

Systematics of the Octopoteuthidae
Berry, 1912 (Cephalopoda: Oegopsida)

Jesse T. Kelly

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Dr. J. Mark Hanson

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ATTESTATION OF AUTHORSHIP

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

Signed _____ Date July 30, 2019

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DEDICATION

This work is dedicated to my grandmothers, Catharina Jongsma (née Masteling) and M. Jean Kelly (née Shouldice), for their steadfast support of post-secondary education, despite it being an experience neither were privileged to have themselves.

Also, to all whose work this study was based upon, researchers who laboured to understand the natural world without modern conveniences such as genetics and international travel, some even without the context of evolution or plate tectonics.

1. ABSTRACT

Squids of the family Octopoteuthidae Berry, 1912, have been known to science for nearly 250 years and have been collected from every ocean except the Arctic and Antarctic. They are an ecologically important group, having been recorded in the diets of pinnipeds, sea birds, predatory fishes, and cetaceans, and are considered one of the most important cephalopod prey groups for sperm whales. Despite this, the family has been poorly studied due to the difficulty in identifying its species, and the diversity and systematics of the family are poorly understood. Ten formal species descriptions have been published, of which six to eight are generally recognised but only two are easily identified. Challenges to clarifying octopoteuthid systematics include the loss of important type specimens, and resolving the status of dubious taxa, potential junior synonyms, and undescribed species. No study has previously sought to resolve the systematics of the entire family.

Within this context, a global revision of the Octopoteuthidae is presented based on the examination of ~900 specimens from 12 international repositories. Extant type material was examined, and efforts made to locate previously established or suggested lost type specimens. Original descriptions and illustrations were reviewed for all historic taxa, and a critical review is given of all previously affiliated taxa. Descriptions and illustrations are provided for the 16 octopoteuthid species recognized herein, of which 10 are novel. Two genera are presently maintained within the family, *Octopoteuthis* and *Taningia*, containing 11 and 5 species, respectively. Within *Octopoteuthis*, four morphologic species groups were identified based primarily on photophore patterning. Descriptions are given for as much of each species' ontogeny as material allowed, and traditional and novel morphologic characters are critically appraised in relation to their utility within the Octopoteuthidae.

A full description of the type species of the family and genus *Octopoteuthis*, *Octopoteuthis sicula* Rüppell, 1844, is given and, in light of this, *Octopoteuthis danae* Joubin, 1931, is considered a junior synonym. The second Atlantic species with two photophores on the posterior ventral mantle is designated *Octopoteuthis megaptera* (Verrill, 1885). Consistent with previous works, *Octopoteuthis persica* Naef, 1923, is considered a junior synonym of *Taningia danae* Joubin, 1931, and *Octopoteuthis*

longiptera Akimushkin, 1963, treated as *nomen dubium*; the status of *Octopoteuthis indica* Naef, 1923 remains unresolved but is discussed. Similarly, definitive resolution of the specific status of ‘*Cuciotheuthis unguiculata*’ (Molina, 1782) and ‘*Enoploteuthis hartingii*’ Verrill, 1880, could not be achieved; however, new insights were made and their implications examined.

The morphology-based review was complemented by concurrent multi-gene, phylogenetic analyses of 130 specimens from 13 of the 16 proposed species—the largest, and first targeted, genetic examination of the Octopoteuthidae. Genetic support was found for all morphologically defined species for which sequences were obtained. Intra- and interfamilial relationships are discussed based on a synthesis of genetic and morphologic data, and the formal rank of the newly recognised species groups is considered.

Octopoteuthid species were generally found to inhabit either single ocean basins or portions thereof, with several being more widely spread (usually throughout the southern hemisphere); species distributions were generally found to comprise a system of connected water currents. Inferences regarding octopoteuthid reproductive biology and spawning strategy are made based on accumulated observations during specimen examinations. Species-specific beak-to-body-size regressions were calculated for five species, and a review of known octopoteuthid predators is provided. With the recognition of their greater diversity and more defined species ranges, the evolutionary history of the family is briefly discussed.

2. INTRODUCTION

Squids of the family Octopoteuthidae Berry, 1912 (“eight-armed” squids), have been known to science for nearly 250 years. They have been collected from every ocean except the Arctic and Antarctic, occupying temperate and tropical waters at depths up to 2100 m (Gomes-Pereira & Tojeira 2014). Octopoteuthid squids are ecologically important in the diets of many marine predators, including pinnipeds (*e.g.*, Klages 1996; Goodman-Lowe 1998), sea birds (*e.g.*, Imber 1973; Imber & Russ 1975; James & Stahl 2000), predatory fishes (*e.g.*, Okutani & Tsukada 1988; Smale 1996; Cherel & Duhamel 2004) and cetaceans (*e.g.*, Kubodera & Miyazaki 1993; Gómez-Villota 2007), and are of particular importance in the diets of toothed whales. In the diet of sperm whales, *Physeter macrocephalus*, octopoteuthids are considered to be the most important family by biomass (Clarke 1996), and many of the available large individuals of *Taningia* in collections are ex-gut-content specimens (*e.g.*, Clarke 1967). Octopoteuthids are unpalatable to humans, due to the high concentrations of ammonia incorporated into their body tissues for buoyancy assistance (Clarke *et al.* 1979), and are not commercially exploited.

The Octopoteuthidae are characterised by the lack of tentacles in post-larval life stages (having been resorbed by ML <60 mm), and arms with two series of hooks. Additional familial characters include all or some arms terminating in large photophores, and large muscular fins in adults (their length 65–85% dorsal mantle length (ML), and width 80–110% ML) that are fused dorsally along the midline. As adults, species of *Octopoteuthis* are generally medium-sized squids (ML 200–270 mm), with two species capable of exceeding ML 500 mm. Species of *Taningia* are large to giant-sized (ML 830–1310* mm), and elsewhere have been reported to reach ML 1700 mm (Nesis 1987).

Since the first species description (*Octopoteuthis sicula* Rüppell, 1844), four genera, 13 species and two subspecies have been attributed to the Octopoteuthidae and given an array of names and affiliations. When taken together with some authors’ assertion that the first octopoteuthid was actually described 60 years earlier (*i.e.*, *Sepia unguiculata* Molina, 1782), 24 combinations of genus and species names have been applied to octopoteuthid taxa (excluding variant generic and specific spellings) in published literature (see Historical Resume). Recent accounts place the number of valid genera and species at two and six (Stephen 1985a), two and eight (Nesis 1987), and two and

seven (Young & Vecchione 2009), due to uncertainties in the genus *Octopoteuthis*; *Taningia* has previously been considered monotypic.

While descriptions of local taxa have been included in regional reviews (*e.g.*, Young 1972; Lipka 1975), a global, morphology-based review has never before been undertaken for this family. Previous systematic treatment has been limited to genus-level reviews (Clarke 1967; Stephen 1985a; Roper & Vecchione 1993) or familial reviews based on published literature (Clarke 1966; Nesis 1987). Despite their constraints, these efforts have identified dubious taxa, suggested junior synonyms, and indicated the existence of additional undescribed taxa; however, they have not succeeded in stabilising the family as a whole, mostly due to difficulties within the genus *Octopoteuthis*.

The taxonomic instability of the family is a result of several converging factors: original species descriptions lacking sufficient detail and illustration; the loss (four) or poor condition (two) of type specimens; original descriptions published in six languages and often based on early life stages that are rarely indicative of adult morphology; inconsistent assessment of taxonomically significant characters (*e.g.*, accessory claws, tail length); the generally poor, incomplete condition of specimens; and the lack of tentacles, which in other families generally bear characters useful to species identification (*e.g.*, Bolstad 2010). These factors have hindered both past efforts to clarify the systematics of the Octopoteuthidae and more recent identification of newly collected material. As a result, recent studies reporting on octopoteuthids have only identified specimens to genus or family (*e.g.*, Judkins *et al.* 2016).

The inability to identify specimens to species has fundamentally impeded further study into octopoteuthid biology and ecology, including their role in marine food webs. Live observations of *Taningia* individuals interacting with a baited camera trap revealed them to be active swimmers and (potentially) predators, not a “sluggish, inactive squid” as was previously thought (Kubodera *et al.* 2007). However, published information on their diet is limited to the contents of only three stomachs (indeed, the only three reported for the entire family), rendering estimation of their predation pressure on community structure or individual species impossible (Santos *et al.* 2001a; González *et al.* 2003). Octopoteuthid beaks, often recovered from predator stomachs, have generally been identified only to genus or family (*e.g.*, Perrin *et al.* 1973; Imber 1976),

necessitating the use of genus-wide regression equations for estimating body size and mass from lower beak measures. However, genus-wide patterns do not always accurately represent the species they contain, which can reduce the accuracy of inferences drawn from such data, such as the relative importance of a group in the diet of marine predators.

This research programme was undertaken to stabilise the systematics of the Octopoteuthidae. All previously reported taxa (see Table 31) were critically reviewed; valid taxa redescribed to modern standards of detail, illustration, and imaging; and unrecognised taxa synonymised (see Systematics). A complementary phylogenetic investigation was performed to test morphology-based species distinctions and explore present morphologic and geographic patterns within an evolutionary context (see Genetics). This thesis follows the taxonomic tradition for in-text citations whereby only citations for original taxon authorities are given in “author, date” form; all other references are given as “author date”.

2.1. Historical Resume

The first recognised octopoteuthid, *Octopoteuthis sicula* Rüppell, 1844, was described from Messina, Italy, and its lack of tentacles, large fins, and arm hooks garnered it both a new species and genus. The genus owed its name to the combination of unspecified “characteristics of the species *Octopus*, *Loligo*, and *Enoploteuthis*”, while the specific name derived from its locality (*i.e.*, Sicily). Rüppell’s letter was meant only to bring attention to the species and he deferred to a colleague, Krohn, for its proper publication. The following year, Krohn (1845) published a more detailed description including the first illustrations of the species but, although referencing discussion with Rüppell, inexplicably gave the generic name as ‘*Octopodoteuthis*’.

Two years later, Krohn (1847) again changed the generic name upon discovering that juvenile *O. sicula* did, in fact, bear tentacles. With the species possessing ten appendages at one point in its life, the prefix “octo” no longer seemed accurate, and the new name ‘*Verania*’ (= *Octopoteuthis*) was proposed, honouring his friend and colleague V é rany. ‘*Verania*’, (or occasionally ‘*Veranya*’, *e.g.*, Chenu 1859), prevailed in the literature until the end of the 19th century as most authors agreed with the inaccurate connotation of

‘*Octopodoteuthis*’ (e.g., Tiberi 1880; Fischer 1887; Ficalbi 1899). However, its usage ceased following Pfeffer’s (1900) synonymy of ‘*Verania*’ with ‘*Octopodoteuthis*’. Thereafter, the latter, ‘*Octopodoteuthis*’, was used almost exclusively until the early 1970’s. However, both of Krohn’s generic names were contrary to nomenclature laws, and thus, while not meaning to supplant him, credit for describing the first octopoteuthid species is given to Rüppell.

Vérany (1851), the seeming third party in the discovery and description of *O. sicula*, gave an insightful history of the discovery of the species as well as the first illustration of an octopoteuthid gladius. In addition, he clarified the difference between three common genera of hooked squid at the time: *Onychoteuthis*, with hooks on tentacles only, *Enoploteuthis*, with hooks on arms and tentacles, and ‘*Verania*’, with hooks only on the arms. This designation remains valid although it was not immediately adopted (e.g., Chenu 1859).

While the unique morphology of *O. sicula* gave the species immediate validity, its familial placement remained uncertain. Gray (1847) first placed the species amongst the octopods in the family Octopodidae. Two years later he moved *O. sicula* to his newly defined Onychoteuthidae (Gray 1849). The species was alternately placed among the families Teuthidae (Vérany 1851; Woodward 1851; Verrill 1882; since elevated to become the Order Teuthida), Onychoteuthidae (e.g., Adams & Adams 1858; Fischer 1887), and Enoploteuthidae (e.g., Pfeffer 1900; Hoyle 1909) for the next 60 years before Chun (1910) erected the family ‘Veranyidae’ (= Octopoteuthidae).

The terminal swellings of the arms of *O. sicula* were initially believed to constitute hectocotyli (Pfeffer 1884, 1900; Weiss 1888), modified male arm tips used to transfer spermatophores to females. However, the unlikelihood that only male octopoteuthids were being caught was quickly noted (Appellöf 1889; Jatta 1896), and soon after Pfeffer (1912) permitted the possibility that the swellings might constitute light organs – a change in direction after previously asserting the genus contained no light organs (Pfeffer 1900, 1908). Two years previously, Chun’s (1910) detailed examination of *Octopoteuthis* viscera led him to conclude that the “muscular warts” identified by Appellöf (1889) were likely photogenic, the first suggestion of the presence of photophores in the family. Berry (1920) similarly suggested *O. sicula* might have “photogenic organs on the ink sac”, although his source for this information was not given.

The second species of the genus, '*Ancistrocheirus*' *megaptera* (= *Octopoteuthis megaptera*) Verrill, 1885, was described from a specimen taken at 1300 m off New Jersey, U.S.A. No comparison was made to *O. sicula* despite striking similarities in gross morphology and his apparent familiarity with '*Verania*' (Verrill 1880, 1882). Instead, Verrill compared his new species to "A. *Veranyi* [*sic*], recorded from the Indian Ocean" (possibly *Abralia veranyi*, although at the time this species was recorded only from the Mediterranean [Hoyle 1886a]). Surprisingly, the discovery of a second species in such a unique genus received almost no notice – save Hoyle (1886a, b) – and *O. megaptera* was not mentioned in press for three decades.

Attempting to clarify some aspects of cephalopod nomenclature, Berry (1912) illustrated that '*Veranyidae*' Chun, 1910 was invalid, being based on the generic name '*Verania*', a junior synonym of *Octopoteuthis*. He recommended the use of either Octopoteuthidae or Octopodoteuthidae, depending on whether Krohn's emendation became accepted, with *O. sicula* as the type species by monotypy. No reference was made to *O. megaptera*.

However, in his work on cephalopods of the Plankton Expedition, Pfeffer (1912) maintained the Octopoteuthidae as a subfamily (Octopodoteuthinae) of the Enoploteuthidae. In his lengthy description of *O. sicula*, Pfeffer divided the species into two forms, the oceanic and the Mediterranean, based primarily on size and skin structure. These later became the basis for Grimpe's (1922) two subspecies, *O. sicula* '*atlantica*' and *O. sicula* '*mediterranea*,' designations that were largely unrecognised. Pfeffer (1912) also allied *O. megaptera* and *O. sicula* for the first time, placing them in the same subfamily. However, he considered differences in position and shape of the arm hooks to be so great that a new genus, '*Octopodoteuthopsis*' (= *Octopoteuthis*), was required to accommodate *O. megaptera*. Nevertheless, he remained uncertain about the validity and taxonomic placement of his new genus. Other authors found it unnecessary, and with an alliance established now between *O. sicula* and *O. megaptera*, many believed that *O. megaptera* simply represented a second species of *Octopoteuthis* (Thiele 1935; Robson 1948; Adam 1952). Despite this, '*Octopodoteuthopsis*' continued to appear in the literature until the 1970's (Roeleveld 1975), possibly a result of Voss's (1956a, 1956b, 1958, 1962, 1967) continued usage.

Pfeffer's (1912) final contribution to the systematics of the Octopoteuthidae was placing '*Cuciototeuthis*' within the Octopoteuthidae. The history of '*Cuciototeuthis*' Steenstrup, 1882 dates back to the eighteenth century when Molina (1782) published essays on the natural

history of Chile. Therein, he gave an account, possibly partially paraphrased from the journal of Joseph Banks (Banks 1896), the naturalist onboard the first voyage of Captain James Cook, of a giant hooked “cuttlefish” floating dead at the surface off Chile in 1769. Molina named the species ‘*Seppia[sic] unguiculata*’, and formally described it in five words: cuttlefish body tailless, arms clawed (see Appendix A). Both Molina and Banks specifically detailed the unique double row of arm hooks, likening them to those of a cat in that they were retractable into fleshy sheaths. The combination of the limited original description, lack of additional material, and fantastical nature of the account, resulted in a litany of new names proposed for the taxon in the following years, without any resolution or additional description. ‘*Sepia unguiculata*’ (e.g., Gmelin 1789; Bosc 1802; Blainville 1827; Férussac 1835) became ‘le poulpe unguiculé’ (Montfort 1802), ‘*Onychoteuthis molinae*’ (Lichtenstein, 1818), ‘*Loligo unguiculata*’ (Blainville 1823; Férussac 1825), ‘*Enoploteuthis molinae*’ (d’Orbigny 1845), and ‘*E. unguiculata*’ (Gray 1849; Woodward 1851; Adams & Adams 1858).

While preparing a catalogue of the Hunterian Museum in 1829, Owen came across several jars of fragments of a large cephalopod, some of which had been labeled with “J.B.” (Owen 1881). He was informed by a colleague that jars of alcohol had been provided to Joseph Banks for preservation of specimens during his voyage. Among the debris were an arm fragment approximately 23 cm long and bearing two series of hooks, a buccal bulb, a heart, and a dried posterior portion of a mantle with fins. These were taken by him to constitute the remains of Banks’ specimen. While a full description of this material and his account of encountering it was not published until 1881, he first referred to the unusual arm in 1830, and in accompanying handwritten notes dated his attribution of the other fragments to Molina’s specimen to March, 1834 (see Appendix B). Thirty years later, in a footnote in John Hunter’s posthumous essays on natural history, Owen published his conclusion that these pieces all derived from Molina’s original specimen (Hunter 1861). A similar reference was made to the specimen by Leach (1818) and Gray (1849), who independently stated that an arm of a large cephalopod – which bore “distinct strong and free hooks” (*vide* Leach) – was deposited at the Royal Museum of the College of Surgeons (= the Hunterian Museum). Unfortunately, most of the Hunterian fragments were destroyed in the bombings of WWII, with the exception of the buccal bulb mount (Clarke 1967).

Publication of comparable material was not made for nearly a hundred years, until Harting (1861) described and illustrated fragments of a ‘gigantic’ *Enoploteuthis* that, “can be

assumed still with some probability... is the same as that of the fragments which are preserved in the Hunterian Museum” (see Appendix C). Harting’s *Enoploteuthis* was recovered from the stomach of a shark caught in the Indian Ocean, and among the fragments were two large arms bearing two series of sheathed hooks. Although he refrained from ascribing a name to his specimen, Verrill (1880), seemingly most interested in assuring every specimen was attributed a name, erected ‘*E. hartingii*’ for it, but made no effort to critically compare it with either ‘*S. unguiculata*’ or ‘*E. molinae*’ which he also referenced. Owen (1881) further contributed to the chaos by proposing to rename ‘*E. molinae*’ as ‘*E. cookii*’. Based on the morphology of ‘*Onychoteuthis raptor*’ (*nomen dubium fide* Bolstad 2010), Owen gave a flawed reconstruction of ‘*E. cookii*’, attributing it an onychoteuthid-shaped body with hooked arms but also long, hooked tentacles.

Steenstrup (1882) erected a new genus, ‘*Cuciotheuthis*’ [*sic*], for ‘*Sepia unguiculata*’ (Molina, 1782) on the basis of its unique arm-hook morphology, being sufficiently different from both *Enoploteuthis* and *Onychoteuthis*. The name derived from the Greek word “χοῦχι” (“coco fruit”), a morphologic reference to the swollen shape of the armature and an acoustic reference to Captain Cook. Steenstrup repeatedly employed the *-us* suffix, while using the convention *-is* for several other genera (*e.g.*, *Enoploteuthis*), a spelling which was only (but consistently) maintained by Hoyle (1886, 1904, 1909, 1910). Other contemporaries converted it to ‘*Cuciotheuthis*’ (Joubin 1895, 1898, 1899, 1900, 1902; Pfeffer 1900, 1912), a spelling that prevails to this day (as with *Architeuthis* Steenstrup, 1857, originally ‘*Architeuthus*’). Applying nomenclature laws, Steenstrup gave precedence to the specific name ‘*unguiculata*’ (Molina, 1782) over ‘*molinae*’ (Lichtenstein, 1818) and ‘*cookii*’ (Owen, 1881). Thus, he attributed the name ‘*C. unguiculata*’ to Molina’s original description and the characteristic arm preserved at the Hunterian, but did not extend it to the additional material described by Owen (*i.e.*, buccal bulb, heart, mantle-fin piece). Although referencing Harting’s specimen, Steenstrup appears to have been unaware of Verrill’s designation. For the next several years both ‘*C. unguiculata*’ and ‘*E. hartingii*’ were recognised as separate species, since authors could not satisfactorily reconcile the two (Verrill 1881, 1882; Fischer 1887).

Pfeffer’s (1912) alliance of ‘*Cuciotheuthis*’ with the Octopoteuthidae was possible as a more coherent picture of the species had emerged by that time. This was largely due to the efforts of, and new material introduced by, French zoologist Joubin (1895, 1898, 1900) who

reported on a complete arm crown, taken from a sperm whale stomach, and a nearly complete specimen found floating at the surface. Photographs show eight arms bearing two series of hooks and broad fins extending the length of the mantle (Joubin 1900). The combination of Pfeffer's systematic expertise and Joubin's new material afforded '*C. unguiculata*' greater taxonomic stability, and its placement among octopoteuthids was readily accepted.

While still reported most extensively from the Mediterranean (*e.g.*, Degner 1925; Digby 1949), as interest in surveying the oceans increased *O. sicula* was reported from further afield: first off Ireland by Massy (1907); then south of the Azores (Murray & Hjort 1912; Joubin 1920); Japan (Sasaki 1916); around the Philippines (Voss 1963); off western USA (Pearcy 1965); eastern Canada (Mercer 1968); the Indian Ocean (Silas 1968); from the Gulf of Guinea (Arkhipkin & Shchetinnikov 1989) and around South Africa (Hoving *et al.* 2008). Similarly, the known distribution of *O. megaptera* expanded from the western north Atlantic and Gulf of Mexico (*e.g.*, Voss 1956a; Lipka 1975; Cairns 1976; Lu & Roper 1979) to the waters of New Zealand (Nesis 1979); the northern coast of South America (Okutani 1983); Namibia (Nesis 1991); eastern Japan (Kubodera & Tsuchiya 1993); and the western coast of Turkey (Salman *et al.* 2002).

Between 1920 and 1940, the number of named octopoteuthid species tripled with the description of two pairs of species. '*Octopoteuthis indica*' and '*O. persica*' Naef, 1923, were based on illustrations of larval octopoteuthids made by Chun (1910). The basis for the designation of '*Octopoteuthis indica*', from off the Indian coast of South Africa, was based on its less-developed arm crown at a comparable size to *O. sicula* from the Mediterranean, although no diagnostic characters were given. *Octopoteuthis 'persica'*, from the Gulf of Aden, differed from *O. sicula* and *O. indica* most notably in that only Arms II bore terminal swellings, which Naef noted constituted photophores as in all other known octopoteuthids. Less than ten years later, the second pair of octopoteuthids was described from specimens collected during the '*Dana*' cruises. *Octopoteuthis 'danae'* Joubin, 1931 was described from a juvenile specimen caught off the Bermuda Islands, and was differentiated from congeners by the presence of three pairs of photophores on the head and body and the absence of suckers on the arms. The second species, *Taningia danae* Joubin, 1931, described from a juvenile specimen caught off the Cape Verde Islands, was placed into a new genus as it bore photophores only at the tips of Arms II, separating it from all known octopoteuthids. While immediately noting the similarities in gross morphology between *Taningia* and

‘*Cuciototeuthis*’, and acknowledging their likely affinity, Joubin maintained his new genus on the basis of the differences in fin musculature development, despite this comparison being between a post-larval *T. danae* (total length 68 mm) and a maturing ‘*Cuciototeuthis*’ (total length 380 mm).

The next two octopoteuthid species, ‘*Octopodoteuthis*’ (= *Octopoteuthis*) *nielseni* Robson, 1948 and ‘*Octopodoteuthis*’ (= *Octopoteuthis*) *longiptera* Akimushkin, 1963, were both inadequately described and only compared to the type species, *O. sicula*. Robson based his description on two small, damaged specimens taken from the Galapagos Islands, and differentiated his *O. nielseni* from *O. sicula* based on the form of its “adhesive organ”, radular tooth morphology, lack of arm membranes, and in having longer Arms III. Akimushkin described ‘*O. longiptera*’ from a specimen recovered from a sperm whale stomach taken off central Brazil, which differed most significantly from *O. sicula* in fin morphology, with fin length comprising 135% of fin width compared to 57–66% in *O. sicula*. He extrapolated the species distribution to the north-western Pacific based on the abundance of its “highly characteristic beaks” which, illustrated but not described, were common in the stomachs of sperm whales there. The holotype of *O. ‘longiptera’* has since been lost (Young 1972).

In the 1960’s, Clarke began publishing on cephalopod systematics based on material from sperm whale stomach contents obtained from the whaling industry. In 1966 he gave the first systematic review of the Octopoteuthidae, considering *Octopoteuthis danae*, *sicula*, ‘*longiptera*’, *megaptera* (listed uncertainly in ‘*Octopodoteuthopsis*’) and *Taningia danae* as valid taxa (Clarke 1966). He noted that *O. nielseni*, *indica* and ‘*persica*’ were all based on larval specimens and could prove to be synonymous with *O. sicula*, given its wide geographic range. In a prelude to a subsequent publication, Clarke synonymised *E. ‘molinae’* Harting, 1861, and several specimens of ‘*C. unguiculata*’ (Joubin 1898, 1900; Clarke 1956; Rees & Maul 1956; Clarke 1962a) with *T. danae*. The following year, in a paper devoted solely to *T. danae*, he indicated that Owen’s material was never definitively established as belonging to Molina’s specimen, preventing its synonymy (Clarke 1967). More importantly, this publication introduced a significant amount of new material (twelve complete specimens and several heads) covering most of the ontogeny of *T. danae*. From this, Clarke was able to describe and illustrate in detail the physical and anatomical morphology, discuss variations observed in his specimens, and comment on aspects of the species’ biology (*e.g.*,

distribution, diet, fecundity). This work solidified the status of *T. danae* and made it known to a wider scientific audience.

Further clarifications within the family were provided by Roper *et al.* (1969). In a review undertaken to purge obsolete designations, they reiterated that ‘*Octopodoteuthis*’, ‘*Verania*’/‘*Veranya*’ and ‘*Octopodoteuthopsis*’ were junior synonyms of *Octopoteuthis* Rüppell. They selected Berry’s (1912) Octopoteuthidae as the familial name, after which no variants were used in the literature.

The most functional original description to date of an octopoteuthid was provided for a new species from the seas off southern California, *Octopoteuthis deletron* Young, 1972. *Octopoteuthis deletron* bore a single posterior ventral mantle photophore (PVMP), a character that distinguished it from all previously described octopoteuthids and gave immediate validity to the species. In defining this new species, Young gave a concise, critical review of the family. He considered *O. ‘longiptera’* to be a *nomen dubium* and discussion of *O. indica* was deferred as the small size of the holotype precluded adequate comparisons to congeners. Young also questioned the validity of the three Atlantic species of *Octopoteuthis*, believing either *O. danae* or *O. megaptera* would prove to be a junior synonym of *O. sicula*. He also briefly mentioned the existence of a single PVMP species in the Atlantic, designated *Octopoteuthis* sp. A, but never formally described it.

Young (1972) also recognised the terminal swellings on Arms II of Naef’s *O. ‘persica’* as a generic trait of *Taningia* Joubin, and proposed transferring it there. This was misinterpreted as synonymising *O. ‘persica’* with *T. danae* by later authors (*e.g.*, Clarke 1980; Stephen 1985a). Vecchione & Roper (1992) petitioned the International Commission on Zoological Nomenclature (ICZN) to give *T. danae* precedence over the senior epithet ‘*persica*’, an effort to stabilise the species, which was granted on the basis that *T. danae* was used predominantly in the literature (ICZN 1994).

Octopoteuthis rugosa Clarke, 1980, was originally described in the greatest detail of all octopoteuthid species, and from specimens recovered from stomachs of sperm whales off South Africa. Unfortunately, despite three pages of description and twenty illustrations, the diagnostic characters for his new species were based on generic, sex-specific, maturity-specific, or misinterpreted characters (Stephen 1985a).

The most comprehensive review of octopoteuthids to date has been a Master's thesis on the genus *Octopoteuthis* in which Stephen (1985a) concluded that only six species were valid (*O. sicula*, *megaptera*, *danae*, *deletron*, sp. A and *T. danae*, although the last was not reviewed) based primarily on photophore pattern. He documented a new character, an eyeball photophore, finding it diagnostic for *O. megaptera* although also present on some specimens labeled *O. nielseni*. On this basis he rejected *O. nielseni*, believing it to be a Pacific form of *O. megaptera*, and considered it along with *O. 'longiptera'*, *indica*, *'persica'* and *rugosa* as *nomina dubia*. However, emphasis was placed on Atlantic material, with the north-western and south-eastern Pacific and Indian Oceans being notable gaps in geographic coverage.

Nesis (1987) compiled an identification guide for cephalopod species around the world and listed the Octopoteuthidae as comprising two genera with eight or nine species. He gave keys to identify *T. danae*, and *O. danae*, *deletron*, *megaptera*, *sicula*, *nielseni*, *rugosa* and sp. A, though *O. longiptera* was excluded due to its incomplete description.

In something of an update to Clarke (1967), Roper and Vecchione (1993) published a detailed account of *Taningia danae*, reporting on the largest complete specimen to date (ML 1600 mm) taken off Massachusetts, USA, plus sixteen paralarval and juvenile specimens from Bermuda and several others from the south Atlantic and Pacific Oceans. They also gave a historical review of '*C. unguiculata*', discussed the bioluminescent capabilities of *T. danae*, and gave an extensive review of its geographic distribution.

In addition to *Octopoteuthis* sp. A Young, 1972, other undescribed octopoteuthid taxa have been alluded to in the literature: Japanese workers have reported over 300 specimens of an *Octopoteuthis* species with a single PVMP but considerably wider fins than *O. deletron* (Okutani *et al.* 1976; Okutani & Satake 1978; Okutani & Tsukada 1988); a considerably rarer "giant" *Octopoteuthis* species has been mentioned in the literature for 40 years (*Octopoteuthis* 'sp. B' *sensu* Clarke & MacLeod 1976, 1982; *Octopoteuthis* sp. 'Giant' *sensu* Clarke 1986; *Octopoteuthis* sp. 'Giant' *sensu* Gómez-Villota 2007); and a second form of *Taningia* has been reported for 50 years, noted for its papillated funnel (the aperture bearing dozens of lanceolate papillae) and nodulated skin (Clarke 1967, 1980; Hoving *et al.* 2010). Specimens attributable to each of these forms were examined in the present study.

With the family becoming increasingly recognised as unstable, fewer publications focused on its systematics (Jereb *et al.* [2016] being the only exception in the last 20 years). Recent publications have instead shifted to focus on aspects of octopoteuthid ecology and behaviour. These include *in situ* observations of hunting behaviour (Kubodera *et al.* 2007), investigations into their reproductive biology and mating strategies (Hoving *et al.* 2008, 2010, 2011), defensive behaviour (Bush 2012), and inter- and intraspecific communication (Bush & Robison 2007; Bush *et al.* 2009). However, all of these studies save one were based on either *T. danae* or *O. deletron*, the most readily identifiable species of the family.

3. MATERIALS & METHODS

3.1. Morphology

Material examined

Original descriptions and, where possible, type material of all previously described nominal octopoteuthid taxa were examined. Preserved and fresh specimens were loaned from, or examined at, the following institutions, between June 2011 and January 2018:

AM — Australian Museum, Sydney, New South Wales, Australia

MBARI — Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA

MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

MV — Museum Victoria, Melbourne, Victoria, Australia

NHMUK — Natural History Museum, London, UK

NIWA — National Institute of Water & Atmospheric Research Ltd, Wellington, New Zealand

NMNZ — Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand

NSMT — National Museum of Nature and Science, Tsukuba, Japan

SBMNH — Santa Barbara Museum of Natural History, Santa Barbara, CA, USA

USNM — National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

ZMH — Zoologisches Museum der Universität Hamburg, Hamburg, Germany

ZMUC — Zoological Museum, University of Copenhagen, Copenhagen, Denmark

Additional specimens were obtained from A. Escáñez, M. Haimovici, H.-J. Hoving, K. Sajikumar, and R. Young for examination, some of which were, at the time of writing, not yet accessioned at a permanent repository; these are identified by their collection data (*e.g.*, station, vessel, or date). Some of these specimens, and several lots of older or ex-gut-content specimens from other collections, have only partially recorded collection data; these have been reported as completely as possible. Collection data enclosed in single quotation marks (‘’) are *fide* label, and unverified by the author (*e.g.*, sex of an unexamined specimen). Collection data are generally reported in the following format:

Accession number, sex, size (*e.g.*, ML), latitude (DDM), longitude (DDM), locality, collection depth (m), bottom depth (m), collection date (dd/mm/yyyy), collection time (00:00), *vessel name*, station, collection method, collected by (*e.g.*, individual, institution, expedition, programme).

Specimens are reported in Material Examined sections in order of decreasing latitude and secondarily by dorsal mantle length (in multiple specimen lots, by ML of the largest specimen). Sexes reported were determined solely by the author, with “sex indet.” used to indicate specimens too juvenile or damaged for confident determination, or where dissection was unjustified. Maturity staging was based on qualitative observations of reproductive tissues, and defined into three stages for males and four for females. Immature males were individuals with narrow, thin terminal organs that barely protruded anteriorly of the gill artery; maturing males were those with thickening and lengthening terminal organs that still did not protrude beyond the anterior mantle margin; and mature males were those with fully thickened terminal organs that extended well beyond the anterior mantle margin and contained developed spermatophores (often accessible from distal tip or via dissection), and were often also themselves implanted with spermatangia (likely self-implanted during capture). Immature females were individuals with very small, thin, narrow nidamental glands, often difficult to discern amongst the connective tissues overlying the viscera; maturing females were those with thickening and lengthening nidamental glands, oviducal glands becoming apparent laterally under the gill arteries; mature females had either ripe ova (large, orange coloured, slightly translucent, detached) in the oviducts or ovary (or both), very large, prominent nidamental glands, and thickened oviducal glands which extended anteriorly of the gill arteries; and resting females were individuals with greatly reduced nidamental and oviducal glands, typically only undeveloped oocytes in ovary, nidamental (and occasionally oviducal) glands with a ‘sheathed’ appearance (see *O. sicula* description below). Specimens that were unable to be positively attributed to species were excluded from further reporting (33 of 891 specimens examined).

Some specimens were examined early in the study and attributed to species before the full diversity of the family was recognised, and re-examination was not possible within the study’s time limit. Those specimens were included in Comparative Material of the species they were most likely attributable (with some exceptions, see Remarks under each species for explanation). For species with few positively identified specimens, this

supplemental material was plotted on distribution maps to gain insight into the species' potential full range (*e.g.*, *O. nielsenii*). For already well-represented species (*e.g.*, *O. rugosa*), distribution plots only depict positively identified specimens.

Additional collection acronyms used in text are:

Acc. No. — Accession number

AUT — Auckland University of Technology, Auckland, New Zealand

BAMZ — Bermuda Aquarium, Museum and Zoo

BT — bottom temperature

BTT — bottom trawl

C — central

CASIZ — California Academy of Science, Invertebrate Zoology, San Francisco, CA, USA

CSIRO — Commonwealth Scientific and Industrial Research Organisation (Australia)

DMNH — Delaware Museum of Natural History, Wilmington, DE, USA

E — east

EtOH — ethanol

FMMWT — fine-mesh midwater trawl

FV, FRV, FSV — fisheries vessel, fisheries research vessel, fisheries survey vessel

IKMWT — Isaacs-Kidd midwater trawl

IYGPT — international Young gadoid pelagic trawl

JAMARC — Japan Marine Fishery Resources Research Centre, Tokyo, Japan

MFish — New Zealand Ministry of Fisheries (now Ministry for Primary Industries, MPI)

MfN — Museum für Naturkunde, Berlin, Germany

MM — Manchester Museum, University of Manchester, Manchester, UK

MMS — Minerals Management Service (formerly; USA)

MNCN — Museo Nacional de Ciencias Naturales, Madrid, Spain

MRC — Malcolm R. Clarke Collection (NHMUK)

MWT — midwater trawl

N — north

NMFS — National Marine Fisheries Service (USA)

NMSZ — National Museum of Scotland, Edinburgh, UK

NMW — National Museum Wales, Cardiff, UK

NOAA — National Ocean and Atmospheric Administration (USA)
NORFANZ — New Zealand and Australia Norfolk Ridge-Lord Howe Rise Biodiversity
Voyage
OAA — Ocean Acre Area
RCSHC – Royal College of Surgeons, Hunterian Collection, London, UK
RV — research vessel
S — south
SAM — South African Museum, Cape Town, South Africa
SEFSC — Southeast Fisheries Science Center (USA)
SOP — MPI Scientific Observer Programme (New Zealand)
ST — surface temperature
stn — station
SWAPS — Sperm Whale Acoustic Prey Survey (USA)
TMAG — Tasmanian Museum and Art Gallery, Hobart, Australia
USNOAP — United States Navy, Ocean Acre Project
UWO — University of Western Ontario, London, Canada
W — west
YPM — Yale Peabody Museum of Natural History, New Haven, CT, USA

Distribution maps were based solely on specimens examined herein, with the exception of a few additional specimens that were not examined but which genetic analyses clearly allied with taxa of known morphology and genetics. Material was available from most major ocean currents (Fig. 1), with the following currents best represented in each ocean basin:

Pacific — Kuroshio, California, Equatorial Counter, East Australian
Atlantic — Gulf Stream, North Atlantic Drift, Canary, Brazil
Indian — South Equatorial

Material from the western equatorial Atlantic, the central and southeastern Pacific, and the Indian Ocean was scarce, and very little to no material was available from the eastern equatorial Pacific and latitudes below 50°S.

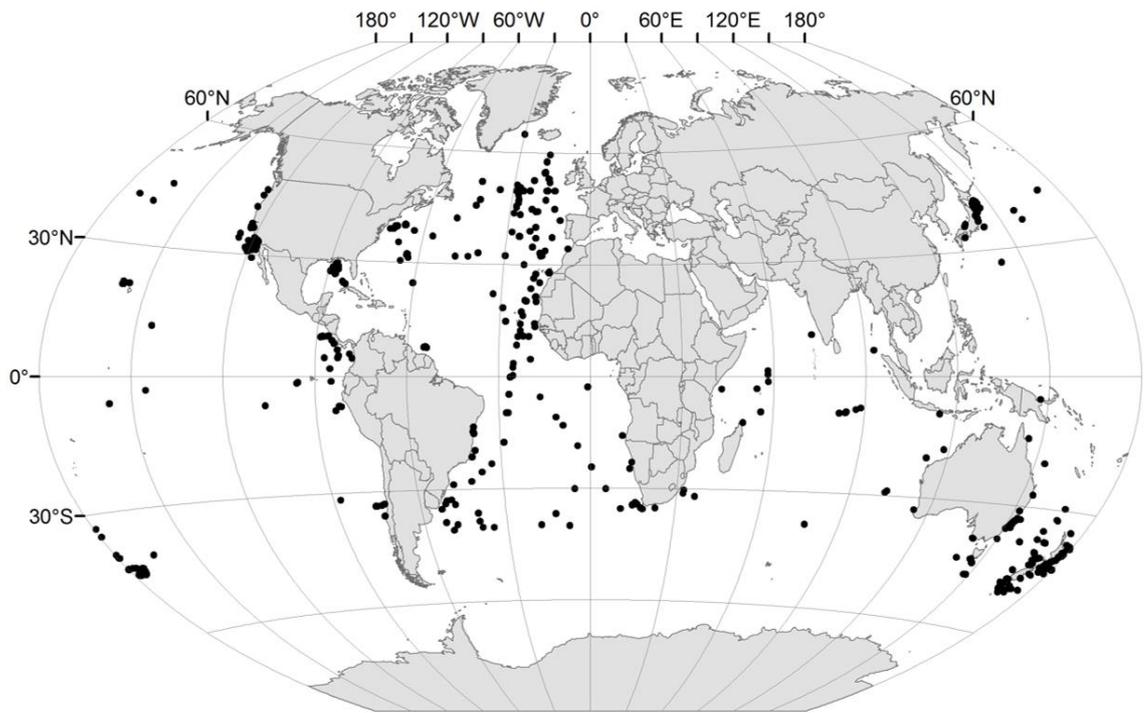


Fig. 1— Geographic distribution of octopoteuthid material examined in this study, June 2011–January 2018.

The synonymy for each species is limited to publications containing substantial morphologic detail, such as species descriptions with specific character state distinctions, illustrations, and/or images, or where the exact material was re-examined herein. Publications of insufficient detail were excluded.

Morphologic examinations

Species descriptions and specimen measurements, indices and counts follow Roper & Voss (1983) with some modification. Standard external measurements and terminology are illustrated in Fig. 2; measurement indices were calculated as a percentage of the dorsal mantle length (*e.g.*, mantle width index, $MWI = MW / ML$; see definitions below). Measurements of brachial crown appendages were taken on the more complete side of the specimen, and indicated in text and tables as “R” (right) or “L” (left) (*e.g.*, Arm IVR). Ranges were given in the format of lowest value (X), mean (Y), and largest value (Z) in the format X–Y–Z. Where fewer than three specimens were available for a species or the range was less than 5%, only the mean is reported (as ~x%). Measurements of damaged features are indicated by an asterisk (*), regenerating features by a superscript r (^r), and specimens missing a tail by a cross (†). For specimens $ML < 50$ mm, measurements to one decimal place are reported.

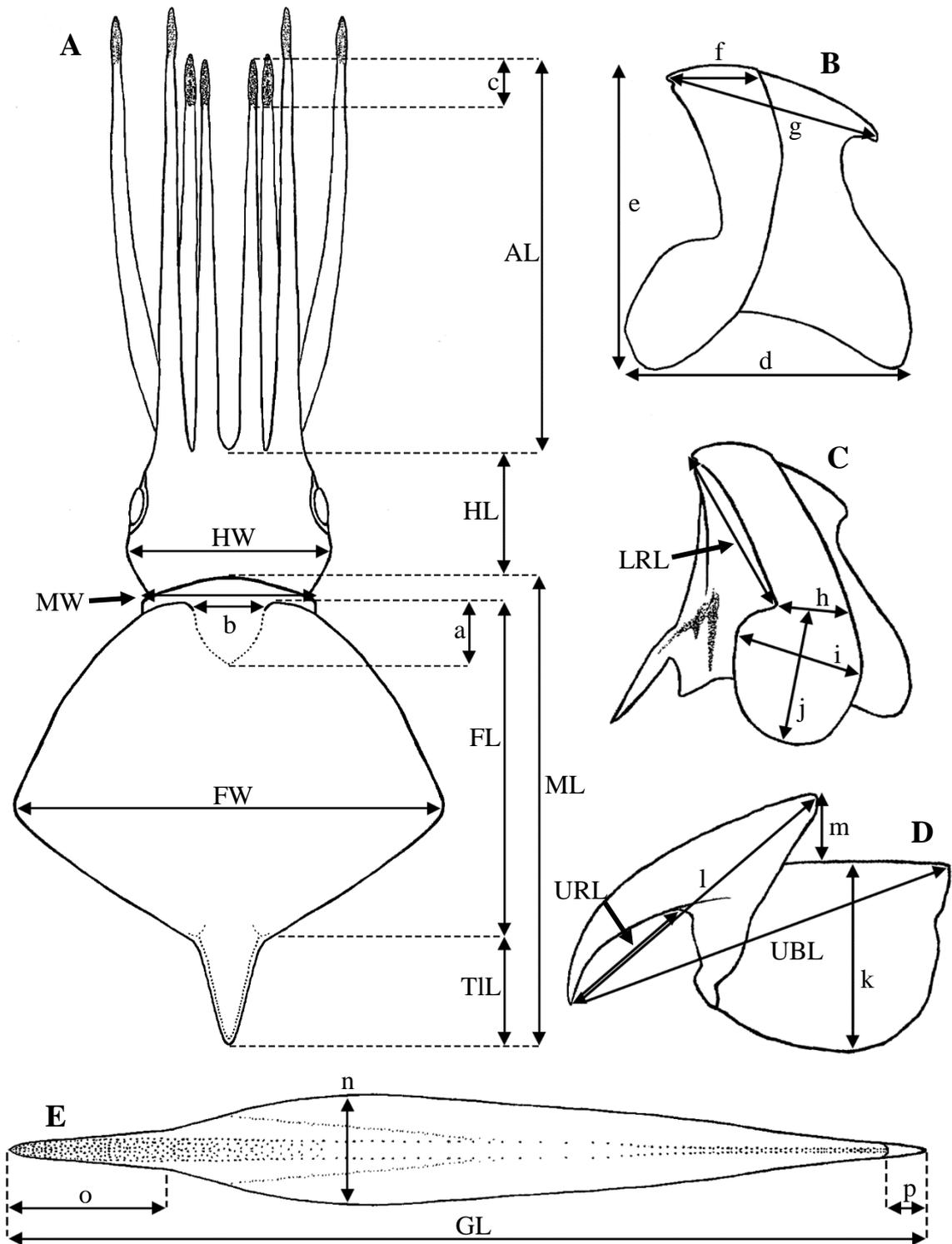


Fig. 2— Octopoteuthid measures. Acronyms of standard measurements are defined in text; additional measures as follows. A) Gross morphology: (a) depth of anterior fin insertion, (b) width of anterior fin insertion, (c) arm tip photophore length; B) lower beak, lateral profile: (d) baseline, (e) depth, (f) hood length, (g) crest length; C) lower beak, oblique: (h) wing width at jaw angle, (i) maximum wing width, (j) wing length; D) upper beak, lateral profile: (k) depth, (l) hood length, (m) hood height; E) gladius: (n) maximum width, (o) free rachis length, (p) conus length.

