(2), 291–306. https://doi.org/10.1080/00288330.1974.9515506

Kousteni, V., Karachle, P. K., Megalofonou, P., & Lefkaditou, E. (2018). Cephalopod prey of two demersal sharks caught in the Aegean Sea (eastern Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, *98*(1, SI), 81–88. https://doi.org/10.1017/S002531541700159X

Laptikhovsky, V. V., Nigmatullin, C. M., Hoving, H. J. T., Onsoy, B., Salman, A., Zumholz, K., & Shevtsov, G. A. (2008). Reproductive strategies in female polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* (Cephalopoda: Sepiolidae). *Polar Biology, 31*(12), 1499–1507.

Leach, W. E. (1817). Synopsis of the orders, families and genera of the class Cephalopoda. *The Zoological Miscellany; being descriptions of new or interesting animals.* 3(30): 137-141.

Lee, P. N., McFall-Ngai, M. J., Callaerts, P., & de Couet, H. G. (2009). The Hawaiian bobtail squid (*Euprymna scolopes*): a model to study the molecular basis of eukaryote-prokaryote mutualism and the development and evolution of morphological novelties in cephalopods. *Cold Spring Harbor Protocols, 2009*(11), doi:10.1101/pdb.emo135

Livingston, M.E., Bull, B., Stevens, D.W. (2002). *Migration patterns during the life-cycle of hoki (*Macruronus novaezelandiae*): an analysis of trawl survey data in New Zealand waters 1991–2002.* Retrieved from https://fs.fish.govt.nz/Page.aspx?pk=113&dk=22668

Mangold, K. (1987). Reproduction. In 'Cephalopod Life Cycles'. (Ed. PR Boyle.) pp. 157–200.

Meier, R., Zhang, G., & Ali, F. (2008) The use of mean instead of smallest interspecific distance exaggerates the size of the 'barcoding gap' and leads to misidentification. *Systematic Biology*, 57, 809–813.

Meynier, L., Stockin, K. A., Bando, M. K. H., & Duignan, P. J. (2008). Stomach contents of common dolphin (*Delphinus* sp.) from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research*, *42*(2), 257–268. https://doi.org/10.1080/00288330809509952

Morrison, M. A., Francis, M. P., Hartill, B. W., & Parkinson, D. M. (2002). Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuarine Coastal and Shelf Science*, *54*(5), 793–807.

Nabhitabhata, J., Nilaphat, P., Promboon, P., & Jaroongpattananon, C. (2005). Life cycle of cultured bobtail squid, *Euprymna hyllebergi* Nateewathana, 1997. *Phuket Mar Biol Cent Res Bull, 66*, 351-365.

Naef, A. (1912). Teuthologische Notizen, 2: Die Gattungen der Sepioliden. *Zoologischer Anzeiger*. 39(7):241-248.

Naef. A. (1916). Ueber neue Sepioliden aus dem Golf Von Neapel. *Pubblicazioni della Stazione Zoologica di Napoli* 1(1-10), 4.

Naef, A. (1921). Das system der dibranchiaten Cephalopoden und die mediterranen arten derselben. *Mitteilungen aus der Zoologischen Station zu Neapel*. 22(16):527-542.

Önsoy, B., Laptikhovsky, V., & Salman, A. (2008). Reproductive biology of the Patagonian bobtail squid, *Semirossia patagonica* (Sepiolidae: Rossiinae) in the south-west Atlantic. *Journal of the Marine Biological Association of the United Kingdom, 88*(5), 1019–1023.

Orbigny, A. d', Férussac, A. de (1834–1848). *Histoire naturelle generale et particuliere des Cephalopodes acetabuliferes vivants et fossiles*. JB Baillière, Paris.

Orbigny, A. d' 1845–[1847]. *Mollusques Vivants et Fossiles, ou Description de Toutes les Espèces de Coquilles et de Mollusques*. Paris, France: Adolphe Delahays.

Orsi Relini, L., & Massi, D. (1991). The butterfly squid *Stoloteuthis leucoptera* in the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom, 71*(1), 47–51. doi:10.1017/S0025315400037383

Owen, R. (1835). Mollusca Cephalopoda, pages xcii-xcix. In J. Ross, *Narrative of a second voyage in search of a North West Passage, 1829-1833*. (Volume II, Appendix, Natural History), 120 + cxliv pages. London: A.B. Webster.

Parin, N. V., Mironov, A. N., & Nesis, K. N. (1997). Biology of the Nazca and Sala y Gomez submarine ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific Ocean: Composition and distribution of the fauna, its communities and history. *Advances in Marine Biology, 32*, 145–242.

Poupart, T. A., Waugh, S. M., Bost, C. A., Kato, A., Miskelly, C. M., Rogers, K. M., & Arnould, J. P. (2019). Foraging ecology of a winter breeder, the Fiordland penguin. *Marine Ecology Progress Series*, *614*, 183-197.

Powell, A. W. B. (1979). *New Zealand Mollusca: marine land and freshwater shells*. Auckland, New Zealand: Collins.

Probert, P. K., Batham, E. J., & Wilson, J. B. (1979). Epibenthic macrofauna off southeastern New Zealand and mid-shelf bryozoan dominance. *New Zealand Journal of Marine and Freshwater Research*, *13*(3), 379–392.

Quoy, J.R., & Gaimard, J.P. (1832). Mollusques. In Voyage de découvertes de l'Astrolabe pendant les annes 1826–1829. *Zoologie, 2*(1), 1–320.

Ratnasingham, S., & Hebert, P. D. N. (2007). BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). *Molecular Ecology Notes, 7*(3), 355–364.

Reid, A., Jereb, P. (2005). Family Sepiolidae. In: Jereb P. & Roper C.F.E., *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol. 1.* FAO Species Catalogue for Fishery Purposes, 4: 153–207.

Reid, A. (2009). *Sepioloidea magna* sp. nov.: A New Bottletail Squid (Cephalopoda: Sepiadariidae) from Northern Australia. *The Beagle: Records of the Museums and Art Galleries of the Northern Territory, 25*, 103–109.

Reid, A. (2016). *Cephalopods of Australia and Sub Antarctic Territories*. Clayton, Australia: CSIRO Publishing.

Robson, G.C. (1924). Preliminary Report on the Cephalopoda (Decapoda) procured by the S.S. "Pickle". *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*. 3:1-14.

Rodrigues, M., Garci, M. E., Guerra, Á., & Troncoso, J. S. (2009). Mating behavior of the Atlantic bobtail squid *Sepiola atlantica* (Cephalopoda: Sepiolidae).

Romeo, T., Battaglia, P., Peda, C., Perzia, P., Consoli, P., Esposito, V., & Andaloro, F. (2012). Pelagic cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content of large fish predators. *Helgoland Marine Research*, *66*(3), 295–306. https://doi.org/10.1007/s10152-011-0270-3

Roper, C. F., & Voss, G. L. (1983). Guidelines for taxonomic descriptions of cephalopod species. *The Biology and Resource Potential of Cephalopods. Memoirs of the National Museum of Victoria,* 52–53.

Salcedo-Vargas, M. A. (1995). Systematic value of the ultrastructure of the sucker surface in the squid family Mastigoteuthidae (Mollusca: Cephalopoda). *Contributions to Zoology, 65,* 65–77.

Salman, A. (1998). Reproductive biology of *Sepietta oweniana* (Pfeffer, 1908) (Sepiolidae: Cephalopoda) in the Aegean Sea. *Scientia Marina, 62*(4), 379–383.

Salman, A. (2010). Reproductive biology of *Neorossia caroli* (Cephalopoda: Sepiolidae) in the Aegean Sea. *Scientia Marina, 75*(1), 9–15.