Where material allowed, species descriptions were divided into as many as four life stages: adults and subadults (specimens lacking all remnants of tentacles); juveniles (also lacking any trace of tentacles but where important indices differed from the larger life stage); post-larvae (specimens with atrophying, presumed non-functional tentacles); and paralarvae (specimens with functional full-length tentacles; Young & Harman 1988). In general, indices reported in text for the largest life stage were based on measurements of specimens listed in tables; indices for some characters (*e.g.*, AL) were calculated from supplementary specimens due to the high frequency of damage (see Remarks for *Octopoteuthis* sp. Giant Pacific nov.). For brevity, only two or three specimens of the smaller size classes combined were included in tables of measurements, although a greater number of specimens was used to create the full description where possible. Select morphometric indices were plotted against ML for *O. sicula* and *O. deletron*, two species with good ontogenetic coverage, to illustrate changes in body proportions. Ontogenetic trends were identified by fitting regression models (linear, exponential, logarithmic, or power functions) to the untransformed data; the model of best fit was determined by the greatest R^2 value. The same analysis was used to generate species-specific regression equations of beak measures (LRL, URL) against body size (ML, body mass) for five species (*O. sp. I NZ*, *O. rugosa*, *O. deletron*, *T. danae*, *T. fimbria* sp. nov.).

Specimen measurement acronyms and terms used in text include:

AH — arm hook count (in pairs; *e.g.*, 30 pairs of hooks, 60 individual hooks in total)

AL, ALI — arm length, arm length index (AL / ML)

AS — arm sucker counts (in pairs; *e.g.*, 8 pairs of suckers, 16 individual suckers in total)

CL, CLI — club length, club length index (CL / ML)

CS — club sucker count (in pairs)

EML — estimate mantle length

est. — estimated

FL, FLI — fin length, fin length index (FL / ML)

Fresh — not fixed in preservative (*i.e.*, no formalin, alcohol; *e.g.*, fresh ML)

FW, FWI — fin width, fin width index (FW / ML)

GL — gladius length

HL, HLI — head length, head length index (HL / ML)

HW, HWI — head width, head width index (HW / ML)

L — left side

ML — mantle length (dorsal mantle length, DML, unless otherwise specified)

MW, MWI — mantle width, mantle width index (MW / ML)

NM — not measured, counted, recorded (character was not quantified during examination)

R — right side

TRSL — total reproductive system length

TL, TLI — tentacle length, tentacle length index (TL / ML)

TIL — tail length

UBL — upper beak length (Fig. 2)

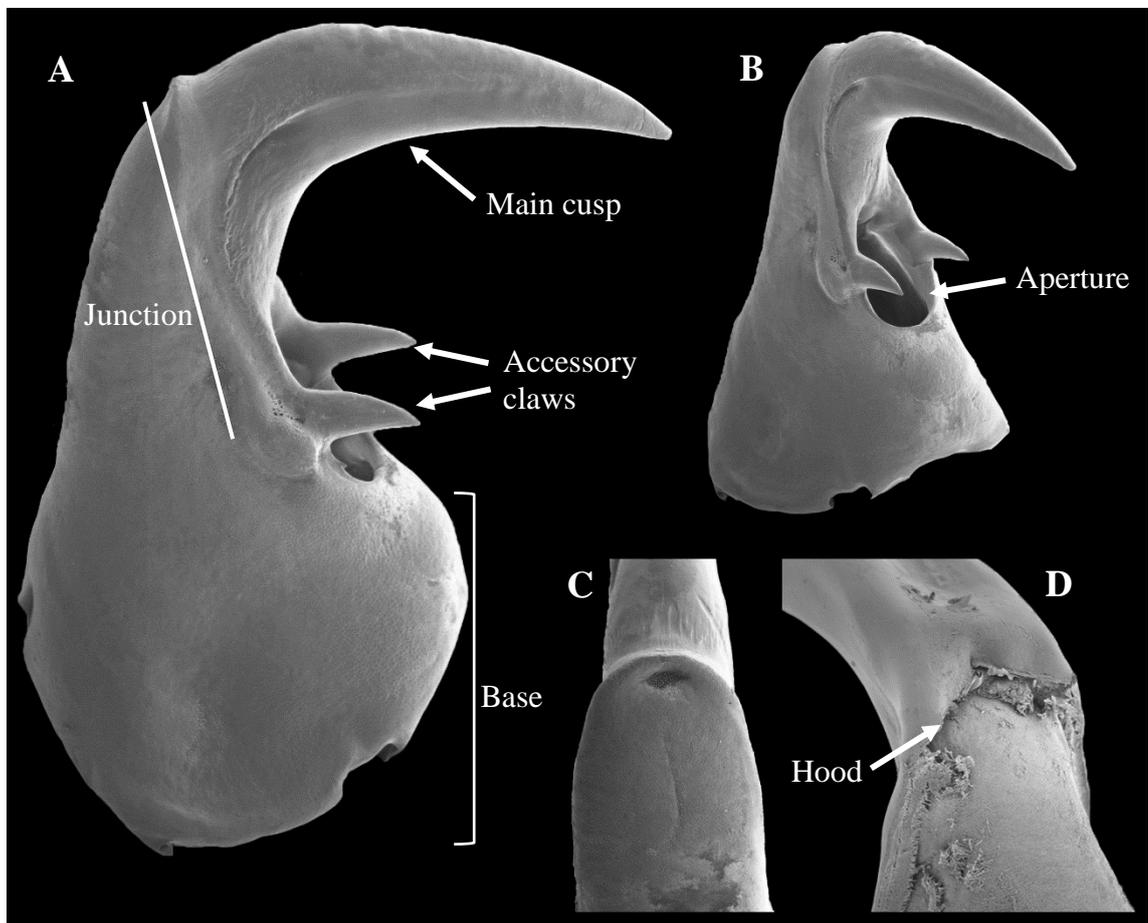


Fig. 3— Octopoteuthid arm hook terminology, based on Young & Harman (1998) with minor adaptations. A–C) *Octopoteuthis rugosa*, NIWA 76639, sex indet., ML 85 mm; D) *Taningia danae*, NIWA 76658, ♂, ML 260 mm. A–C) 5V hook, Arm IIIIR: (A) lateral profile with line indicating junction of main cusp and base, (B) oral oblique, (C) aboral; D) 4V hook, Arm IVR, aboral oblique with hood and inserted tissue.

Counts of arm hooks, arm suckers, and tentacle club suckers are reported as pairs of hooks or suckers in text and tables, never as total numbers of individual hooks or suckers. This method was chosen as it underscores the consistent, ordered presentation of the armature, in addition to reducing seeming variability (*i.e.*, the difference between 28 to 32 pairs of hooks compared with 56 to 64 hooks). In some cases, a single centred sucker or hook occurred distally on arm tips, instead of a complete pair; these are reported as the number of complete pairs “+1” (*e.g.*, AS 6+1). In tables, hook and sucker counts are reported only for the complete arms or tentacles measured, and are listed in order of Arms I to IV. Arm hook terminology follows Young & Harman (1998) with some modification (Fig. 3). Individual hooks are identified according to dorsal or ventral series and numbered from proximal-most to distal-most (*e.g.*, arm hook 4D = fourth hook in the dorsal series, counting distally from the arm base).

Lower beak descriptions and terminology follow Clarke (1980) and were oriented with the dorsal surface along the baseline; upper beak descriptions and terminology follow Young *et al.* (2000), with the ventral surface oriented along upper beak length (Fig. 2). Herein, upper beak length is equivalent to crest length, *fide* Young *et al.* 2000. Octopoteuthid lower beaks display a unique character shared only with *Lepidoteuthis*, here termed a ‘shelf’ (Fig. 4): a lateral or dorsolateral protrusion of the anterior lateral wall fold fusing it to the inner surface of the hood for the anterior 40–70% of the hood’s length. Radula and palatine palp descriptions and measurements follow Bolstad (2010) and Braid (2013). Epidermal tubercle and funnel projection descriptions are based on Roper & Lu (1990).

Anterior fin insertion depth was measured along the midline from the anterior-most point of the fin margin to the posterior-most point of the indentation; anterior fin insertion width was measured level with the anterior-most fin margins (Fig. 2).

For the majority of *T. fimbria* sp. nov. specimens (72%, 13/18 whole specimens), the posterior tip of the mantle beyond the posterior fin attachment (the “tail”) was missing. In the few intact specimens examined, the tail comprised 20% ML (mean of six individuals of sufficient quality, ML 312–884 mm); thus, to include measurements of damaged specimens in the description an estimated mantle length (EML) was calculated by dividing the measured DML by 0.80. This EML was used to obtain indices for

damaged specimens (Table 23). Within the description of *T. fimbria*, use of “ML” indicates pooling of DML/EML measurements and calculations.

Owing to the incomplete nature of their original descriptions and absence of subsequently published re-examinations, the type material of *O. sicula* and *O. nielseni* were re-described. Original descriptions of the type material of *O. deletron*, *O. ‘danae’*, *O. rugosa*, and *T. danae* were considered sufficiently detailed, and the type material for *O. megaptera*, ‘*O. longiptera*’, ‘*O. indica*’, and ‘*T. persica*’ could not be located.

For scanning electron microscopy (SEM), samples were first manually cleaned of soft tissue and then transferred daily to incrementally higher concentrations of ethanol (*i.e.*, from general storage of 70–80% EtOH to 100% EtOH). Samples were then critical-point dried either at University of Auckland or UWO, sputter coated in gold-palladium, and imaged at AUT or UWO. Due to mechanical constraints of the SEM, lateral profiles of arm hooks were obtained at 60–70° of tilt, as opposed to 90° in illustrations.

For conclusive characterisation of soft-tissue structures, samples were prepared for histological examination. Samples were embedded in xylol followed by paraffin in accordance with the protocols given in Braid (2013). Staining was performed with standard haematoxylin and eosin (H&E) and Mallory’s trichrome stain at UWO.

3.2. Genetics

Samples and specimens

Tissue samples were obtained from institutions and collecting programmes from around the world (Table 1). Samples were maintained at -80°C either unfixed (*i.e.*, no EtOH) when possible or in 100% EtOH. Some specimens that were sequenced were not available for morphologic examination. In such cases, that material is listed in species descriptions under “Additional genetic samples,” with available collection data and source. The same outgroup species, *Pholidoteuthis* sp. (BAlep 557/12) from Hawaii, was included in both the single-gene trees and the combined phylogeny. This sequence was chosen as it belongs to the lepidoteuthid families clade—a well-supported monophyletic group comprising the Lepidoteuthidae, Pholidoteuthidae, and

Table 1. Tissue samples and genetic sequences analysed for the present study. Unaccessioned specimens are identified by their collection data. Source indicates the collector of tissue used for sequencing in this study, or reference for previously published sequences. Not all samples below were included in all phylogenies.

Species	Specimen ID	COI	16S rRNA	<i>cyt b</i>	Source
Octopoteuthidae					
<i>Octopoteuthis</i>					
<i>O. sicula</i>					
	USNM 1283031	X			A. Lindgren
	USNM 1283032	X	X	X	A. Lindgren
	USNM 1283039 ^a	X	X	X	A. Lindgren
	USNM 1283040	X			M. Vecchione
	DE0304/3	X	X	X	M. Vecchione
	DE0304/3	X			M. Vecchione
	DE0304/6	X			M. Vecchione
	DE0304/9	X			A. Lindgren
	DE0506/5	X			M. Vecchione
	DE0506/15	X			M. Vecchione
	DE0611/8	X			A. Lindgren
	Escáñez 11-4-D	X	X	X	A. Escáñez
	Escáñez 11-4-N	X			A. Escáñez
	Escáñez 11-5-D	X			A. Escáñez
	Escáñez 12-I-N	X	X	X	A. Escáñez
	Mar Eco #004303; SS 31-1125;	EU735402	EU735266		Lindgren 2010
	LS 360				
	5 specimens, 3 Mediterranean localities	GU812407	GU812406		Cuccu <i>et al.</i> 2013; Jereb <i>et al.</i> 2016
<hr/>					
<i>O. fenestra</i> sp. nov.	NIWA 62695	X			Present study
	NIWA 76606	X	X	X	Present study

Table 1 (cont.). Tissue samples and genetic sequences analysed for the present study.

Species	Specimen ID	COI	16S rRNA	<i>cyt b</i>	Source
<i>O. fenestra</i> (cont.)	NIWA 76606 –spermatangium	X			Present study
	NIWA 76607	X			Present study
	NIWA 76607 – spermatangium	X			Present study
	NIWA 76635	X	X	X	Present study
	NIWA 76636	X	X		Present study
	NIWA 76638	X			Present study
	NIWA 85959	X			Present study
	NIWA 89384	X	X	X	Present study
	NIWA 89388	X	X	X	Present study
	NIWA 95934	X			D. Stevens
	NIWA 106190	X			Present study
	TAN1401/69	X	X	X	H. Braid
	NMNZ M.306361	X			Present study
	NMNZ M.306362	X			Present study
	<i>O. megaptera</i>	USNM 1192580	X		
PC10/B82		X	X	X	M. Vecchione
PC10/SW8		X	X	X	M. Vecchione
PC10-01/092		X	X	X	M. Vecchione
Escáñez 5-I-N		X	X		A. Escáñez
Escáñez 6-0-N		X	X	X	A. Escáñez
<i>O. rugosa</i>	NIWA 76634	X	X	X	Present study
	NIWA 76639	X	X	X	Present study
	NIWA 76647	X	X	X	Present study
	NIWA 95937	X			D. Stevens
	NIWA 95943	X	X	X	D. Stevens
	TAN1401/53	X	X	X	H. Braid
	SAM S4084	X	X	X	A. Lindgren

Table 1 (cont.). Tissue samples and genetic sequences analysed for the present study.

Species	Specimen ID	COI	16S rRNA	cyt b	Source
<i>O. rugosa</i> (cont.)	Annie 6	X			A. Lindgren
<i>O. laticauda</i> sp. nov.	BAlep 330/9	X	X	X	A. Choy/R. Young
	BAlep 503/1	X	X	X	A. Choy/R. Young
	NewHorizon4/26/93	X	X		A. Choy/R. Young
	NSMT Mo75879	X	X	X	T. Kubodera
	NSMT DNA 377	X			T. Kubodera
	NSMT DNA 378	X	X	X	T. Kubodera
	Hokusei Maru 1994	AF000055	EU735216		Carlini & Graves 1999; Lindgren <i>et al.</i> 2004; Lindgren 2010
<i>O. sp. IO nov.</i>	OJMF3	X			S. Kumar
<i>O. deletion</i>	DNA 1	X	X		Present study
	DNA 2	X	X		Present study
	DNA 3	X			Present study
	DNA 4	X			Present study
	OD 12	X			H. Hoving
	OD 13	X			H. Hoving
	OD 14	X	X	X	H. Hoving
	OD 15	X			H. Hoving
	OD 16	X			H. Hoving
	OD 17	X			H. Hoving
	OD 18	X			H. Hoving
	OD 19	X			H. Hoving
	OD 20	X			H. Hoving
	OD 21	X			H. Hoving
	OD 22	X			H. Hoving
	OD 23	X			H. Hoving
	OD 24	X	X	X	H. Hoving

Table 1 (cont.). Tissue samples and genetic sequences analysed for the present study.

Species	Specimen ID	COI	16S rRNA	<i>cyt b</i>	Source
<i>O. deletron</i> (cont.)	OD 25	X	X	X	H. Hoving
	OD 26	X			H. Hoving
	OD 27	X			H. Hoving
	OD 28	X			H. Hoving
	OD 29	X			H. Hoving
	OD 30	X			H. Hoving
	OD 31	X			H. Hoving
	OD 33	X			H. Hoving
	OD 34	X			H. Hoving
	OD 35	X			H. Hoving
	OD 36	X			H. Hoving
	OD 37	X			H. Hoving
	OD 38	X			H. Hoving
	OD 39	X	X	X	H. Hoving
	OD 40	X			H. Hoving
	OD 41	X			H. Hoving
	OD 45	X			H. Hoving
	OD 47	X			H. Hoving
	OD 48	X	X	X	H. Hoving
	OD 51	X			H. Hoving
	OD 54	X			H. Hoving
	OD 55	X			H. Hoving
	OD 56	X			H. Hoving
	OD 62	X			H. Hoving
	OD 71	X			H. Hoving
	OD 72	X			H. Hoving
	OD 73	X			H. Hoving

Table 1 (cont.). Tissue samples and genetic sequences analysed for the present study.

Species	Specimen ID	COI	16S rRNA	cyt b	Source
<i>O. deletron</i> (cont.)	OD 75	X			H. Hoving
	OD 76	X			H. Hoving
	OD 77	X			H. Hoving
	NSMT Mo71580	X	X	X	T. Kubodera
	NSMT Mo71581 ^b	X	X	X	T. Kubodera
	NSMT Mo71967	X	X	X	T. Kubodera
	NSMT DNA 447	X			T. Kubodera
	NSMT DNA 448	X			T. Kubodera
	Monterey del (NMNZ M.317511)	X			K. Bolstad
	NSMT, 1999	AY557541	EU735217		Lindgren <i>et al.</i> 2004; Lindgren 2010
	<i>O. sp. Giant Pacific</i>	OG1	X		S. O'Shea
<i>Taningia</i> <i>T. danae</i>	BAMZ 2012 280 017	X	X	X	S. Smith
	MNCN 239 ^c	X	X	X	B. Alvarez
	NIWA 75790	X			Present study
	NIWA 76658	X	X	X	Present study
	NIWA 76663	X	X		Present study
	NIWA 94142	X			Present study
	NMNZ M.284745	X			K. Bolstad
	NMNZ M.305062	X	X	X	B. Marshall
	NMNZ M.306360	X	X	X	Present study
	TMAG E24300	X			S. Grove
	<i>T. fimbria</i> sp. nov.	NMNZ M.306357 TAN1117/59	X X	X X	X X

Table 1 (cont.). Tissue samples and genetic sequences analysed for the present study.

Species	Specimen ID	COI	16S rRNA	<i>cyt b</i>	Source
<i>T. fimbria</i> (cont.)	TAN1412/36	X	X	X	Present study
<i>T. rubea</i> sp. nov.	NSMT Mo71582	X	X	X	T. Kubodera
	NSMT Mo76347	X	X	X	T. Kubodera
	NSMT Mo85593 (DNA 389)	X	X	X	T. Kubodera
<i>T. sp. IV</i>	BAlep 344/6	X	X	X	A. Choy/R. Young
	BAlep 667/1	X	X	X	A. Choy/R. Young
<i>T. sp. V</i>	ZMH 79906	X	X	X	B. Hausdorf
	PC10-01	X	X	X	M. Vecchione
Pholidoteuthidae					
<i>Pholidoteuthis</i>					
<i>P. sp.</i>	BAlep 557/12	X	X	X	A. Choy/R. Young

^a = *O. 'megaptera'* of Lindgren (2010): EU735358 (COI), EU735258 (16S); re-sequenced herein.

^b = likely same specimen as *O. 'sacula'* of Lindgren *et al.* (2004), *O. deletion* of Lindgren (2010): AY557541 (COI), EU735217 (16S). Sample of NSMT Mo71581 sequenced herein.

^c = *T. danae* of Rey *et al.* (2008, unpublished): AY393902 (COI), AY393901 (16S); re-sequenced herein.

Octopoteuthidae (Roper & Lu 1990; O'Shea *et al.* 2007; Lindgren 2010)—and is, therefore, related to octopoteuthids but less so than they are to each other.

DNA extraction and sequencing

Three mitochondrial gene regions were selected for amplification and sequencing: the 658 basepair (bp) region of the 5' end of cytochrome *c* oxidase subunit I (COI); 16S rRNA; and *cytochrome b* (*cyt b*). Primer sequences and reaction profiles for each gene are given in Table 2; COI primers were modified slightly from universal invertebrate primers (Folmer *et al.* 1994) to be cephalopod specific (Braid *et al.* 2014). DNA was extracted using a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following manufacturer's instructions. PCR amplification was carried out in 12.5 µl reaction volumes comprising 2 µl of DNA, 6.25 µl 10% trehalose, 2 µl ddH₂O, 1.25 µl 10X buffer, 0.625 µl MgCl₂ (50 mM), 0.1 µl forward primer (10 µM), 0.1 µl reverse primer (10 µM), 0.0625 µl 10 mM dNTPs, and 0.06 µl Platinum Taq polymerase (5U/µl). PCR products were visualised in 2% agarose E-gels (Invitrogen) or 1% agarose gels stained with GelRed (Biotium). Sequencing reactions for PCR products used BigDye v3.1 and the same primers used for the initial PCR; sequencing products were sent to either ACA Genomics Facility (Guelph, Canada) or Macrogen (Seoul, South Korea) for sequencing. Bi-directional sequence contig assemblies were created and edited using Sequencher v 4.9 (Gene Codes). Sequences were screened for potential contamination by using the Basic Local Alignment Search Tool (BLAST) through GenBank.

Phylogenetic analysis

To test the ability of the three gene regions at separating morphologically hypothesised species, separate maximum-likelihood phylogenies were constructed for each gene. Combined, multi-gene phylogenies were also constructed to analyse higher relationships within the family. Sequences were aligned via the MAFFT algorithm (Katoh *et al.* 2002) as implemented in Geneious Pro 9.1.5 (Biomatters, Auckland, New Zealand); alignments were then trimmed manually, and concatenated in Geneious. To determine the most appropriate partitioning scheme for phylogenetic analyses, jModelTest (Darriba *et al.* 2012) and PartitionFinder 1.1.1 (Lanfear *et al.* 2012) were run on concatenated alignments for the maximum-likelihood analysis with all substitution models included. jModelTest was used to determine the best single partitioning scheme

Table 2. Primer sequences for each gene region and PCR reaction profiles.

Gene region	Primer pair	Primer sequence (5'–3')	Reaction profiles
COI	LOC1490_CephF	TTTCAACAATCATATAAGATATTGG	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
	HCO2198_CephR (modified from Folmer <i>et al.</i> 1994)	ACTTCTGGGTGACCAAAAAATCA	
16S rRNA	16Sar (Simon <i>et al.</i> 1994)	CGCCTGTTTATCAAAAACAT	Hot start of 94°C for 2 min; 35 cycles of 94°C for 30 s, 52°C for 40 s, 72°C for 1 min; extension at 72°C for 10 min, hold 4°C indefinitely
	16Sb (Xiong & Kocher 1991)	CTCCGGTTTGAACTCAGATCA	
<i>cyt b</i>	CEF H (Santacilara <i>et al.</i> 2007)	TTATGGKTGRGTRYTDCGTTAT	Hot start of 95°C for 3 min; 35 cycles of 95°C for 30 s, 50°C for 1 min, 72°C for 90 s; extension at 72°C for 7 min, hold 4°C indefinitely
	CEF L (Santacilara <i>et al.</i> 2007)	TACHCCYCCWARTTTTWTAGGAAT	

for the 16S rRNA single-gene phylogeny (a non-coding gene); PartitionFinder was used to test partitioning by codon position for the COI and *cyt b* single-gene phylogenies (both coding genes), and by gene and codon position for the combined phylogenies (resulting in a maximum of seven possible partitions). Optimal schemes (those with the greatest associated relative weight, ω_i) as selected by Bayesian Information Criterion (BIC) and corrected Akaike Information Criterion (AICc) supported partitioning by codon for both COI and *cyt b* (Table 3). Outputs from PartitionFinder did not include values for ω_i , which were calculated using:

$$\omega_i = \frac{e^{\frac{-1}{2\Delta_i}}}{\sum_{r=1}^R \left(e^{\frac{-1}{2\Delta_i}} \right)}$$

where Δ_i is the difference between the BIC or AICc score of the i^{th} model and the smallest BIC or AICc score. BIC-selected models resulted in higher weight values than AICc-selected models in all but two cases (difference for both was <0.1), and were thus used for generating all phylogenies. All phylogenies were created using GARLI 2.0.1 (Zwickl 2006) with 1000 bootstrap replicates, which is generally sufficient for most trees (Pattengale *et al.* 2010). Two multigene phylogenies were constructed: a strict combined phylogeny comprising only individuals with all three gene regions sequenced; and an inclusive combined phylogeny which included all individuals with at least one sequenced region.

Mean pairwise intra- and interspecific distances were calculated from aligned COI sequences using the K2P model (Kimura 1980) in MEGA 6 (Tamura *et al.* 2013). Single-gene phylogenies were submitted to <http://species.t-its.org/> for maximum likelihood Bayesian Poisson tree processes (bPTP) analysis (Zhang *et al.* 2013) to evaluate how the three gene regions delimited species.

Table 3. Optimum models for three gene regions as selected by Bayesian Information Criterion (BIC) and corrected Akaike Information Criterion (AICc), with corresponding scores and weights. Bolded models indicate the two cases where the AICc selected model had a greater weight than the BIC selected model.

Partition(s)	BIC model	Score	weight	AICc model	Score	weight
Single						
COI	HKY+I+G	8429.98	0.724	HKY+I+G	7619.76	0.660
16S	TIM3+I+G	3970.79	0.409	TIM3+I+G	3525.73	0.479
<i>cyt b</i>	HKY+G	6256.15	0.565	TVM+I+G	5855.11	0.322
Multiple						
Single gene						
COI						
COI_1	F81+I	662.55	0.841	F81+I	649.26	0.381
COI_2	TrN+G	4193.63	0.822	GTR+G	4173.48	0.315
COI_3	TrNef+G	1297.16	0.666	TrNef+G	1287.18	0.331
<i>cyt b</i>						
<i>cyt b</i> _1	K81+G	1345.56	0.317	TIM+I+G	1325.73	0.324
<i>cyt b</i> _2	F81+I	847.46	0.625	TVM+I	825.45	0.339
<i>cyt b</i> _3	HKY+G	3119.84	0.663	K81uf+G	3103.49	0.196
Combined						
Strict						
COI_1: <i>cyt b</i> _2	F81+I	1512.89	0.843	TVM+I+G	1490.30	0.351
COI_2	TrN+G	3720.90	0.840	TrN+G	3701.08	0.472
COI_3	TrNef+I	1222.96	0.462	TrNef+I	1212.98	0.269
16S: <i>cyt b</i> _1	K81uf+I+G	4592.87	0.771	TVM+I+G	4554.77	0.690
<i>cyt b</i> _3	HKY+G	3128.71	0.512	TVM+G	3111.99	0.179
Inclusive						
COI_1: <i>cyt b</i> _2	F81+I	1528.99	0.871	F81+I	1512.95	0.190
COI_2	TrN+G	4299.95	0.831	TrN+G	4280.16	0.352
COI_3	TrNef+G	1333.77	0.716	TrNef+G	1323.79	0.387
16S: <i>cyt b</i> _1	K81uf+I+G	4640.10	0.757	TVM+I+G	4602.04	0.680
<i>cyt b</i> _3	HKY+G	3118.19	0.614	HKY+G	3101.98	0.258

_ = codon partition within gene region

4. CHECKLIST OF SPECIES

Family Octopoteuthidae Berry, 1912

Genus *Octopoteuthis* Rüppell, 1844

<i>Octopoteuthis sicula</i> Rüppell, 1844	}	<i>sicula</i> species group
<i>Octopoteuthis nielseni</i> Robson, 1948		
<i>Octopoteuthis fenestra</i> sp. nov.		
<i>Octopoteuthis megaptera</i> (Verrill, 1885)	}	<i>megaptera</i> species group
<i>Octopoteuthis rugosa</i> Clarke, 1980		
<i>Octopoteuthis laticauda</i> sp. nov.		
<i>Octopoteuthis</i> sp. IO		
<i>Octopoteuthis deletron</i> Young, 1972	}	<i>deletron</i> species group
<i>Octopoteuthis leviuncus</i> sp. nov.		
<i>Octopoteuthis</i> sp. Giant Pacific	}	“Giant” species group
<i>Octopoteuthis</i> sp. Giant Atlantic		

Genus *Taningia* Joubin, 1931

Taningia danae Joubin, 1931
Taningia fimbria sp. nov.
Taningia rubea sp. nov.
Taningia sp. IV
Taningia sp. V

5. SYSTEMATICS

Family Octopoteuthidae Berry, 1912

Veranyidae Chun, 1910: 143.

Octopodoteuthidae Berry, 1912: 645.

Octopodoteuthidae (not Berry 1912) — Naef, 1916: 15.

Diagnosis. Tentacles lacking in juvenile to adult stages (ML >60 mm); arms with biserial hooks enclosed in thick fleshy sheaths; some or all arms terminate in a single large photophore; fins rhombic, large (length 65–85% ML), broad (width 80–110% ML); buccal connectives attach ventrally to Arms IV; six weak buccal supports.

Description. Medium- to large-bodied squids (maximum observed ML 552 mm in *Octopoteuthis*, 1310* mm in *Taningia*), with gelatinous tissue overlying epidermis of mantle, head, and arms in post-larval stages. Mantle conical to weakly goblet shaped: widest anteriorly, tapering in anterior third then nearly cylindrical to posterior fin attachment before tapering along tail (extension of mantle beyond posterior fin attachment). Fins muscular; fused dorsally along midline; subterminal, continuing posteriorly along tail as narrow strip of tissue, fusing beyond posterior tip; anterior fin insertion forms distinct ‘U’-shaped notch; posterior fin insertion poorly demarcated. Arms all subequal in length; with paired low, non-trabeculate protective membranes orally; arm hook series slightly offset longitudinally relative to each other. Tentacles (ML <59 mm) simple, with proximal club demarcation a slight expansion of stalk. Clubs short with 4–6 pairs of suckers; simple, distally tapering to blunt tip; regions poorly defined with no distinction apparent between manus and dactylus; carpus comprising single pair of suckers, considerably smaller than manus suckers. Eyes with anterior sinus, strong crescent-shaped posterior muscle. Funnel pocket present, bordered by two bridles; funnel aperture directed ventrally. Photophores associated with ink sac region. Lower beak with shelf (lateral or dorsolateral protrusion of anterior lateral wall fold fusing it to the inner surface of the hood; Fig. 4). Upper beak lateral walls trapezoidal to rectangular. Radula with 7 series of teeth. Six weak buccal supports: one between Arms I, one at each of Arms II–III, one between Arms IV. Two pores present in ventral visceral mesentery. Males with terminal organ, without hectocotylus; females with paired, bilobed nidamental and oviducal glands.

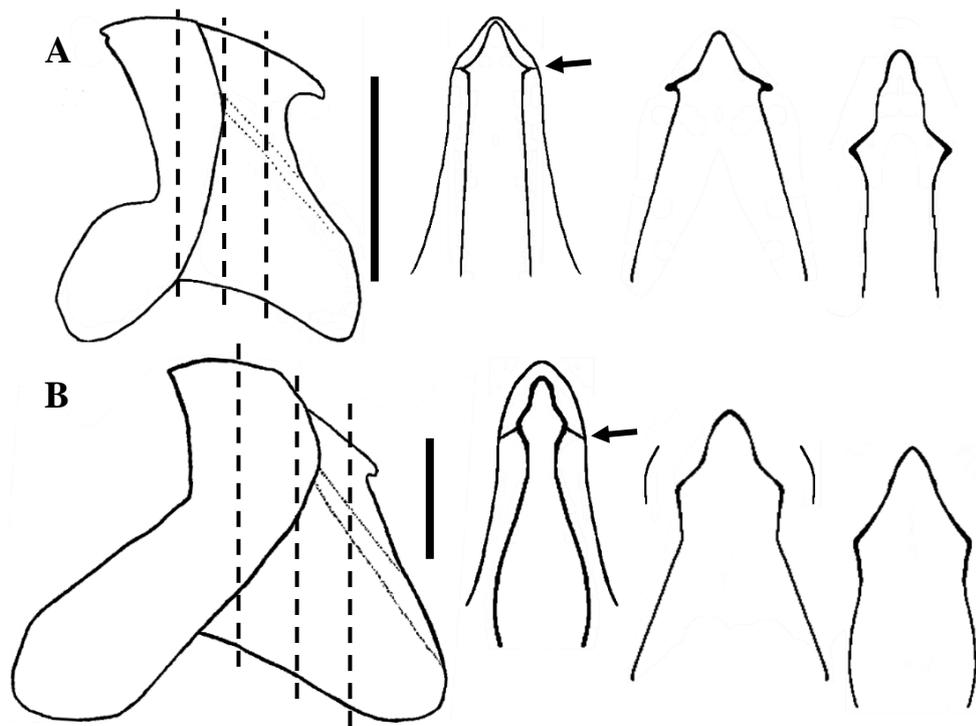


Fig. 4—Cross-sections through lower beak showing shelf (arrows) along lateral wall ridge in (A) *Octopoteuthis* and (B) *Taningia*. Scale bars = 10 mm.

Remarks. Both Berry (1912) and Naef (1916) designated the Octopo(do)teuthidae as the proper name for the family containing *O. sicula*. Berry stated that the proper spelling, Octopoteuthidae or Octopodoteuthidae, would depend on which spelling variant was accepted at the genus level. Four years later Naef listed “Octopodoteuthidae nov.” without citing Berry (1912), and despite referencing Berry (1913). As in Berry’s (1912) work, Naef used nomenclature rules to give precedent to ‘*Octopodoteuthis*’ over ‘*Veranya*’ but gave no reference to *Octopoteuthis* or the spelling variant issue. While it remains possible that Naef was unaware of Berry’s previous familial designation, it may also be that he took Berry’s ambiguity as lacking sufficient distinction for him to retain authorship. It is possible Naef was stating outright his support for Krohn’s (1845) variant, and thus derive the familial name of ‘Octopodoteuthidae’.

Despite their ephemeral nature, tentacles, both their morphology and early loss, characterise octopoteuthids. However, given the taxonomic disarray of the family, this review has prioritised differentiating adult specimens and little time was devoted to paralarval identification and the diagnostic character for this life stage, tentacles (Young & Harman 1988). A brief treatment of octopoteuthid tentacular morphology is given in the following sections: genus *Octopoteuthis* Remarks, *T. danae* post-larval description, *O. laticauda* paralarval description, and the post-larval descriptions of *O. sicula*, *O. nielsenii*, *O. deletron*, *O. sp. IO*.

5.1. *Octopoteuthis* Rüppell, 1844

Octopodoteuthis (Rüppell, 1844) — Krohn, 1845: 47–49.

Verania Krohn, 1847: 38–39. Type species *Octopoteuthis sicula* Rüppell, 1844, by monotypy.

Veranya (Krohn, 1847) — Chenu, 1859: 29.

Octopodoteuthopsis Pfeffer, 1912: 222–223. Type species *Ancistrocheirus megaptera* Verrill, 1885, by monotypy.

Type species. *Octopoteuthis sicula*, Rüppell, 1844, by monotypy.

Diagnosis. All arms terminating in a single, long, slender photophore; arm length 85–115% ML, Arms II longest; buccal connectives paired for Arms I and III, attaching both dorsally and ventrally; mantle cartilage narrow anteriorly.

Description (Figs 5, 6). Medium-sized squids (maximum observed ML 552 mm in *O.* sp. Giant Pacific nov.) separable into four species groups based on photophore pattern (see below for group descriptions). Fins rhombic, large (length 65–85% ML), broad (width 80–110% ML); anterior margins of fins slightly convex; posterior margins straight to slightly convex. Arms slender, Arms II and III generally longer than I and IV; arm hooks variably with accessory claws. Tentacles completely lost by ML 26 mm, excluding “Giant” species group (atrophying tentacles still present at ML 47 mm). Tentacle and arm suckers domed: infundibular ring aperture small, basally set relative to whole sucker creating vaulted internal cavity. Lower beak depth between jaw angle and rostral tip comprises more than half of overall depth; upper beak rostrum long. Buccal connectives formed from basal continuation of protective membranes fusing to buccal membrane. Six pores in buccal membrane. Maturing and mature females with rugose furrows in gelatinous tissue along circumference of anterior mantle, decreasing in length dorsally. Tail often curved postero-ventrally. Dorsal funnel organ cordiform, short free tip antero-medially pointed ventrally, low lateral ridges extend posteriorly from tip along middle of each lobe following outer contour; ventral components form irregular parallelogram without sculpture.

Remarks. Almost all photophores in *Octopoteuthis* are either embedded in body tissue or located along an interior surface, discernible only through dissection, particularly in large adults (Fig. 6): posterior ventral mantle photophores (PVMP) are located just

anterior to the posterior fin–mantle junction, underneath the outer gelatinous tissue layer near its junction with the muscle tissue; *recti abdominis* photophores along the dorsal surface of each muscle; lateral head photophores (LHP) along the postero-lateral head typically in close proximity to the olfactory papillae, posterior to the eye, basally attached to the cephalic cartilage, underlying outer gelatinous tissue; medial eyelid photophores (MEP) on the inner surface of the ventral eyelid, antero-medially; eyeball photophores (EP) antero-dorsally on each eyeball, at junction of iris and sclera; arm-base photophores are embedded ventrally at bases of Arms II–IV, with those of Arms III and IV greater in size than those of Arms II; and arm series photophores along the ventrum of the brachial nerves of Arms III and IV only. Generally, photophores are more visible in small or fresh specimens, where tissues are either thinner or more translucent. In species with paired PVMP, it can be necessary to straighten out the tail (*i.e.*, align it dorsally with the main longitudinal axis of the animal) to properly determine the chromatophore patterning around the photophores.

A brief opportunistic description of a tentacle club at high magnification, the first to-date, from an unexamined *Octopoteuthis* from the south Atlantic is as follows. Club with 10 intact suckers likely corresponding to 6 pairs (Fig. 5E). Carpal suckers proximal to club, on tentacle stalk; diameter ~50% basal-most intact manus sucker; dentition damaged. Manus suckers large, second pair largest, subsequent suckers gradually decreasing, diameter of distal-most ~125% that of carpal. Dentition similar across manus: infundibular ring smooth, diameter ~40% sucker diameter; papillated ring comprising singular central ring of irregular polygonal-faced pegs, intermediate ring of irregular polygonal-faced pegs singular proximally becoming doubled laterally and tripled distally, singular peripheral ring of ovoid to oblong-faced pegs; rim damaged.

The above is comparable to previous descriptions with the notable exception being a greater number of suckers: all previous reports stated a maximum of either four pairs or eight suckers (Krohn 1847; Vérany 1851; Appellöf 1889; Chun 1910; Naef 1923; Stephen 1985a, 1985b) except for Okutani & McGowan (1969), which stated that larger paralarvae of *O. deletron* have 10 club suckers. While the minuscule carpal pair may have been missed by some, Chun clearly figured them in both *Octopoteuthis* and *Taningia*, and still only reported three pairs distally. With the herein established adult species designations, future work will attempt to establish species-specific paralarval identification characters.

In trawl-caught specimens, arms are rarely intact due to the presence of multiple autotomy fracture planes along their length (Bush 2012). Specimens from stomach contents of predators, or specimens of the “Giant” species group (see Remarks, that section) more frequently retain complete arms.

Fig. 5 (following page)—*Octopoteuthis* general morphology (‡ indicates differing morphology in Giant species group, see group description). A, B) *O. rugosa*: (A) NMNZ M.091409, ♂, ML 109 mm; (B) SAM S4084, ♀, fresh ML ~200 mm; C, G) *O. deletron*: (C) unexamined MBARI specimen; (G) SBMNH 34966, holotype, ♂, ML 96 mm; D) unexamined *Octopoteuthis* sp., sex indet., ML unknown, MarEco cruise, 2009; E) *O. megaptera*, USNM 814610, ♀, ML 110 mm; F) *O. laticauda* sp. nov., USNM 729746, ♂, ML 73 mm; H) *O. fenestra* sp. nov., top (NMNZ. M.277829, paratype, ♀, ML 218 mm), *O. sp. Giant Pacific* nov., bottom (NIWA Z10746, ♀, ML 552 mm). A–C) Arm tip photophores: (A) oral view with distal suckers and protective membranes, (B) with slight bulb at tip, (C) bifurcated photophore, likely a result of regeneration (photo by K. Bolstad); D) paralarval *Octopoteuthis* tentacle club and sucker morphology (SEMs by K. Bolstad); E) *recti abdominis* muscles (*ab*) and rectum (*r*): natural state (left), right side dissected (right) revealing dorsal photophore (*ph*); F) rectum-*recti* region *in situ*; G) funnel organ; H) comparison between mated adult females of ‘Giant’ and small-bodied species. Scale bars = A, G) 2 mm; B, C, E, F) 5 mm; D) 0.25 mm (insets 50 μm).

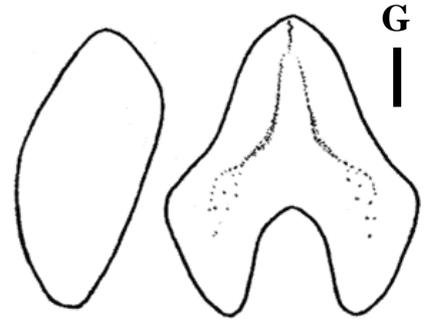
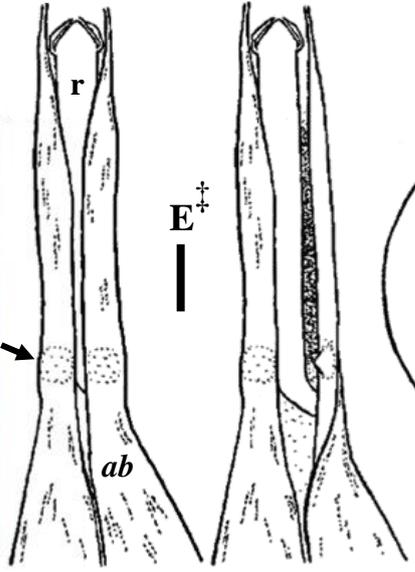
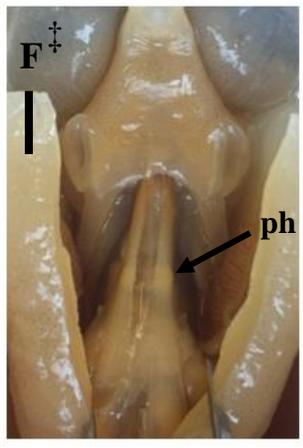
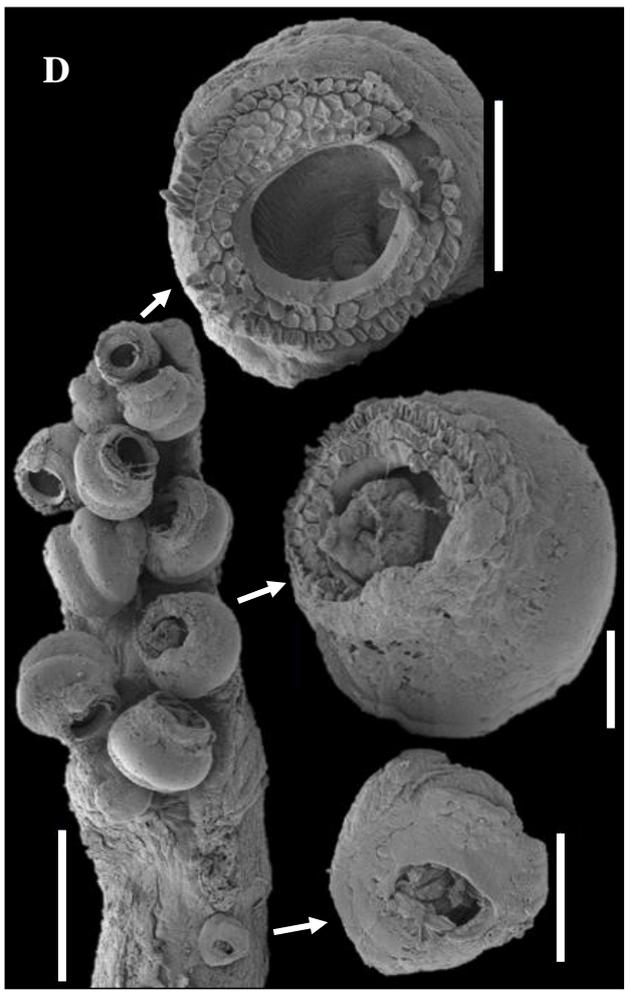


Table 4. Comparison of taxonomically significant characters among *Octopoteuthis* species.

Taxon	PVMP	Chrom. patch	LHP	<i>recti</i>	MEP	EP	Arm II conn.	Ant. fin margin Adult	Juv.	Tail length Adult	Juv.	Acc. claws	Basal hook	Known distribution
<i>sicula</i> group														
<i>sicula</i>	2	Single	2	2	0	0	Single	Ant.	Mod.	Short	Short	Var.	VVDD	Atlantic
<i>nielsenii</i>	2	Single	2	2	0	0	Single	Ant.	Post.	Short	Mod.	Low	VVDD	SE Pacific
<i>fenestra</i> sp. nov.	2	Single	2	2	0	0	Single	Ant.	Mod.	Mod.	Long	Yes	VVDD	SW Pacific
<i>megaptera</i> group														
<i>megaptera</i>	2	Paired	2	2	2	2	Single	Ant.	Mod.	Mod.	Mod.	Yes	VVDD	Atlantic
<i>rugosa</i>	2	Paired	2	2	2	2	Paired	Ant.	Mod.	Mod.	Long	Yes	VVDD	circum. S
<i>laticauda</i> sp. nov.	2	Paired	2	2	2	2	Single	Post.	Mod.	Mod.	Long	Yes	VVDD	W Pacific
sp. IO nov.	2	Paired	2	2	2	2	Single	Ant.	Post.	Long	Long	Yes	VVDD	Indian
<i>deletron</i> group														
<i>deletron</i>	1	Single	2	2	2	0	Paired	Post.	Post.	Mod.	Short	Yes	VVDD	NE Pacific
<i>leviuncus</i> sp. nov.	1	Single	2	2	2	0	Paired	Ant.	Mod.	Mod.	Mod.	No	VVDD	Atlantic
“Giant” group														
Pacific nov.	0	-	0	0	0	0	Single	Ant.	Mod.	Mod.	Mod.	Yes	VVDD	Pacific
Atlantic nov.	0	-	0	0	0	0	Single	Ant.	Ant.	Mod.	Long	Yes	VVDV	Atlantic

Juv. = juvenile, Ant. = anteriorly set, Post. = posteriorly set, Mod. = moderate, Var. = variable, Low = absent to short, circum. = circumglobal

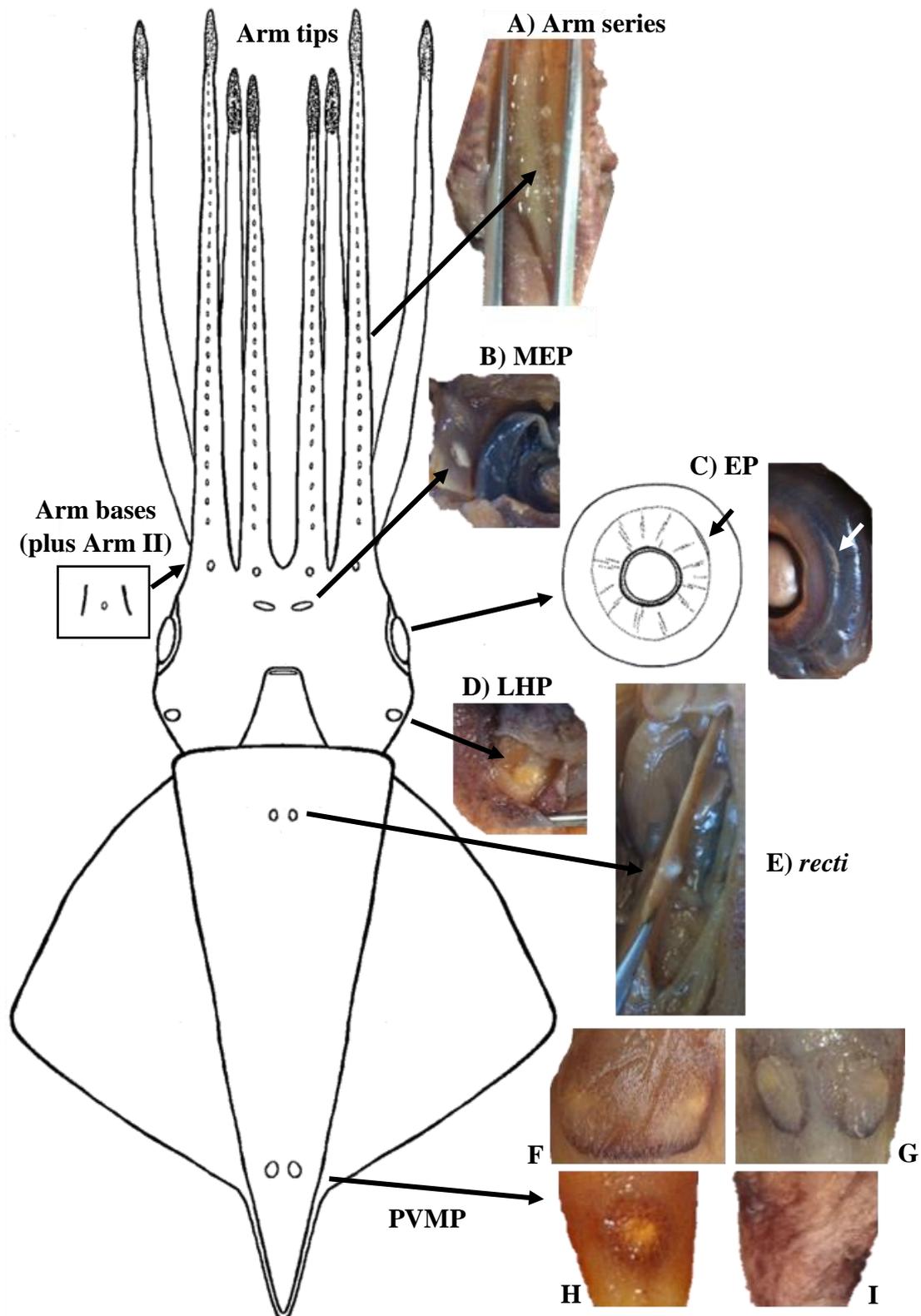


Fig. 6—Photophores in *Octopoteuthis* (terminology adapted from Stephen [1985a]). Arm tips (see Figs 5A–C); A) Arms III, IV series (*O. rugosa*, NIWA 71845, ♀, ML 175 mm); Arm bases II–IV; B) medial eyelid (MEP; *O. megaptera*, USNM 885283, ♀, ML 111 mm); C) eyeball (EP; *O. rugosa*, ZMH 11232, ♂, ML 130 mm); D) lateral head (LHP; *O. fenestra* sp. nov., NIWA 75728, ♂, ML 234 mm); E) dorsally on *recti abdominis* muscles (USNM 885283); posterior ventral mantle (PVMP): F) *O. sicula*, USNM 885298, ♀, ML 75 mm; G) *O. rugosa*, NMNZ M.091633, ♀, ML 109 mm; H) *O. deletron*, SBMNH 265402, ♀, ML 50 mm; I) *O. sp. Giant Pacific* nov., USNM 1283041, ♀, ML 148 mm).

5.1.1. *sicula* Species Group (Fig. 7). With two PVMP overlain together by single large chromatophore patch with distinctly pigmented posterior and lateral margins, often reduced to single ring due to epidermal abrasion; one photophore dorsally on each *recti abdominis* muscle; one LHP on each side of head; single arm-base photophore on Arms II–IV; photophore series along ventral brachial nerve on Arms III and IV only. Arm II buccal connective dorsal. Arms IV with thin densely set transverse pigment bands aborally. Arm hooks without aboral hood on main cusp; basal-most hook pattern VVDD. 3–12 pairs of suckers present at tip of each arm.

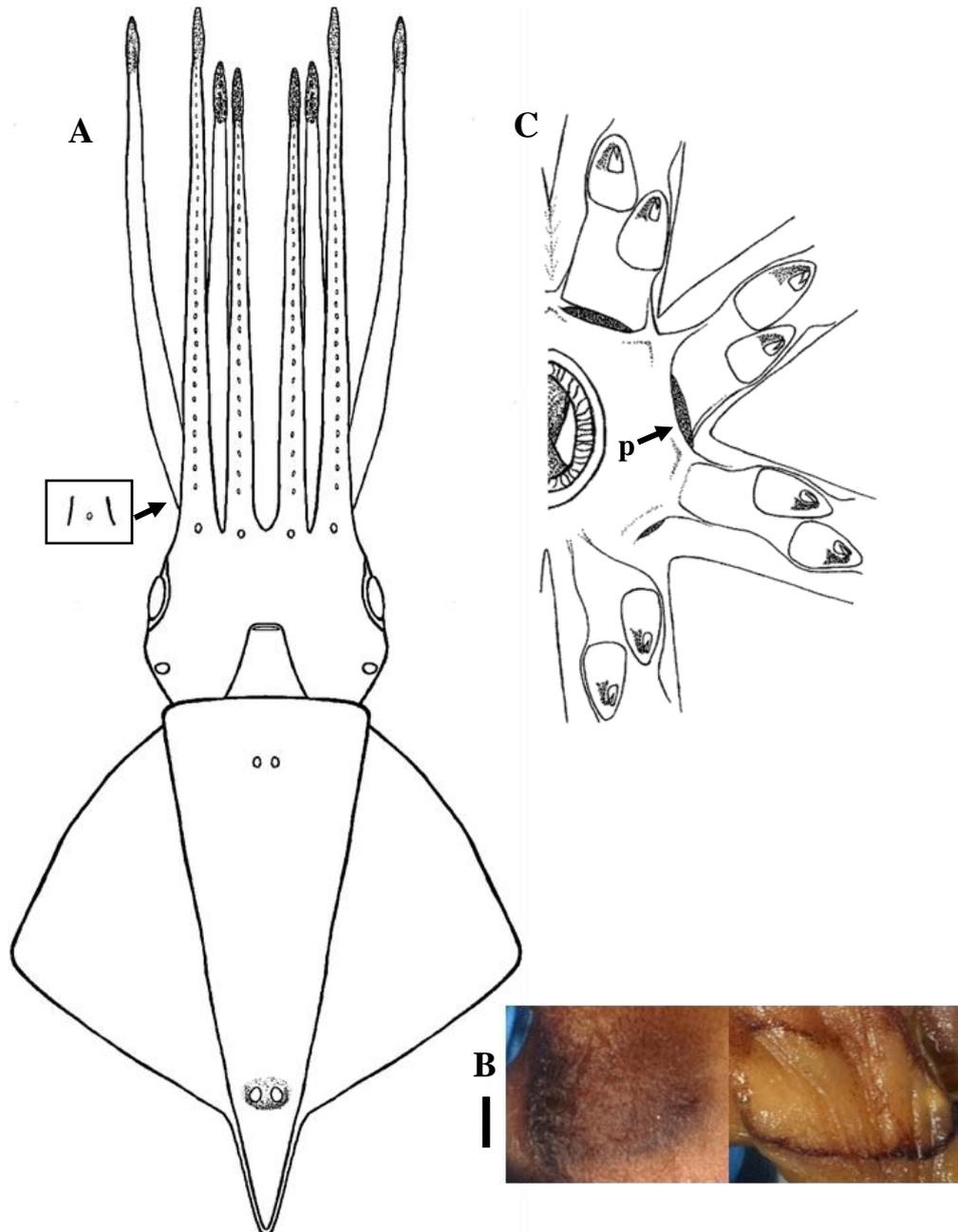


Fig. 7—*sicula* species group general morphology. A) Ventral photophore pattern; B) single chromatophore patch in *O. fenestra* sp. nov.: natural condition (left; NMNZ M.277829, paratype, ♀, ML 218 mm) and abraded, revealing two PVMP (right; NMNZ M.091416, ♂, ML 139 mm); C) oral surface with single dorsal buccal connective Arm II and large pore (p) between Arms II and III. Scale bars = 5 mm.

5.1.1.1. *Octopoteuthis sicula* Rüppell, 1844 (Tables 5–8, Figs 6F, 8–15)

Octopoteuthis sicula Rüppell, 1844: 129–135; Ficalbi (1899): 83–84; Villari & Ammendolia (2009): 9–11, Fig. 1; Cuccu *et al.* (2013): 2–4, Fig. 1, 2, Table 1; Jereb *et al.* (2016): 8–13, Figs 4–6, Table 1, 2.

Octopodoteuthis sicula Krohn, 1845: 47–49, Figs A–F.

Verania sicula Krohn, 1847: 38–39, Pl. 2 Figs D, E; Verany (1851): 86–88, Pl. 28.

Octopodoteuthis danae Joubin, 1931: 185–187, Figs 17, 18; Lindgren (2010): EU735402, EU735266.

Octopoteuthis megaptera (not Verrill, 1885) — Lindgren (2010): EU735358, EU735258.

Not *Octopoteuthis sicula* Percy (1965) (= *O. deletron*); Toll (1982) (= *O. leviuncus* sp. nov.).

Type material (2 specimens). **NHMUK 1845.9.8.13**, Holotype, sex indet., ML 19 mm, Sicily, coll. Rüppell; **ZMUC CEP-89**, holotype (*Octopodoteuthis danae*), ♂, ML 28.3 mm, 35°15'N, 68°20'W, Atlantic Ocean, 150 m, 14/05/1922, 1930 hr, *Dana*, stn 1341V, S 200.

Additional material examined (171 specimens). **ZMH 11195**, sex indet., ML 80 mm, 57°44.4'N, 18°08'W, West of British Isl., 400 m, 29/06/1986, RV *Walther Herwig*, stn 366, cruise #76-2; **ZMH 11217**, ♂, ♀, head only, ML 124*, 111* mm, HL 40 mm, 57°39.2'N, 18°06.3'W, West of British Isl., 800 m, 30/06/1986, RV *Walther Herwig*, stn 384, cruise #76-2; **ZMH 11220**, ♀, ML 70* mm, 57°39.1'N, 18°04.8'W, West of British Isl., 600 m, 29/06/1986, RV *Walther Herwig*, stn 364, cruise #76-2; **ZMH 11205**, 2 sex indet., ML 64*, 63 mm, 57°36.1'N, 18°02.4'W, West of British Isl., 400 m, 28/06/1986, RV *Walther Herwig*, stn 356, cruise #76-2; **ZMH 11213**, 2 ♀, ML 98*, 95 mm, 57°34.8'N, 18°10.1'W, West of British Isl., 800 m, 28/06/1986, RV *Walther Herwig*, stn 363, cruise #76-2; **ZMH 11184**, sex indet., ML 82 mm, 54°47.4'N, 18°09.9'W, West of British Isl., 800 m, 02/07/1986, RV *Walther Herwig*, stn 405, cruise #76-2; **ZMH 11223**, 2 ♂, ML 93, 92 mm, 54°44.8'N, 18°09.8'W, West of British Isl., 800 m, 07/07/1986, RV *Walther Herwig*, stn 451, cruise #76-2; **ZMH 11224**, ♀, ML 128 mm, 54°43.7'N, 18°21.7'W, West of British Isl., 800 m, 06/07/1986, RV *Walther Herwig*, stn 444, cruise #76-2; **ZMH 11211**, ♂, ML 94 mm, 54°39.8'N, 18°15.6'W, West of British Isl., 400 m, 05/07/1986, RV *Walther Herwig*, stn 428, cruise #76-2; **ZMH 11200**, ♂, ML 87 mm, 54°35.6'N, 18°27.9'W, West of British Isl., 600 m, 05/07/1986, RV *Walther*

Herwig, stn 426, cruise #76-2; **ZMH 11174**, ♂, ML 81 mm, 54°33.3'N, 18°16.9'W, West of British Isl., 400 m, 03/07/1986, RV *Walther Herwig*, stn 408, cruise #76-2; **ZMH 11225**, ♀, ♂, head only, ML 100, 89 mm, HL 33 mm, 54°33.3'N, 18°16.9'W, West of British Isl., 400 m, 03/07/1986, RV *Walther Herwig*, stn 408, cruise #76-2; **ZMH 11219**, 2 ♂, ML 107, 95* mm, 54°31'N, 18°26'W, West of British Isl., 800 m, 04/07/1986, RV *Walther Herwig*, stn 425, cruise #76-2; **ZMH 11214**, 2 heads only, HL 45*, 40* mm, 53°03.5'N, 16°36.3'W, West of British Isl., 1800 m, 09/07/1986, RV *Walther Herwig*, stn 463, cruise #76-2; **ZMH 11218**, ♀, ML 180 mm, 52°56.3'N, 16°18.4'W, West of British Isl., 2000–2500 m, 09/07/1986, RV *Walther Herwig*, stn 464, cruise #76-2; **ZMH 11233**, ♀, ML 177 mm, 52°35'N, 22°20'W, Europe, 1250 m, 24/09/1973, RV *Walther Herwig*, stn 700, cruise #6B, coll. Stehmann; **USNM 1283031**, ♀, ML 83 mm, 52°N, 43°W, 160–868 m, 19/06/2009, 1942 GMT, RV *Henry B. Bigelow*, 7, net 4, cruise 2009-02, Norwegian micronekton trawl; **ZMH 11222**, 2 ♀, ML 91, 90* mm, 52°00'N, 16°00'W, West of British Isl., 2000–2500 m, 00/06/1986, RV *Walther Herwig*, no stn, cruise #76-2; **USNM 1283032**, ♂, ML 122 mm, 51°19.2'N, 28°52.2'W, 596–1132 m, 26/06/2009, 0630 GMT, RV *Henry B. Bigelow*, 21, net 4, 2009-02, Norwegian micronekton trawl; **MCZ 370405**, ♂, ML 42 mm, 50°40.8'N, 27°16.75'W, 1280–1828 m, 28/08/1928, 1200–1300, RV *Atlantis*, stn 141, vertical; **MCZ 370406**, ♂, ML 122 mm, 50°00'N, 35°20'W, 914 m, 09/02/1928, 1600–1800, RV *Atlantis*, stn 143; **ZMH 11244**, ♂, sex indet., ML 135*, 115* mm, 49°56.4'N, 16°28.7'W, Europe, 950 m, 19/06/1982, RV *Walther Herwig*, stn 402, cruise #52B; **ZMH 11181**, sex indet., ML 31 mm, 49°50.1'N, 13°42.4'W, Europe, 2700 m, 20/06/1982, RV *Walther Herwig*, stn 404, cruise #52B; **ZMH 11191**, sex indet., ML 145* mm, 49°50.1'N, 013°42.4'W, Europe, 2700 m, 20/06/1982, RV *Walther Herwig*, stn 404, cruise #52B; **ZMH 11161**, ♀, ML 151 mm, 49°49.6'N, 26°28.3'W, 3200 m, 16/06/1982, RV *Walther Herwig*, stn 391, cruise #52B; **ZMH 11203**, sex indet., ML 45 mm, 49°49.5'N, 016°57.6'W, 480 m, 19/06/1982, RV *Walther Herwig*, stn 400, cruise #52B; **ZMH 11245**, ♀, ML 109 mm, 49°49.5'N, 16°57.6'W, Europe, 480 m, 19/06/1982, RV *Walther Herwig*, stn 400, cruise #52B; **ZMH 35998**, 2 ♀, sex indet., ♂, ML 91, 77*, 67, 64 mm, 49°48.4'N, 26°32.8'W, Europe, 500 m, 16/06/1982, RV *Walther Herwig*, stn 390, cruise #52B; **ZMH 11235**, ♀, ML 142 mm, 49°48'N, 25°54.8'W, Europe, 1000 m, 16/06/1982, RV *Walther Herwig*, stn 392, cruise #52B; **ZMH 11464**, 2 ♀, 4 ♂, ML 166, 118*, 145, 136, 134, 120* mm, 49°48'N, 25°54.8'W, Europe, 1000 m, 16/06/1982, RV *Walther Herwig*, stn 392, cruise #52B; **ZMH 11159**, 3 ♀, ML 176, 164, 162 mm, 49°47.90'N, 28°46.8'W, 3200 m, 15/06/1982, RV *Walther*

Herwig, stn 387, cruise #52B; **ZMH 11241**, ♂, ML 30 mm, 49°47.2'N, 13°52.3'W, Europe, 500 m, 20/06/1982, RV *Walther Herwig*, stn 403, cruise #52B; **ZMH 11178**, 3 sex indet., 2 ♀, ML 31, 31, 22*, 28, 28 mm, 49°47'N, 23°29.9'W, Europe, 460 m, 17/06/1982, RV *Walther Herwig*, stn 393, cruise #52B; **ZMH 11165**, 4 ♀, 3 ♂, 2 heads only, ML 201, 189, 182, 140*, 147, 132*, 118* mm, HL 46, 38* mm, 48°35.3'N, 27°38'W, 1000 m, 14/06/1982, RV *Walther Herwig*, stn 385, cruise #52B; **ZMH 11202**, ♂, ML 33* mm, 48°35.3'N, 027°38'W, 1000 m, 14/06/1982, RV *Walther Herwig*, stn 385, cruise #52B; **ZMH 26070**, 4 ♀, sex indet., ML 206*, 196, 188, 179*, 126* mm, 48°35.3'N, 027°38'W, Europe, 1000 m, 14/06/1982, RV *Walther Herwig*, stn 385, cruise #52B; **ZMH 11182**, ♂, ML 38 mm, 47°25'N, 27°19.8'W, Europe, 250 m, 13/06/1982, RV *Walther Herwig*, stn 381, cruise #52B; **USNM 1283028**, ♂, ML 171 mm, 47°18'N, 16°57'W, 0–1000 m, 26/09/1973, RV *Walther Herwig*, 710/73, 1600 mesh Engel trawl; **MCZ 277831**, sex indet., ♂, ML 44, 39 mm, 47°11'N, 42°11'W, (0–)30–35(-0) m, 12/09/1964, (1915–)1930–2315(-2325) hr, RV *Atlantis II*, stn 1030, cruise 13, 6.1–15.6°C, 10' IKMT, coll. R.H. Backus; **ZMH 11237**, ♀, ML 137* mm, 47°02.7'N, 27°19.9'W, Europe, 2200 m, 12/06/1982, RV *Walther Herwig*, stn 380, cruise #52B; **ZMH 11234**, sex indet., ML 132* mm, 46°29.4'N, 27°14.3'W, Europe, 250 m, 12/06/1982, RV *Walther Herwig*, stn 378, cruise #52B; **MCZ 278198**, 2 ♂, ML 42.5, 39.5 mm, 45°40'N, 43°14'W, 0–290 m, 12/09/1964, 0145–0540, stn 1028, 5.0–8.9°C, 10' IKMT, coll. R.H. Backus; **ZMH 11228**, ♂, ML 143 mm, 45°40'N, 027°48.2'W, 3200 m, 11/06/1982, RV *Walther Herwig*, stn 377, cruise #52B; **ZMH 11176**, 3 ♀, ML 57, 36, 35 mm, 45°23.2'N, 27°48.5'W, Europe, 900 m, 11/06/1982, RV *Walther Herwig*, stn 375, cruise #52B; **ZMH 11179**, 2 ♂, 4 ♀, ML 43, 37, 41, 38, 34, 33 mm, 45°23.2'N, 27°48.5'W, Europe, 900 m, 11/06/1982, RV *Walther Herwig*, stn 375, cruise #52B; **USNM 817938**, ♂, ML 88 mm, 44°55.8'N, 21°57'W, 03/05/1979, RV *Anton Dohrn*, stn 373–79, 1600 mesh Engel trawl; **USNM 817940**, ♀, ML 82 mm, 44°55.2'N, 13°27'W, 05/05/1979, RV *Anton Dohrn*, stn 391–79, 1600 mesh Engel trawl; **ZMH 11236**, ♀, ML 135* mm, 44°15.1'N, 19°44'W, Europe, 3200 m, 07/06/1982, RV *Walther Herwig*, stn 343, cruise #52B; **ZMH 11229**, ♀, ML 179* mm, 44°12'N, 020°04.7'W, 1100 m, 07/06/1982, RV *Walther Herwig*, stn 344, cruise #52B; **ZMH 11231**, ♀, ♂, ML 173*, 135* mm, 44°08.5'N, 20°14'W, Europe, 800 m, 07/06/1982, RV *Walther Herwig*, stn 345, cruise #52B; **ZMH 11238**, ♀, ML 77* mm, 43°41.8'N, 28°26.5'W, Europe, 1550 m, 10/06/1982, RV *Walther Herwig*, stn 370, cruise #52B; **ZMH 11246**, ♂, ML 144* mm, 43°21.7'N, 25°58.6'W, Europe, 1230 m, 09/06/1982, RV *Walther Herwig*, stn 359, cruise #52B; **USNM 1283029**, sex indet., ML 38 mm,

42°09.48'N, 49°18.48'W, 31/07/1970, 2-08-C-D, JOAST cruise, trawl, coll. USA Navy; **ZMH 11192**, ♂, ML 170 mm, 41°03'N, 011°09'W, Portugal, 140–160 m, 16/01/1968, RV *Walther Herwig I*, stn 3, cruise #23, coll. Schulz; **NHMUK 20160091**, 2 ♂, ML 60, 51 mm, 40°2.5'N, 19°57.5'W, 0–175 m, 12/05/1961, stn 4769, *Discovery Expedition*, BCMT; **USNM 1283039**, ♂, ML 88 mm, 39°58.2'N, 67°19.8'W, USA, max. depth ~1700 m, 04/06/2004, 1400 GMT, RV *Delaware II*, 5, cruise 409, IYGPT, coll. M. Vecchione; **USNM 1080229**, ♂, sex indet., ML 44, 26 mm, 39°57'N, 67°30'W, Bear Seamount, Massachusetts, USA, 2023–2217 m, 27/07/2002, RV *Delaware II*, 38, Bear Seamount Expedition, IYGPT; **USNM 1283040**, sex indet., ML 43 mm, 39°55.8'N, 67°24'W, USA, max. depth ~700 m, 04/06/2004, 1908 GMT, RV *Delaware II*, 6, cruise 409, IYGPT, coll. M. Vecchione; **USNM 1192570**, ♀, head only, ML 204 mm, AL 133 mm, 39°55.69'N, 67°25.01'W, Bear Seamount, over seamount, USA, 1052 m, 05/09/2012, 0445–0611, FSV *Pisces*, stn 27, Deepwater Biodiversity Cruise - Bear Seamount 2012, PC201205, MWT with 3rd wire, coll. M. Vecchione & S. Bush; **USNM 1188463**, ♀, ML 92 mm, 39°55.30'N, 67°15.15'W, Bear Seamount, east of seamount, USA, 688 m, 31/08/2012, 0002–0032, FSV *Pisces*, stn 4, Deepwater Biodiversity Cruise - Bear Seamount 2012, PC201205, MWT, coll. M. Vecchione & S. Bush; **USNM 1188464**, ♂, ML 139* mm, 39°55.30'N, 67°15.15'W, Bear Seamount, east of seamount, USA, 688 m, 31/08/2012, 0002–0032, FSV *Pisces*, stn 4, Deepwater Biodiversity Cruise - Bear Seamount 2012, PC201205, MWT, coll. M. Vecchione & S. Bush; **USNM 1192511**, ♂, sex indet., ML 124*, 86* mm, 39°47.12'N, 67°27.79'W, Bear Seamount, south of seamount, USA, 1520 m, 31/08/2012, 1544–1645, FSV *Pisces*, stn 7, Deepwater Biodiversity Cruise - Bear Seamount 2012, PC201205, MWT, coll. M. Vecchione & S. Bush; **MCZ 370409**, ♂, ML 100 mm, 39°26'N, 71°0'W, 0-(713)-0 m, 13/10/1962, 1020–1505, stn 913, 64' GMT, coll. R.H. Backus; **USNM 1100393**, ♂, ML 48 mm, 39°26'N, 70°11.4'W, Bear Seamount, Massachusetts, USA, 29/11/2000, RV *Delaware II*, stn 3, Bear Seamount Expedition 11; **MCZ 370408**, sex indet., ML 19* mm, 39°24'N, 70°33'W, 0–549 m, 20/09/1962, 1800–2220, stn 872, 10' IKMT, coll. R.H. Backus; **NHMUK 20160090**, ♀, ML 56 mm, 38°54'N, 21°55.5'W, 7.5–100 m, 13/10/1966, stn 6103, *Discovery Expedition*, WB; **USNM 730364**, 2 sex indet., ML 35, 34 mm, 38°40.8'N, 71°28.8'W, off east coast, USA, 0–550 m, 21/05/1974, RV *Albatross IV*, 74-5-10N, 3 m IKMWT; **NHMUK 20160097**, ♂, ML 48 mm, 38°38.1'N, 28°20.2'W, 105–300 m, 29/10/1970, stn 7447, *Discovery Expedition*, RMT25; **NHMUK 20160092**, ♂, sex indet., ML 54, 49 mm, 37°35'N, 25°22'W, 0–400 m, 17/05/1966, stn 6117, *Discovery Expedition*, EMT; **MCZ 370407**, sex indet., ML 28.5

mm, 37°10'N, 56°30'W, Sargasso Sea, 17-18/08/1931, RV *Atlantis*, stn 1043, haul C3; **NHMUK 20160100**, ♀, sex indet., ML 71*, 26* mm, 32°34.5'N, 17°17.5'W, 0–245 m, 09-10/04/1962, stn 4843, *Discovery Expedition*, BCMT; **USNM 728875**, 2 ♂, ML 176, 172 mm, 32°09'N, 64°10.8'W, Ocean Acre Area, Bermuda, 0–750 m, 24/08/1971, RV *Delaware II*, 80-N, Ocean Acre Project 12, 1400 Engel trawl, coll. USA Navy; **NHMUK 20160094**, ♀, ML 77 mm, 28°02.4'N, 14°09'W, 0–140 m, 11/06/1966, stn 6174, *Discovery Expedition*, EMT; **NHMUK 20160089**, ♂, ML 62 mm, 27°51'N, 14°17'W, 0–420 m, 06/08/1967, stn 6413, *Discovery Expedition*, EMT; **NHMUK 20160099**, ♂, sex indet., ML 65, 62 mm, 27°50'N, 13°59'W, 0–180 m, 04/08/1967, stn 6408, *Discovery Expedition*, EMT; **Escáñez 12_I_N**, ♀, ML 220 mm, 25°14.64'N, 17°13.68'W, 0–800 m, bottom depth 3093 m, 27/04/2015, 2109 hr, RV *Hesperides*, PEL12, 12_I_N, IKMWT; **Escáñez 11_5_D**, sex indet., ML 9.1 mm, 21°25.38'N, 18°25.68'W, 0–100 m, bottom depth 3095 m, 25/04/2015, 1354 hr, RV *Hesperides*, PEL11, 11_5_D, IKMWT; **Escáñez 11_4_D**, sex indet., ML 25.2 mm, 21°25.08'N, 18°26.1'W, 100–200 m, bottom depth 3095 m, 25/04/2015, 1341 hr, RV *Hesperides*, PEL11, 11_4_D, IKMWT; **Escáñez 11_4_N**, sex indet., est. ML 7 mm, 21°21.6'N, 18°32.1'W, 50–100 m, bottom depth 2989 m, 25/04/2015, 0448 hr, RV *Hesperides*, PEL11, 11_4_N, IKMWT; **USNM 885293**, ♀, ML 153* mm, 20°27'N, 21°58.2'W, 1900–2100 m, 18/04/1971, RV *Walther Herwig*, 502-71, 1600 mesh Engel trawl; **ZMH 11189**, ♀, 2 ♂, ML 138, 122, 118 mm, 20°14'N, 021°35'00W, Africa, 40–60 m, 28/01/1968, RV *Walther Herwig I*, stn 10, cruise #23, coll. Schulz; **USNM 814606**, ♀, ML 89 mm, 20°07.2'N, 18°15'W, Cape Verde, 90–200 m, 12/11/1970, RV *Atlantis II*, RHB-2045, 3 m IKMWT, coll. R.H. Backus; **USNM 1283038**, 3 ♀, 4 ♂, ML 152, 104, 45, 149, 145, 133, 131 mm, 14°10.8'N, 18°28.2'W, Senegal, 2000 m, 18/07/1974, RV *Anton Dohrn*, AD 11/74, Gate Expedition; **USNM 885292**, ♀, sex indet., ML 162, 144 mm, 14°04.8'N, 23°12'W, 1900 m, 16/04/1971, RV *Walther Herwig*, 494-71, 1600 mesh Engel trawl; **NHMUK 20160086**, 2 ♀, ML 108, 61 mm, 13°25'N, 18°22'W, 0–900 m, 28/10/1925, *Discovery Expedition*; **ZMH 11168**, ♂, ML 114 mm, 12°16'N, 23°05'W, Africa, 180–200 m, 30/01/1968, RV *Walther Herwig I*, stn 12, cruise #23, coll. Schulz; **USNM 816676**, ♀, ♂, ML 141*, 95* mm, 10°52.2'N, 22°09'W, 592–608 m, 15/04/1971, RV *Walther Herwig*, 490-II-71, 1600 mesh Engel trawl; **USNM 816679**, ♀, ML 126 mm, 10°52.2'N, 22°09'W, 592–608 m, 15/04/1971, RV *Walther Herwig*, 490-II-71, 1600 mesh Engel trawl; **USNM 885073**, 2 ♀, sex indet., ML 75, 49, 22 mm, 10°49.8'N, 22°07.8'W, 100–111 m, 15/04/1971, RV *Walther Herwig*, 490-I-71, 1600 mesh Engel trawl; **NHMUK 20160220**, ♀, ML 51 mm, 10°47.6'N, 20°20.6'W,

50–100 m, 11/03/1972, stn 7824#53, *Discovery* Expedition, RMT8; **ZMH 11221**, sex indet., ML 23 mm, 10°46'N, 23°54'W, 200–300 m, 16/05/1966, RV *Walther Herwig*, stn 182, cruise #15, coll. Schulz; **NHMUK 20160084**, ♀, ML 93 mm, 15°55'S, 10°35'E, 600-700(-0) m, 26/07/1927, stn 269, *Discovery* Expedition, TYF; **NHMUK 20160085**, ♂, ML 93 mm, 15°55'S, 10°35'E, 600-700(-0) m, 26/07/1927, stn 269, *Discovery* Expedition, TYF; **ZMH 33989**, ♂, ML 62 mm, 17°36'S, 28°53'W, Brazil, 160–660 m, 23/05/1966, RV *Walther Herwig*, stn 190, cruise #15, coll. Schulz; **NSMT Unaccessioned**, ♂, ML 79 mm, 22°59'S, 13°59'E, Namibia, 324–335 m, 31/01/1978, V-89; **NIWA 71843**, 2 ♀, ♂, ML 196, 175, 167 mm, 24°41.06'S, 13°19.06'E, Namibia, 836 m, 24/07/1997, stn Z8930; **USNM 1221584**, ♂, ML 154* mm, 39°45'S, 17°40.2'W, 2000 m, 13/03/1971, RV *Walther Herwig*, 384-71, 1600 mesh Engel trawl; **USNM 885298**, 2 ♀, ML 75*, 42 mm, 40°01.8'S, 07°28.2'W, 300–320 m, 18/03/1971, RV *Walther Herwig*, 402-II-71, 1600 mesh Engel trawl; **USNM 816677**, ♀, ML 168 mm, 40°18'S, 35°07.2'W, Argentina, 2000 m, 09/03/1971, RV *Walther Herwig*, 367-71, 1600 mesh Engel trawl.

Unlocalised material examined (24 specimens). **NHMUK 1909/11.27.1**, ♀, ML 95 mm, off W. of Ireland, 27/06/1909, Holt; **NHMUK 1912.3.19.2**, ♀, ML 44 mm, W of Ireland, 19/03/1912, Holt; **NHMUK 20100488**, ♀, ML 70 mm, NE Atlantic, off NW Africa, 04/02/1968, *Discovery* Expedition; **NHMUK 20160096**, ♀, ML 57 mm, NE Atlantic, off NW Africa, 0–170 m, 08/02/1968, stn 6650, *Discovery* Expedition, TMT90; **NHMUK 20160102**, sex indet., ML 43 mm, NE Atlantic, off NW Africa, 0–170 m, 08/02/1968, stn 6650, *Discovery* Expedition, TMT90; **ZMH 11160**, ♀, ML 168* mm, NE Atlantic, 1982, RV *Walther Herwig*, stn 38x, cruise #52B; **ZMH 11162**, ♀, 4 ♂, ML 167*, 98*, 91*, 79*, 72* mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11163**, ♀, sex indet., 3 ♂, ML 171, 147, 127*, 112*, 55* mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11183**, ♀, ML 25 mm, NE Atlantic, 17/06/1982, RV *Walther Herwig*, stn 395, cruise #52B; **ZMH 11212**, ♂, ML 69 mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11227**, 2 ♂, ML 161, 142 mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11230**, ♀, ML 190 mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11242**, ♀, ML 173* mm, NE Atlantic, 00/06/1982, RV *Walther Herwig*, no stn, cruise #52B; **ZMH 11186**, ♂, ML 111* mm, Patagonia, Argentina, 1966, no stn, cruise #15, coll. Schulz; **ZMH aus 32**, ♂, ML 167 mm, no stn.

Additional genetic samples (7 samples). **DE0304/6**, sex unknown, ML unknown, 39°58.9'N, 67°32.3'W, 1415 m, bottom depth 2252 m, 15/05/2003, 0521–0621, RV *Delaware II*, stn 6, 3.862°C, salinity 34.943‰, midwater IYGPT, coll. M. Vecchione; **DE0506/5**, sex unknown, ML unknown, 39°50.89'N, 67°26.44'W, bottom depth 2114–2257 m, 13/04/2005, 1132–1232, RV *Delaware II*, stn 5, midwater IYGPT, coll. M. Vecchione; **DE0506/15**, sex unknown, ML unknown, 39°05.76'N, 67°18.43'W, Bear Seamount slope, 856–1360 m, bottom depth 2712–2970 m, 17/04/2005, 1853–1953, RV *Delaware II*, stn 15, 3.712°C, salinity 36.061‰, midwater IYGPT, coll. M. Vecchione; **DE0304/9**, sex unknown, ML unknown, 39°49.4'N, 67°24'W, 1475 m, bottom depth 2767 m, 16/05/2003, 0547–0647, RV *Delaware II*, stn 9, 3.689°C, salinity 34.932‰, midwater IYGPT, coll. A. Lindgren; **DE0304/3**, 2 sex unknown, 2 ML unknown, 39°49.22'N, 67°27'W, 1583 m, 14/05/2003, 0814–0914, RV *Delaware II*, stn 3, 3.591°C, salinity 34.911‰, midwater IYGPT, coll. M. Vecchione; **DE0611/8 (DMNH 234371)**, sex unknown, ML unknown, 39°52.76'N, 67°32.4'W, bottom depth 2604 m, 17/06/2006, 0220–0544, RV *Delaware II*, stn 8, 3.535°C, salinity 37.618‰, midwater IYGPT, coll. A. Lindgren.

Distribution (Fig. 8A). Temperate and tropical Atlantic, 50°N–40°S, including Mediterranean; presence in Gulf of Mexico, Caribbean Sea uncertain; 0–2200 m, possibly deeper.

Diagnosis. Accessory claws short, broad points; inner angle of main cusp of arm hooks acute in distal 70% of pairs; Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III; anterior fin margin at ~5–7% ML in adults, 8–16% ML in juveniles.

Description (ML 61–206* mm, Figs 6F, 8B–15). Mantle conical to weakly goblet shaped; widest at anterior margin, width 27–35–43 % ML; weakly muscled; tail short, length 12–20–25% ML; dorsal anterior margin smoothly rounded, ventral margin with slight indentation between mantle components of locking apparatus. Fins long (length 70–75–80% ML), very broad (width 89–100–113% ML), greatest width attained at their midpoint, ~50% ML; anterior margin at 4–6–10% ML; width of fin continuation along tail ~2% ML. Paired PVMPs circular, diameter ~1.6% ML; set close together (distance between photophores ~7% ML), medially along posterior ventral mantle. Anterior fin insertion tapering posteriorly to blunt rounded point, depth 13–17–20% ML, width 8–

Table 5. Measurements (mm) of adult and subadult *Octopoteuthis sicula*. Mean indices were calculated from specimens ML >57 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side). For specimens ML <57 mm (juveniles and post-larvae), see Table 6.

Specimen ID	NHMUK	USNM	USNM	USNM	USNM	ZMH	ZMH	ZMH	USNM	USNM	ZMH	ZMH	USNM	USNM	ZMH	ZMH	Mean index
	1845.9.8.13	1192570	728875	1283028	816677	11224	11168	814606	1283031	11212							
Type status	Holotype	None	None	None	None	None	None	None	None	None	None	None	None	None	None	None	
Sex	NM	♀	♂	♂	♀	♀	♂	♀	♀	♂	♂	♀	♀	♀	♂	♂	
DML	19	204	172	171	168	128	114	89	83	69							
MW	8.4	81	67	73	50	43	30	29	29	27							35
FL	14.6	154	137	130	127	89	90	65	61	32							72
FW	24.3	191	183	173	150	114	122	85	88	78							100
HL	7.3	51	49	47	49	27	33	23	26	26							28
HW	7.6	55	56	62*	49	37	30	29	27	15*							30
Side	L	L	R	L	R	R	R	L	R	L							
AL I	11.5	78*	48*	44*	94*	18*	23*	21*	32*	10*							
AL II	16*	154*	95*	67*	106*	52*	47*	30*	47*	77							
AL III	15.7*	104*	45*	80*	94*	47*	22*	29*	58 ^r	54*							
AL IV	9.6	102*	81*	65*	92*	64*	39*	25*	39*	50*							
AH	NM,NM									*							
AS	NM, NM									4							

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

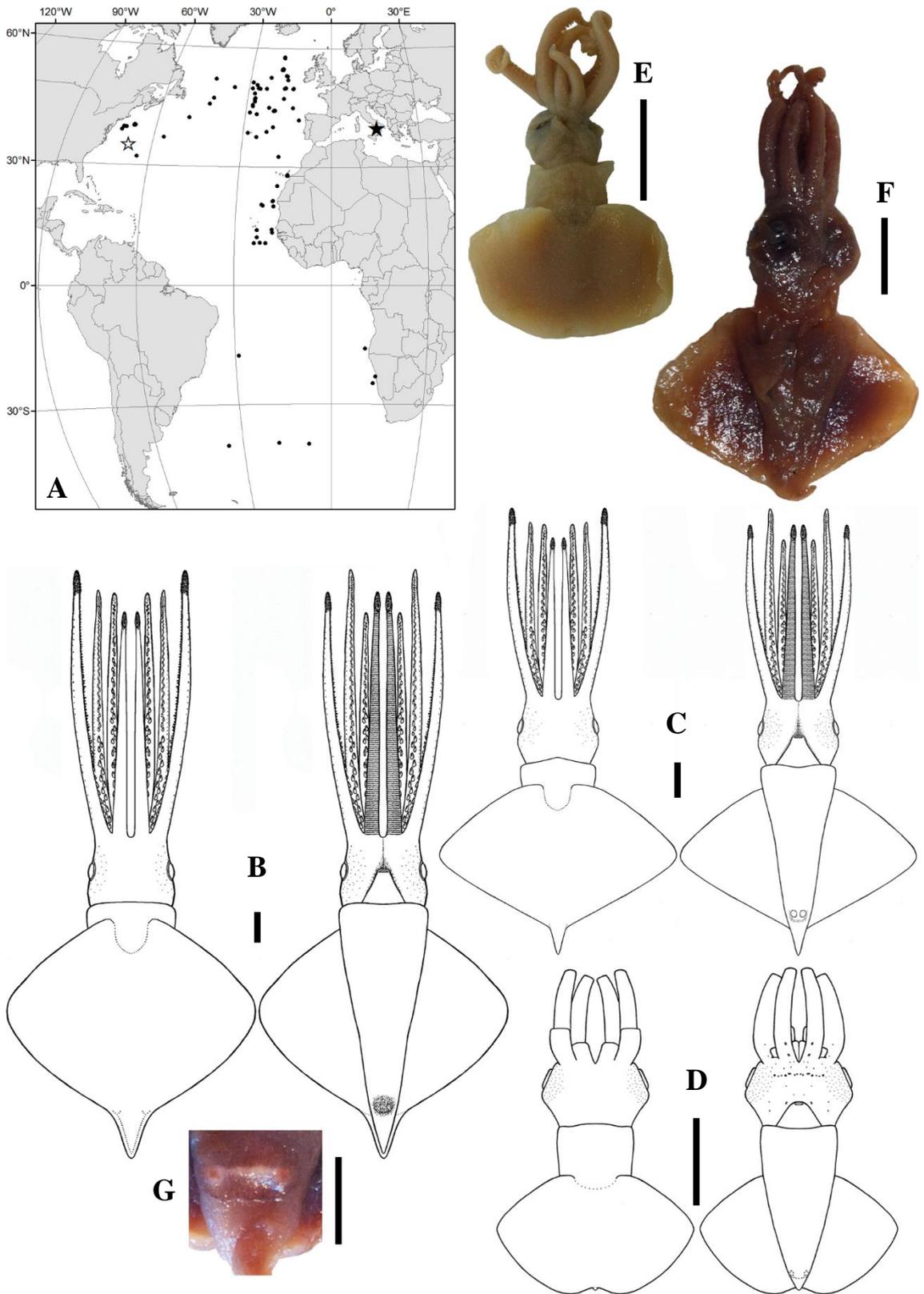


Fig. 8—*Octopoteuthis sicula*. A) Distribution (solid star indicates type locality, hollow star type locality for *O. 'danae'* Joubin, 1931); B) adult; C) juvenile; D) post-larva, (Escáñez_11_5_D, sex indet., ML 9.1 mm); E) NHMUK 1845.9.8.13, holotype, sex unknown, ML 19 mm; F) ZMUC CEP-89, *O. 'danae'* holotype, ♂, ML 28.3 mm; G) atypical PVMP presentation (see juvenile description), ZMH 11203, sex indet., ML 45 mm. Scale bars = B) 25 mm; C, E, F) 10 mm; D, G) 5 mm.

13–16% ML.