Salman, A., & Önsoy, B. (2010). Reproductive biology of the bobtail squid *Rossia macrosoma* (Cephalopoda: Sepiolidea) from the eastern Mediterranean. *Turkish Journal of Fisheries and Aquatic Sciences, 10*(1), 81–86.

Sanchez, G., Setiamarga, D. H., Tuanapaya, S., Tongtherm, K., Winkelmann, I. E., Schmidbaur, H., Umino, T., Albertin, C., Allcock, L., Perales-Raya, C., Gleadall, I., Strugnell, J. M., Simakov, O., & Gleadall, I. (2018). Genus-level phylogeny of cephalopods using molecular markers: current status and problematic areas. *PeerJ, 6*, e4331.

Smith E.A. (1881). Account of the zoological collections made during the survey of H. M. S. Alert. IV. Mollusca and Molluscoida. *Proceedings of the Zoological Society of London*. (1881): 22-44, pls 3-5.

Spencer, H. G., Willan, R. C., Marshall, B., & Murray, T. J. (2016). Checklist of the Recent Mollusca recorded from the New Zealand Exclusive Economic Zone. Retrieved November 26, 2018, from http://www.molluscs.otago.ac.nz/index.html

Spitz, J., Richard, E., Meynier, L., Pusineri, C., & Ridoux, V. (2006). Dietary plasticity of the oceanic striped dolphin, *Stenella coeruleoalba*, in the neritic waters of the Bay of Biscay. *Journal of Sea Research*, *55*(4), 309–320. https://doi.org/10.1016/j.seares.2006.02.001

Steenstrup, J., 1881: *Sepiadarium* og *Idiosepius* to nye Slaegter af Sepiernes Familie. Med Bemaerkninger om de to beslaegtede Former *Sepiolidea* D'Orb. og *Spirula* Lmk. *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, *1*(3). 211-242.

Stilwell, J. D., & Consoli, C. P. (2012). Tectono-stratigraphic history of the Chatham Islands, SW Pacific—The emergence, flooding and reappearance of eastern ‘Zealandia’. Proceedings of the Geologists' Association, 123(1), 170–181.

Summers, W. C. (1983). 6 – Physiological and Trophic Ecology of Cephalopods. In W. D. Russell-Hunter (Ed.), *Ecology* (pp. 261–279). https://doi.org/10.1016/B978-0-12-751406-2.50013-1

Summers, W. C. (1984). Comparative Life History Adaptations of Some Myopsid and Sepiolid Squid. *Northwest Atlantic Fisheries Organization, 895,* 1–6.

Suter, H. (1913). *Manual of the New Zealand mollusca: With an atlas of quarto plates* (Vol. 1). J. Mackay, Government Printer.

Vafidis, D., Kallianiotis, A., Chartosia, N., & Koukouras, A. (2009). The Sepioidea (Cephalopoda, Mollusca) fauna of the Aegean Sea: comparison with the neighbouring seas and notes on their diet composition. *Journal of Biological Research, 11*, 57–71.

Vecchione, M., Young, R. E. & Roper C. F. E. (2013). *Heteroteuthis dagamensis* Robson 1924. Version 03 November 2013 (under construction). The Tree of Life Web Project, http://tolweb.org/Heteroteuthis_dagamensis/20053/2013.11.03.

Winkelmann, I., Campos, P. F., Strugnell, J., Cherel, Y., Smith, P. J., Kubodera, T., Allcock, L., Kampmann, M., Schroeder, H., Guerra, A., Norman, M., Finn, J., Ingrao, D., Clarke, M., & Gilbert, M. T. P. (2013). Mitochondrial genome diversity and population structure of the giant squid *Architeuthis*: genetics sheds new light on one of the most enigmatic marine species. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1759), 20130273.

WoRMS Editorial Board (2020). World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2020-05-18. doi:10.14284/170

Young, R. E. (2010). Sepiadariidae Fischer, 1882. Version 15 August 2010 (under construction). The Tree of Life Web Project, http://tolweb.org/Sepiadariidae/19986/2010.08.15