Head trapezoidal in outline, stocky, length 25–28–37% ML, width 26–30–33% ML, depth 20–25% ML. LHP triangular, length ~6% HL (~1.5% ML). Eyes very large, diameter 65–78–91% HL (18–21–25% ML), with large lenses, diameter ~36% ED. Funnel length 19–23–28% ML; aperture width ~15% of funnel length, level with posterior margin of lens; funnel valve tall, broad; funnel groove shallow. Funnel component of locking apparatus subtriangular (Fig. 9A); groove broadest posteriorly (~80% cartilage width), narrowing antero-medially to slender channel; medial margin of groove concave producing raised plateau medial to groove; lateral margin convex to slightly sinusoidal, with smaller plateau antero-laterally; length ~8% ML, maximum width ~5% ML. Mantle component of locking apparatus oblique, conical, broadly triangular, posteriorly narrowing rapidly antero-medially to slender ridge in anterior half (Fig. 9B); surrounded by narrow groove laterally and anteriorly; length ~8% ML, maximum width ~4% ML. Nuchal cartilage rectangular to oblong with straight parallel or slightly convex lateral margins, anterior and posterior margins rounded, weakly pointed anteriorly (Fig. 9C); dorsal surface with medial groove flanked by ridges (groove and ridges of equivalent width), flanked by broader grooves pointed antero-medially; length ~12% ML, maximum width ~6% ML; set on rhombic cartilaginous pad of equivalent length, width ~170% nuchal cartilage width. Buccal connective on Arms II dorsal (Fig. 7C), ventral protective membrane attaches basally to Arm III; Arms I, III with paired buccal connectives, Arms IV with weakly paired connectives set closely

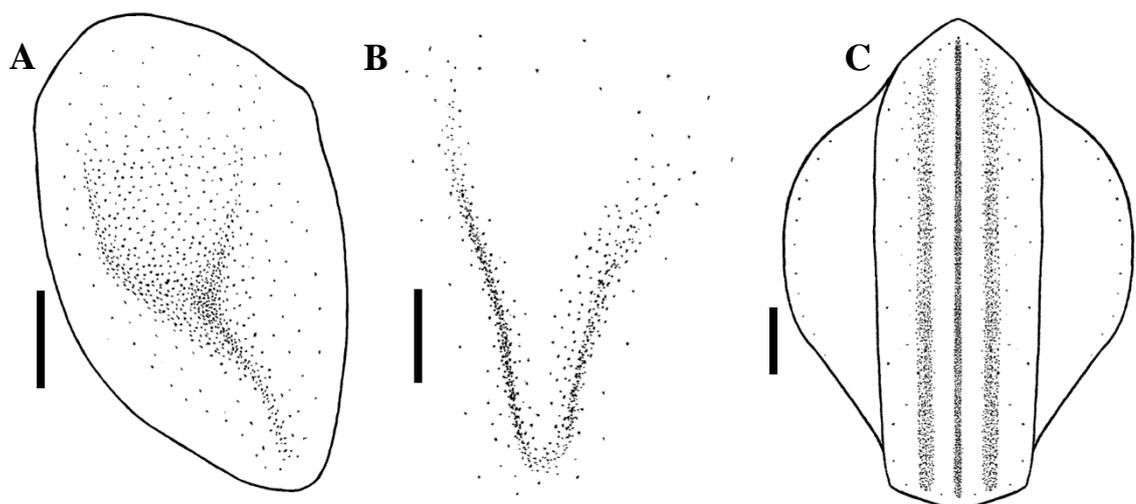


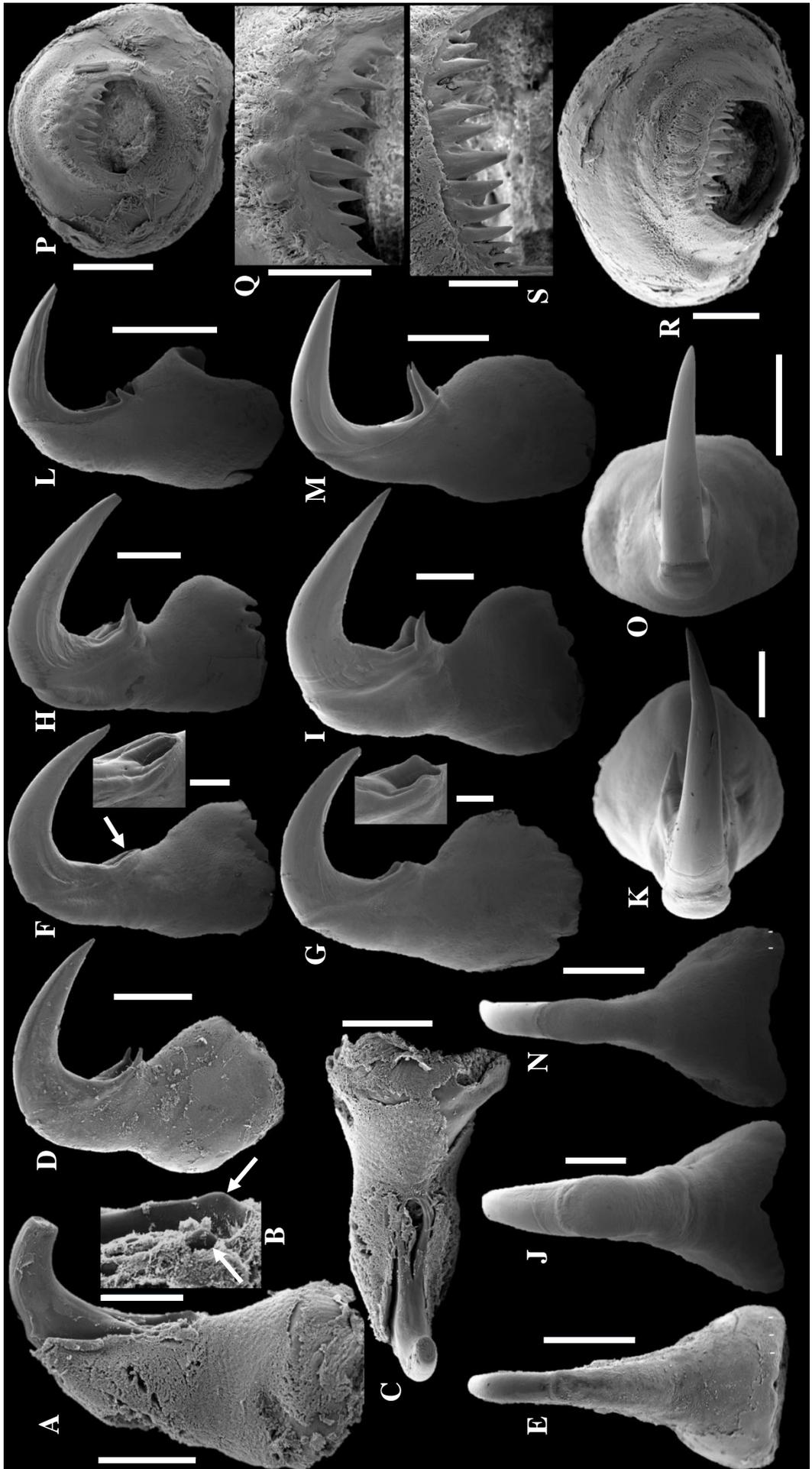
Fig. 9—*Octopoteuthis sicula*. A–C) USNM 1283032, ♂, ML 122 mm. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage. Scale bars = A–C) 2 mm.

together, ventrally. Six pores in buccal membrane: one between paired connectives of Arms I, one between Arms II and III ventral to Arm II buccal connective, and one between Arms III and IV. Olfactory papillae short (height ~2% HL), elliptical (breadth ~2.7% HL), fleshy knobs without sculpture.

Only four subadult specimens with intact, non-regenerating arms (marginally more among juveniles, see below), comprising only two of each of Arms II and III, and one Arm IV; Arm II length ~106% ML, Arm III length ~83% ML, Arm IV length 98% ML; oblong in cross-section becoming circular distally; with 24–29 pairs of hooks in thick fleshy sheaths, followed by 3–8+1 pairs of suckers distally. Arms slender, tapering gradually to tips. Arm-tip photophores occupy distal-most ~7% AL (photophore length ~8% ML); swelling slightly to midpoint, tapering distally to blunt tip or slight bulb; arm hooks terminate proximal to photophore, distal-most suckers overlies photophore proximally. Single large oval photophore embedded deeply in base of Arms II–IV; largest in Arms III (2.9 mm in specimen ML 171 mm; ~6% HL, ~1.7% ML), smallest in Arms II (1.9 mm in specimen ML 171 mm; ~4% HL, ~1.1% ML). Photophore series along ventral Arms III, IV beginning ~25% HL (~7% ML) distally from arm-base photophores; comprising dozens of oval to circular photophores considerably smaller than base photophores (diameter ~1 mm in specimen ML 171 mm), decreasing in size distally; terminating proximal to arm-tip photophore. Gelatinous tissue along aboral arms often produced into low keels from base to tip; keel breadth increases distally relative to arm depth.

Arm hooks robust (Figs 10A–O); largest in pairs 3–6 of Arms II, decreasing gradually in size distally, slight decrease in size proximally. Main cusp long, smoothly curved;

Fig. 10 (following page)—*Octopoteuthis sicula* armature. A–C) NHMUK 1845.9.8.13, holotype, sex indet., ML 19 mm; D, E) ZMUC CEP-89, holotype (*O. danae*), ♂, ML 28.3 mm; F, G) USNM 1283032, ♂, ML 122 mm; H–K) USNM 728875, ♂, ML 176 mm; L–O) NIWA 71843, ♀, ML 196 mm; P–S) Escáñez_12_I_N, ♀, ML 220 mm. A–C) 11V hook, Arm III: (A) lateral profile, (B) accessory claws (arrows) as low corners, (C) oral; D, E) 6D hook, Arm III: (D) lateral profile, (E) aboral; F) 13D hook, Arm II, without (arrow) accessory claws (inset, oblique); G) 4V hook, Arm II (inset, oblique); H) 10D hook, Arm II; I–K) 6V hook, Arm II: (I) lateral profile, (J) aboral, (K) top; L) 18D, Arm III; M–O) 2V, Arm III: (M) lateral profile, (N) aboral, (O) top; P, Q) 7th arm sucker (series, arm unknown): (P) oral, (Q) sucker ring dentition; R, S) 2nd arm sucker (series, arm unknown): (R) oral, (S) sucker ring dentition. Scale bars = A, C, Q, S) 100 µm; B) 25 µm; D–G, P, R) 200 µm; H–K) 0.5 mm; L–O) 1 mm.



finely pointed distally; smooth laterally or with one or two shallow lateral ridges; maintaining similar width aborally and laterally along junction with base; inner angle $\sim 90^\circ$ in basal hooks, acute ($\sim 60\text{--}80^\circ$) among distal 75% of pairs; aperture open, broad oval except in mature male (USNM 728875, ML 176 mm) where aperture rim expanded inward leaving only tall narrow gap. Accessory claws typically present as low points, straight to slightly curved; but variable, ranging from entirely absent (Fig. 10F) to very long straight spurs (Fig. 10M), also as low corners (Fig. 10G) or short broad triangles (Fig. 10L). Aboral hood absent. Bases crenulated, most prominent oro-laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth). Arm suckers in thin fleshy sheaths similar to hooks, sheaths with chromatophores proximally; borne on short stalks; suckers asymmetric, domed, broad laterally (Figs 10P–S); dentate apically, basal $\sim 60\text{--}70\%$ of circumference smooth; series of raised lumps apical of infundibular teeth underlying sheath roughly correspond to tooth series. Basal sucker dentition symmetrical: apical tooth longest, broadest, triangular, pointed; flanked on both sides by six teeth; medial 2–4 teeth pointed, roughly equal in length; lateral teeth rounded, decreasing in length. Dentition of suckers at midpoint symmetrical: apical tooth triangular, broad, pointed; flanked on each side by slightly shorter tooth, then longer tooth equivalent to apical in length but more conical, then three conical teeth decreasing in length.

Tentacles absent, traces only remain in post-larvae (see life stage description below).

Recti abdominis muscles (Figs 5E, F) form discrete muscle bands straddling rectum anteriorly, posteriorly merging and fusing over rectum; weakly attached to rectum and immediately adjacent dorsal tissues dorsally; anteriorly inserting under dorsal component of funnel organ, beyond rectum, posteriorly expanding into thin sheet attaching to ventral surface of visceral mass; single near-circular photophore on dorsal surface of each muscle at $\sim 30\%$ ML anteriorly; small, width 24–56–96% width of muscle band ($\sim 1.7\%$ ML); centred to slightly medially set; pearly white, slightly raised dorsally. Rectum free briefly anteriorly, terminating just inside funnel posterior to dorsal funnel organ concavity; laterally bearing two moderate-length anal flaps, length $\sim 1.8\%$ ML, ovate, anterior tip pointed, chiral dorso-ventrally. Ventral visceral mesentery pore small, diameter $\sim 0.6\%$ ML; pore appears as sphincter in membrane. Gills robust; length $\sim 25\text{--}30\%$ ML, with 26–28 lamellae.

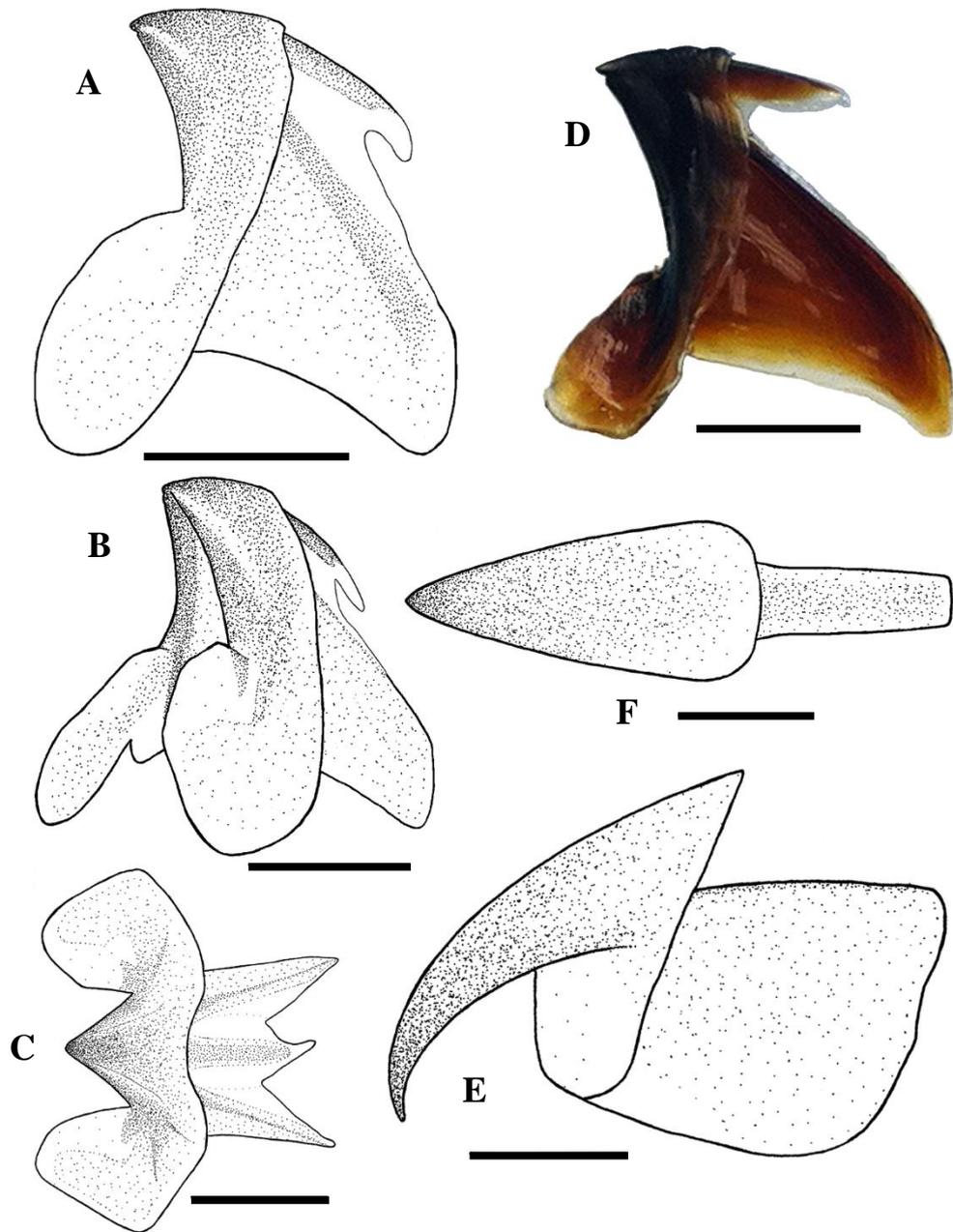


Fig. 11—*Octopoteuthis sicula* beaks. A–C, E, F) USNM 816679, ♀, ML 126 mm, LRL 6.05 mm, URL 7.15 mm; D) NHMUK 20160106, ♀, ML 148 mm, LRL 11.19 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

Lateral profile of lower beak (6.05–8.96 mm LRL, Figs 11A–D) equally long and deep, with distal wing tips extending beyond rostral tip by 10–13–20% baseline; rostral tip with shallow to distinct notch; jaw edge visible, slightly concave, with short jaw-edge extension; jaw angle 90°, rarely obscured by low, rounded wing fold; depth anterior to jaw angle typically greater than posterior. Hood low over crest, length 32–35–38% baseline, with shallow hood groove. Crest distinct, lateral wall between crest and fold unpigmented; length 62–68–77% baseline; tip free with concave ventral margin; straight

to slightly curving. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior ~50% of hood length; posterior lateral wall margin slightly curved; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 193–218–248% that at jaw angle; length 66–85–108% LRL; with cartilaginous pad, decreasing in prominence through ontogeny. Ventral view with very broad, shallow notch in hood; free corners level with inner wing margin. All beaks examined fully pigmented excluding largest (USNM 816677, ♀, ML 168mm, LRL 8.96 mm): hood, crest and lateral wall fully pigmented, wings unpigmented.

Lateral profile of upper beak (7.15–8.17 mm URL, Figs 11E, F) longer than deep, maximum depth ~48% of length. Rostrum long, ~37% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle acute (70–80°) except in large male (USNM 728875, ML 172 mm) where 90° due to loss of shoulder cartilage; low ridge of cartilage present orally along shoulder; oral shoulder margin straight. Hood long (length ~82% UBL), moderately tall (~19% UBL); junction of hood and free shoulder slightly concave. Lateral walls approximately rectangular with maximum depth in posterior quarter, posterior margin straight. Dorsal view with posterior margin of hood straight, posterior margin of crest slightly concave, posterior margin of crest pigmentation slightly concave. Smallest beak examined fully pigmented excluding free shoulder and ventro-anterior quarter; fully pigmented in beaks >7.9 mm URL.

Radula (Figs 12A–C) somewhat variable in morphology among specimens. Rachidian tricuspid: mesocone moderately long, narrowly triangular, straight; lateral cusps long (~50% mesocone height) straight tines or very short (~20% mesocone height) slightly laterally directed blunt nubs; base slightly concave or slightly convex. First lateral tooth basebicuspid: inner cusp narrowly triangular, equal to rachidian in height, straight or slightly medially directed; outer cusp long (50–60% height of inner) medially curved tine or very short (15–20% height of inner) laterally directed nub; base straight. Second lateral tooth simple, conical, ~130% height of rachidian. Marginal tooth simple, conical, ~200% height of rachidian. Marginal plate absent. One specimen (Fig. 12D) with asymmetrical radula: left side with 3 series of teeth lateral to rachidian (normal), right side with 4 series; 8 series of teeth for entire length of radula; first and second right lateral tooth series composed of slightly smaller teeth, both slightly different in

morphology to left first lateral series; lateral-most two series on both sides equivalent. Palatine palp (Fig. 12E) with 36–46 broad, triangular teeth generally with broad rounded base, each 65–190% rachidian height, smallest orally; oral end of palp rounded, recessed relative to majority of tooth-bearing length; depth of tooth-bearing surface decreases posteriorly; anterior margin adentate, dorsal margin regularly dentate, teeth evenly arranged along tooth-bearing surface.

Gladius (139*–250 mm GL, Fig. 12F) very broad and very thin (<0.1 mm thick), delicate, transparent; greatest width (10–12% GL) at ~30% GL; rachis broad, evenly concave; free rachis ~7% GL, pointed anteriorly, smoothly widening posteriorly to maximum width (~2% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden quickly to maximum width, then taper gradually for remainder of length; short conus present (~3% GL); very fragile, into which tissue inserts (the traction of which often results in breakage during dissection). Posterior end of gladius curved ventrally, with vanes bending ventro-medially.

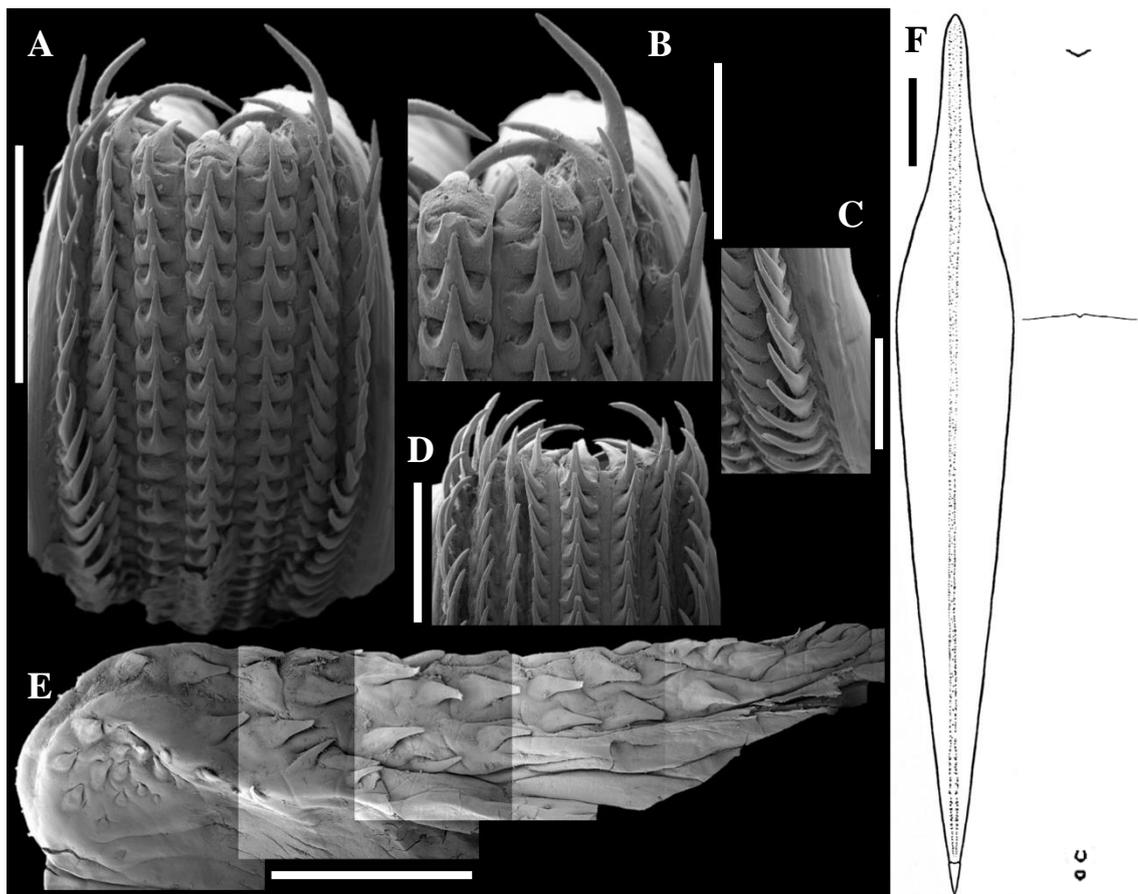


Fig. 12—*Octopoteuthis sicula*. A–C) USNM 816679, ♀, ML 126 mm; D, E) NIWA 71843, ♀, ML 175 mm; F) USNM 1192570, ♀, ML 204 mm, GL 250 mm. A–D) Radulae; E) palatine palp; F) gladius, with cross-sections. Scale bars = A, D) 1 mm; B, C) 0.5 mm; E) 2 mm; F) 25 mm.

Colour (preserved) in adults deep purple to pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose furrows in females; arm tips over photophores dark purple; chromatophore patch overlying posterior ventral mantle photophores darkest postero-laterally. Inner mantle surfaces and viscera unpigmented. Fresh specimens similar but colours more brilliant: pigmentation redder, non-pigmented tissues whiter or translucent.

Juvenile specimens (ML 25.2–57 mm, Figs 8C, F) as above, with the following exceptions. Mantle conical, width 32–40–46% M; tail short, length 5–15–21% ML; PVMP diameter ~2.5% ML, spaced ~9% ML apart, outline of overlying chromatophore pattern discernable in smallest specimen as single rings of larger darker black-purple chromatophores connected posteriorly, posterior chromatophore band present by ML 30 mm. *Recti* photophores ~2% ML. Fins very wide (113–125–137% ML); anterior margin of fin more posteriorly set relative to adults, at 8–12–16% ML. Head length 35–42–47% ML, width 32–37–46% ML. Arm length 67–82–102% ML; formula II>III>IV>I. Arms with two series of fully developed hooks, smallest specimen already with developed accessory claws. Tentacles entirely lacking. Single specimen with light-coloured transverse bar between anterior PVMP (Fig. 8G); appearing continuous with organs, similarly coloured, occupying similar depth in tissues.

Post-larval specimens (ML 7–9.5 mm, Fig. 8D) as above, with the following exceptions (measurements based on Escáñez_11_5_D, sex indet., ML 9.1 mm, excepted where noted). Posterior ventral mantle tip recessed relative to posterior fin margins, no tail. Faint rings of single chromatophores visible in approximate location of PVMP, not connected posteriorly in species-group diagnostic pattern; photophores not discernable. Fin width 115% ML; anterior fin margin more posteriorly set, at 26% ML. Head length 62% ML. Arm hooks already developed: specimen ML 7 mm with at least some arm hooks (damage prevented more detailed observations), specimen ML 9.5 mm with hooks proximally to at least second pair if not basal-most pair. Tentacles broken in smallest specimen but already atrophying, width at tentacle base ~30% width of adjacent arm; in specimen ML 9 mm only vestigial tentacle nubs remain, gelatinous, translucent, without definition or armature, length 4% ML, width at base 21% width of adjacent arm.

Redescription of type material (holotypes of *O. sicula* and *O. 'danae'*, Figs 8E, F).

NHMUK 1845.8.9.13, *O. sicula* holotype, ML 19 mm, sex indet., in fair condition.

General condition of fins, mantle, funnel, and arm hooks very good; damage to head causing arm crown to detach, tissue snip missing from ventral medial mantle (taken by author in 2015), ventral mantle dissected medially; colouration dulled, monochromatic. Major morphometric indices (Table 5) align closely with mean juvenile indices, differences and important indices as follows. Mantle weakly goblet-shaped; tail very short, length ~8% ML; two PVMP discernible, chromatophore patterning unknown due to fading. Fins broadly rhombic (128% ML), with convex anterior and posterior margin; very posteriorly set, anterior margin at 20% ML; retaining characteristic octopoteuthid anterior and posterior insertion morphology. Head trapezoidal, broadest posteriorly; nuchal cartilage oblong. Arms short: Arm IL 60% ML, Arm IVL 50% ML; Arm IIIR in early stages of regeneration. Arm hooks fully developed basally; accessory claws present as slightly raised corners on aperture lip; aperture tear-shaped, rounded basally; base crenulated. Funnel and funnel components of locking apparatus in very good condition; funnel set in shallow groove between eyes; aperture oriented ventrally; locking components subtriangular, broad groove narrowing antero-medially to shallow channel. Eyes small, 17% ML. *Recti abdominis* photophores visible; all other photophores (except arm tip photophores) undetectable due to damage or fading. Status of tentacle remnants unknown at present (at least indiscernible macroscopically); life history stage remains unclassified at present. **ZMUC CEP-89**, *O. danae* holotype, ML 28.3 mm, ♂, in good condition. All body regions in good condition; left eyelid tissue dissected anteriorly, ventral mantle dissected medially; colouration typical of preserved specimen. Measurements reported in Table 6; important indices or differences from juvenile description as follows. Mantle broad anteriorly (width 48% ML) due to minor compression of mantle; tail 14% ML; two PVMP, chromatophore pattern not characterised at time of examination. Fins broad (116% ML), rhombic, margins straight; anterior fin margin at 14% ML. Head trapezoidal, width 47% ML; LHP present; eyes in sufficient condition to identify MEP and EP, neither found; nuchal cartilage oblong. Single arm complete, Arm IVR 69% ML; Arms II–IV with photophores embedded deeply in base, those of III and IV greater in size than II; photophore series along ventrum of axial nerve in Arms III, IV. Arm hooks with narrow smoothly curved main cusps, lateral sides smooth; broad laterally; accessory claws prominent; aperture asymmetrically lens-shaped. Funnel, locking components in good condition, as above in NHMUK 1845.8.9.13; funnel organ in good condition, as described above for

Octopoteuthis. Recti abdominis photophores visible. Tentacles lacking. Immature male, terminal organ just anterior of gill artery.

Table 6. Measurements (mm) of a selection of *Octopoteuthis sicula* juvenile and post-larval specimens, including the holotype of *O. danae* Joubin, 1931. Mean indices were calculated from specimens with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side).

Specimen ID	ZMUC CEP-89	ZMH 11176	USNM 885073	USNM 1283029	Escáñez 11_5_D	Mean index	Escáñez 11_5_D
Type status	Holotype (<i>O. danae</i>)	None	None	None	None		None
Sex	♂	♀	♀	Indet.	Indet.		Indet.
DML	28.3	57	49	38	25.2		9.5
MW	13.6	24	21	17	11.6	45	4.1
FL	21.6	49	39	24	20.6	77	7.3
FW	32.7	73	62	48	30.8	124	11
HL	11.0	27	21	15	8.9	41	5.9
HW	13.4	18	18*	14.2	11.5	40	3.6
Side	R	R	R	R	R		R
AL I	NM*	36*	8*	9*	18		1.1*
AL II	NM*	58*	3*	6*	22.7		1.8*
AL III	NM*	40*	7*	8*	17.2*		4.7*
AL IV	18.8	35*	17*	15*	17.5	68	5.3*
AH	26				*, *, 26		
AS	5				*, **, *		
TL							0.4

* indicates damaged character not used to calculate indices.

Biology. Plots of select morphometrics through ontogeny (Fig. 13) indicated decreasing trends for fin width, head length and width relative to mantle length. Fin length was remarkably consistent, with most values ranging between 70 and 85% ML and fitted values varying <1.5% ML across ML range of nearly 200 mm; eye diameter was similarly consistent, although this index is inherently less variable due to the smaller absolute size of the eyes relative to the mantle. Tail length and the anterior fin margin showed a distinct, inverse relationship with respect to mantle length, relationships all the more noteworthy given that these are very small absolute measures but taxonomically significant characters in some species.

The maturity stages of 108 specimens with undamaged mantles were assessed. The smallest mature specimen examined was ML 93 mm (NHMUK 20160085, ♂); males begin maturing at ML 62–88 mm, reaching sexual maturity at ML 93–122 mm; the largest male examined was ML 176 mm. The smallest reproductive female was ML 151

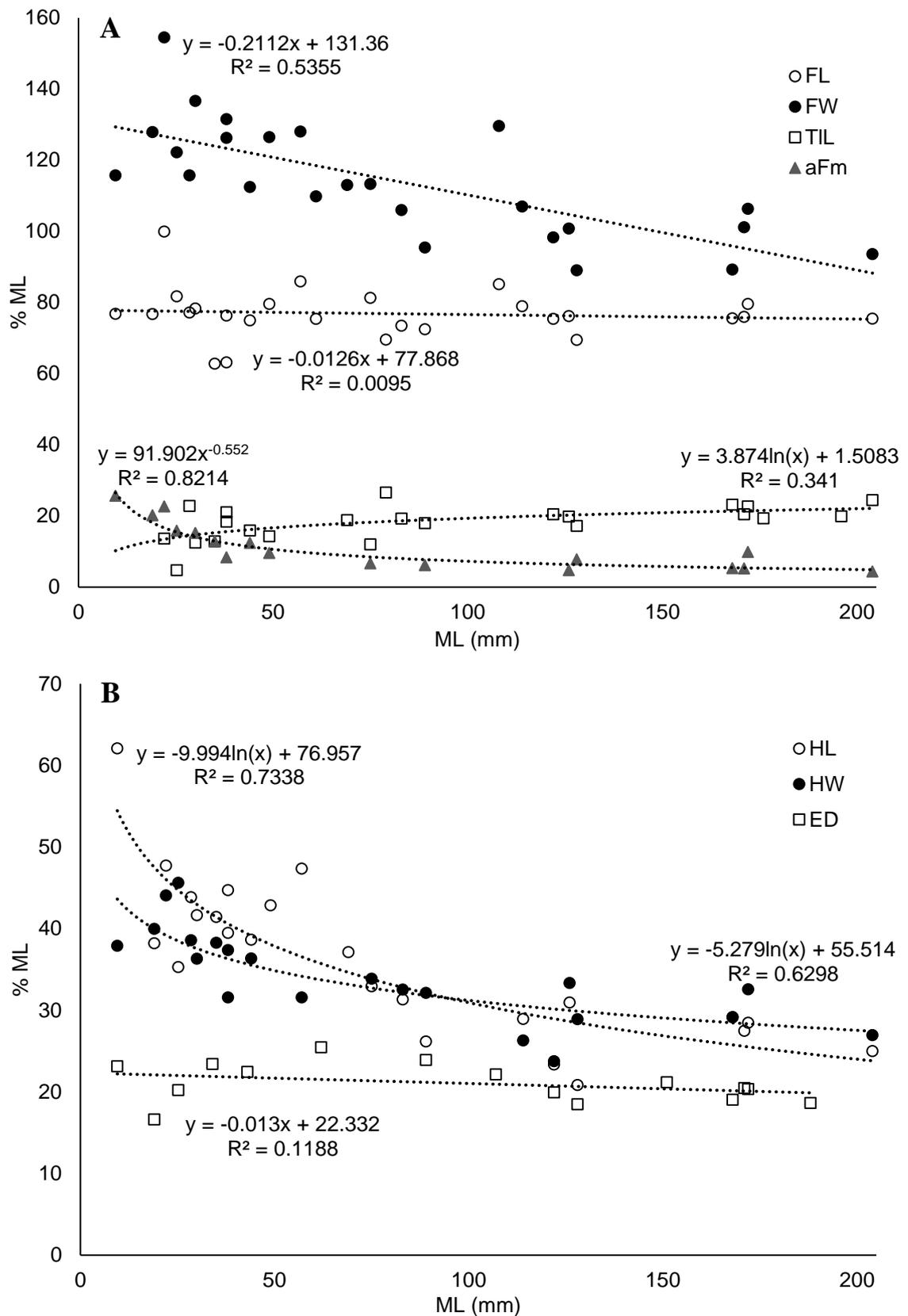


Fig. 13—*Octopoteuthis sicula*, selected morphometric indices through ontogeny. A) fin length (FL; hollow circles), fin width (FW; solid circles), tail length (TIL; hollow squares), level of anterior fin margin (aFm; grey triangles); B) head length (HL; hollow circles), head width (HW; solid circles), eye diameter (ED; hollow squares). Regression equations and R^2 values of models of best fit are shown.

mm (ZMH 11161, in resting stage, presumed spawned); females begin maturing at ML 70–91 mm, reaching sexual maturity at ML 151–162 mm; the smallest mature female examined was ML 152 mm (USNM1283038), the largest was ML 204 mm.

Opportunistic observations were made on 23 reproductive females (Figs 14B–G). Female reproductive system comprised posteriorly situated ovary; paired oviducts, laterally set in mantle posterior to gills underneath sheet of connective tissue, each anteriorly adjoining bilobed oviducal gland protruding anteriorly from under gill artery; paired, bilobed nidamental glands attached to ventral membrane of visceral mass. Measurements reported in Table 7: mature females with considerably enlarged nidamental glands (length 40–53% ML), developed oviducal glands (length 14–22% ML), and ovum-filled oviducts (length 13–23% ML, ovum diameter 2.2–2.4 mm); oviducts with 11 or 12 convolutions. Ovaries showed group-synchronous ovulation, containing eggs at different stages of development: undeveloped oocytes very small (mean diameter 0.5 mm), whitish to light cream coloured, attached in strings to ovary; maturing oocytes slightly greater in diameter, cream coloured, attached; developed ova large (mean diameter 1.6 mm), orange, slightly translucent, detached from ovary. A well-defined and distinctly different reproductive morphology was also observed in females of a size range overlapping that of mature females, herein termed ‘resting stage’. Resting females with considerably reduced nidamental and oviducal glands

Table 7. Measurements of reproductive organs for mature ($n = 6$) and resting ($n = 4$) female *O. sicula*. For nidamental gland (NGI), oviducal gland (OGI), oviduct (Od) measures, length (L) along posterior–anterior axis, width (W) transverse axis, depth (D) dorsal–ventral axis. Ov = ovary, dia. = diameter.

Structure	Mature		Resting	
	Range (mm)	% ML	Range (mm)	% ML
ML	173*–206*		142*–201	
NGI L	80–103	40–53	28.5–42.0	15–24
W	10.8–24	6–12	4.3–6.5	2–4
D	6.4–12	3–6	1.5–2.54	0.8–1.4
OGI L	29–39.2	14–22	12.2–14.1	7
W	3.8–8.3	2–5	2.4	1.3–1.4
D	2.4–5.6	1–3	2.9–3.0	1.6
Od L	22.3–44.7	13–23	34.6	20
W	6.1–10.7	3–5	1.37	0.8
D	4.3–7.9	2–4		
Ov oocyte dia.	0.35–0.70			
Ov ovum dia.	1.2–1.8			
Od ovum dia.	2.2–2.4			

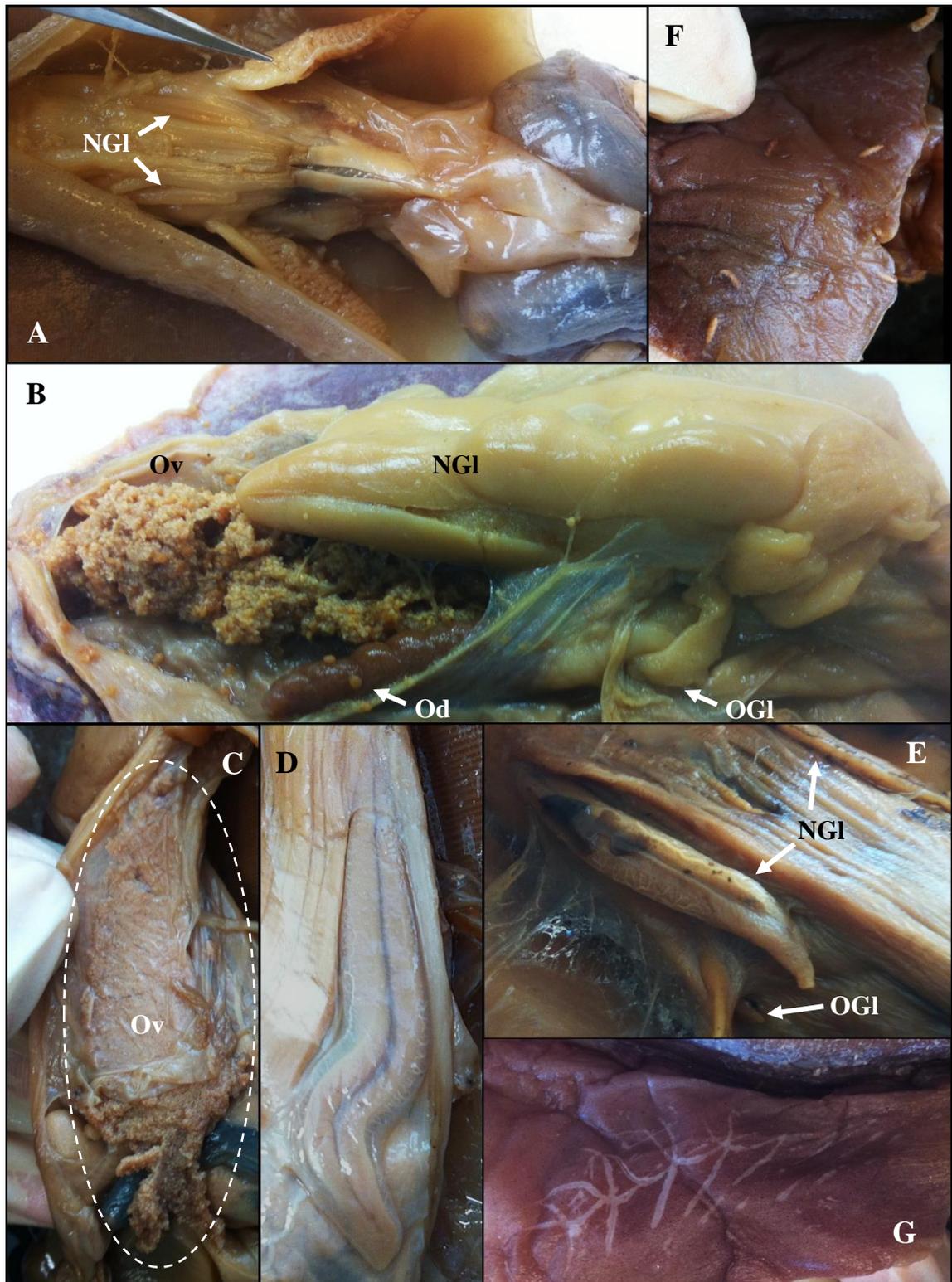


Fig. 14—*Octopoteuthis sicula*. Female maturity staging and reproductive system. A) Maturing (USNM 814606, ML 89 mm), nidamental glands (NGI) developing; B) mature (NIWA 71843, ML 196 mm), nidamental and oviducal (OGI) glands enlarged, oviducts (Od) with ova, ovary (Ov) with developed ova, undeveloped oocytes; C–E) resting: (C) ovary thin with only attached, undeveloped oocytes, (D) regressing sheathed nidamental gland, (E) greatly reduced nidamental and oviducal glands (C, D: ZMH 11229, ML 179* mm; E: ZMH 26070, ML 188 mm); F, G) ZMH 11237, ML 137* mm: (F) long thin spermatangia implanted along right lateral mantle, (G) unusual scratches along external left lateral mantle.

relative to mature specimens (indices 200–300% smaller, Table 7); nidamental (occasionally oviducal) glands sheathed: outer membrane loosely encasing inner glandular tissue, inner tissue with slight bends often independent of casing; oviducts similar in length but empty, compressed; ovaries contain dense mass of undifferentiated, undeveloped oocytes.

Reproductive morphology observations were made on eight males (Fig. 15, measurements reported in Table 8). In immature males, section of terminal organ anterior to gill artery very short (~4% ML), narrow, thin. In maturing males, total reproductive system length (TRSL) ~50% ML; terminal organ lengthening anteriorly, length distal to gill artery ~40% TRSL (~15% ML), not extending beyond anterior mantle margin; thin, broadening laterally, width at gill artery ~6% TRSL (~3% ML); testis ~47% TRSL, maximum width ~9% TRSL, depth ~5.1% TRSL. Mature males with greatly developed reproductive system: TRSL ~75% ML; distal terminal organ extends beyond anterior mantle margin (~39% ML), length beyond gill artery 55–65% ML; maximum width ~16% TRSL (8–12% ML) at ~60% TRSL, width at gill artery (~6% ML); testis kidney shaped, length 44% TRSL (~33% ML), width ~16% TRSL (~12% ML); thin (~4% ML, ~6% TRSL), composed of striated tissue. Two of three mature males with implanted spermatangia, presumably self-implanted during capture.

Implanted spermatangia in females (Fig. 14F) long, slender (width ~25% length; length 2.25–2.99 mm, width 0.58–0.85 mm), embedded superficially in outer gelatinous tissue

Table 8. Measurements of reproductive organs for immature ($n = 3$), maturing ($n = 2$), and mature ($n = 3$) male *O. sicula*. For total reproductive system length (TRSL), terminal organ (TO), and testis measures, length (L) along posterior–anterior axis, width (W) transverse axis, depth (D) dorsal–ventral axis. dist. = distal.

Structure	Immature		Maturing		Mature	
	Range (mm)	% ML	Range (mm)	% ML	Range (mm)	% ML
ML	39–42.5		100*–122		167–172	
TRSL			48.6	~45	126	75
TO L dist. M					64–67	37–40
L dist. gill	1–3	3–6	16–20	13–16	94–109	55–65
max. W					12.5–20.0	8–12
W at gill			2.8–3.5	~3	7.9–11.3	5–7
Testis L			22.8	~20	55	33
max. W			4.4	~4	19.7	12
D			2.5	~2	7.3	4

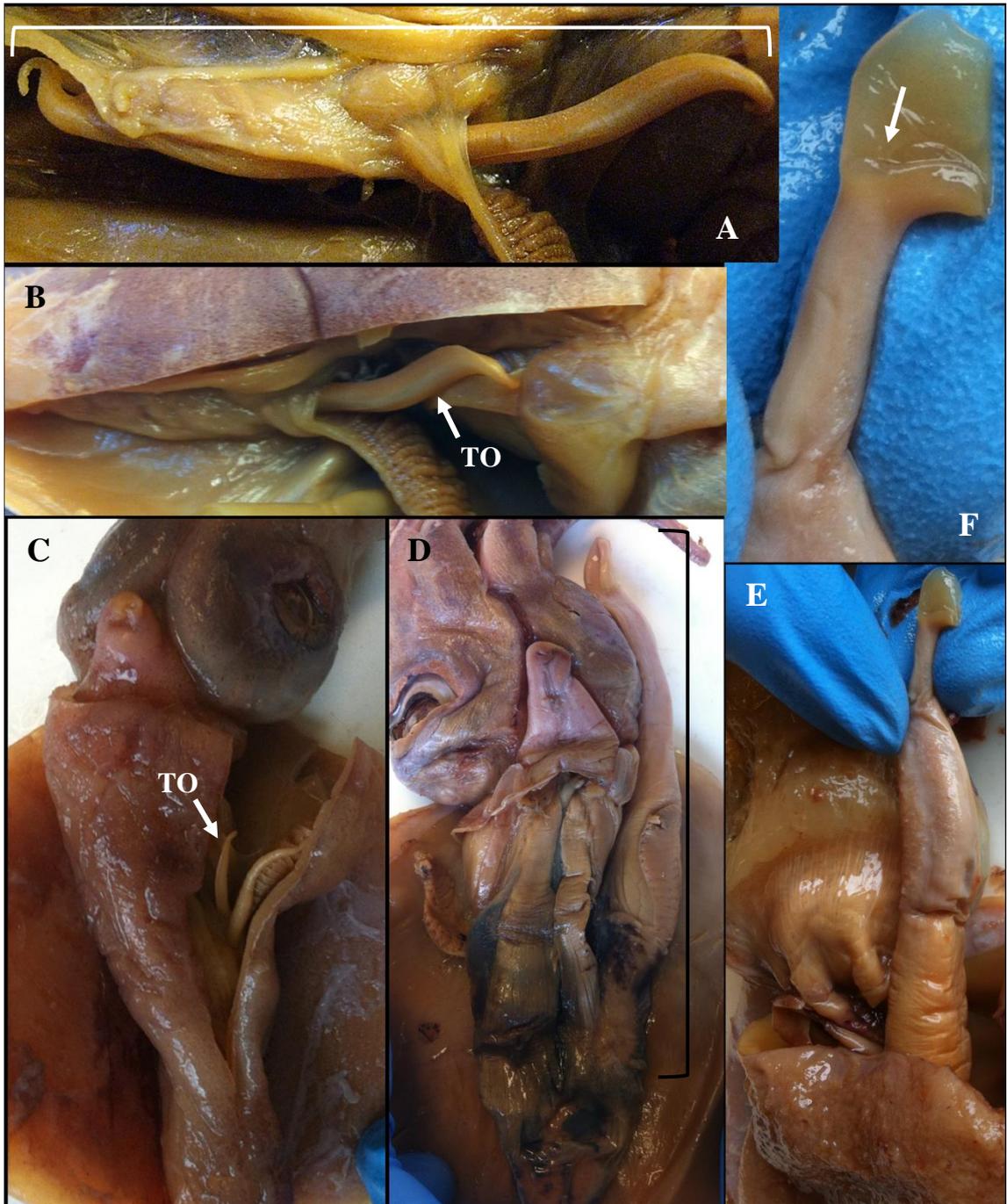


Fig. 15—*Octopoteuthis sicula*. Male maturity staging and reproductive system. A, B) Maturing: (A) lateral view of reproductive system, (B) terminal organ (TO) developing (MCZ 370406, ML 122 mm); C) early maturing (USNM 1283032, ML 122 mm); D) mature (USNM 1283028, ML 171 mm), developed reproductive system *in situ*; E, F) mature: (E) terminal organ extending well beyond anterior mantle margin, (F) distal tip morphology, opening (arrow) (USNM 728875, ML 176 mm).

layers; long aboral thread (3.1 mm, 104% sperm mass length) emergent from tissues; those implanted in males identical. Single lot (NIWA 71843, ML 167–196 mm) of two mature females, one mature male, each with identical, small, teardrop-shaped implanted spermatangia; sperm mass width ~65% length (width 0.78–1.19 mm, length 1.43–1.76

mm), thread length 1.31 mm (~92% sperm mass length); spermatophores of male, 13.2 mm long, 0.37 mm wide. Dividing the body into 9 regions (dorsal, ventral, lateral surfaces of arms, head, mantle) of female specimens: spermatangia equally frequent in head and mantle (38%), followed by arms (18%); most common along dorsal head and dorsal arm bases (both 18%), followed by dorsal mantle (15%) and lateral head and lateral mantle (both 12%). However, for specimens where mature males were caught at same station, possibility of net-induced implantation cannot be excluded.

Remarks. *Octopoteuthis sicula* co-occurs considerably with *O. megaptera*, and to a lesser extent with *O. leviuncus* sp. nov. and *O. rugosa*. It is readily separated from *O. megaptera* and *O. rugosa* by the absence of MEPs and EPs, and from all three in having two PVMPs overlain by a single chromatophore patch (versus two PVMPs overlain by two separate patches in *O. megaptera* and *O. rugosa*, and a single PVMP with a single patch in *O. leviuncus*). In addition, adult specimens of *O. sicula* tend to have a stockier gross morphology compared to adult *O. megaptera*. When collection locality is unknown, specimens of *O. sicula* can be difficult to distinguish from the other members of this species group. The reduced or absent accessory claws described above were uncommon in small *O. sicula* and never observed in adults, while *O. nielseni* is characterised by reduced or absent accessory claws (with rare exceptions, see below); juvenile *O. nielseni* tend to have more posteriorly set fins than juvenile *O. sicula* (anterior fin margin at 11–19% and 8–16% ML, respectively). Adult *O. sicula* differ from *O. fenestra* sp. nov. in having fewer and less prominent lateral ridges on arm hooks and a tendency toward shorter tails (length 12–20–25% compared to 17–23–28% ML), juveniles in having narrower fins (FW 113–132% vs 114–117% ML, respectively).

The holotype of *O. sicula*, collected from Messina, Italy, could not be traced for Stephen's (1985a) review of the genus, but was located at the NHMUK (*vide* Lipinski *et al.* 2000), likely having been deposited there shortly after its description (Gray 1849). Select characters of the holotype were reviewed by Jereb *et al.* (2016), but morphometrics were not reported. Herein, the holotype was examined on two occasions and, while generally in good condition, key taxonomic characters (*e.g.*, photophores, chromatophores) were indistinguishable due to fading. Two PVMP were identified, and arm hooks were in sufficient condition to permit SEM imaging, but these were insufficient for specific identification; historic descriptions did not refer to the necessary

missing characters. Unfortunately, specimens from the type locality (Mediterranean Sea) of sufficient size and quality to distinguish salient characters were not available during this study. However, to stabilise the genus, establishment of the type species' morphology is essential.

Herein, only two morphological forms of *Octopoteuthis* with two PVMP were identified from the north Atlantic: form A with both PVMPs overlain together by a single chromatophore patch and no MEPs or EPs; and form B with each PVMP separately overlain by a single chromatophore patch, with MEPs and EPs. Jereb *et al.* (2016) reported on ten specimens from the Mediterranean, of which seven were matched to form A either morphologically (Figs 5, 6), genetically (all sequenced specimens), or both, including one from the Straits of Messina (specimen *D*₁; Villari & Ammendolia 2009, Fig. 1); the remaining specimens were insufficiently described to attribute them to species. Jereb *et al.* concluded that only a single species of *Octopoteuthis* was present in the Mediterranean which, while somewhat premature, may be a necessary leap in order to stabilise the genus; additional reports of *Octopoteuthis* from the Mediterranean were not suggestive of a second resident form, albeit mostly due to lack of detail (Degner 1925; Digby 1949; Salman *et al.* 1999). As such, the north Atlantic *Octopoteuthis* with two PVMP overlain by a single chromatophore patch is herein designated *O. sicula* Rüppell, 1844. The holotype of *O. 'danae'* Joubin, 1931, collected near Bermuda, also demonstrated form A morphology. As such, it is designated a junior synonym of *O. sicula* and its type specimen proposed as a neotype for *O. sicula*. Should a neotype from closer to the type locality of *O. sicula* be considered more appropriate, the specimen originally reported by Villari and Ammendolia (2009, Fig. 1; specimen *D*₁, Jereb *et al.* 2016), from the Straits of Messina and clearly showing the single chromatophore patch, is proposed as a neotype following re-examination.

Overall gross morphology and reproductive morphometrics corresponded well with those of Hoving *et al.* (2008) for male and female *O. sicula* off South Africa. While both maturing and resting females, as defined herein, can have small nidamental glands, in maturing individuals nidamental glands were lengthening and thickening but still typically straight and attached tightly to the visceral mass (as in immature females); the inner tissues of the glands were indistinguishable from the encasing membrane. In resting females, inner glandular tissue appeared somewhat detached from the outer casing, and were often curved at some point along their length; vessels were also often

visible along the membranes of resting females. For further critique of the resting stage, see Discussion.

Females from a continuous size range (ML 151–204 mm) were staged as either mature or resting, a span equivalent to 25% of the species' maximum size. This suggests that individuals may continue to feed and grow during the reproductive phase of their lives. Resting individuals had both relatively substantial digestive glands (*i.e.*, energy storage) and typically robust musculature (mantle, fins, arms) compared to other stages, supporting this hypothesis; no specimens were ever observed in a spent state as occurs in other groups (*e.g.*, onychoteuthids, Bolstad and Hoving 2016).

While significant gaps exist in temporal coverage of examined adult females (material was available from six months, and few individuals from each month), mature females were only captured during June, July and September (ML 152–206* mm, $n = 10$), along with the vast majority of resting females (ML 140*–201 mm, $n = 16$); maturing females caught in June and July ranged from ML 91 to 142 mm ($n = 13$). Females caught during January, March, and April were staged as either maturing (ML 126–138 mm, $n = 2$) or resting (ML 141*–168 mm, $n = 4$), and the largest female caught in October (ML 108 mm) and November (ML 89 mm) were both maturing. Males were excluded from consideration as no variation was observed in their reproductive morphology.

Within a relatively narrow seasonality (June–July), mature and resting individuals were collected from localities across most of the species' currently recognised range, suggesting that suitable oceanographic parameters for spawning occur throughout the Atlantic during this timeframe. When mature or resting individuals were collected, they were more often caught in groups than were groups of exclusively immature or maturing individuals. Of the 105 stations sampled, stations that captured at least one adult (mature or resting, male or female; $n = 38$) caught a significantly higher number of individuals on average than stations where adults were not collected (Welch's *t*-test for unequal variances and sample sizes, $t = 1.867$, $df = 46$, one-tailed $P = 0.0342$). This is best demonstrated from a station in the mid-North Atlantic which landed fifteen *O. sicula* (ZMH 11165, 11202, 26070), twelve of which were mature or resting (the remaining three comprised one immature specimen and two heads likely also from adults). An additional four stations caught four or more adults (totaling 13% of stations which caught adults), compared to only four stations (6%) which caught four or more

exclusively immature or maturing individuals. This clustering of mature individuals suggests that adults may form small spawning groups, or that water layers targeted by trawls were also frequented by mature specimens.

5.1.1.2. *Octopoteuthis nielsenii* Robson, 1948 (Table 9, Figs 16–17)

Octopoteuthis nielsenii Robson, 1948: 120–121, Figs 2–4; Young (1972): 43, *Dana* specimen.

Octopoteuthis Rüppell, 1844 — Young (1972): 43, *Eltanin* specimen (now USNM 817351).

Type material (2 specimens). **NHMUK 1947.7.7.10**, Syntype, sex indet., ML 18 mm, 4°50'N, 87°00'W, 60 miles S of Cocos Island, 0–1090 m, 02/06/1925, 1430 hr, *Arcturus* Oceanographic Expedition, stn. 74, T-70, No. 34, SY *Arcturus*, tow net, coll. W. Beebe; **NHMUK 20180142**, Syntype, sex indet., est. ML ~13* mm, 4°50'N, 87°00'W, 60 miles S of Cocos Island, 0–732 m, 02/06/1925, 1430 hr, *Arcturus* Oceanographic Expedition stn. 74, T-69, No. 33, SY *Arcturus*, tow net, coll. W. Beebe.

Additional material examined (19 specimens). **USNM 814598**, ♀, ML 27 mm, 11°52.8'N, 144°48'W, off Hawaii, USA, 46–50 m, 18/10/1969, RV *Townsend Cromwell*, stn 46-17, Cobb MWT, Sango Expedition; **USNM 814604**, ♂, ML 58 mm, 11°49.2'N, 144°51'W, off Hawaii, USA; **SBMNH 51435**, ♂, ML 21.9 mm, 10°25'N, 86°12'W, off Cabo Velas, Guanacaste, Costa Rica, 969 m, 05/05/1973, RV *Velero IV*, stn 18880, IKMWT; **SBMNH 51354**, ♂, ML 32 mm (mantle only), 10°22'N, 88°00'W, off Cabo Velas, Guanacaste, Costa Rica, 3347 m, 10/05/1973, RV *Velero IV*, stn 18880, IKMWT, coll. R. Pieper; **SBMNH 49345**, sex indet., ML 23.6 mm, 10°22'N, 86°28'W, off Cabo Velas, Guanacaste, Costa Rica, 3658 m, 05/05/1973, RV *Velero IV*, stn 18883, IKMWT, coll. R. Pieper; **SBMNH 51237**, ♂, ML 148 mm, 10°17.1'N, 87°45.5'W, Cabo Velas, Guanacaste, Costa Rica, 3234 m, 11/05/1973, RV *Velero IV*, stn 18926, IKMWT, coll. R. Pieper; **SBMNH 49452**, ♂, ML 36 mm, 08°27.5'N, 84°12.5'W, Costa Rica, 914 m, 26/05/1973, RV *Velero IV*, stn 19033, IKMWT, coll. R. Pieper; **SBMNH 49463**, sex indet., ML 16.5 mm, 06°49.4'N, 82°56.3'W, Guanacaste, Costa Rica, 15/06/1973, RV *Velero IV*, stn 19077, IKMWT, coll. R. Pieper; **SBMNH 51289**, sex indet., ML 32.5* mm, 04°49.8'N, 82°39'W, off Guanacaste, Costa Rica, depth unknown (possibly 300 m), 10/06/1973, RV *Velero IV*, stn 19118, IKMWT, coll. R. Pieper; **NHMUK 20150468**, ♀, ML 36.5 mm, 04°45'N, 78°02'W, Columbia, 910 m, 03/04/1938, Beebe 38903, stn 233, Eastern Pacific Zaca Expedition, net T-1; **USNM 1283043**, ♀, ML 33 mm, 07°35'S, 82°22'W, NW of Trujillo, La Libertad, Peru, 10 m, 13/03/1966, RV *Anton Bruun*, SEPBO/14/570, 70 cm net; **USNM 817351**, ♀, ML 121 mm, 07°46.5'S, 81°30'W, Peru, 683 m, 07/06/1962, RV *Eltanin*, USARP/3/34,

IKMWT, coll. University of Southern California, Department of Zoology; **USNM 1283042**, ♀, ML 34.4 mm, 08°47'S, 83°32'W, W of Trujillo, La Libertad, Peru, 500–700 m, 12/03/1966, RV *Anton Bruun*, SEPBO/14/569A, IKMWT; **USNM 1283044**, sex indet., ML 46.6 mm, 31°48'S, 87°31.2'W, NW of San Fernandez Islands, Chile, 23/02/1966, RV *Anton Bruun*, SEPBO/14/557; **MCZ 278555**, sex indet., ML 28 mm, 33°16'S, 72°36'W, Chile, 0-(165-170)-(350-370)-0 m, 05/01/1966, 0145–0630 (+4) hrs, RV *Anton Bruun*, stn 2, cruise XIII, 10' IKMWT (BDT, Foxton trousers); **MCZ 278524**, ♂, ML 32 mm, 33°32'S, 73°35'W, Chile, 0-(100)-0 m, 01–02/02/1966, 2355–0310 (+5) hrs, RV *Anton Bruun*, stn 53, cruise XIII, 10' IKMWT; **MCZ 278486**, sex indet., ML 14 mm, 33°42'S, 75°53'W, Chile, 0-280-0 m, 30/01/1966, 1823–1913 (+5) hrs, RV *Anton Bruun*, stn 45, cruise XIII, 10' IKMWT (BDT); **MCZ 278531**, sex indet., ML 39 mm, 33°46'S, 75°17'W, Chile, 0-(270)-0 m, 31/01/1966, 0329–0540 (+5) hrs, RV *Anton Bruun*, stn 47, cruise XIII, 10' IKMWT (BDT); **NIWA 105442**, ♀, ML 77 mm, 36°23.09'S, 73°33.95'W, Chillan, Chile, 440 m, stn 251.

Comparative material (6 specimens). **SBMNH 49911**, sex indet., ML NM, 10°15'N, 88°30'W, off Cabo Velas, Guanacaste, Costa Rica, 3246 m, 09/05/1973, RV *Velero IV*, stn 19910, IKMWT, coll. R. Pieper; **SBMNH 49434**, sex indet., ML NM, 10°08'N, 88°41.14'W, off Cabo Velas, Guanacaste, Costa Rica, 3347 m, 09/05/1973, RV *Velero IV*, stn 18906, IKMWT, coll. R. Pieper; **SBMNH 49435**, 3 sex indet., ML NM, 09°15'N, 84°55.58'W, off Cabo Blanco, Puntarenas, Costa Rica, 50 m, 17/05/1973, RV *Velero IV*, stn 18951, IKMWT, coll. R. Pieper; **SBMNH 49440**, sex indet., ML NM, 08°34'N, 84°15'W, Guanacaste, Costa Rica, 300 m, 18/10/1966, RV *Velero IV*, stn 19028, IKMWT.

Distribution (Fig. 16A). Eastern tropical and southern Pacific, 11°N–36°S, 144–72°W; 0–1100 m.

Diagnosis. Accessory claws very low points or absent, rarely prominent; inner angle of main cusp of all arm hooks acute; Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III; anterior fin margin at 5–7% ML in adults, 11–19% ML in juveniles.

Description (ML 121–148 mm, Figs 16B–17). Mantle conical to weakly goblet shaped; widest at anterior margin, width ~41% ML; weakly muscled; tail thick, length ~17%

Table 9. Measurements (mm) of *Octopoteuthis nielsenii*. Mean indices were calculated from specimens ML >120 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	NHMUK 1947.7.7.10	SBMNH 51237	USNM 817351	Mean index	USNM 1283044	MCZ 278531	NHMUK 20150468	SBMNH 49452	USNM 1283043	SBMNH 51435	SBMNH 49463
Type status	Syntype	None	None		None	None	None	None	None	None	None
Sex	Indet.	♂	♀		Indet.	NM	♀	♂	♀	♂	Indet.
DML	18	148	121		46.6	39	36.5	36	33	21.9	16.5
MW	9.4	72	40	41	18	17	17.6	20	18	14.4	8.9
FL	15.9	109	91	74	40.7	27.5	26.5	28.5	26	19.8	13.6
FW	25.5	145	112	95	58	47	44.9	46	47.4	29.8	22.1
HL	9.2	53	42	35	14.5	15	15.5	14.5	12.7	9.5	6.9
HW	9.7	58	36	34	11*	16.5	16.9	14.5	12.1	8.7	6.9
Side	R	L	R		R		R	L	R	R	R
AL I	9.5*	57*	62*		43.3	NM	17*	19*	20*	9.9*	15.2
AL II	21*	68 [†]	67*		29*	NM	26*	36	23*	13.6*	21.1
AL III	11*	77 [†]	67*		45.8	NM	16*	21*	22*	15.6*	18.2
AL IV	10*	32*	63*		38.3	NM	16*	17*	20*	14.2*	13.3 (L)
AH					26, 30, 29			23			NM
AS		6, 6			4+1, 4, 4+1			4			NM
TL											0.5

* indicates damaged character, † indicates regenerating feature, not used to calculate indices.

ML; dorsal anterior margin slightly produced medially, ventral margin with slight indentation between mantle components of locking cartilage. Fins large (length ~74% ML), broad (width ~95% ML); anterior margin at 6% ML; greatest fin width attained at ~60% ML; width of fin continuation along tail ~3% ML. Paired posterior ventral mantle photophores circular, diameter ~1.3% ML; very closely set, distance between photophores ~3.6% ML; embedded basally in gelatinous tissue layer near junction with mantle muscle tissue; together covered by single opaque chromatophore patch, often abraded during collection giving appearance of single chromatophore ring encircling both photophores. Anterior fin insertion broad 'V'-shaped, depth ~18% ML, width ~14% ML.

Head trapezoidal in outline, length ~35% ML, width ~34% ml, depth ~20–30% ML. Single triangular photophore present laterally, posterior to each eye (underlying olfactory papillae), length ~5% HL (~2% ML). Eyes large, diameter ~67% HL (~23% ML), with large lenses, diameter ~35% ED. Funnel length ~29% ML, funnel groove shallow; aperture width ~20% of funnel length, level with posterior lens margin; funnel valve tall, broad. Funnel and mantle components of locking apparatus, nuchal cartilage as in *O. sicula*: funnel component subtriangular, length ~12% ML, maximum width ~7% ML; mantle component obliquely set, length ~10% ML, maximum width ~4% ML; nuchal cartilage oblong, pointed or rounded anteriorly, length ~10% ML, maximum width ~4% ML, tapering posteriorly. Buccal connectives and pores as in *O. sicula*. Olfactory papillae short (length ~4% HL), elliptical (breadth ~2.5% HL), fleshy knobs without sculpture.

No complete, non-regenerating arms among adult specimens (see description of juvenile specimens below); oblong to circular in cross-section. Arm hook pairs not counted, regenerating arms with six pairs of suckers at tips. Single large, oval photophore embedded deeply in base of Arms II–IV, smaller in Arms II. Photophores of Arms III, IV series oval, much smaller than arm-base photophores; presumed to extend to arm tip. All arms with gelatinous aboral tissue, depth ~30% arm depth proximally.

Arm hooks robust (Fig. 17); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp long, smoothly curved; smooth laterally, rarely with shallow lateral ridges; breadth aborally maintained along junction with base or narrowing; inner angle acute in basal hooks (70–80°), becoming increasingly acute distally (50–60°); aperture

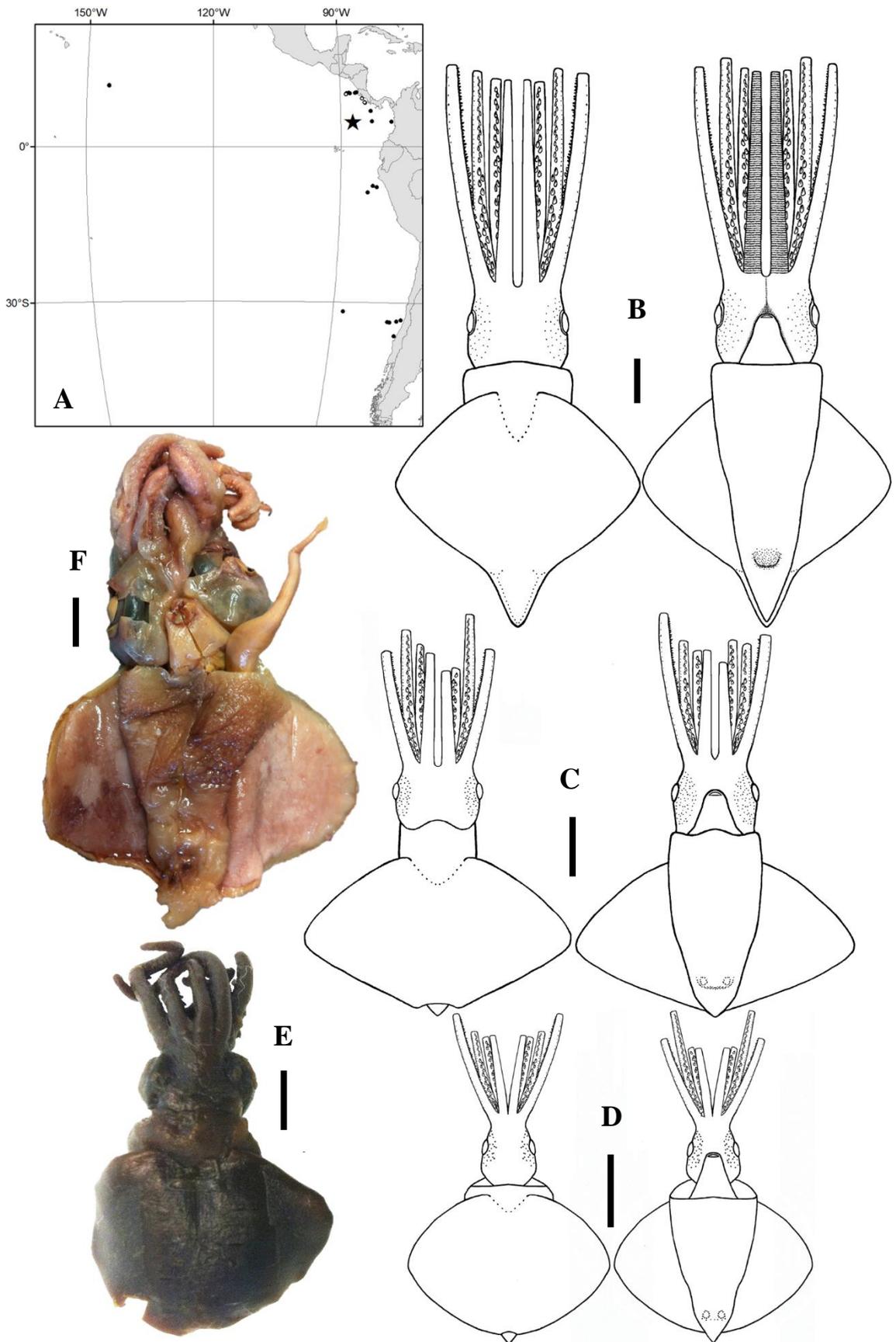


Fig. 16—*Octopoteuthis nielseni*. A) Distribution, star indicates type locality, hollow circles Comparative Material; B) adult; C) juvenile (USNM 1283043, ♀, ML 33 mm); D) post-larva (SBMNH 51435, ♂, ML 21.9 mm); E) NHMUK 1947.7.7.10, syntype, sex indet., ML 18 mm; F) SBMNH 51237, ♂, ML 148 mm. Scale bars = B, F) 25 mm; C, D) 10 mm; E) 5 mm.

open, oval to teardrop shaped. Accessory claws typically absent or as very low points; rarely as prominent slightly curved cusps. Aboral hood absent. Bases crenulated, most prominent oro-laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth). Arm sucker morphology not examined due to limited material.

Tentacles absent, only traces remain in post-larvae (see below).

Recti abdominis and rectum morphology (Fig. 5E, F) as in *O. sicula*. *Recti* photophores near-circular, at ~30% ML anteriorly; diameter ~2% ML; nearly centred, comprising ~70% of *recti abdominis* width. Anal flaps of moderate length, ~2% ML. Ventral visceral mesentery pore small, diameter ~0.5% ML. Gills robust, length ~27% ML, with 26–29 lamellae.

Lower and upper beak, radula, palatine palps, and gladius not examined due to scarcity of subadult and adult specimens.

Colouration (preserved) in adults deep purple to pink over all external body surface where epidermis remains intact; overlying gelatinous tissue unpigmented; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patch overlying posterior ventral mantle photophores darkest posteriorly. Inner mantle surfaces and viscera unpigmented. Small individuals with large, distinct chromatophores evenly spaced across all external surfaces.

Juvenile specimens (ML 23.6–46.6 mm, Fig. 16C) comprise majority of available material; characters and indices differ from above as follows. Mantle broad, width 39–48–56% ML; tail length 13–17% ML; posterior ventral mantle photophores spaced ~14% ML apart, photophore diameter ~4.3% ML. Fins long (71–78–87% ML), very broad (121–128–144% ML); anterior margin of fin at 11–15–19% ML; anterior fin insertion shallow (depth 12–15–18% ML), broad (width 18–22–26% ML). Head length 31–38–42% ML, width 37–41–46% ML; eye diameter 17–22–27% ML, lens diameter 27–31–36% ED; funnel length ~30% ML, aperture width ~23% funnel length. Arm length 69–95–128% ML; formula II>III>I>IV; with 23–30 pairs of hooks in fleshy sheaths followed by 4 or 4+1 pairs of suckers; all arms narrow gradually to tips. Arm-tip photophores occupy distal-most 5–7–10% AL (length ~7% ML); proximally slightly



Fig. 17—*Octopoteuthis nielsenii* armature. A–C) NHMUK 1947.7.7.10, syntype, sex indet., ML 18 mm; D–G) USNM 817351, ♀, ML 121 mm; H–M) SBMNH 51237, ♂, ML 148 mm. A–C) proximal hook (~5th, 6th pair), Arm III: (A) lateral profile, (B) without accessory claws, (C) oblique oral; D) 19D hook, Arm III; E–G) 3V hook, Arm III: (E) lateral profile, (F) aboral, (G) top; H, I) 20V hook, Arm IIR: (H) lateral profile, (I) oblique aperture without accessory claws; J–M) 20V hook, Arm IIR: (J) lateral profile, (K) oblique aperture without accessory claws, (L) aboral, (M) top. Scale bars = A, C) 100 μm; B) 50 μm; D–H, J, L, M) 0.5 mm; I, K) 200 μm.

expanded, distally quickly tapering to slender tip; suckers overlie photophore proximally; arm description included single post-larval specimen (SBMNH 49462, ML 16.5 mm) as indices, counts did not differ significantly from juveniles. Tentacles entirely lacking. Gill length ~38% ML.

Post-larval specimens (ML 16.5–21.9 mm, Fig. 16D), characters and indices differing from above as follows. Mantle broad, ~60% ML; posterior ventral mantle photophores discernable to ML 21.9 mm (SBMNH 51435), associated chromatophore pattern allows species identification to ML 16.5 mm (SBMNH 49463): pair of circular gaps in sparse chromatophores along posterior ventral mantle. Fins long (length ~86% ML), very broad (width ~135% ML); anterior margin of fin at ~17% ML; anterior fin insertion depth ~15% ML, width ~19% ML. Head length ~43% ML, width ~41% ML. Single specimen with complete arms, indices and counts included above in juvenile arm description. Basal-most armature in specimen ML 16.5 mm nearly fully developed hook; in specimen ML 21.9 mm, basal-most hook with adult morphology. Tentacles atrophying, reduced to translucent, gelatinous nubs without structure or definition; length ~3% ML.

Redescription of type material (2 syntypes, Fig. 16E). **NHMUK 1947.7.7.10** and **NHMUK 20180142**, in poor condition (the latter exceptionally so). Both previously severely dehydrated (reported in Stephen [1985a]), subsequently reconstituted (via trisodium orthophosphate, Steedman's Solution). Bodies stiff, brittle; colour monotonous brown. NHMUK 1947.7.7.10 broken into three pieces, tissue snip missing from posterior left fin margin; unaccessioned syntype brittle nondescript mass, fins and one arm just discernible. The few morphometrics obtained from NHMUK 1947.7.7.10 align well with mean post-larval indices, reasonably well (69–81–100% of original measures) with those reported by Robson (1948). Ventral mantle damaged; *recti abdominis* photophores discernible, all other photophores undetectable due to condition. Fin length 88% ML, broadly rhombic (142% ML); posteriorly set; with broad shallow anterior fin insertion. Head length (51% ML), trapezoidal, broadest posteriorly (width 54%). Eyes well preserved, large, 44% HL (22% ML). No arms complete. Arm hook general morphology possibly affected by dehydration; accessory claws as short, broad pointed corners along aperture rim. Status of tentacle remnants unknown (Robson gave no reference to tentacles), specimen's attribution into post-larval or juvenile life stage withheld.

Biology. Smallest mature specimen examined ML 148 mm (SBMNH 51237, ♂). Most developed female specimen examined ML 121 mm (USNM 817351). Implanted spermatangia with long, slender sperm mass (e.g., 2.36 x 0.59 mm in specimen ML 148 mm); comparable to morphology observed in *O. sicula*.

Remarks. *Octopoteuthis nielseni* was the sole *Octopoteuthis* species encountered from the southeast Pacific. Two specimens from southeast of Hawaii suggest possible co-occurrence with *O. laticauda* in that region, but can be separated by the single chromatophore patch overlying the PVMPs and the absence of MEPs and EPs (Table 4). *Octopoteuthis nielseni* is similar morphologically to both *O. sicula* and *O. fenestra* sp. nov., the latter of which is also a resident of the south Pacific (although exclusively in the west). Accessory claws are reliably prominent throughout ontogeny in *O. fenestra* sp. nov., and provide the strongest character for separating it *O. nielseni* (for differentiation from *O. sicula*, see *O. sicula* Remarks).

Robson (1948) reported his specimens at ML 26 mm, which would likely group them with juvenile specimens examined herein. However, tissue shrinkage due to dehydration reduced gross morphometrics to 69–81–100% of their original size, notably the ML to 69% of its original length. Given the uncertainty in accurate proportions being maintained through tissue contraction, NHMUK 1947.7.7.10 was excluded from all mean index calculations and described separately. Detailed collection data for the syntypes can be found in Beebe (1926).

Four lots were listed under Comparative Material as they were unable to be confidently attributed morphologically to *O. nielseni* due to their small size and the current lack of taxonomic characters at such sizes. However, they were collected from the same region and, for three lots, cruise that collected seven other lots of *O. nielseni*. Given the scarcity of specimens for *O. nielseni*, these lots were included in the species' distribution plot (Fig. 16A hollow circles).

5.1.1.3. *Octopoteuthis fenestra* sp. nov. (Table 10, Figs 5H, 6D, 7B, 18–22)

Type material (6 specimens). **NIWA 62695**, Holotype, ♀, ML 190 mm, 42°45.29'S, 179°58.68'W, 755 m, 13/06/1996, TAN9608/8, Z8497, BTT; **NMNZ M.287225**, Paratype, ♂, ML 43 mm, 40°39.22'S, 165°34.61'W, Valerie Guyot, Louisville Ridge, 17–101 m, 1957 m, 23/03/1995, RV *Tangaroa*, TAN9503/27; **NMNZ M.287224**, Paratype, ♀, ML 39 mm, 40°55.04'S, 177°24.85'E, E of Castlepoint, New Zealand, 17–110 m, bottom depth 2134 m, 31/03/1995, RV *Tangaroa*, TAN9503/65; **NIWA 71835**, Paratype, ♂, ML 158 mm, 42°49.96'S, 177°12.06'W, 809 m, 21/07/1995, FV *San Waitaki*, Z8339, trawl; **NIWA 71844**, Paratype, ♂, ML 213 mm, 43°09.7'S, 173°51.24'W, 945–966 m, 07/08/1996, TAN9609/54, fine-mesh MWT; **NMNZ M.277829**, Paratype, ♀, ML 208 mm, 48°17'S, 166°08'E, New Zealand, 50–145 m, 16/03/2007, FV *Taiwa Maru* 8, 2388/2.

Additional material examined (39 specimens). **NIWA 84375**, ♂, ML 46 mm, 41°55'S, 175°30'E, 20–100 m, 00/02/1998, TAN9802/200, E6, fine-mesh MWT; **NIWA 84388**, ♀, ML 54 mm, 42°30'S, 175°30'E, 20–100 m, 00/02/1998, TAN9802/196, E10, fine-mesh MWT; **NIWA 84380**, ♀, ML 183 mm, 42°42'S, 180°00'W, 915 m, 06/10/1999, TRIP1278/09, Z9868; **NMNZ M.074363**, ♂, ML 195 mm, 42°43'S, 178°15'W, NW of Chatham Islands, New Zealand, 18/09/1979, FV *Mys Babuskina*, B01/106/79; **NIWA 106190**, ♀, ML 185 mm, 42°43.47'S, 178°05.47'E, Chatham Rise, 985–996 m, 19/08/2015, 1148–1208, TAN1511/126, BTT; **NIWA 75728**, ♂, ML 234 mm, 42°42'S, 169°48'E, 742 m, 20/06/2011, 2310–0100, TRIP3340/94, MWT; **NIWA 71837**, ♀, ML 125 mm, 42°47.17'S, 179°52.5'W, 978–1030 m, 21/06/1999, TAN9908/25, BTT; **NIWA 71836**, ♂, ML 153 mm, 42°47.83'S, 176°40.99'E, 999 m, 19/07/1995, TAN9508/71, Z8309; **NIWA 85959**, sex indet., ML 70* mm, 42°47.92'S, 179°49.76'E, 1036–1038 m, 15/06/2012, 1336–1406, TAN1208/18, BTT; **NIWA 76638**, ♀, ML 222* mm, 42°47.98'S, 177°10.92'W, 929–930 m, 10/07/2007, TAN0709/27, BTT; **NIWA 76606**, ♀, ML 180 mm, 42°48.17'S, 177°18.78'W, 903–910 m, 14/07/2007, TAN0709/62, BTT, OPI/DWO; **NIWA 85958**, sex indet., ML 32 mm, 42°48.65'S, 179°54.41'E, 984–988 m, 15/06/2012, 1859–1929, TAN1208/20, BTT; **NIWA 76607**, ♀, ML 214* mm, 42°48.82'S, 177°15.6'W, 881–890 m, 11/07/2007, TAN0709/33, BTT; **NIWA 95934**, sex indet. (beaks only), fresh ML 206 mm, LRL 13.61 mm, 42°49.71'S, 179°16.62'E, 1053 m, 20/06/2005, 1824–1845, TAN0509/8, BTT; **NIWA 89384**, sex indet., ML 34 mm, 42°50.08'S, 176°23.04'W, 0–850 m, 01/01/2013,

TAN1301/74, fine-mesh MWT; **NIWA 89388**, ♀, ML 175 mm, 42°52.23'S, 179°45.23'E, 863–871 m, 00/01/2013, TAN1301/50, BTT; **NMNZ M.063768**, ♂, ML 196 mm, 42°58.20'S, 174°35.50'E, western Chatham Rise, New Zealand, 836 m, 14/03/1979, RV *James Cook*, J03/26/79; **NIWA 76635**, ♀, ML 177 mm, 42°48.82'S, 177°15.6'W, 1205–1222 m, 18/07/2007, TAN0709/91, BTT; **NMNZ M.118353**, ♂, ML 201 mm, 43°13.5'S, 175°02.80'W, off Chatham Islands, New Zealand, 772 m, 07/01/1994, RV *Tangaroa*, TAN9401/34; **NIWA 71840** (beaks **NIWA 84698**), sex indet., ML 211 mm, 43°51.78'S, 174°17.16'W, 789 m, 12/07/2000, SWA0001/17, Z10750; **NMNZ M.091749**, ♀, ML 196 mm, 44°01.6'S, 178°25.4'E, SE of Mernoo Bank, western Chatham Rise, New Zealand, 785–793 m, 09/12/1985, RV *James Cook*, J21/08/85; **MV F159988**, sex indet., ML 166 mm, 44°11.73'S, 147°09.69'E, Pedra, 1128–1130 m, bottom depth 1128–1139 m, surface temperature 12.5°C, 10/11/92, 09:42–11:00, SS04/92 54, demersal trawl, RV *Southern Surveyor*; Cruise SS04/92, station 54; **MV F78304**, ♂, ML 132* mm, 44°13.6'S, 147°16.73'E, Off Tasmania, 775–900 m, 16/07/1993, MIDOC net, CSIRO Division of Fisheries; **NIWA TAN1401/69**, sex indet., ♂, ML 187, 155 mm, 44°24.58'S, 178°23.7'W; **NIWA 76636**, ♀, VML 222 mm, 44°29.09'S, 174°53.76'W, 1199–1201 m, 22/07/2007, 2106 hr, TAN0709/116, trawl; **NIWA 71834**, ♀, ML 188* mm, 44°37.13'S, 177°53.94'W, 1112 m, 13/10/1998, TAN9812/48, Z9447; **NMNZ M.117830**, ♂, ML 149 mm, 44°40.33'S, 175°21.40'W, off Chatham Islands, New Zealand, 925–1020 m, 29/10/1993, RV *Tangaroa*, TAN9309/134; **NMNZ M.91410**, ♀, ML 49 mm, 44°44.80'S, 173°04.10'E, SE of Timaru, New Zealand, 880–915 m, 19/02/1984, RV *James Cook*, J04/19/84, BTT; **NMNZ M.091416**, ♂, ML 139 mm, 44°55.7'S, 174°05.5'E, SE of Banks Peninsula, New Zealand, 1080–1103 m, 15/06/1984, RV *James Cook*, J10/37/84B; **NMNZ M.117419**, 2 ♂, ML 192, 168 mm, 45°58.18'S, 171°13.77'E, SE of Cape Saunders, New Zealand, 912–992 m, 25/06/1992, FV *Giljanes*, 9201/024, coll. M. Clark; **NMNZ M.306361**, ♂, ML 156 mm, 46°34.22'S, 166°23.15'E, Puysegur Bank, New Zealand, 732–774 m, 06/12/2003, RV *Tangaroa*, TAN0317/70; **NMNZ M.117886**, ♀, ML 208 mm, 46°37.14'S, 166°16.32'E, Puysegur Bank, New Zealand, 814–852 m, 04/12/1993, RV *Tangaroa*, TAN9310/67; **NMNZ M.287222**, ♀, ML 89 mm, 46°39.85'S, 166°18.31'E, Puysegur Bank, New Zealand, 964–966 m, 19/12/1990, FV *Amaltal Explorer*, AEX9/002/177; **NMNZ M.306362**, ♂, ML 162 mm, 46°44.22'S, 166°09.82'E, Puysegur Bank, New Zealand, 928–947 m, 07/12/2003, RV *Tangaroa*, TAN0317/78; **NIWA 71841**, ♀, ML 162 mm, 47°12'S, 148°42'E, 916–1041 m, 27/07/2000, Z10306, TRIP1374/27, BTT; **MV F159464**, ♀, ML 157 mm, 47°10'S,

147°42'E, South Tasman Rise, 10/01/1992, K. Staisch and A. Hinson, A; **MV F159999**, ♀, ML 178 mm, 47°11'S, 148°47'E, South Tasman Rise, 1115 m, K. Staisch and A. Hinson; **NMNZ M.091660**, ♂, ML 62 mm, 47°34'S, 164°54.2'E, Macquarie Ridge, New Zealand, 490 m, bottom depth 1750 m, 30/07/1985, RV *Kaiyo Maru*, KM/111C1/85, Bongo nets; **NIWA 62694**, ♀, ML 169 mm, 48°41.75'S, 170°33.06'E, 850 m, 15/12/2000, TAN0012/82, Z10631.

Unlocalised material examined (1 specimen). **NIWA 84382**, OS LIA 01, ♀, ML 192* mm, unlocalised [southern Australia], *Adriatic Pearl*, coll. L. Triantafillos.

Distribution (Fig. 18A). From southern Tasmania to off eastern New Zealand, 41–49°S, 147°E–166°W; 15–1250 m.

Diagnosis. Accessory claws very prominent; inner angle of main cusp of all arm hooks 90°; Arm II buccal connective dorsal, ventral protective membrane typically fusing laterally to Arm III proximally in females or basally to Arms III in males; anterior fin margin at ~5–11% ML in adults, 11–13% ML in juveniles.

Description (ML 62–234 mm, Figs 18B–22). Mantle conical to slightly goblet shaped; widest at anterior margin, width 40–46–52% ML; weakly muscled; tail thick, long, length 17–23–28% ML; dorsal anterior margin slightly produced medially, ventral margin with slight indentation between mantle components of locking cartilage. Fins large (length 71–76–81% ML), very broad (width 92–106–128% ML); anterior margin at 5–8–12% ML; greatest fin width attained at 50–60% ML. Paired posterior ventral mantle photophores circular, diameter 1.1–1.8–3.1% ML; closely spaced, distance between photophores 7–11–14% ML; embedded basally in gelatinous tissue layer near junction with mantle muscle tissue; together covered by single opaque chromatophore patch, often abraded during collection giving appearance of single chromatophore ring encircling both photophores. Anterior fin insertion blunt posteriorly, depth ~15% ML, width 12–16–24% ML.

Head trapezoidal in outline, length 29–32–37% ML, width 29–32–39% ML, depth 20–30% ML. Single triangular photophore present laterally, posterior to each eye (underlying olfactory papilla), length ~5% HL (~2% ML); occasionally with small, faint, whitish patch approximately same location as inner eyelid photophore of

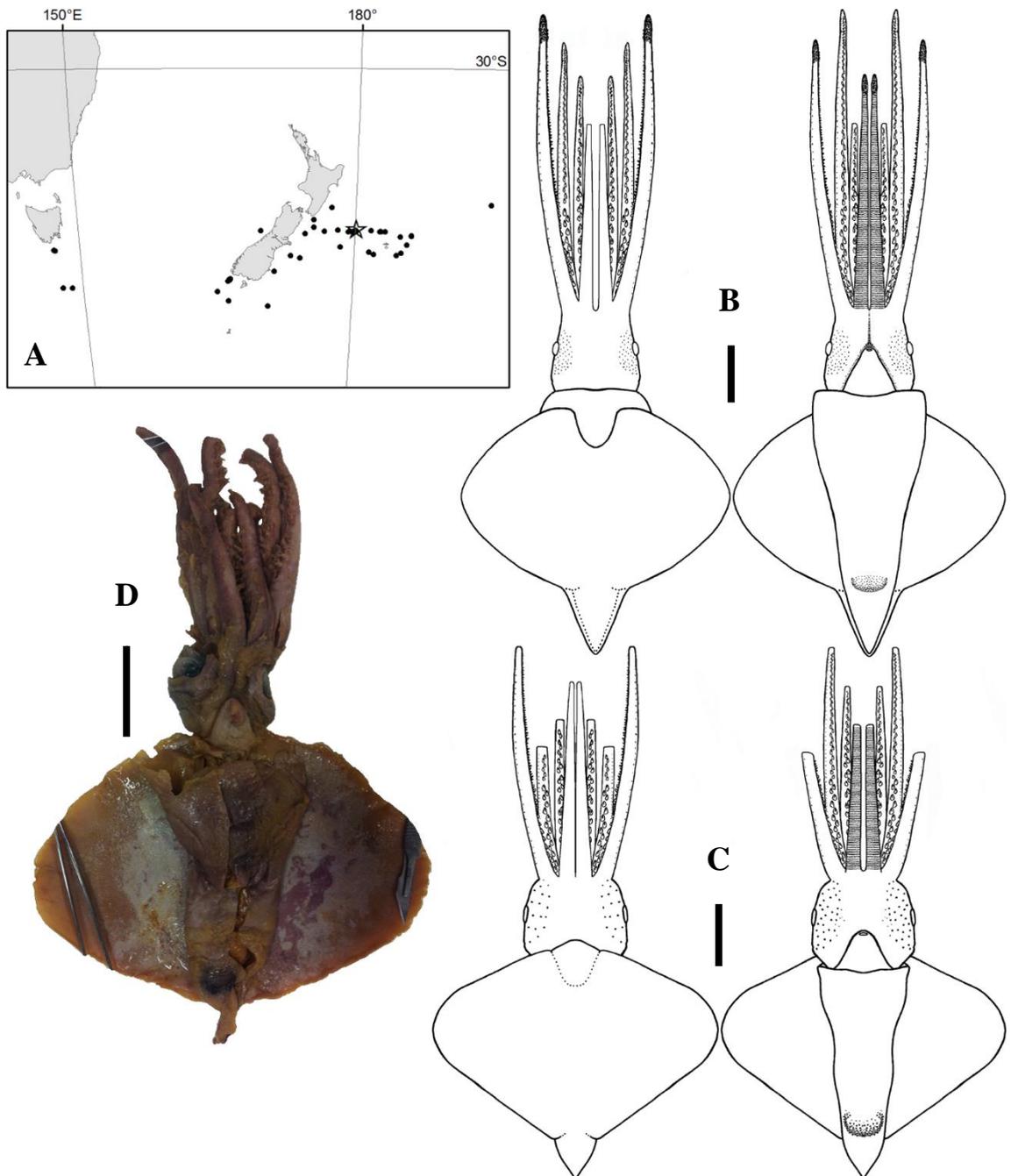


Fig. 18—*Octopoteuthis fenestra* sp. nov. A) Distribution, star indicates type locality; B) adult; C) juvenile (NMNZ M.287224, paratype, ♀, ML 39 mm); D) NIWA 62695, holotype, ♀, ML 190 mm. Scale bars = B, D) 50 mm; C) 10 mm.

megaptera species group but never discrete organ. Eyes large, diameter 39–49–70% HL (12–16–26% ML), with large lenses, diameter ~40% ED. Funnel length 25–27–30% ML, funnel groove shallow; aperture width ~15% funnel length, level with midpoint of eye; funnel valve tall, broad. Funnel and mantle components of locking apparatus, nuchal cartilage as in *O. sicula*: funnel component subtriangular length ~8% ML, maximum width ~4% ML; mantle component oblique, length ~8% ML, maximum width ~5% ML; nuchal cartilage oblong, slightly pointed anteriorly, length ~13% ML, maximum width ~5% ML, set on rhombic cartilaginous pad of equivalent length, width

~9% ML. Dorsal Arm II buccal connective formed from dorsal protective membrane fusing to buccal membrane, occasionally broadly; ventral protective membrane discrete, usually fusing laterally to Arm III proximally in females or reducing in depth proximally and fusing basally to Arms III in males; buccal connectives of Arms I, III, IV as in *O. sicula*. Six pores in buccal membrane: one between paired connectives of Arms I, one between connectives of Arms II (in females) or between dorsal connectives of Arms II and III (in males), one between Arms III and IV (occasionally reduced to pocket in membrane). Olfactory papillae short (length ~3% HL), elliptical (breadth ~3% HL), fleshy knobs without sculpture.

Only two adults examined with complete non-regenerating arms, comprising two of each of Arms II–IV. Arms slender, Arm II length ~121% ML, Arm III length ~109% ML, Arm IV length ~95% ML; oblong to circular in cross-section; with up to 35 pairs of hooks in thick fleshy sheaths, followed by 3 to 12 pairs of suckers distally. Arms taper gradually to tips, from ~6% AL at base to ~3% at midpoint. Arm-tip photophores occupy distal-most ~9% AL (photophore length ~10% ML); of consistent thickness or swelling slightly from photophore base to midpoint; distally tapering to blunt tip or with slight bulb at tip; arm hooks terminate proximal to photophore, suckers overlie proximal third of photophore. Arm-base photophore diameter ~2% AL, smaller in Arms II. Photophore series along ventral Arms III, IV beginning ~10% AL distally from arm-base photophores; comprising ~25–35 oval photophores much smaller than base photophores, terminating proximal to arm tip photophore. Arms with gelatinous tissue aborally, as in *O. sicula*.

Arm hooks robust, tall, upright (Fig. 19); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp long, smoothly curved, without significant broadening aborally or laterally at junction with base, typically with multiple prominent lateral ridges; inner angle ~90° in at least proximal ~60% of hook pairs; aperture open, broad oval proximally becoming narrower and teardrop shaped distally. Accessory claws very prominent, long slightly curved claws or long straight spurs. Aboral hood absent. Bases crenulated, most prominent laterally. Proximal hooks with relatively larger bases (width and breadth). Arm suckers not examined due to limited material.

Tentacles absent from all material examined (likely lost during post-larval stages as in other *Octopoteuthis* spp.).

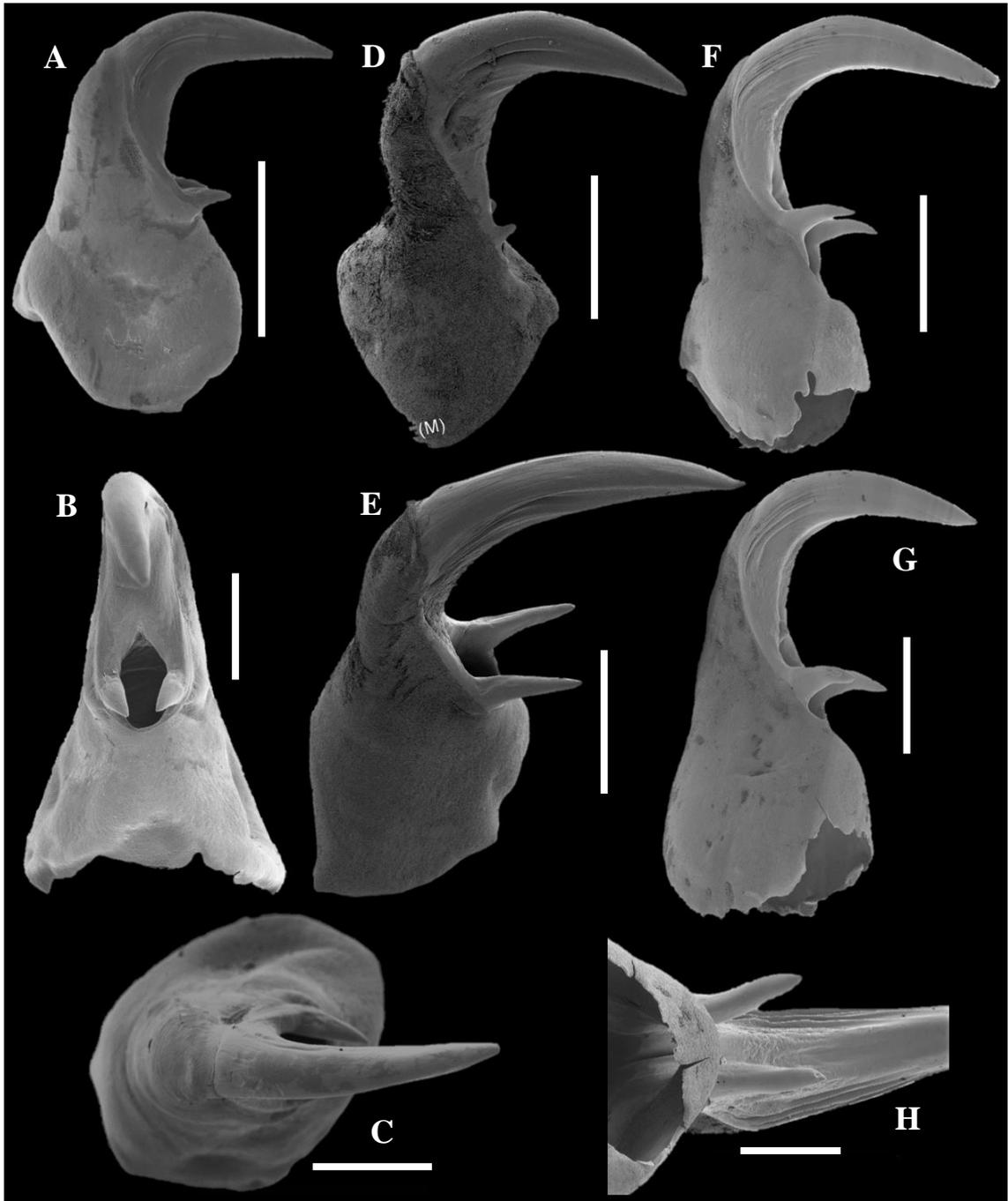


Fig. 19—*Octopoteuthis fenestra* sp. nov. armature A–C) NIWA 76636, ♂, ML 115 mm; D, E) NIWA 76635, ♀, ML 177 mm; F–H) NMNZ M.063768, ♂, ML 196 mm. A–C) 3D hook, Arm II: (A) lateral profile, (B) oral, (C) apical; D) 21V hook, Arm IVL; E) 3V hook, Arm IVL; F) 17V hook, Arm III; G, H) 4D hook, Arm III: (G) lateral profile, (H) basal view of lateral ridges of main cusp. Scale bars = A, E–G) 1 mm; B–D, H) 0.5 mm.

Recti abdominis muscles and rectum morphology (Fig. 5E, F) as in *O. sicula*. *Recti* photophores near-circular, at ~30% ML anteriorly; length ~1.3% ML, width ~1.1% ML; centred to slightly laterally set, comprising 40–50% of *recti abdominis* width. Anal flaps long, length ~2.5% ML. Ventral visceral mesentery pore small, diameter ~0.5% ML;

pore appears as sphincter in membrane. Gills robust; length ~25–30% ML, with 26–28 lamellae.

Lateral profile of lower beak (7.33–10.70 mm LRL, Figs 20A–D) slightly deeper than long, with distal wing tips extending beyond rostral tip by 13–16–19% baseline; rostral tip with deep notch, creating distinctly pointed tip; jaw edge visible, slightly concave due to slight bend in distal third of LRL, with short jaw-edge extension; jaw angle typically 80–95°, obscured slightly by low, rounded wing fold; depth anteriorly from jaw angle greater than posterior. Hood low over crest, length 33–36–39% baseline, usually with shallow hood groove beginning at rostral notch and continuing along hood in line with lateral wall folds. Crest very distinct, typically with narrow strip of lateral wall between fold and crest remaining unpigmented at all sizes; length 69–72–76% baseline; tip free, with concave notch between crest and lateral wall; sloped in nearly straight line. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior 60% of hood length; posterior lateral wall margin straight; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 200–213–220% that at jaw angle, length 70–79–91% LRL, with cartilaginous pad. Ventral view with very broad, very shallow notch in hood; free corners in line with wing breadth midpoint at sizes <~8 mm LRL, narrowing to medial ~30% of wing breadth in sizes >~10 mm LRL. Entire beak excluding wing pigmented by LRL ~7 mm; wings fully pigmented by LRL ~11 mm.

Lateral profile of upper beak (3.01–13.17 mm URL, Figs 20E, F) longer than deep, maximum depth 45% of length. Rostrum very long, ~37% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~80°; low ridge of cartilage present orally along shoulder; oral shoulder margin straight, ventrally protruding as ‘tooth’; cartilage reduced dorsally in largest beaks. Hood long (length 76–78–82% UBL), height 14% UBL; junction of hood and free shoulder straight to slightly concave. Lateral walls approximately rectangular with maximum depth at midpoint, posterior margin straight. Dorsal view with posterior margin of hood and crest straight or slightly concave, posterior margin of crest pigmentation slightly concave. Lateral wall pigmentation begins along crest, darkening antero-ventrally with margin of pigmentation at ~45° to axis of UBL. Crest and lateral wall unpigmented at URL <~4 mm; breadth of posterior lateral wall pigmented by URL ~8 mm, free shoulder and anterior lateral wall

transparent; lateral wall fully pigmented by URL ~ 11 mm, free shoulder partially pigmented; free shoulder fully pigmented in URL $> \sim 13$ mm.

Radula (Figs 21A–C) with tricuspid rachidian: mesocone long or very long, narrowly triangular or conical; lateral cusps short ($\sim 30\%$ mesocone height), straight to slightly laterally directed pointed nubs; base straight to concave. First lateral tooth bicuspid or weakly tricuspid: main cusp equal to rachidian in height, conical to narrowly triangular, straight to slightly medially directed; when present, inner cusp very low blunt corner,

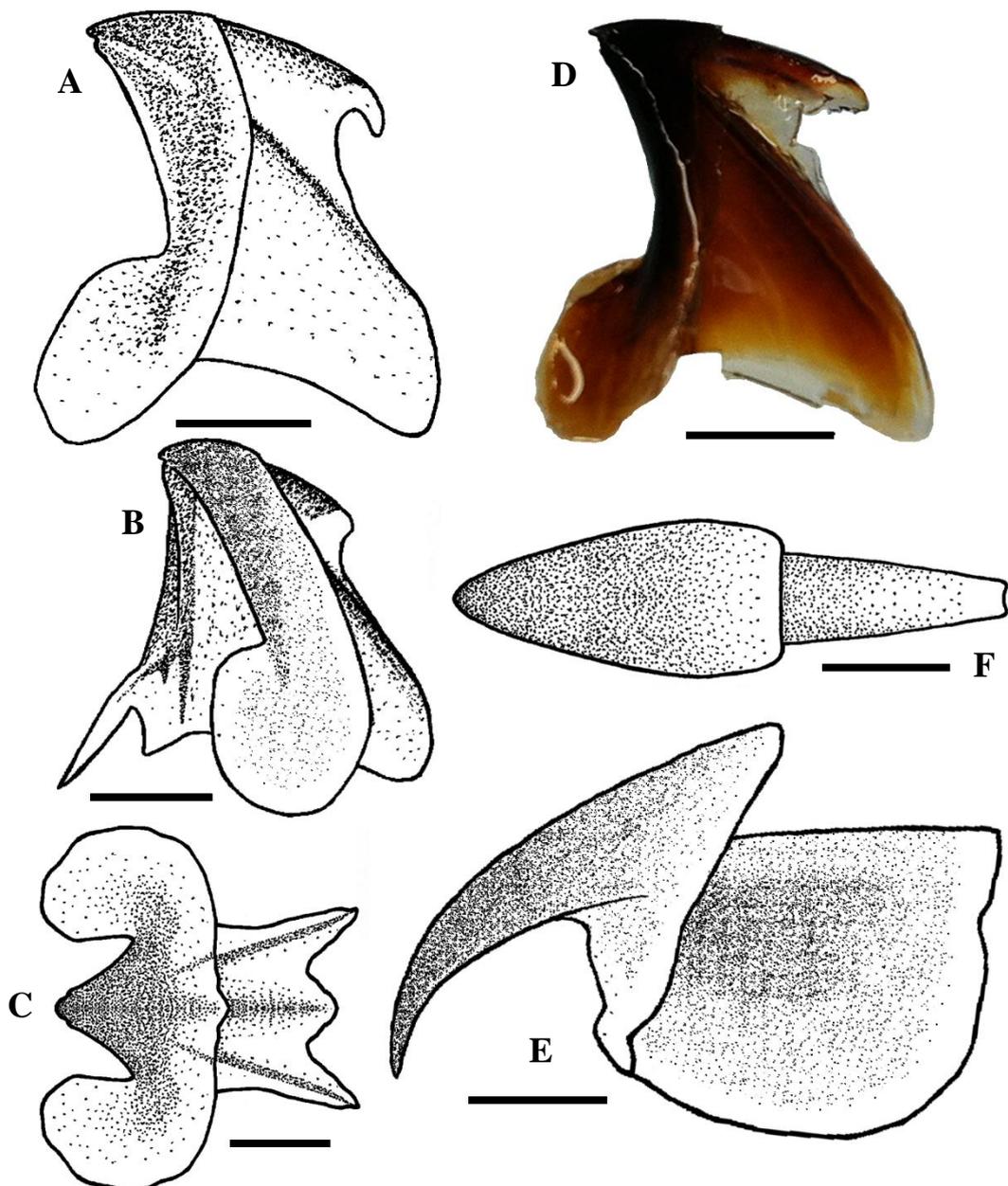


Fig. 20—*Octopoteuthis fenestra* sp. nov. beaks. A–C, E, F) NIWA 76635, ♀, ML 177 mm, LRL 10.7 mm, URL 10.85 mm; D) NIWA 71844, paratype, ♂, ML 213 mm, LRL 10.09 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

~10% height of main cusp; lateral cusp prominent, height ~20% of main cusp; base straight to slightly concave. Second lateral tooth conical, ~130% height of rachidian; simple in specimens with bicuspid first lateral tooth; with corner or low ridge on medial base in specimens with weakly tricuspid first lateral. Marginal tooth simple, conical, 150–200% height of rachidian. Series of regular nubs lateral to marginal tooth series. Palatine palp with 50–60 stout triangular (Fig. 21D) or long narrow teeth (Fig. 21E), each 35–80% or 60–215% rachidian height, smallest along posterior surface; oral end of palp rounded, recessed relative to majority of tooth-bearing length; dorsal margin dentate, densely so posteriorly, teeth evenly arranged along tooth-bearing surface.

Gladius (176*–185* mm GL, Fig. 21F) broad and very thin (<0.1 mm thick), frail, transparent; greatest width (~15% GL) at ~40% GL; free rachis ~8% GL, pointed anteriorly, broadening posterior to maximum width (~3% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden posteriorly to maximum width, then taper

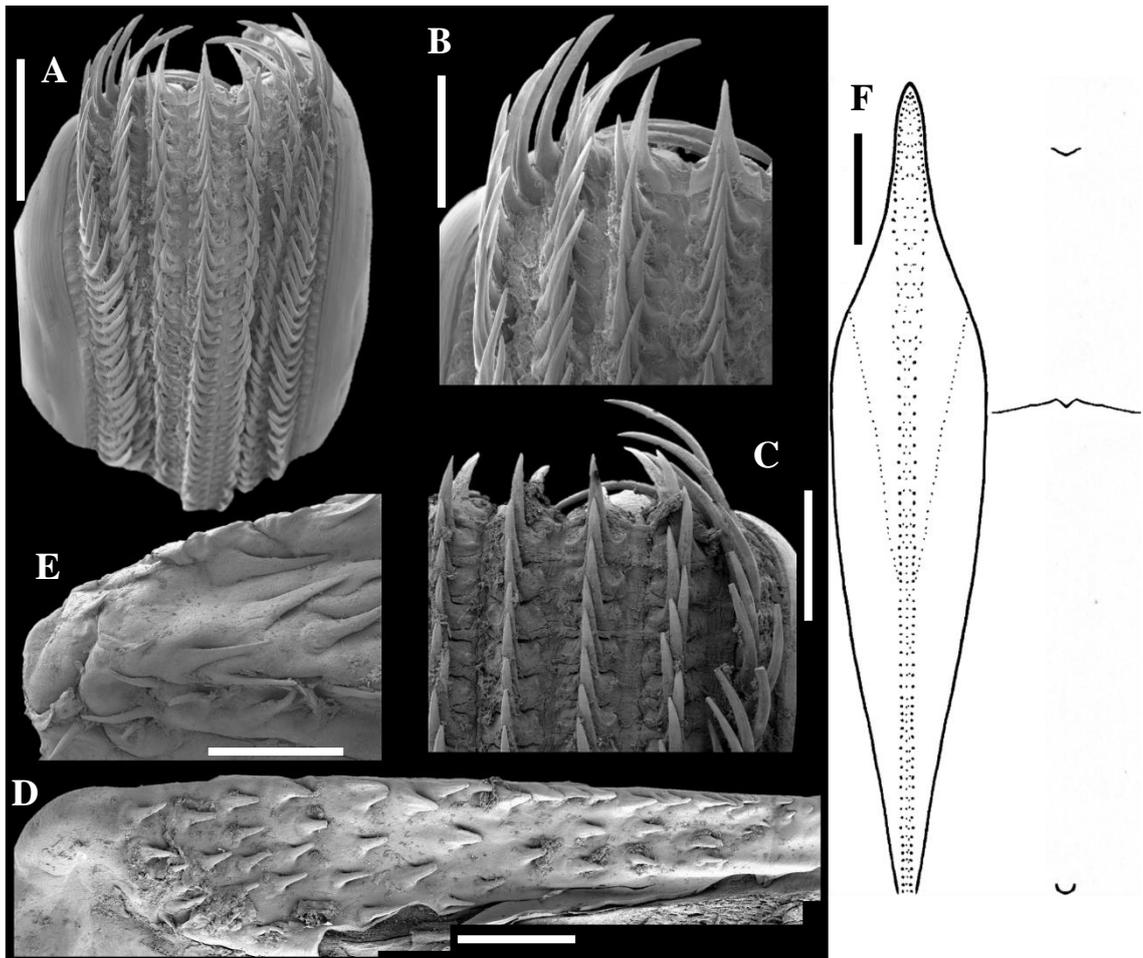


Fig. 21—*Octopoteuthis fenestra* sp. nov. A, B) NMNZ M.306361, ♂, ML 156 mm; C, E) NIWA 71844, paratype, ♂, ML 213 mm; D) NIWA 62694, ♀, ML 169 mm; F) NIWA TAN1401/69, sex indet., ML 187 mm, GL 185* mm. A–C) Radulae; D, E) palatine palp; F) gladius, with cross-sections. Scale bars = A, B, D, E) 1 mm; C) 0.5 mm; F) 25 mm.

gradually for remainder of GL; conus unknown due to damage; rachis broad, evenly concave.

Colour (preserved) in adults deep purple to pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose furrows in females; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patch overlying posterior ventral mantle photophores darkest posterior-laterally. Inner mantle surfaces and viscera unpigmented. Fresh specimens similar but colours more brilliant.

Juvenile specimens (ML 32–49 mm, Fig. 18C) as above, with the following exceptions. PVMP spaced ~14% ML apart; tail length 15–17–22% ML. Fins moderate in length (66–70–72% ML), wide (~116% ML); anterior margin of fin at ~12% ML. Head length 32–42–45% ML, width 32–40–44% ML; eye diameter ~51% HL (~21% ML). One specimen with three intact arms: Arms I length ~101%, Arm II length 133% ML. Tentacles entirely lacking. *Recti abdominis* photophores nearly full width of muscle.

Etymology. The specific epithet *fenestra* (“window, an opening for light”) was chosen to recognise the taxonomic significance of the postero-ventral mantle chromatophore patch. The differing morphology of the chromatophore patch was first established during comparisons between *O. fenestra* sp. nov. and *O. rugosa* from New Zealand collections, and was crucial in the initial delimitation of *Octopoteuthis* species.

Biology. Smallest mature specimen examined ML 156 mm (NMNZ M.306361, ♂). Smallest presumed reproductive female ML 175 mm (NIWA 89388, implanted with spermatangia). Spermatangia globular (length 1.73–2.06 mm, width 1.10–1.27 mm), with short rounded sperm mass as in *O. rugosa* and other *Octopoteuthis* species but not *O. sicula* and *O. nielseni*; genetic sequences obtained from implanted spermatangia from two female *O. fenestra* sp. nov. were conspecific (single lot of *O. sicula* from off Namibia [NIWA 71843, 2 females, 1 male, all mature] also with globular implanted spermatangia). Mated females sparsely implanted, most commonly in rugose furrows of anterior ventral mantle, along ventral head and arm bases; one specimen with several spermatangia in buccal membrane. Male reproductive system greatly enlarged in mature adults: terminal organ extends beyond anterior mantle margin by ~30% ML; length of organ anterior of gill artery ~55% ML, diameter at gill artery ~7% ML.

Relationships between LRL and URL against ML and body mass were best described by power equations (Fig. 22). Relationships fit the data well ($R^2 > 0.8$) despite small sample sizes (LRL: $n = 19$; URL: $n = 15$) and a skew toward adults. Females appear to have greater beak measures than do males of the same ML. Previous genus regressions (Clarke 1980; Lu & Ickeringill 2002) overestimated body size relative to the regressions calculated herein, although they corresponded well to the raw measures of ML and body mass for male and sex indeterminate specimens.

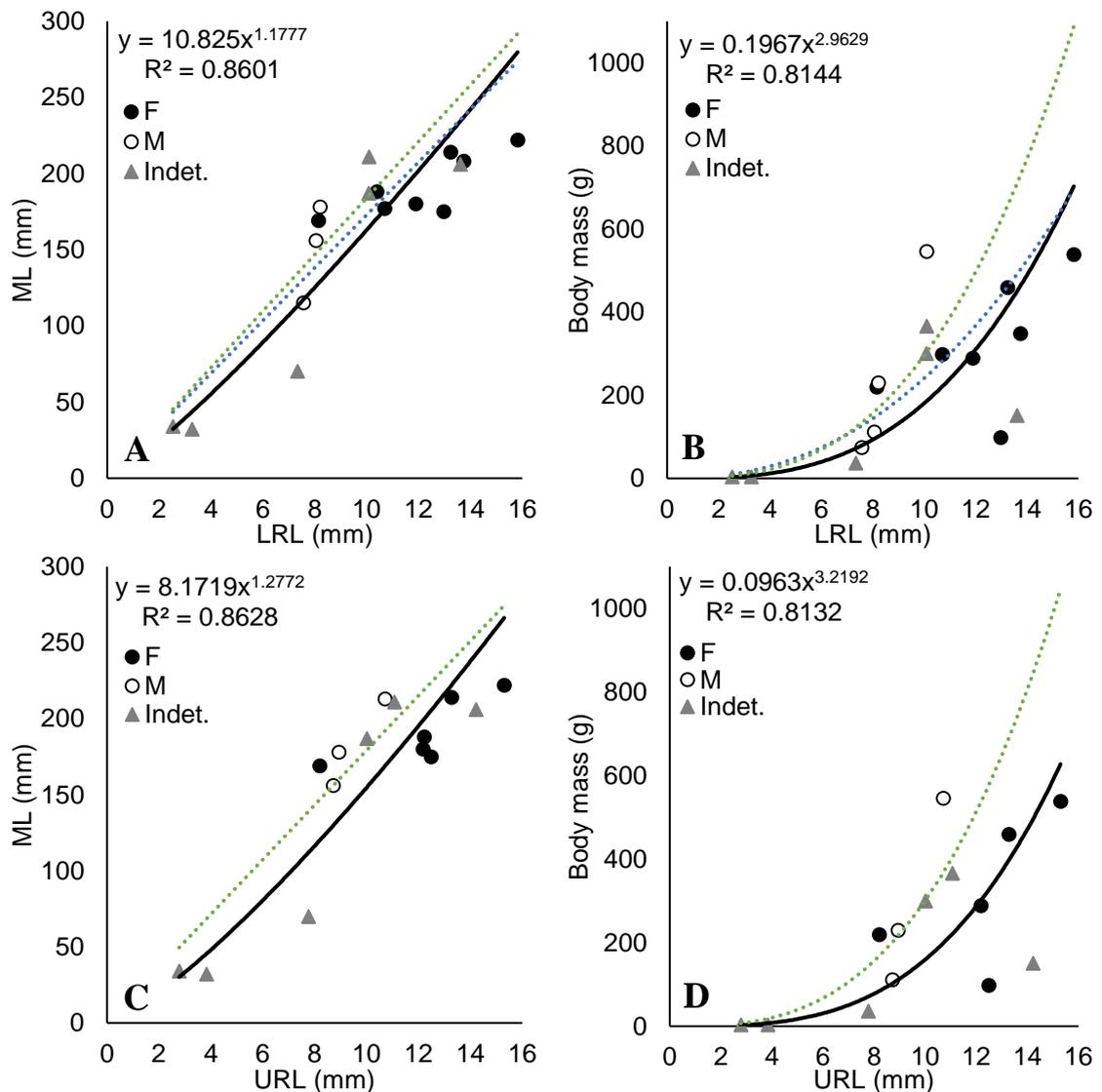


Fig. 22—*Octopoteuthis fenestra* sp. nov. Regressions of lower rostral length (LRL) against (A) dorsal mantle length (ML) and (B) preserved wet body mass, by sex; upper rostral length (URL) against (C) ML and (D) preserved wet body mass, by sex. Models of best fit (greatest R^2 value) are plotted in black against genus regressions of Clarke (1980; blue), Lu and Ickeringill (2002; green).

Remarks. *Octopoteuthis fenestra* sp. nov. is frequently collected from the same region as *O. rugosa*. However, specimens of these species can be readily separated by the single chromatophore patch overlying paired PVMP, absence of MEPs and EPs, and a single dorsal buccal connective on Arms II in *O. fenestra* sp. nov. (compared to paired chromatophore patches, MEPs, EPs and Arm II buccal connectives in *O. rugosa*).

Some specimens of *O. fenestra* sp. nov. appear to have faint whitish patches in the region of MEPs; however, these were never the distinct, pearly, rounded organs as in the *megaptera* and *deletron* species groups.

5.1.2. *megaptera* Species Group. With two PVMP overlain by separate chromatophore patches (occasional medial overlap), often reduced to rings due to epidermal abrasion; one photophore dorsally on each *recti abdominis* muscle; one LHP, MEP, EP on each side of head; one photophore at base of each of Arms II–IV; photophore series along ventral brachial nerve of Arms III and IV. Arms IV with thin densely set transverse pigment bands aborally. Arm hooks with prominent accessory claws; without aboral hood on main cusp; basal-most hook pattern VVDD. 2–14 pairs of arm-tip suckers.

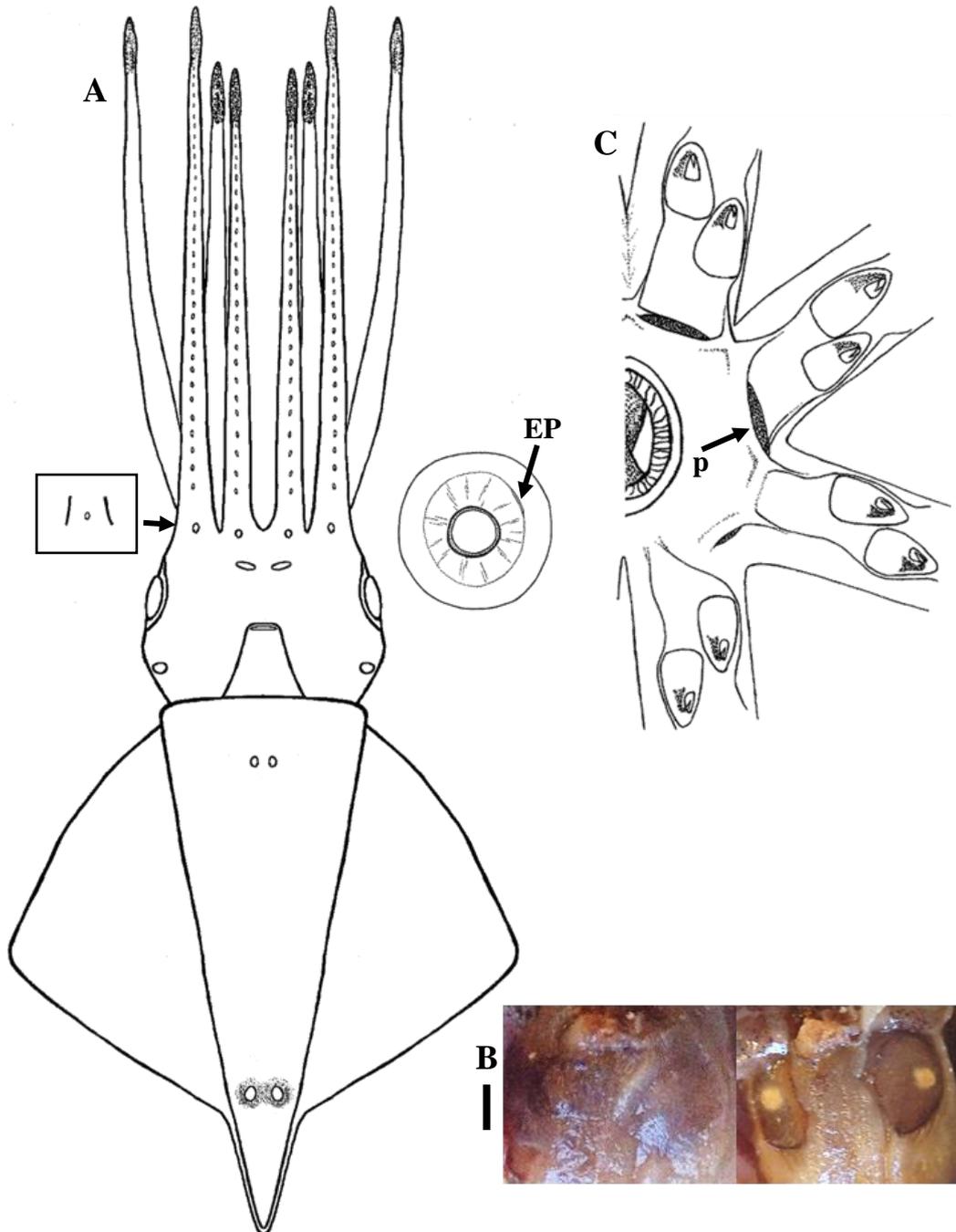


Fig. 23—*megaptera* species group general morphology. A) Ventral photophore pattern; B) paired chromatophore patches in *O. megaptera* (USNM 1221577, ♀, ML 135 mm): natural state (left) and dissected (right); C) oral surface as in *O. megaptera, laticauda* and sp. IO nov.: single dorsal buccal connective Arm II and large pore (p) between Arms II and III (for *O. rugosa*, see species description). Scale bar = 5 mm.

5.1.2.1. *Octopoteuthis megaptera* (Verrill, 1885) (Table 11, Figs 5E, 6B, 6E, 23B, 24–29)

Ancistrocheirus megaptera Verrill, 1885: 399–400, Pl. 42, Figs 1, 1a.

Type material (not examined; reported lost by Roper and Sweeney [1978]). **USNM 40128**, Holotype (no longer extant, see Roper & Sweeney 1978), sex unknown, ML 44 mm, 39°12'N, 72°03.5'W, 1292 m, 13/09/1884, RV *Albatross*, stn 2235, large beam trawl.

Material examined (104 specimens). **USNM 817939**, ♂, ML 116 mm, 44°55.8'N, 21°55.2'W, 03/05/1979, RV *Anton Dohrn*, 374-79, 1600 mesh Engel trawl; **USNM 1192550**, ♂, ML 49.5 mm, 40°02.86'N, 67°27.92'W, N of Bear Seamount, 964 m, 4.4°C at depth, 02/09/2012, 11:45:59–12:15:59, FSV *Pisces*, 15, MWT, M. Vecchione, S. Bush; **USNM 1077449**, ♀, ML 35 mm, 39°55.98'N, 67°28.5'W, Bear Seamount, Massachusetts, USA, 1993–2097 m, 25/07/2002, RV *Delaware II*, 30, IGYPT; **USNM 1080228**, sex indet., ML 24 mm, 39°52.02'N, 67°20.52'W, Bear Seamount, Massachusetts, USA, 2134–2545 m, 27/07/2002, RV *Delaware II*, 40, IGYPT, M. Vecchione, Bear Seamount Expedition; **USNM 1192531**, sex unknown, ML unknown [damaged mantle tissue only], 39°43.63'N, 67°30.63'W, S of Bear Seamount, 1066 m, 4.3°C at depth, 01/09/2012, 06:19:56–07:19:29, FSV *Pisces*, 10, MWT, M. Vecchione, S. Bush; **USNM 730363**, sex NM, ML NM, 38°40.2'N, 72°33'W, off USA east coast, 0–630 m, 19/05/1974, RV *Albatross IV*, 74-5-08N, 3 m IKMWT; **USNM 815744**, ♂, sex indet., ML 44, 22* mm, 38°23.2'N, 63°48.4'W, 01/03/1982, RV *Kaiyo Maru*, KMT33, Kaiyo Maru trawl; **ZMH 11177**, ♂, ML 65 mm, 37°22'N, 013°42'W, Africa, 140–160 m, 17/01/1968, RV *Walther Herwig I*, 1968, stn 4, cruise #23, Schulz; **USNM 575596**, sex NM, ML NM, 29°13.8'N, 87°40.2'W, S of Mobile, Alabama, USA, 26/04/1961, RV *Oregon*, 3250, 60 ft MWT; **USNM 575124**, sex NM, ML NM, 29°10.2'N, 87°55.2'W, S of Mobile, Alabama, USA, 896–1097 m, 12/06/1953, RV *Oregon*, 796, 40 ft flat trawl; **USNM 1179446**, sex indet., ML 41 mm, 28°28.58'N, 87°34.89'W, eastern Gulf of Mexico, 2528–2571 m, 27/02/2010, RV *Pisces*, 22, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179397**, sex NM, ML NM, 28°24.56'N, 87°2.27'W, eastern Gulf of Mexico, 960–1124 m, 21/02/2010, RV *Pisces*, 14, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179398**, sex indet., ML 47 mm, 28°24.56'N, 87°2.27'W, eastern Gulf of Mexico, 960–1124 m, 21/02/2010, RV *Pisces*, 14, Aleutian wing trawl, NOAA, MMS Collections,

SWAPS; **USNM 1179477**, sex indet., ML 27 mm, 28°8.74'N, 88°20.08'W, eastern Gulf of Mexico, off Louisiana, USA, 2017–2133 m, 01-02/03/2010, RV *Pisces*, 34, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179500**, sex NM, ML NM, 28°8.63'N, 88°45.75'W, eastern Gulf of Mexico, off Louisiana, USA, 1522–1826 m, 01/03/2010, RV *Pisces*, 37, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179501**, ♀, ML 31 mm, 28°8.63'N, 88°45.75'W, eastern Gulf of Mexico, off Louisiana, USA, 1522–1826 m, 01/03/2010, RV *Pisces*, 37, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179516**, sex NM, ML NM, 28°8.63'N, 88°45.75'W, eastern Gulf of Mexico, off Louisiana, USA, 1522–1826 m, 01/03/2010, RV *Pisces*, 37, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179409**, sex NM, ML NM, 27°57.89'N, 86°57.17'W, eastern Gulf of Mexico, 2913–3006 m, 22/02/2010, RV *Pisces*, 15, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179428**, sex NM, ML NM, 27°35.18'N, 87°10.03'W, eastern Gulf of Mexico, 3060–3069 m, 24/02/2010, RV *Pisces*, 20, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179463**, ♂, ML 35 mm, 27°34.22'N, 87°41.04'W, eastern Gulf of Mexico, 2801–2896 m, 23/03/2010, RV *Pisces*, 26, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179420**, sex indet., ML 35 mm, 27°33.15'N, 86°46.74'W, eastern Gulf of Mexico, 3135–3180 m, 23/02/2010, RV *Pisces*, 16, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179697**, ♀, est. ML 45 mm, 27°24.8'N, 89°7.22'W, off Louisiana, USA, 1820–1935 m, 28/07/2009, RV *Gordon Gunter*, 12, 174 ft MWT, NOAA, MMS Collections, SWAPS; **USNM 1179508**, ♂, ML 94 mm, 27°1.46'N, 89°22.93'W, central Gulf of Mexico, 2446–2659 m, 18–28/02/2010, RV *Pisces*, 50, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179515**, sex indet., ML 30* mm, 27°01.46'N, 89°22.93'W, central Gulf of Mexico, 2446–2659 m, 18–28/02/2010, RV *Pisces*, 50, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179473**, sex indet., ML 21 mm, 26°40.8'N, 87°28.72'W, eastern Gulf of Mexico, 2831–2835 m, 20/03/2010, RV *Pisces*, 28, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179439**, sex NM, ML NM, 26°29.95'N, 87°21.04'W, eastern Gulf of Mexico, 2795–2916 m, 25/02/2010, RV *Pisces*, 21, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179470**, sex NM, ML NM, 26°24.22'N, 87°29.12'W, eastern Gulf of Mexico, 2996–3008 m, 24/03/2010, RV *Pisces*, 30, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179472**, sex indet., ML 23 mm, 26°24.22'N, 87°29.12'W, eastern Gulf of Mexico, 2996–3008 m, 24/03/2010, RV *Pisces*, 30, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 817942**,

♀, ML 155 mm, 24°42'N, 60°30'W, 23/03/1979, RV *Anton Dohrn*, 46-I-79, 1600 mesh Engel trawl; **USNM 1179636**, sex unknown, ML 40 mm, 24°36.81'N, 84°23.03'W, SE Gulf of Mexico, off Florida, USA, 2484–3487 m, 17/02/2010, RV *Pisces*, 87, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179637**, sex indet., ML 108 mm, 24°36.81'N, 84°23.03'W, SE Gulf of Mexico, off Florida, USA, 2484–3487 m, 17/03/2010, RV *Pisces*, 87, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179640**, ♀, ML 52 mm, 24°17.76'N, 84°02.74'W, SE Gulf of Mexico, off Florida, USA, 1608–1643 m, 17/03/2010, RV *Pisces*, 89, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179641**, sex indet., ML 39 mm, 24°17.76'N, 84°02.74'W, SE Gulf of Mexico, off Florida, USA, 1608–1643 m, 17/03/2010, RV *Pisces*, 89, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179642**, sex indet., ML 43 mm, 24°17.76'N, 84°02.74'W, SE Gulf of Mexico, off Florida, USA, 1608–1643 m, 17/03/2010, RV *Pisces*, 89, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179643**, ♀, ML 70 mm, 24°17.76'N, 84°02.74'W, SE Gulf of Mexico, off Florida, USA, 1608–1643 m, 17/03/2010, RV *Pisces*, 89, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179644**, ♂, ML 74 mm, 24°17.76'N, 84°02.74'W, SE Gulf of Mexico, off Florida, USA, 1608–1643 m, 17/03/2010, RV *Pisces*, 89, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **USNM 1179655**, sex indet., ML 39 mm, 23°56.27'N, 83°10.41'W, SE Gulf of Mexico, off Florida, USA, 1095–1268 m, 14/03/2010, RV *Pisces*, 92, Aleutian wing trawl, NOAA, MMS Collections, SWAPS; **ZMH 11216**, ♀, ML 197 mm, 20°14'N, 021°35'W, Africa, 40–60 m, 28/01/1968, RV *Walther Herwig I*, 1968, stn 10, cruise #23, Schulz; **USNM 814610**, ♀, ML 110 mm, 18°28.8'N, 29°13.2'W, Cape Verde Basin, 150–155 m, 26/11/1970, RV *Atlantis II*, RHB-2086, 3 m IKMWT, R.H. Backus; **USNM 1221579**, ♂, sex indet., ML 97, 85 mm, 17°24'N, 22°57'W, 293–305 m, 17/04/1971, RV *Walther Herwig*, 498-II-71, 1600 mesh Engel trawl; **USNM 885280**, ♀, ML 115 mm, 17°22.2'N, 22°58.2'W, Cape Verde, 102–105 m, 17/04/1971, RV *Walther Herwig*, 498-I-71, 1600 mesh Engel trawl; **ZMH 11180**, ♂, ML 74 mm, 16°14'N, 22°24'W, Africa, 140–160 m, 29/01/1968, RV *Walther Herwig I*, 1968, stn 11, cruise #23, Schulz; **ZMH 11201**, ♂, ML 89 mm, 08°29'N, 24°07'W, Africa, 140–160 m, 31/01/1968, RV *Walther Herwig I*, 1968, stn 13, cruise #23, Schulz; **NSMT Mo61156**, 2♀, ML 138, 89* mm, 07°53'N, 54°05'W, 850 m, 29/06/1980, JAMARC; **NSMT Mo60776**, ♂, ML 120 mm, 07°51'N, 54°07'W, off Suriname, 835 m, 23/07/1981, JAMARC; **NSMT Mo61134**, ♂, ML 115 mm, 07°51'N, 54°02'W, 810 m, JAMARC; **NSMT Mo61135**, ♀, ♂, ML 81, 79 mm, 07°51'N, 54°14'W, 830 m, 08/10/1979, JAMARC; **NSMT Mo61138**, ♀, 2♂, ML 175,

108*, 73 mm, 07°51'N, 54°18'W, 200 m, 27/04/1980, JAMARC; **NSMT Mo61157**, ♀, ML 181 mm, 07°51'N, 54°07'W, 760 m, 14/10/1979, JAMARC; **NSMT Mo61136**, ♀, ML 104 mm, 07°50'N, 54°09'W, off Suriname, 810 m, 14/06/1980, BTT, JAMARC; **NSMT Mo61137**, ♀, ML 177 mm, 07°50'N, 54°17'W, off Suriname, 740 m, 13/10/1979, JAMARC; **NSMT Mo61154**, ♂, ML 112* mm, 07°50'N, 54°01'W, off Suriname, 810 m, 27/06/1980, BTT, JAMARC; **NSMT Mo60857**, ♂, ML 112* mm, 07°48'N, 54°39'W, 780 m, 06/08/1981, JAMARC; **NSMT Mo61152**, ♂, ♀, ML 113, 71 mm, 07°48'N, 54°13'W, off Suriname, 532 m, 29/09/1979, JAMARC; **NSMT Mo61158**, 2♀, ML 177, 96 mm, 07°48'N, 54°12'W, off Suriname, 750 m, 26/06/1980, BTT, JAMARC; **NSMT Mo61153**, ♀, ML 99 mm, 07°40'N, 53°43'W, 600 m, 18/06/1979, JAMARC; **USNM 1221577**, ♀, ML 135 mm, 04°37.8'N, 19°40.8'W, 746–756 m, 13/04/1971, RV *Walther Herwig*, 482-III-71, 1600 mesh Engel trawl; **USNM 885288**, ♂, 2♀, ML 103, 34, 29 mm, 04°36'N, 19°40.2'W, 246–256 m, 13/04/1971, RV *Walther Herwig*, 482-II-71, 1600 mesh Engel trawl; **USNM 885285**, sex indet., 2♂, ♀, ML 109, 102, 86, 86 mm, 04°34.2'N, 19°39'W, 100–104 m, 13/04/1971, RV *Walther Herwig*, 482-I-71, 1600 mesh Engel trawl; **USNM 885289**, 2 sex indet., ML 34, 32 mm, 04°34.2'N, 19°39'W, , 100–104 m, 13/04/1971, RV *Walther Herwig*, 482-I-71, 1600 mesh Engel trawl; **Escáñez 06_0_N**, sex indet., ML 15.3 mm, 03°27.36'N, 25°09.24'W, 0–800 m, bottom depth 4170 m, 15/04/2015, 21:47, RV *Hesperides* ICM_CSIC, PEL6, 06_0_N, trawl, A. Escáñez; **ZMH 11199**, ♂, ML 52* mm, 00°20'N, 25°20'W, Africa, 70–90 m, 02/02/1968, RV *Walther Herwig I*, 1968, stn 15, cruise #23, Schulz; **Escáñez 05_I_N**, sex indet., ML 8.1 mm, 00°09.42'S, 26°17.64'W, 0–800 m, bottom depth 3482 m, 13/04/2015, 22:26, RV *Hesperides* ICM_CSIC, PEL5, 05_I_N, trawl, A. Escáñez; **ZMH 11197**, ♀, ML 105 mm, 04°43'S, 026°39'W, Africa, 2000 m, 04/02/1968, RV *Walther Herwig I*, 1968, stn 17, cruise #23, Schulz; **USNM 730682**, ♀, ML 144 mm, 05°30'S, 16°28.2'W, 1850–1900 m, 09/04/1971, RV *Walther Herwig*, 467-71, 1600 mesh Engel trawl; **ZMH 11171**, ♀, sex indet., ML 135, 120 mm, 09°41'S, 27°39'W, Brazil, 160–400 m, 21/05/1966, RV *Walther Herwig*, 1966, stn 188, cruise #15, Schulz; **ZMH 11210**, sex indet. (head only), HL 51 mm, 09°41'S, 27°39'W, Brazil, 160–400 m, 21/05/1966, RV *Walther Herwig*, 1966, stn 188, cruise #15, Schulz; **ZMH 11173**, ♀, ML 145 mm, 09°43'S, 27°07'W, Brazil, 80–100 m, 05/02/1968, RV *Walther Herwig I*, 1968, stn 19, cruise #23, Schulz; **USNM 885283**, ♀, ML 111 mm, 13°07.2'S, 09°01.8'W, 990–1010 m, 06/04/1971, RV *Walther Herwig*, 455-III-71, 1600 mesh Engel trawl; **Haimovici E499**, sex indet., ML 26 mm, 13°23.83'S, 38°37.54'W, Bahia, Brazil, 761 m, 4.6°C at depth, 08/06/2000, RV *Thalassa*, E 499, Bahia II cruise,

ARROW BTT, M. Haimovici; **Haimovici E505**, ♂, ML 128 mm, 14°36.61'S, 38°49.35'W, Bahia, Brazil, 1067 m, 2.7°C at depth, 10/06/2000, RV *Thalassa*, E 506, Bahia II cruise, ARROW BTT, M. Haimovici; **Haimovici E507**, ♂, ML 51 mm, 15°08.6'S, 38°40.64'W, Bahia, Brazil, 1026 m, 3°C at depth, 11/06/2000, RV *Thalassa*, E 507, Bahia II cruise, ARROW BTT, M. Haimovici; **Haimovici E524**, ♂, ML 56 mm, 19°43.66'S, 38°39.84'W, Bahia, Brazil, 925 m, 3.4° at depth, 27-Jun-00, RV *Thalassa*, E 524, Bahia II cruise, ARROW type bottom trawl, M. Haimovici; **Haimovici E550**, ♂, ML 159 mm, 21°26.32'S, 39°49.11'W, Bahia, Brazil, 1598 m, 2.7°C at depth, 07/07/2000, RV *Thalassa*, E 550, Bahia II cruise, ARROW BTT, M. Haimovici; **ZMH 11172**, ♀, ML 165 mm, 23°20'S, 33°22'W, Brazil, 140–160 m, 09/02/1968, RV *Walther Herwig I*, 1968, stn 23, cruise #23, Schulz; **USNM 1221580**, sex indet. (head only), HL NM, 24°19.2'S, 00°22.8'E, 296–300 m, 02/04/1971, RV *Walther Herwig*, 439-II-71, 1600 mesh Engel trawl; **ZMH 11170**, ♂, ML 132 mm, 25°27'S, 036°56'W, Brazil, 90–160 m, 26/05/1966, RV *Walther Herwig*, 1966, stn 193, cruise #15, Schulz; **ZMH 11175**, ♂, ML 102 mm, 27°57'S, 40°52'W, Brazil, 110–580 m, 27/05/1966, RV *Walther Herwig*, 1966, stn 194, cruise #15, Schulz; **ZMH 10794**, ♂, ML 77 mm, 32°44'S, 48°43'W, Brazil, 70–580 m, 29/05/1966, RV *Walther Herwig*, 1966, stn 196, cruise #15, Schulz; **ZMH 11226**, ♀, ML 165 mm, 34°00'S, 47°34'W, Brazil, 130–150 m, 14/02/1968, RV *Walther Herwig I*, 1968, stn 28, cruise #23, Schulz; **USNM 885282**, sex NM, ML NM, 38°37.8'S, 52°1.8'W, 240–262 m, 05/03/71, RV *Walther Herwig*, 350-II-71, 1600 mesh Engel trawl.

Unlocalised material examined (4 specimens). **USNM 1192580**, sex indet., ML 15 mm, Bear Seamount, 07/09/12, FSV *Pisces*, 36, plankton trawl, M. Vecchione, S. Bush; **NSMT Mo61155**, ♀, ML 46 mm, off Suriname, JAMARC; **ZMH 11166**, 2♀, ML 128, 115 mm, Argentina, 1966, RV *Walther Herwig*, 1966, no stn, cruise #15, Patagonia, Schulz.

Additional genetic samples (3 samples). **PC10-B0625-2888-MTB082-SD**, sex unknown, ML unknown, 28°00.82'N, 87°57.43'W, 0–724 m, 25/06/2011, 1604–1727, RV *Pisces*, cruise 10, IH trawl, M. Vecchione; **PC10-B0708-2791-MTSW8-SN**, sex unknown, ML unknown, 26°59.16'N, 91°05.50'W, 0–709 m, 08/07/2011, 0327–0450, RV *Pisces*, cruise 10, IH trawl, M. Vecchione; **PC10-01 stn 092**, sex unknown, ML unknown, 23°56.27'N, 83°10.41'W, 14/03/2010, RV *Pisces*, M. Vecchione.

Distribution (Fig. 24A). Temperate to tropical Atlantic, including Gulf of Mexico, 58°N–40°S; 0–3500 m.

Diagnosis. Arms long (~92% ML); Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III; arm hooks narrow aborally; anterior fin margin at 6–14% ML; tail long (17–32% ML).

Description (ML 65–197 mm, Figs 24B–29). Mantle conical to weakly goblet shaped; widest at anterior margin, width 29–34–45% ML; weakly muscled; tail long, length 17–25–32% ML; dorsal anterior margin weakly pointed medially, ventral margin with slight indentation between mantle components of locking apparatus. Fins moderately long (length 61–66–71% ML), broad (width 79–89–103% ML), greatest width attained at 40–50% ML; anterior margin at 6–9–14% ML; width of fin continuation along tail ~3% ML. Paired PVMPs circular, diameter ~1.6% ML; set laterally along posterior ventral mantle, distance between photophores ~10% ML. Anterior fin insertion blunt posteriorly, rounded, depth 10–13–16% ML, width 11–14–17% ML.

Head trapezoidal in outline, length 29–31–35% ML, width 23–26–29% ML, depth 20–25% ML. LHP triangular, length ~5% HL (~2% ML); MEPs narrowly oblong, level with anterior margin of lens, oriented ~45° to body axis, length ~8% HL (~2% ML), width ~2% HL (~0.5% ML); EPs crescent shaped, length ~13% HL (~4% ML), width ~0.8% HL (~0.3% ML). Eyes large, diameter 53–62–73% HL (~18% ML), with large lenses, diameter 30–37–44% ED. Funnel length ~23% ML; aperture width ~20% of funnel length, level with posterior margin of lens; funnel valve tall, broad; funnel groove shallow. Funnel component of locking apparatus subtriangular (Fig. 25A); groove broadest posteriorly (~80% cartilage width), narrowing antero-medially to slender channel; medial margin of groove concave leaving raised plateau medial to groove; lateral margin convex to slightly sinusoidal, with smaller plateau antero-laterally; length ~9% ML, maximum width ~5% ML. Mantle component of locking apparatus oblique, conical, broadly triangular, posteriorly narrowing rapidly to slender ridge in anterior half (Fig. 25B); surrounded by narrow groove laterally and anteriorly; length ~7% ML, maximum width ~4% ML. Nuchal cartilage oblong, bluntly pointed anteriorly (Fig. 25C); with medial groove flanked by ridges (groove and ridges of equivalent width), flanked by broader grooves pointed antero-medially; length ~12% ML, maximum width ~5% ML; set on rhombic cartilaginous pad of equivalent length,

Table 11. Measurements (mm) of *Octopoteuthis megaptera*. Mean indices were calculated from specimens ML >56 mm with undamaged dimensions, and 'Side' indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	ZMH	NSMT	USNM	ZMH	Mean index	USNM 885288	USNM 885288	Escáñez 06_O_N						
Type status	None	None	None	None	None	None	None	None	None	None		None	None	None
Sex	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂		♀	♀	sex indet.
DML	197	175	144	115	102	89	65	65	65	65	34	34	29	15.3
MW	62	78	46	41	30	27	21	21	21	21	34	13	10	5.7
FL	120	108	94	75	72	63	45	45	45	45	66	26	23	12.2
FW	155	161	120	102	89	82	67	67	67	67	89	39	39	23.8
HL	45	61	42	36	33	31	21	21	21	21	31	11	12	7.9
HW	38*	48	33	31	26	22	19	19	19	19	26	9	10	7
Side	R	R	R	L	R	L	L	L	L	L		L	R	L
AL I	80*	151	30*	60*	69*	35*	25*	25*	25*	25*		25* (R)	20	7.4*
AL II	45*	169	131*	69*	33*	47*	23*	23*	23*	23*		36	21*	9.8*
AL III	67*	168	53*	50*	72*	37*	21*	21*	21*	21*		29	16*	11*
AL IV	67*	141	34*	67*	67*	27*	26*	26*	26*	26*		24 (R)	3*	8.2*
AH		28, 34, 34, 30											*	*
AS		5+1, 4, 4+1, 5+1											*	*

* indicates damaged character, not used to calculate indices.

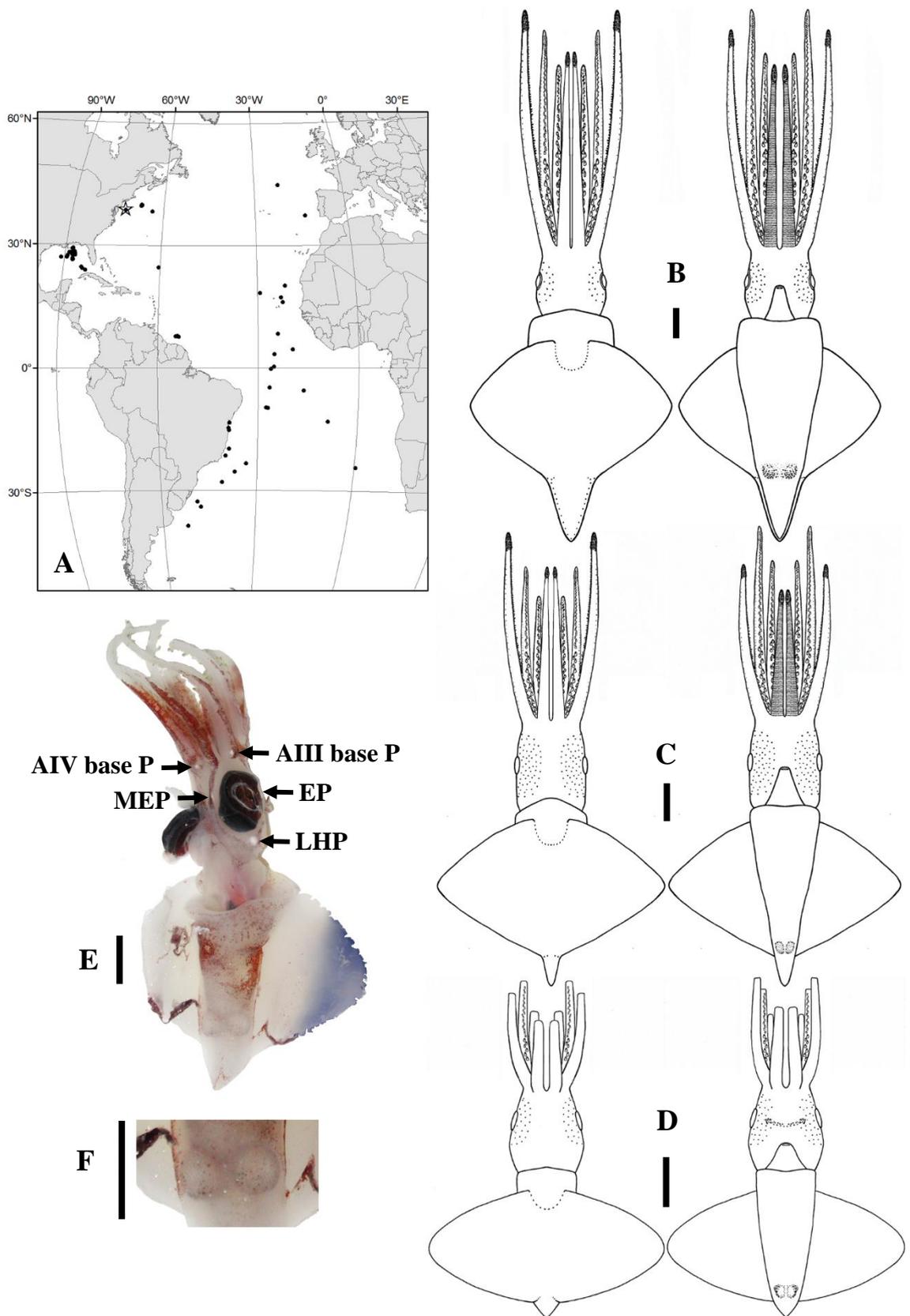


Fig. 24—*Octopoteuthis megaptera*. A) Distribution (star indicates type locality); B) adult; C) example specimen ML 29–56 mm (see Remarks); D) example specimen ML 15.3–26 mm (Escanez_06_0_N, sex indet., ML 15.3 mm); E, F) USNM 1192550, ♂, ML 49.5 mm (photo by M. Vecchione). Scale bars = B) 25 mm; C, E, F) 10 mm; D) 5 mm.

width ~8% ML. Buccal connective on Arms II dorsal (Fig. 23C; 25D, E), rarely paired on the right side only in males; Arms I, III with paired buccal connectives, Arms IV with weakly paired connectives set closely together, ventrally; in males only, buccal and basal protective membranes greatly developed proximally (Figs 25E, F), breadth greatest between Arms I (~50–60% arm base width) decreasing ventrally with no connective between Arms IV. Six pores typically in buccal membrane: one between paired connectives of Arms I, one between Arms II and III ventral to Arm II buccal connective, and one between Arms III and IV (occasionally reduced to pocket in membrane). Olfactory papillae short (length ~3% HL), elliptical (breadth ~4%HL), fleshy knobs without sculpture.

Arms slender, length 78–92–117% ML; formula II>III>I>IV; oblong in cross-section, becoming circular distally; with 26–36 pairs of hooks in thick fleshy sheaths, followed by 2–6 pairs of suckers distally. Arms taper gradually to tips, from ~7% AL at base to

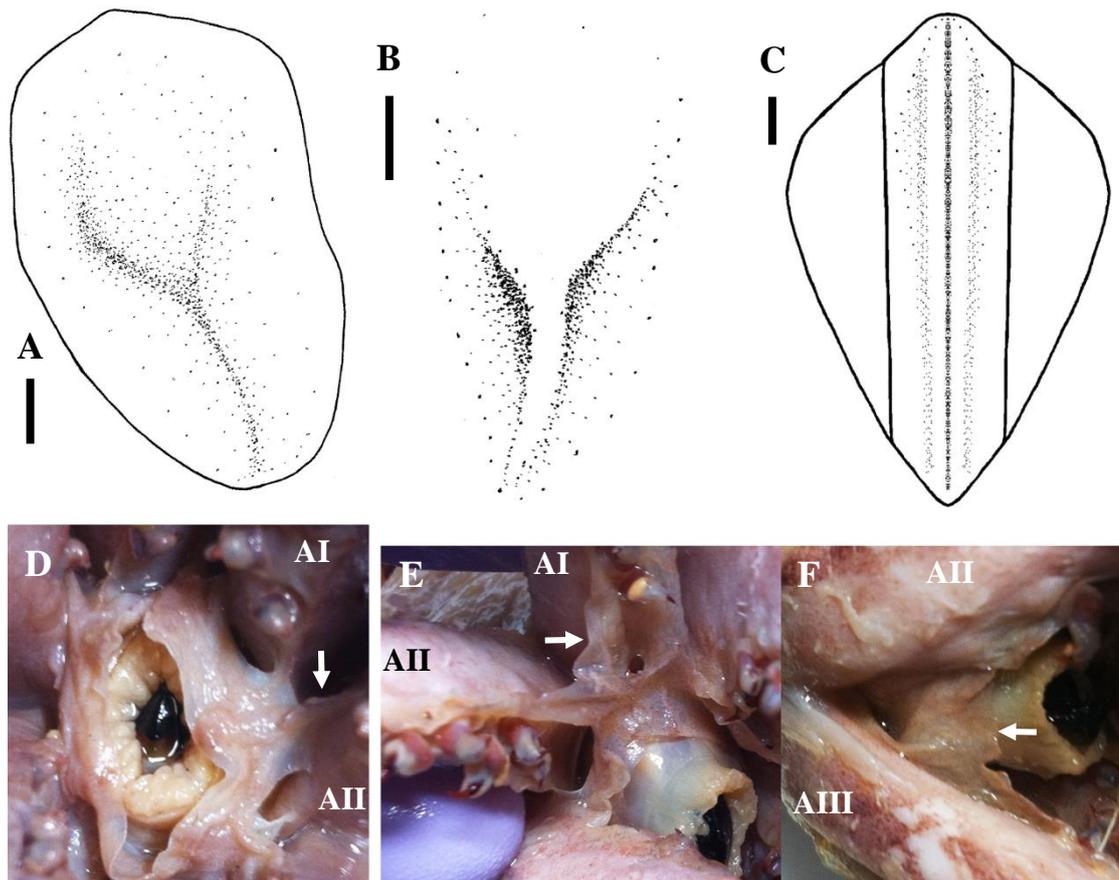


Fig. 25—*Octopoteuthis megaptera*. A, B) ZMH 11172, ♀, ML 165 mm; C) NSMT Mo61138, ♀, ML 175 mm; D) NSMT Mo61137, ♀, ML 177 mm; E, F) NSMT Mo61138, ♂, ML 108* mm. A) Funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage; D) female with low buccal connectives (arrow); E, F) male with expanded buccal connectives (arrows). Scale bars = A–C) 2 mm.

~3% at midpoint. Arm-tip photophores occupy distal-most ~7% AL (photophore length ~6% ML); swelling slightly to midpoint, tapering distally to blunt tip or slight bulb; arm hooks terminate proximal to photophore, suckers overlies proximal third of photophore length. Single large oval photophore embedded deeply in base of Arms II–IV, smaller in Arms II. Photophore series along ventral Arms III, IV beginning after gap distal to base photophores; comprising dozens of oval to circular photophores considerably smaller than base photophores; terminating proximal to arm-tip photophore. Gelatinous tissue along aboral arms often produced into low keels from base to tip; keel breadth increases distally relative to arm depth.

Arm hooks robust (Fig. 26); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp moderately long, smoothly curved, without significant broadening laterally or aborally at junction with base, typically with single prominent lateral ridge; inner angle right to slightly obtuse in proximal 50% of hook pairs, becoming slightly acute (~80°) in distal pairs; aperture open, narrow to broad oval. Accessory claws very prominent, slightly curved. Aboral hood absent. Bases crenulated, most prominent laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth) and shorter main cusps. Arm suckers asymmetric, domed.

Tentacles absent from all material examined (see Remarks).

Recti abdominis muscles (Figs 5E–F, 29) form discrete muscle bands straddling rectum anteriorly, posteriorly merging and fusing over rectum; weakly attached to rectum and immediately adjacent dorsal tissues dorsally; anteriorly inserting under dorsal component of funnel organ, beyond rectum, posteriorly expanding into thin sheet attaching to ventral surface of visceral mass; single near-circular photophore on dorsal surface of each muscle at ~30% ML anteriorly; pearly white, slightly raised dorsally; diameter ~2% ML; centred, comprising 70–100% of muscle width. Rectum free briefly anteriorly, terminating just inside funnel posterior to dorsal funnel organ concavity; laterally bearing two moderate-length anal flaps, length ~1% ML, ovate, anterior tip pointed, chiral dorso-ventrally. Ventral visceral mesentery pore diameter ~0.7% ML; pore appears as sphincter in membrane. Gills robust; length ~25% ML, with 26–30 lamellae.

Lateral profile of lower beak (4.54–6.57 mm LRL, Figs 27A–D) equally long and deep, with distal wing tips extending beyond rostral tip by ~19% baseline; rostral tip with shallow notch; jaw edge visible, slightly concave due to slight bend in distal third of LRL, with short jaw-edge extension; jaw angle 90°, slightly obscured by low, rounded wing fold; depth anterior to jaw angle greater than posterior. Hood low over crest, length ~31% baseline, without hood grooves. Crest distinct, lateral wall between crest and fold unpigmented; length ~69% baseline; tip free with concave ventral margin; sloped in nearly straight line. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior ~60% of hood length; posterior lateral wall margin straight; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width ~270% that at jaw angle, length ~98% LRL, with cartilaginous pad. Ventral view with very broad,

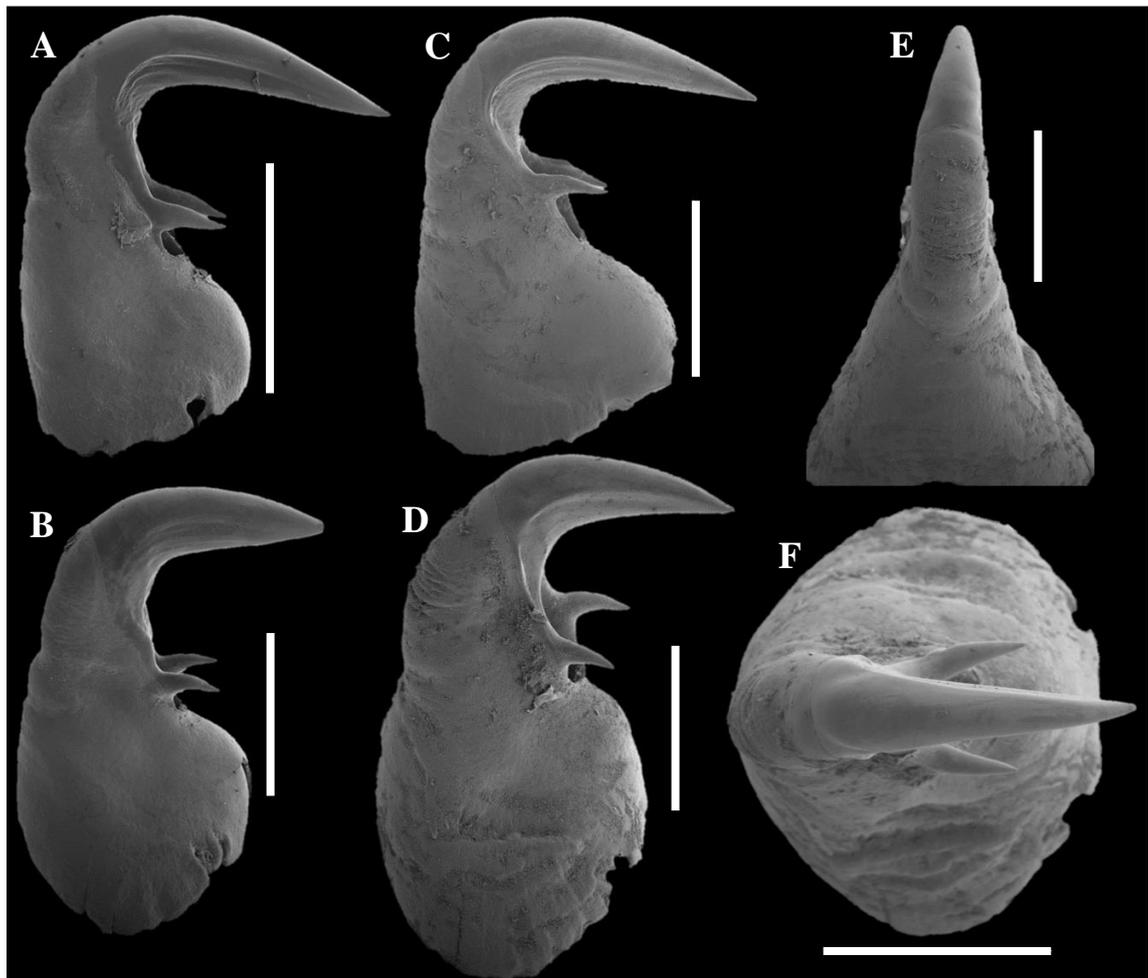


Fig. 26—*Octopoteuthis megaptera* armature. A, B) ZMH 11170, ♂, ML 132 mm; C–F) NSMT Mo61158, ♀, ML 177 mm. A) 15D hook, Arm IIIIR; B) 3D hook, Arm IIIIL; C) 14D hook, Arm IIIIL; D–F) 4V hook, Arm IIIIL: (D) lateral profile, (E) aboral, (F) top. Scale bars = A–F) 1 mm.

shallow notch in hood; free corners level with inner wing margin. Both beaks examined fully pigmented (ML 144, 52* mm).

Lateral profile of upper beak (5.32–7.45 mm URL, Figs 27E, F) longer than deep, maximum depth ~45% of length. Rostrum very long, ~38% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~80°; low ridge of cartilage present orally along shoulder; oral shoulder margin straight, ventrally protruding in ‘tooth’. Hood long (length ~76% UBL), moderately tall (~17% UBL); junction of hood and free shoulder straight. Lateral walls approximately rectangular with maximum depth in posterior third; posterior margin straight. Dorsal view with posterior margin of hood straight, posterior margin of crest concave, posterior margin of crest pigmentation concave. Both beaks examined fully pigmented (ML 144, 52* mm).

Radula (Figs 28A–C) with tricuspid rachidian: mesocone moderately long, conical, straight; lateral cusps short (~30% mesocone height), straight to slightly laterally directed blunt nubs; base straight. First lateral tooth weakly tricuspid: mesocone ~100–120% height of rachidian, conical, straight; lateral cusps very low triangular ridges, laterally directed, ~10% height of mesocone, outer cusp more prominent than inner; base slightly convex. Second lateral tooth generally simple, conical, ~125–175% height of rachidian, some rows with very low inner ridge akin to inner cusp of first lateral teeth. Marginal tooth simple, conical, ~200–275% height of rachidian. Marginal plate absent. Palatine palp (Fig. 28D) with ~47 narrowly triangular teeth (possibly an additional ~10 lost due to damage), each 80–230% rachidian height; dorso-anterior oral surface and margin adentate, teeth more densely arranged along posterior oral surface than anterior.

Gladius (96–142 mm GL, Fig. 28E) broad and very thin (<0.1 mm thick), delicate, transparent; greatest width (~13% GL) at ~30% GL; free rachis 8–10% GL, pointed anteriorly, broadening posterior to maximum width (~2% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden posteriorly to maximum width, then taper gradually for remainder of GL; short conus present, 3–4% GL, into which tissue inserts (the traction of which often results in breakage during dissection); rachis broad, evenly concave.

Colour (preserved) in adults deep purple to dark pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose furrows in females; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patches overlying posterior ventral mantle photophores darkest postero-laterally. Inner mantle surfaces and viscera unpigmented. Fresh specimens similar but colours more brilliant: pigmentation redder, non-pigmented tissues whiter or translucent.

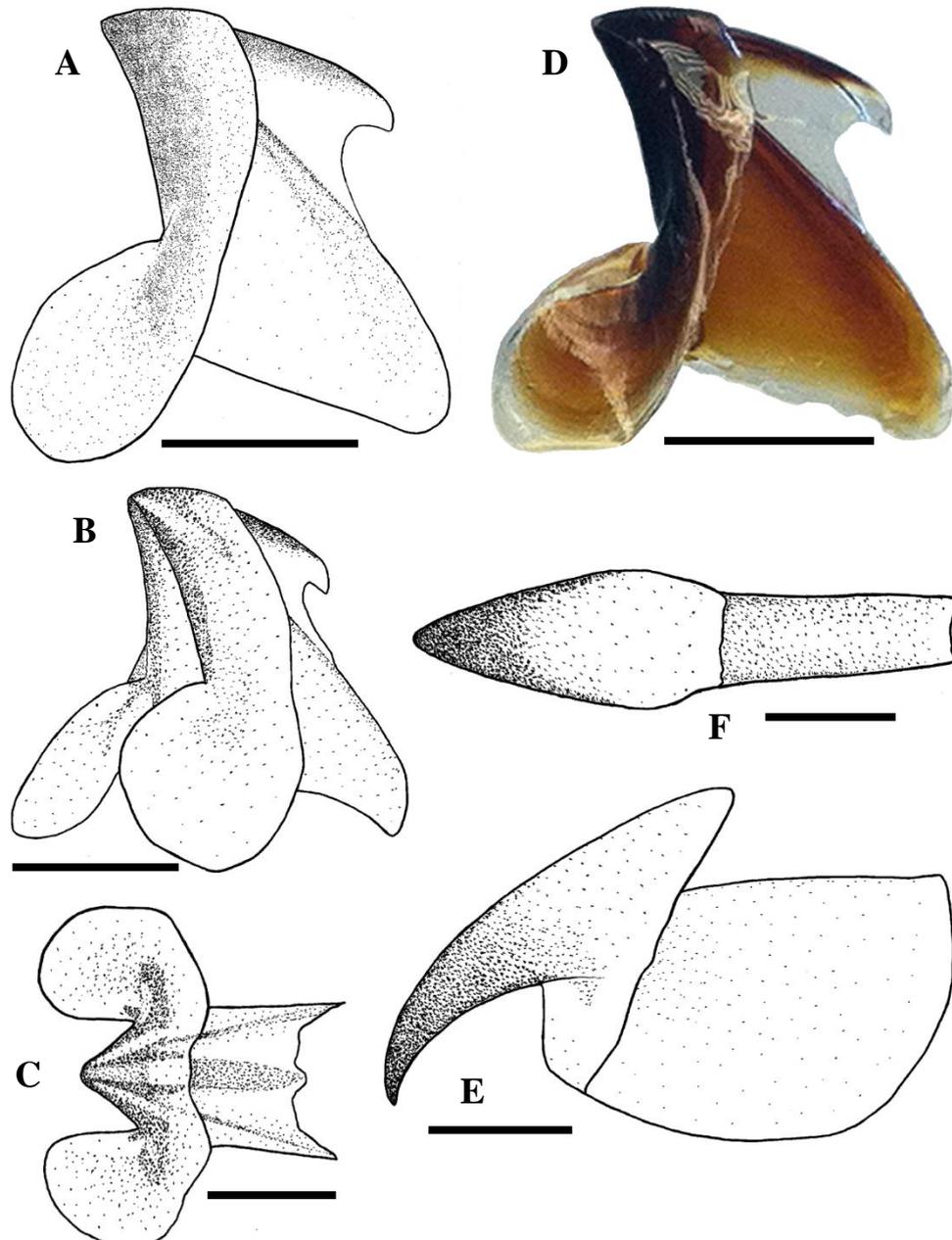


Fig. 27—*Octopoteuthis megaptera* beaks. A–F) USNM 730682, ♀, ML 144 mm, LRL 6.57 mm, URL 7.45 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

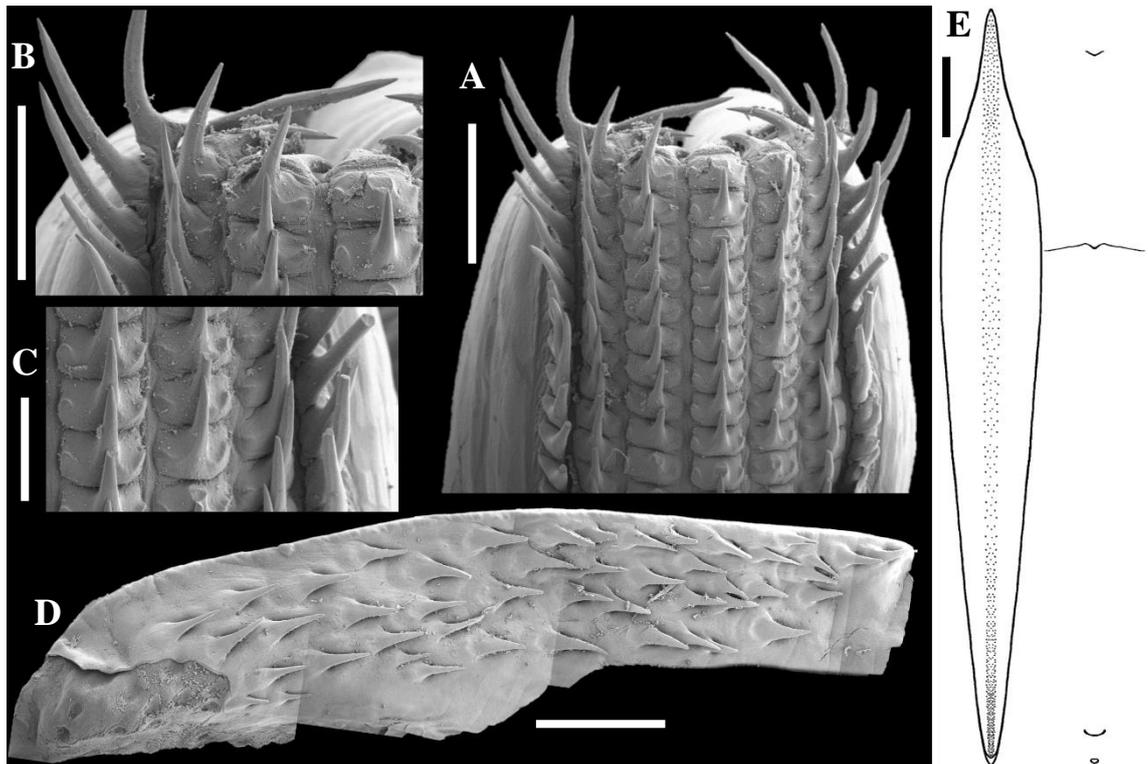


Fig. 28—*Octopoteuthis megaptera*. A–D) USNM 730682, ♀, ML 144 mm; E) USNM 885285, sex indet., ML 109 mm, GL 96 mm. A–C) Radulae; D) palatine palp; E) gladius, with cross-sections. Scale bars = A, D) 1 mm; B, C) 250 μ m; E) 10 mm.

Specimens ML 29–56 mm (Figs 24C, E, F; see Remarks below) as above, with the following exceptions. Mantle width \sim 38% ML; tail length 9–16–23% ML. Fins very wide (width 109–123–142% ML); anterior margin at \sim 11% ML. Head length 32–44–54% ML, width 27–31–35% ML; eyes very large, diameter \sim 82% HL (\sim 35% ML). Tentacles entirely lacking. Smallest specimens in this size class with wider fins, shorter tails, and more posteriorly set fins.

Specimens ML 15.3–26 mm (Fig. 24D; see Remarks below) differed from above as follows. Tail length \sim 15% ML. Fin length 80–83% ML, width 156–165% ML; anterior fin margin at 12–14% ML. Head length 46–52% ML, width 34–46% ML. Tentacles lacking (see Remarks).

Biology. Species achieves sexual maturity at very small sizes: smallest mature specimen examined ML 74 mm (ZMH 11180, ♂; some shrinkage due to dehydration), with terminal organ extending outside mantle and spermatophores exiting organ; a second male, ML 79 mm (NSMT Mo61135), also mature. Smallest mature female ML 99 mm (NSMT Mo61153), with ripe eggs (diameter 1.12 mm), spermatangia implanted along ventral tail; a second female of ML 105 mm (ZMH 1197) appeared to be in resting

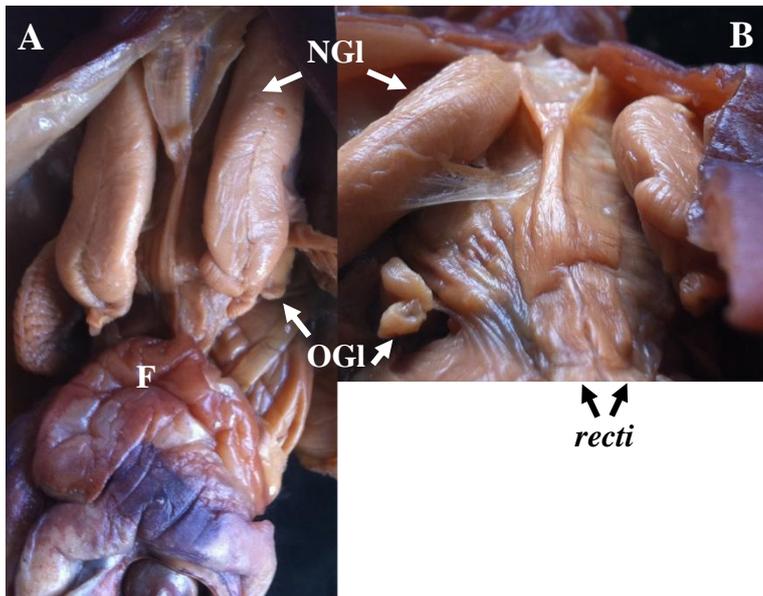


Fig. 29—*Octopoteuthis megaptera*. Position of nidamental (NGI) and oviducal (OGI) glands in relation to the funnel (F) and *recti abdominis* muscles (*recti*) in a well-preserved, mature female (ZMH 11216, ♀, ML 197 mm). A) Ventral view; B) posterior view.

state (*i.e.*, presumed already spawned). Single, well-preserved mature female (ZMH 11216, ML 197 mm) with nidamental glands developed medially into *recti abdominis* muscles, anterior tips in close proximity to anterior oviducal gland tips, all terminating just posterior to wide base of funnel (Fig. 29). Largest male specimen examined ML 159 mm (Haimovici E550). Implanted spermatangia with short, oblong sperm mass; most frequently implanted along tail and around PVMP.

Remarks. *Octopoteuthis megaptera* Verrill, 1885, was described from a mutilated juvenile specimen without reference to any photophores, only figured dorsally with an inset for a section of the oral arm surface, and was not subsequently mentioned in the literature until Adam (1952) suggested it had been lost. Shortly after, Voss (1956a) reported it as no longer extant at the USNM, and it was subsequently confirmed as lost by Roper and Sweeney (1978) following a thorough review of the USNM, YPM, and MCZ collections. Attempts were made herein to determine whether William Hoyle, the only contemporary author to refer to *O. megaptera*, may have taken the type overseas; unfortunately, it was not located at either NMW or MM. While Pfeffer (1912) gave a detailed treatment of *O. megaptera*, it is clear from the text that he did not re-examine the specimen. Roper and Sweeney (1978) acknowledged in a footnote that several late 19th and early 20th century USNM types were lost pre-1950 during an extended period of insufficient curatorial attention; Verrill's holotype for *O. megaptera* appears to have been one such casualty.

Although initially rarely cited, *O. megaptera* has appeared frequently in recent literature and remains the senior-most available name for the remaining north Atlantic *Octopoteuthis* species with two PVMP. Herein, morphometric comparisons were made between those reported by Verrill (1885) and those of comparably sized specimens of north Atlantic *Octopoteuthis* forms A (= *O. sicula*) and B (see *O. sicula* Remarks). Unfortunately, no significant, reliable differences were found between these two forms at this life stage and, in general, it appears that standard morphometrics bear little taxonomic significance among *Octopoteuthis* species. However, other characters can be used to identify a distinct north Atlantic *Octopoteuthis* species: two PVMP each overlain separately by a chromatophore patch, with MEPs and EPs present. This taxon is herein designated *O. megaptera* Verrill, 1885, which is the senior-most available name and one with continued and current usage.

Given the morphologic similarity and taxonomic instability of the genus, types are needed for all valid species. The specimen registered under USNM 1192550 (♂, ML 49.5 mm, 40°02.86'N, 67°27.92'W, N of Bear Seamount, 964 m, 4.4°C at depth, 02/09/2012, 11:45:59–12:15:59, FSV *Pisces*, 15, MWT, M. Vecchione and S. Bush) was collected from near the type locality, is similar in size to the lost holotype, and possesses the diagnostic buccal connective and photophore pattern of *O. megaptera*. This specimen is proposed as a suitable neotype for *O. megaptera* Verrill, 1885.

In the South Atlantic, some difficulty was encountered in differentiating specimens of *O. megaptera* from those of *O. rugosa* where the buccal connectives were damaged. Life history characteristics were found to be helpful supplementary characters, in that *O. megaptera* can reach maturity at body sizes ~60–70% those observed in among mature *O. rugosa*: male *O. megaptera* mature around ML ~80 mm compared to ML ~140 mm in *O. rugosa*, females around ML ~100 mm compared to ML ~145 mm. For sufficiently small but fully mature specimens, this character alone can differentiate an individual of these two species. Additionally, the greatly developed proximal protective and buccal connectives reported for male *O. megaptera* (Figs 25E, F) were not found in *O. rugosa*. Elsewhere in its range *O. megaptera* co-occurs with *O. sicula* and, to a lesser extent, *O. leviuncus* sp. nov.: it can readily be separated from both by the two PVMP overlain by separate chromatophore patches, compared to the single patch in *O. sicula* (overlying two PVMP; see *O. sicula* Remarks) and *O. leviuncus* (overlying a single PVMP).

In addition to precocious reproductive capacity, *O. megaptera* appears to develop adult morphology at smaller sizes than other *Octopoteuthis* species. Of the few beaks examined, full beak pigmentation had already developed by LRL 4.54 mm, smaller than other species including in *O. deletron* (LRL 5.2–5.98 mm) for which 90 beaks were available. Similarly, current material suggests that tentacles are lost at smaller sizes in *O. megaptera* than in other species. Tentacles could not be distinguished, nor any remnants of them, in two specimens ML 15 mm (Escáñez 06_O_N, USNM 1192580) and no tentacular structures were confidently identified in the smallest specimen examined (Escáñez 05_I_N, ML 8.1 mm), although the specimen had suffered some damage. As such, juvenile and post-larval life stages for *O. megaptera* could not be established developmentally, and the smaller two size-classes described above were based solely on variation in morphometric indices. Although capable of reaching sexual maturity at smaller sizes than other species of *Octopoteuthis*, *O. megaptera* still achieves similarly large proportions as adults, with the largest specimen examined herein ML 197 mm.

5.1.2.2. *Octopoteuthis rugosa* Clarke, 1980 (Table 12, Figs 3A–C, 5A, 5B, 6A, 6C, 6G, 30–35, 40G)

Type material (2 specimens). **NHMUK 1973100**, Holotype, ♀, ML 162 mm, off Donkergat, Cape Province, South Africa, 29/09/1963, from stomach of sperm whale no. 2336; **NHMUK 1973101**, Paratype, ♂, ML 147 mm, off Donkergat, Cape Province, South Africa, from stomach of sperm whale no. 2336.

Additional material examined (99 specimens). **ZMH 35995**, ♂, ML 175 mm, 23°20.00'S, 033°22.00'W, Brazil, 140–160 m, 09/02/1968, RV *Walther Herwig I*, stn 23, cruise #23; **MV F159987**, ♂, ML 184 mm, 27°13.68'S, 153°54.98'E, Moreton Bay, 600 m, 31/03/1983, FV *Iron Summer*, shot 6, R. Morton; **MV F159996**, sex indet., ML 28 mm, 29°15'S, 102°19.8'E, 52 m, 29/10/1992, FV *Shoei Maru*; **NMNZ M.172953**, ♂, ML 125 mm, 29°31.75'S, 167°38.05'E, South of Norfolk Island, 200–1200 m, 15/05/2003, RV *Tangaroa*, NORFANZ stn 23, TAN0308; **NHMUK 20160087**, ♂, ML 56 mm, 32°00.8'S, 36°21.7'E, 0–1000 m, 06/05/1936, stn 1764, *Discovery Expedition*, net N 450 B; **NMNZ M.091442**, ♀, ML 42 mm, 32°11.70'S, 167°15.30'E, WNW of Three Kings Islands, New Zealand, 75–80 m, bottom depth 1255–1630 m, 24/10/1985, RV *James Cook*, J16/22/85, MWT; **NMNZ M.091499**, ♀, ML 44 mm, 32°18.90'S, 167°40.50'E, WNW of Three Kings Islands, New Zealand, 150 m, bottom depth 1451–1565 m, 24/10/1985, RV *James Cook*, J16/20/85, MWT; **AM C.303928**, ♀, ML 230 mm, 32°52.00'S, 152°48.00'E, off Newcastle, 1006–1052 m, 08/06/1989, 1020–1220, FRV *Kapala*, BTT, K.J. Graham; **AM C.303928**, ♀, ML 211 mm, 32°52.00'S, 152°48.00'E, off Newcastle, 1006–1052m, 08/06/1989, 1020–1220, FRV *Kapala*, K89-11-02, BTT, K.J. Graham; **MV F160001**, ♂, ML 160 mm, 33°03'S, 114°37'E, NW of Bunbury, Western Australia, 1000–1050 m, bottom depth 1000–1050 m, 29/05/1992, 1300–1500, FV *Star of Crimea*, shot 11, demersal trawl, F. Ewing & A. Grice; **MV F51082**, 2 sex indet., ML 76, 39 mm, 33°04.7'S, 154°07.9'E, Tasman Sea, 22/09/1979, 0005–0055, *Sprightly*, SP19/79/08, 8 m rectangular MWT; **AM C.269846**, ♂, ML 48 mm, 33°05'S, 153°05'E, East of Newcastle, NWS, 28/11/1979, FRV *Kapala*, K79-19-03, MWT, K.J. Graham; **AM C.269847**, ♂, ML 228 mm, 33°07'S, 153°11'E, off Newcastle, 28/11/1979, FRV *Kapala*, K79-19-06, K.J. Graham; **NMNZ M.074492**, ♂, ML 57 mm, 33°14.0'S, 179°14.0'W, NE of East Cape, over Kermadec Trench, 695 m, bottom depth 3000 m, 04/12/1976, RV *James Cook*, J17/09/76; **AM C.451852**, ♂, ML 91 mm, 33°28.00'S, 152°34.00'E, 97km E of Broken Bay, 630 m, bottom depth 3658 m,

14/12/1977, 530 hrs, FRV *Kapala*, K77-24-10, Engel MWT, J.P. Paxton; **AM C.476742**, 5 ♂, 4 ♀, sex indet., ML 79, 73, 53, 44, 43, 77, 49, 41, 41, 35.5 mm, 33°28'S, 152°33'E, off Broken Bay, 100 km east of Bay, New South Wales, Australia, 900 m, bottom depth 4200 m, 14/12/1977, FRV *Kapala*, K77-24-10, J.P. Paxton; **AM C.476741**, ♂, ML 155 mm, 33°31'S, 152°20'E, East of Broken Bay, New South Wales, 578 m, bottom depth 1829–2926 m, 12/12/1977, 2300 hrs, FRV *Kapala*, K77-24-02, MWT, K.J. Graham; **AM C.476740**, 2 ♀, ML 238, 216 mm, 33°32'S, 152°11'E, off Broken Bay, 1097 m, 26/09/1984, 1415 hr, FRV *Kapala*, K84-16-10; **ZMH 11193**, ♂, ML 172 mm, 33°43'00S, 051°02.00'W, Uruguay, 800 m, 31/07/1966, RV *Walther Herwig*, stn 439, cruise #15; **NHMUK 20160088**, ♂, ML 44 mm, 33°50.5'S, 15°46.00'E, 0–1200 m, 04/06/1930, stn 405, *Discovery* Expedition, net TYFB; **AM C.451853**, 2 ♀, ♂, ML 49, 41, 42 mm, 33°53.00'S, 152°02.00'E, 64 km E of Sydney Heads, 800 m, bottom depth 1830 m, 14/12/1977, 1330–1930, FRV *Kapala*, K77-24-11, Engel MWT, J.P. Paxton; **MV F51430**, ♀, ML 31.5 mm, 33°54'S, 151°54'E, E of Port Jackson, 0–300 m, 26/01/1982, S01/82/55, Engels 308 MWT, G. Poore; **AM C.476747**, ♂, ML 43 mm, 34°05'S, 151°55'E, Tasman Sea, off Sydney, NSW, 0–950 m, bottom depth 1920–2835 m, 25/03/1971, FRV *Kapala*, K71-03-06, J. Paxton; **USNM 885287**, ♂, ML 79 mm, 34°15'S, 16°34.8'E, South Africa, 1550 m, 28/03/1971, RV *Walther Herwig*, 417-71, 1600 mesh Engel trawl; **AM C.380778**, 2 ♂, ML 46, 26 mm, 34°20.00'S, 151°56.00'E, 80 km E of Port Kembla, 0–800 m, bottom depth 2925–3650 m, 14-15/12/1977, 2050–0030, FRV *Kapala*, K77-24-12, 20x15 m Engel MWT, J.P. Paxton; **ZMH 73899**, ♀, ML 89 mm, 34°25.00'S, 014°47.00'E, South America, 105–305 m, 28/03/1971, RV *Walther Herwig*, stn 419, cruise #36; **USNM 885286**, 4 ♀, ML 61, 57, 44, 40 mm, 34°25.2'S, 14°46.8'E, 105–112 m, 28/03/1971, RV *Walther Herwig*, 419-I-71, 1600 mesh Engel trawl; **USNM 885276**, ♀, ML 59 mm, 34°25.8'S, 14°43.2'E, 300–305 m, 28/03/1971, RV *Walther Herwig*, 419-II-71, 1600 mesh Engel trawl; **USNM 885290**, sex indet., ML 58 mm, 34°25.8'S, 14°43.2'E, 300–305 m, 28/03/1971, RV *Walther Herwig*, 419-II-71, 1600 mesh Engel trawl; **AM C.391754**, ♀, ML 244 mm, 34°27.00'S, 151°38.00'E, off Botany Bay, Australia, 550 m, bottom depth 1463–1829 m, 23/05/1978, 2000 hr, FRV *Kapala*, K78-08-01, MWT, K.J. Graham; **NMNZ M.074516**, sex indet., ML 38 mm, 35°0'S, 179°29'W, NE of East Cape, over Kermadec Trench, New Zealand, 338 m, bottom depth 3000 m, 04/12/1976, RV *James Cook*, J17/06/76, MWT; **MV F159473**, ♂, ML 41 mm, 35°04.3'S, 151°12.6'E, off Nowra, Australia, 1350–1411 m, 15/07/1986, 1830–1930, RV *Franklin*, FR5/86, SLOPE 10, 8 m rectangular MWT, M.F. Gomon; **NHMUK 20160083**, sex indet., ML 32.5 mm,

35°13'S, 17°50.5'E, off Capetown, 800–950 m, 12/06/1930, stn 407, *Discovery* Expedition, net N 405 H; **NHMUK 20160093**, 2 ♂, ML 45, 31 mm, 35°13.00'S, 17°50.5'E, 800–950 m, 12/06/1930, stn 407, *Discovery* Expedition, net N 450 H; **NHMUK 20160118**, sex indet., ML 30.5 mm, 35°13.00'S, 17°50.5'E, 800–950 m, 12/06/1930, stn 407, *Discovery* Expedition, N 450 H; **AM C.391763**, ♀, ML 263 mm, 35°30.00'S, 150°51.00'E, off Ulladulla, Australia, 978–1024 m, 25/10/1983, 1020 hr, FRV *Kapala*, demersal fish trawl, K.J. Graham; **USNM 885279**, ♀, ML 151 mm, 35°31.8'S, 10°54'E, 300–305 m, 29/03/1971, RV *Walther Herwig*, 423-II-71, 1600 mesh Engel trawl; **NHMUK 19980431**, sex indet., ML 24 mm, 35°35.00'S, 18°25.25'E, 31/08/1930, stn 420, *Discovery* Expedition; **ZMH 35999**, 2 ♂, ML 110, 86 mm, 36°24.8'S, 40°00.00'W, 650–700 m, 09/01/1976, RV *Walther Herwig II*, stn 108-I, cruise #20; **NHMUK 20160106**, ♀, ML 148 mm, 37°S, 165°E, Tasman Sea, 14/11/1970, from sperm whale stomach; **NMNZ M.287249**, ♀, ML 41.2 mm, 37°21.70'S, 178°45.60'E, NNE of East Cape, New Zealand, bottom depth 1380 m, 20/11/1976, RV *James Cook*, J16/73/76, plankton trawl; **NIWA 71833**, ♀, ML 161 mm, 37°25.04S, 168°09.07'E, 900 m, 03/03/1999, Z9724, 1204/16; **NIWA 71845**, ♀, ML 175 mm, 37°34.99'S, 179°08.18'E, East Cape, New Zealand, 934–971 m, 24/04/1992, TAN9203/135; **NHMUK 20130458**, sex indet. (head only), HL 62 mm, 38°S, 159°E, from sperm whale stomach; **NIWA 71839**, ♂, sex indet., ML 61, 56 mm, 38°00'S, 179°40.01'E, 20–100 m, bottom depth 3197 m, 15/02/1998, RV *Tangaroa*, TAN9802/100, Z11018, FMMWT, NIWA; **NIWA 84378**, ♀, ML 67 mm, 38°00'S, 179°20'E, 20–100 m, bottom depth 2536 m, 02/1998, RV *Tangaroa*, TAN9802/108, FMMWT, NIWA; **NIWA 84387**, ♂, ML 52 mm, 38°00'S, 178°45'E, 20–100 m, bottom depth 316 m, 02/1998, TAN9802/110, FMMWT, NIWA; **MV F51075**, ♀, ML 31 mm, 38°01.4'S, 150°14.1'E, Great Australian Bight, 23 km WSW of Point Culver, 0–70 m, 28/11/1981, *Soela*, S05/81/5, IYGPT; **ZMH 11232**, ♀, ♂, ML 132, 130 mm, 38°34.8'S, 39°58.8'W, Argentina, 200–220 m, 08/01/1976, RV *Walther Herwig II*, stn 107, cruise #21, 1600 mesh Engel trawl; **NIWA 84383**, ♀, ML 49 mm, 39°31.99'S, 178°35'E, 20–100 m, 02/1998, RV *Tangaroa*, TAN9802/125, Z9919, FMMWT, NIWA; **NIWA 84385**, ♂, 2 ♀, ML 67, 57, 44 mm, 39°37.99'S, 179°00'E, 20–100 m, bottom depth 3354 m, 02/1998, RV *Tangaroa*, TAN9802/127, FMMWT, NIWA; **NIWA 76647**, ♀, ML 131 mm, 39°43.21'S, 178°09.64'E, 846 m, 21/03/2010, TAN1003/16, BTT, Mfish, NIWA; **NIWA 95943**, sex indet. (beaks only), LRL 8.25 mm, 39°49.32'S, 167°19.05'E, 1044–1083 m, 30/06/2009, FV *Thomas Harrison*, THH0901/31, NIWA; **NMNZ M.091409**, ♂, ML 109 mm, 39°57.20'S, 167°53.70'E, Challenger Plateau, New Zealand,

980–1027 m, 14/11/1984, RV *James Cook*, J19/14/84, BTT; **NIWA 84384**, ♂, ML 65 mm, 40°00'S, 179°40'W, 20–100 m, bottom depth 3237 m, 02/1998, RV *Tangaroa*, TAN9802/134, FMMWT, NIWA; **NIWA 71838**, ♀, ML 138 mm, 40°00.6'S, 178°08.40'E, 700 m, 21/09/1995, Z8377, NIWA; **NMNZ M.287226**, ♂, ML 46 mm, 40°0.830'S, 177°58.410'E, S of Mahia Peninsula, North Island, New Zealand, 14–99 m, bottom depth 1529 m, 29/03/1995, RV *Tangaroa*, TAN9503/55; **USNM 885281**, ♀, ML 139 mm, 40°36'S, 39°12'W, 316–328 m, 08/03/1971, RV *Walther Herwig*, 363-II-71, 1600 mesh Engel trawl; **NIWA 84376**, ♂, ML 77 mm, 40°40.01'S, 178°00.00'E, 20–100 m, bottom depth 2458 m, 02/1998, RV *Tangaroa*, TAN9802/173, FMMWT, NIWA; **USNM 1283035**, ♀, ML 37 mm, 40°46.2'S, 49°55.8'W, Argentine Basin, 100 m, 19/11/1975, RV *Walther Herwig*, 05/1976, 1600 mesh Engel trawl; **NIWA 84386**, ♂, ML 71 mm, 41°25.01'S, 176°30'E, 20–100 m, bottom depth 1149–1419 m, 02/1998, RV *Tangaroa*, TAN9802/178, FMMWT, NIWA; **NMNZ M.287223**, ♂, ML 106 mm, 41°35.80'S, 169°9.40'E, Challenger Plateau, New Zealand, 1011–1018 m, 16/10/1983, FV *Arrow*, A03/136/83; **NIWA 84377**, ♀, ML 74 mm, 42°12', 177°30.00'E, 20–100 m, bottom depth 2548 m, 02/1998, RV *Tangaroa*, TAN9802/188, FMMWT, NIWA; **NIWA 96212**, ♂, GL 96 mm, 42°44.34'S, 178°08.16'E, Chatham Rise, New Zealand, 50–950 m, 17/11/2011, TAN1116/117, MWT; **NIWA 71846**, ♀, ML 106 mm, 42°45.32'S, 179°55.93'E, 1108–1140 m, 24/06/1997, TAN9708/13, FMMWT, NIWA; **NMNZ M.091633**, ♀, ML 109 mm, 42°47.10'S, 169°30.90'E, W of Hokitika, New Zealand, 470 m, bottom depth 1250 m, 24/07/1985, RV *Kaiyo Maru*, KM/107B1/85, Bongo nets; **NIWA 95937**, sex indet. (beaks only), LRL 5.40 mm, 42°53.06'S, 176°39.36'W, 0–750 m, 01/2013, TAN1301/76, FMMWT, MPI, NIWA; **NIWA TAN1401/53**, ♀, ML 134 mm, 43°06.08'S, 174°43.98'W, 871 m, 10/01/2014, BTT; **MV F51073**, ♂, ML 66 mm, 43°30'S, 140°E, 1000 m, 21/10/1968, 36/3/103, 3 m IKMWT, Australian Antarctic Division; **NIWA 76639**, sex indet., ML 85 mm, 44°01.15'S, 174°30.66'W, 1060–1082 m, 21/07/2007, TAN0709/107, trawl, Mfish, NIWA; **MV F78255**, ♂, ♀, ML 73, 68 mm, 44°12.87'S, 147°04.77'E, off Tasmania, 200–300 m, bottom depth 1214 m, 12/04/1993, 1840 hr, RV *Southern Surveyor*, SS03/93/21, net 3, Midoc net, CSIRO Division of Fisheries; **NMNZ M.091642**, ♂, ML 124 mm, 44°27.30'S, 165°3.10'E, off Fiordland, New Zealand, 480 m, bottom depth 4559 m, 26/07/1985, RV *Kaiyo Maru*, KM/109A/85.

Unlocalised material examined (14 specimens). **NHMUK 20160082**, 4 ♀, 3 sex indet., ML 244, 210, 195, 185, 160, 150*, 146* mm, Durban, South Africa, 1963, 2248

(D1901); **USNM 1283034**, ♀, ML 158 mm, St. Paul and Amsterdam Island, 26/07/1986, RV *Marion Dufresne*, RMT 188, cruise 50; **NIWA OS AP 101**, ♀, ML 109 mm, unlocalised [southern Australia]; **NIWA OS LIA 02**, ♂, ML 56 mm, unlocalised [southern Australia], *Adriatic Pearl*, L. Triantafillos; **NMNZ M.302297**, ♂, ML 146 mm, New Zealand, no stn; **NIWA 84381**, ♀, ML 199, *Adriatic Pearl*, OR-AP-01; **NIWA 71847**, sex indet., ML 189 mm, no stn; **NIWA 76634**, sex indet., ML 95 mm, TAN0709-no stn.

Additional genetic samples (2 samples). **SAM S4084**, ♀, fresh ML ~200 mm, 35°13'S, 22°54'E, 521 m, 14/04/2007, RV *Africana*, A27372; **Annie6**, ?♀, ML ~210 mm, unlocalised [Australia], G. Jackson & K. Bolstad.

Distribution (Fig. 30A). Southern hemisphere between 23° and 44°S; 0–1400 m.

Diagnosis. Arms long (80–110% ML); Arm II buccal connectives paired, equal in depth, attaching both dorsally and ventrally; arm hooks narrow aborally; anterior fin margin at 5–12% ML; tail long (17–32% ML).

Description (ML 73–263 mm, Figs 30B–34). Mantle conical to weakly goblet shaped; widest at anterior margin, width 29–37–47% ML; weakly muscled; tail thick, long, length 17–25–32% ML; dorsal anterior margin slightly pointed medially, ventral margin with slight indentation between mantle components of locking apparatus. Fins large (length 64–71–77% ML), broad (width 85–96–104% ML), greatest width attained at 40–50% ML; anterior margin at ~8% ML; width of fin continuation along tail ~5% ML. Paired PVMPs circular, diameter ~1.6% ML; set laterally along posterior ventral mantle, distance between photophores 8–10–13% ML. Anterior fin insertion blunt posteriorly, depth ~14% ML, width ~14% ML.

Head square to trapezoidal in outline, length 26–33–37% ML, width 28–32–35% ML, depth 20–30% ML. LHP triangular, length ~5% HL (~2% ML); MEPs oblong, level with mid-eye, oriented 30–60° to body axis, length ~7% HL (~2% ML), width ~2% HL (~1% ML); EPs crescent shaped, length ~13% HL (~5% ML), width ~1.5% HL (~0.5% ML). Eyes large, diameter 37–47–58% HL (12–16–20% ML), with large lenses, diameter ~35% ED. Funnel length ~23% ML; aperture width ~13% of funnel length,

Table 12. Measurements (mm) of *Octopoteuthis rugosa*. Mean indices were calculated from specimens ML >46 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side).

Specimen ID	NHMIJK	NIWA	ZMH	USNM	NIWA	ZMH	NMNZ	ZMH	NIWA	ZMH	NMNZ	ZMH	NIWA	Mean index	NMNZ
Type status	Holotype	None	None	None	None	None	None	None	None	None	None	None	None		None
Sex	♀	♀	♂	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀		♂
DML	162	199	172	158	131	130	109	89	74	89	109	89	74		46
MW	55	78	50	57	62	54	37	28	28	54	37	28	28	37	20
FL	125	139	127	104	94	98	75	61	47	98	75	61	47	71	34
FW	164	181	179	135	136	132	101	80	72	132	101	80	72	96	50
HL	48	62.5	61	41	56*	47	39	33	25	47	39	33	25	33	19
HW	30*	60*	49	50	30*	42	36	29	26	42	36	29	26	32	18
Side	L	R	R	L	R	R	R	L	R	R	R	L	R		R
AL I	115	91*	100*	78*	43*	60*	42*	34*	18*	60*	42*	34*	18*		21*
AL II	125*	81*	95*	97*	63*	71*	57*	30*	36*	71*	57*	30*	36*		44*
AL III	128	70*	72*	117	50*	71*	65*	40*	37*	71*	65*	40*	37*	77	21*
AL IV	55*	164	71*	75*	69*	54*	82 ^r	17*	46*	54*	82 ^r	17*	46*		20*
AH	29, 27	*		*											
AS	3, 2+1	10+1		8+1											

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

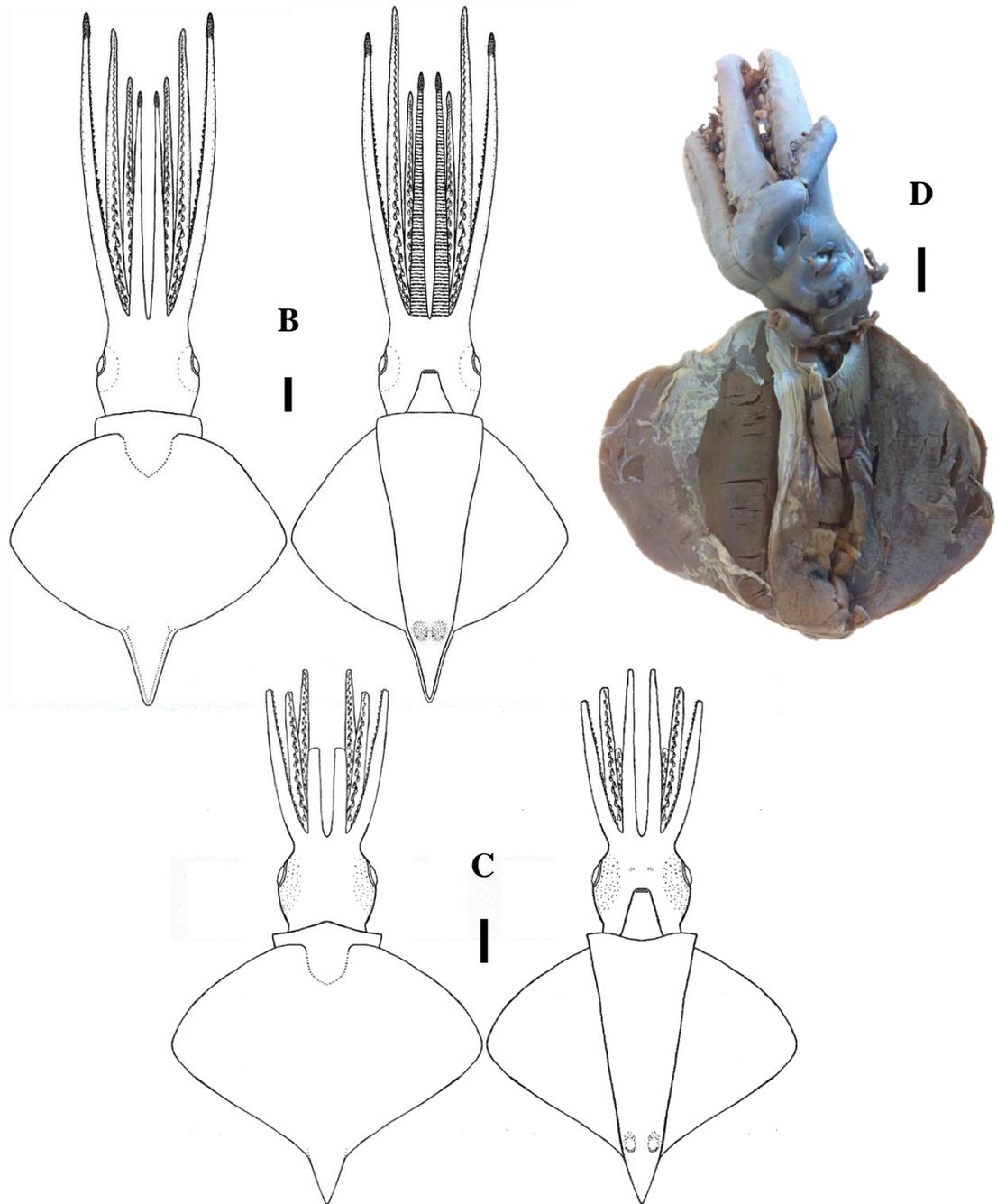
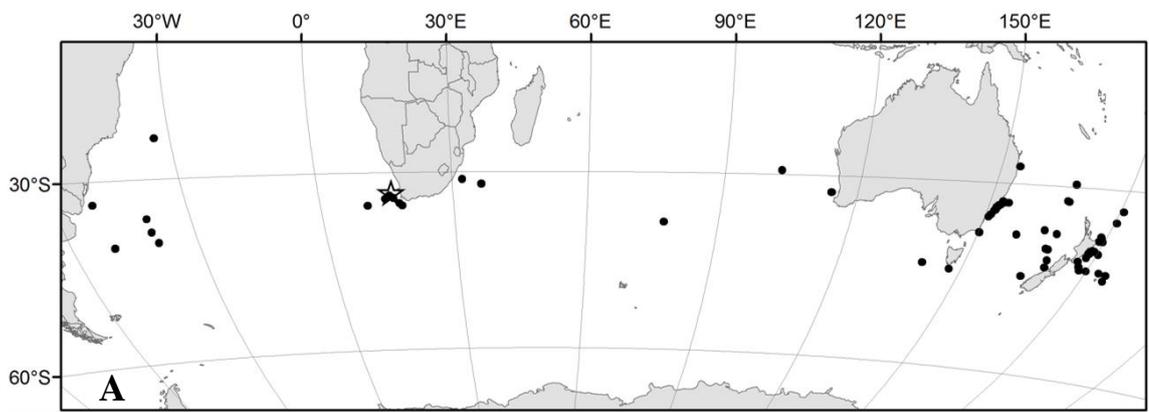


Fig. 30—*Octopoteuthis rugosa*. A) Distribution (star indicates type locality); B) adult; C) juvenile; D) NHMUK 1973100, holotype, ♀, ML 162 mm. Scale bars = B, D) 20 mm; C) 10 mm.

level with midpoint of eye; funnel valve tall, broad; funnel groove shallow. Funnel and mantle components of locking apparatus, nuchal cartilage as in *O. megaptera*: funnel component subtriangular (Fig. 31A), length ~9% ML, maximum width ~4% ML; mantle component oblique, conical (Fig. 31B), length ~9% ML, maximum width ~4% ML; nuchal cartilage oblong, slightly pointed anteriorly (Fig. 31C), length ~11% ML, maximum width ~4% ML; set on rhombic cartilaginous pad of equivalent length, width ~5% ML. Buccal connectives paired on Arms I–III (Fig. 31D, E); Arm IV weakly paired, set closely, ventrally. Six pores in buccal membrane: one between paired connectives of each of Arms I and II, one between Arms III and IV (occasionally reduced to pocket in membrane). Olfactory papillae short (length ~3% HL), elliptical (breadth ~3% HL), fleshy knobs without sculpture.

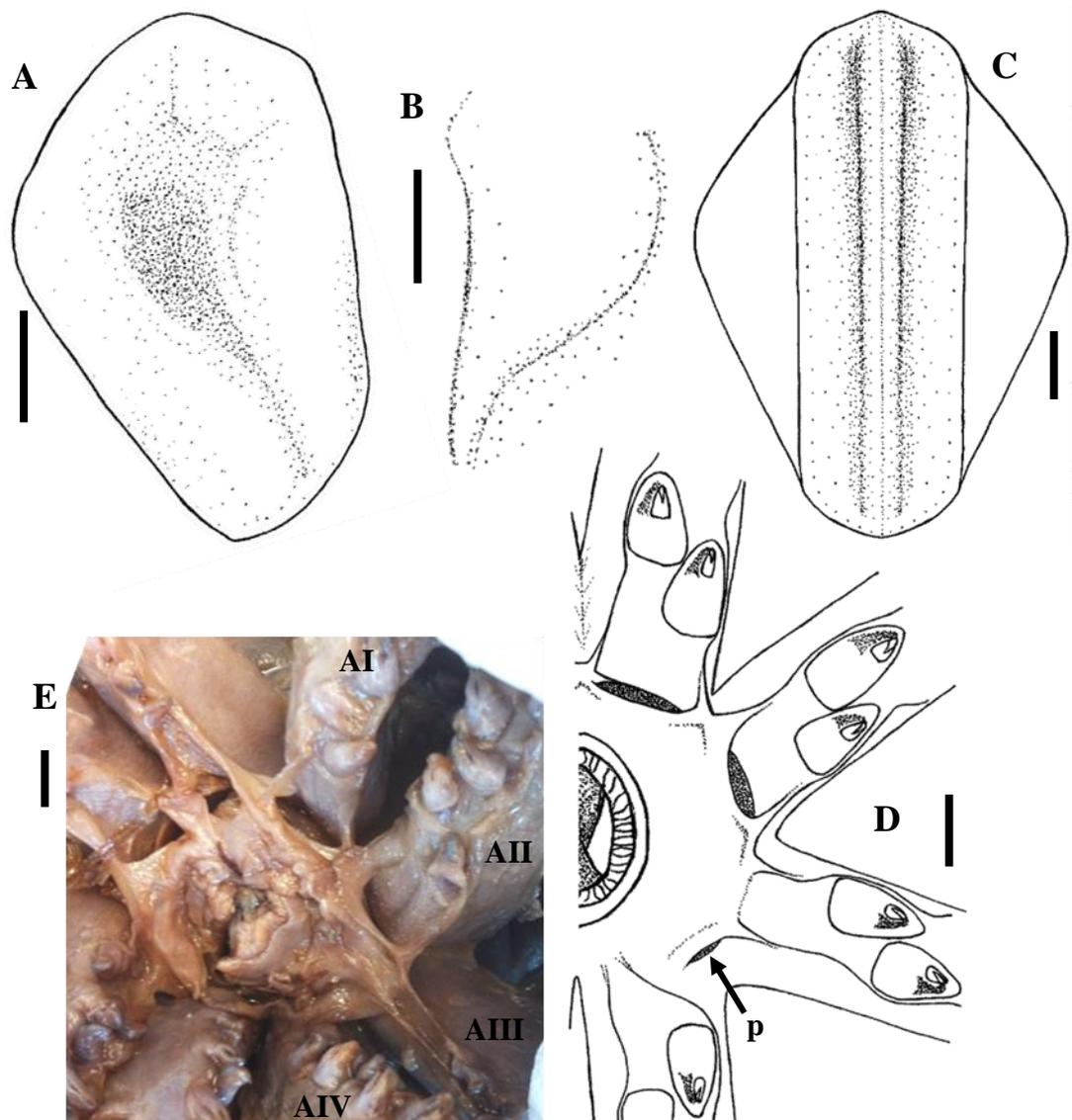


Fig. 31—*Octopoteuthis rugosa*. A) NMNZ M.287223, ♂, ML 106 mm; B, C) ZMH 11232, ♂, ML 130 mm; E) NHMUK 20160082, isolated head. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage; D, E) oral surface with paired Arm II buccal connectives, pores (p). Scale bars = A–C) 2 mm; D, E) 4 mm.

Arms slender, length 69–97–146% ML; formula II=III>I=IV; oblong to circular in cross-section; with 24–31 pairs of hooks in thick fleshy sheaths, followed by 4–14 pairs of suckers distally. Arms taper gradually to tips: width ~7% AL at base, narrows to ~4% at midpoint. Arm tip photophores occupy distal-most ~7% AL (photophore length ~6% ML); swelling slightly from photophore base to midpoint, distally tapering to blunt tip or very slight bulb at tip; arm hooks terminate proximal to photophore, suckers overlies proximal third of photophore. Arm-base photophore diameter ~2% AL, smaller in Arms II. Photophore series along ventral Arms III, IV beginning ~9% AL distally from base photophores; comprising ~25–35 oval photophores much smaller than arm-base photophores; terminating proximal to arm-tip photophore. Arms with gelatinous tissue aborally as in *O. megaptera*.

Arm hooks robust (Fig. 32 A–G); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp long, smoothly curved, without significant broadening aborally or laterally at junction with base, typically with single prominent lateral ridge; inner angle ~90° in proximal ~40% of hook pairs, becoming increasingly acute (~60–80°) distally; aperture open, broad. Accessory claws very prominent, slightly curved. Aboral hood absent. Bases crenulated, most prominent laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth) and shorter main cusps. Arm suckers asymmetric, domed; proximal suckers with tricuspid apical tooth, flanked by 2–4 pairs of simple teeth decreasing in size laterally (Fig. 32H, I); distal suckers with triangular apical cusp flanked by 4 pairs of simple long, narrow teeth; teeth occupy apical 50% of circumference, remainder of sucker ring smooth.

Tentacles absent from all material examined (likely lost during post-larval stages as in other *Octopoteuthis* spp.).

Recti abdominis muscles and rectum morphology as in *O. megaptera*; *recti* photophores near-circular, at ~30% ML anteriorly; pearly white, slightly raised dorsally; length ~2% ML, width ~2% ML; centred to slightly medially set, comprising 80–100% of muscle width. Anal flaps moderate-length, ~2% ML. Ventral visceral mesentery pore small, diameter ~0.5% ML. Gills robust; length ~25–30% ML, with 26 or 27 lamellae.

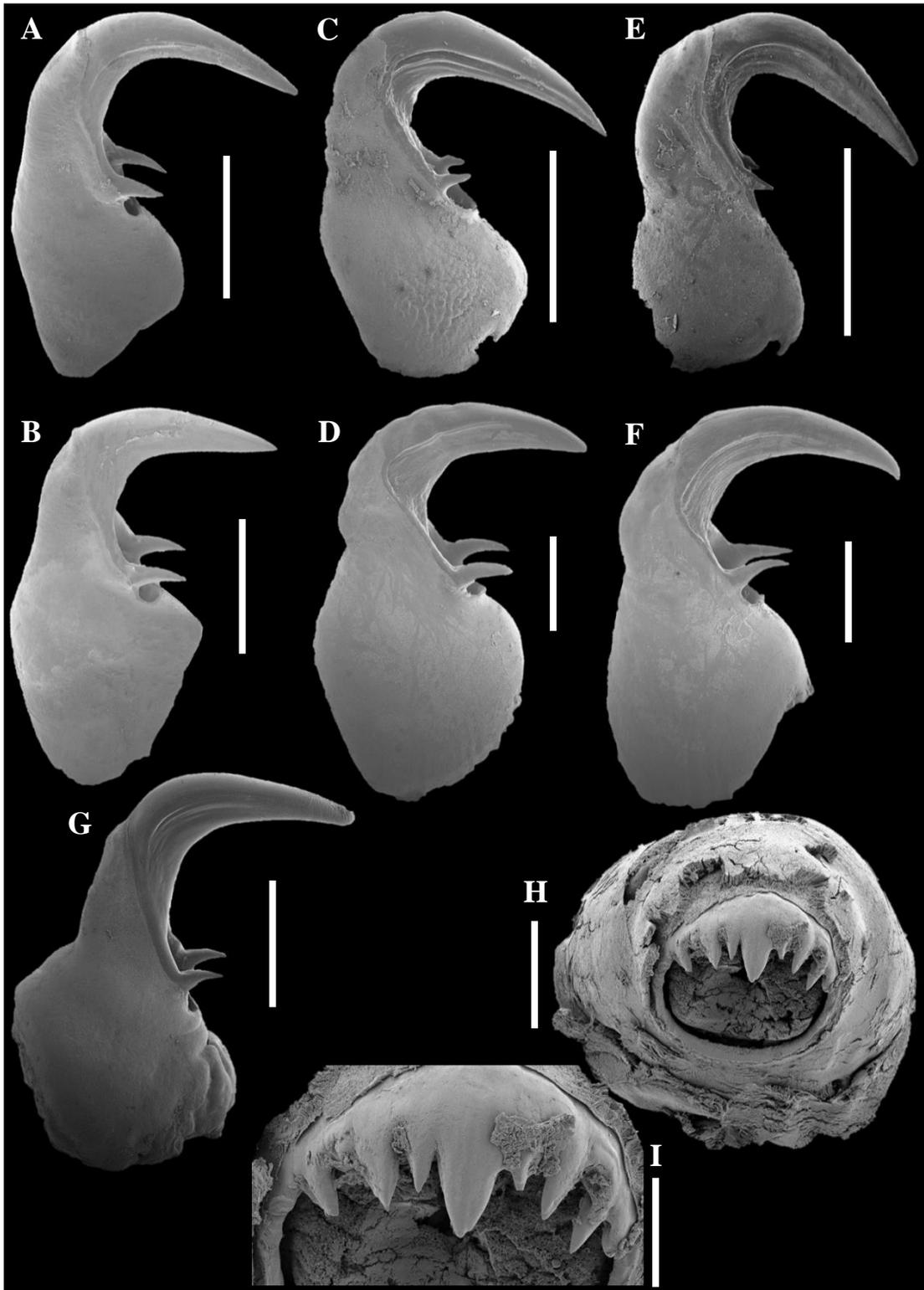


Fig. 32—*Octopoteuthis rugosa* armature. A, B) NIWA 76647, ♀, ML 131 mm; C, D) AM C.476740, ♀, ML 238 mm; E, F) MV F159987, ♂, ML 184 mm; G) NHMUK 1973100, holotype, ♀, ML 162 mm; H, I) NMNZ M.091642, ♂, ML 124 mm. A) 12D hook, Arm III L; B) 2V hook, Arm III L; C) 22D hook, Arm III R; D) 2D hook, Arm III R; E) 20D hook, Arm III; F) 2D hook, Arm III; G) arm hook, unknown location; H, I) 1V sucker, Arm III R. Scale bars = A–G) 1 mm; H) 200 μ m; I) 100 μ m.

Lateral profile of lower beak (5.31–11.19 mm LRL, Figs 33A–D) equally long and deep, with distal wing tips extending beyond rostral tip by 14–20–26% baseline; rostral tip with shallow notch; jaw edge visible, slightly concave due to slight bend in distal third of LRL, with short jaw-edge extension; jaw angle 90–100°, slightly obscured by low, rounded wing fold; depth anterior to jaw angle greater than posterior in largest beak, otherwise equal to posterior. Hood low over crest, length 29–35–40% baseline, without hood grooves. Crest distinct, some of anterior lateral wall between crest and fold pigmented, proportionally increasing with size; length 67–69–73% baseline; tip free with concave notch between crest and lateral wall; sloped in nearly straight line. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior ~70% of hood length; posterior lateral wall margin straight; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 173–202–227% that at jaw angle, length 75–97–106% LRL, with cartilaginous pad. Ventral view with very broad, shallow notch in hood; free corners level with medial ~30% of wing breadth. Entire beak excluding wing pigmented by LRL ~5 mm (ML ~85 mm); patches of pigmentation distally on wing by LRL ~8 mm; wings fully pigmented by LRL ~11 mm (ML ~150 mm).

Lateral profile of upper beak (6.04–9.74 mm URL, Figs 33E, F) longer than deep, maximum depth 45% of length. Rostrum very long, 34–37–42% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~80°; low ridge of cartilage present orally along shoulder; oral shoulder margin straight, ventrally protruding in ‘tooth’. Hood long (length 75–79–83% UBL), moderately tall (~17% UBL); junction of hood and free shoulder very slightly concave. Lateral walls approximately rectangular with maximum depth at midpoint, posterior margin straight. Dorsal view with posterior margin of hood straight, posterior margin of crest straight or slightly concave, posterior margin of crest pigmentation slightly concave. Lateral wall pigmentation begins along anterior crest, progressing posteriorly until crest fully pigmented; continues ventrally along posterior lateral wall, finally progressing anteriorly to free shoulder along a ~45° to axis of UBL. Breadth of posterior lateral wall pigmented by URL ~6 mm, free shoulder and anterior lateral wall transparent; in largest beak examined (URL 9.74 mm), lateral wall fully pigmented, free shoulder unpigmented.

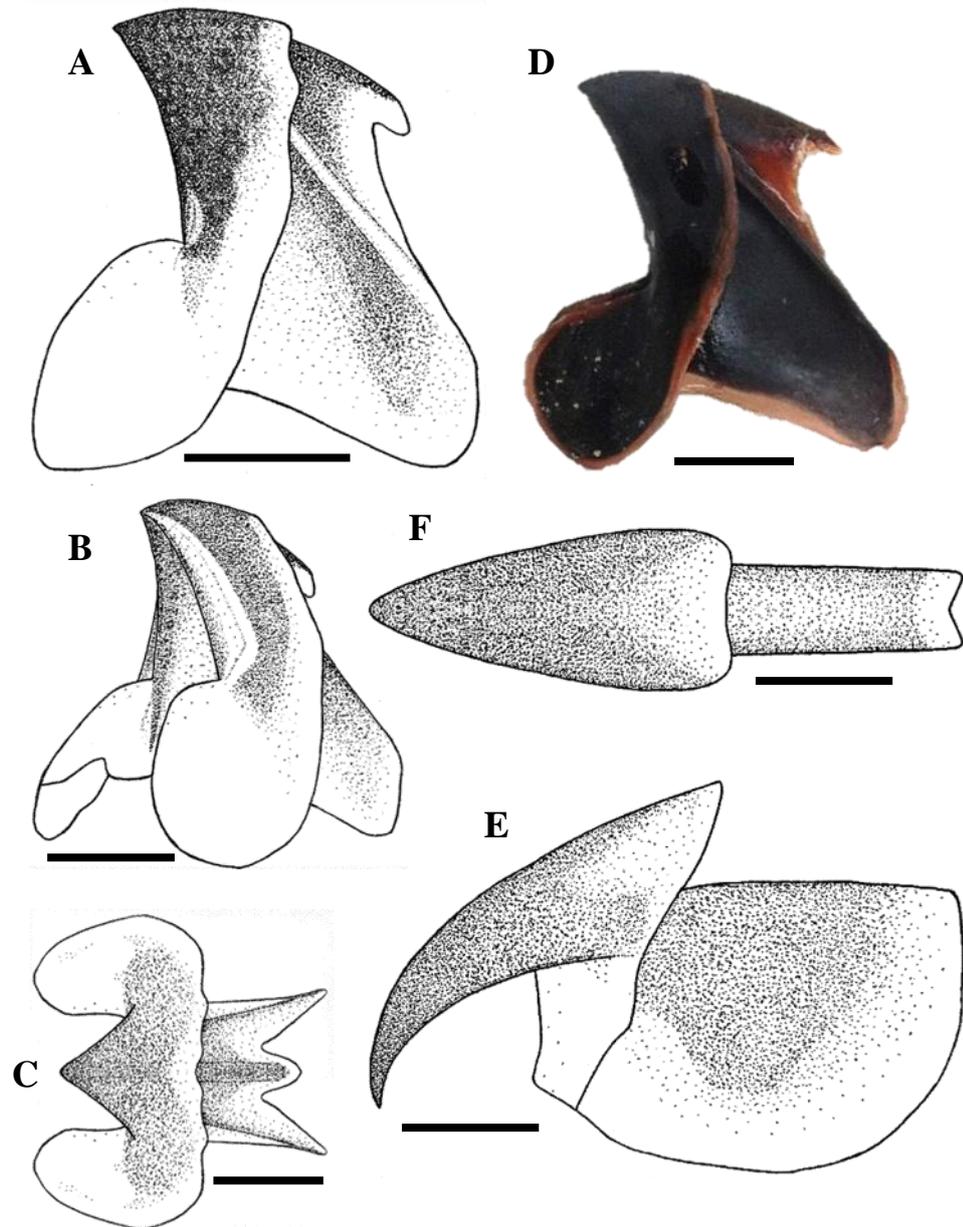


Fig. 33—*Octopoteuthis rugosa* beaks. A–C, E, F) NIWA 95943, sex indet. (beaks only), LRL 8.25 mm, URL 9.74 mm; D) NHMUK 20160106, ♀, ML 148 mm, LRL 11.19 mm, ex-gut-content. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

Radula tooth morphology variable among specimens (Fig. 34A–C); rachidian tricuspid, mesocone moderately long, conical to triangular, base straight to slightly concave; lateral cusps ~30–45% mesocone height, ranging from short and straight or laterally directed to curved and medially directed to broad and blunt. First lateral tooth bicuspid, slightly shorter than rachidian, base straight to slightly convex; inner cusp conical to slightly triangular, slightly medially directed; outer cusp ~40–50% height of inner cusp, ranging from short and straight or laterally directed to curved and slightly medially directed to broad and blunt. Second lateral tooth simple, conical, ~110–125% height of

rachidian. Marginal tooth conical, ~150–200% height of rachidian. Marginal plate present. Palatine palp (Fig. 34D) with 30–42 narrowly triangular teeth, each 70–130% rachidian height; dorso-anterior oral surface and margin adentate, teeth evenly arranged along remainder of oral surface.

Gladius (96–230 mm GL, Fig. 34E) broad and very thin (<0.1 mm thick), delicate, transparent; greatest width (10–12% GL) at ~40% GL; free rachis 7–9% GL, pointed anteriorly, broadening posterior to maximum width (~2% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden posteriorly to maximum width, then taper gradually for remainder of GL; short conus present, 3–5% GL, into which tissue inserts (the traction of which often results in breakage during dissection); rachis broad, evenly concave.

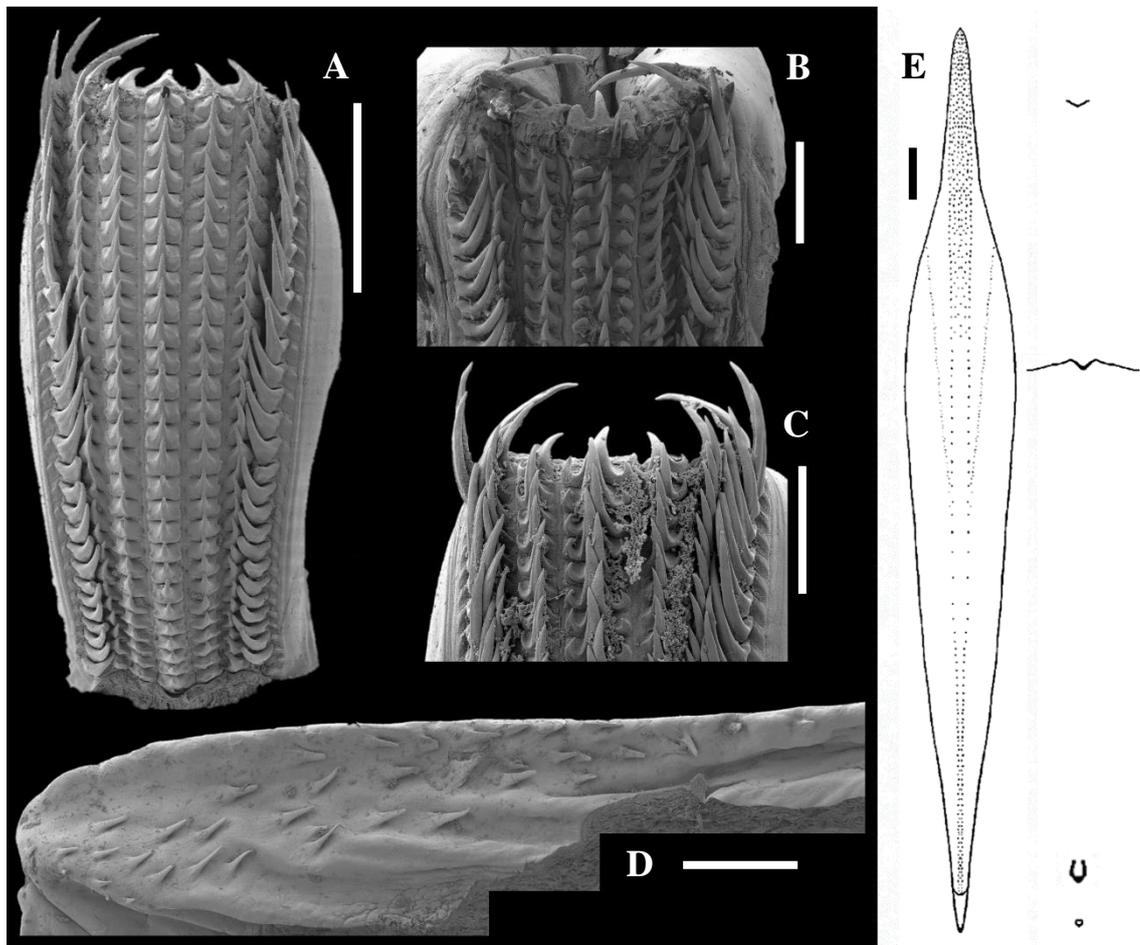


Fig. 34—*Octopoteuthis rugosa*. A) NMNZ M.172953, ♂, ML 105 mm; B) NIWA 71833, ♀, ML 157 mm; C) NIWA OS AP 101, ♀, ML 109 mm; D) NIWA 71838, ♀, ML 138 mm; E) NIWA TAN1401/53, ♀, ML 134 mm. A–C) Radulae; D) palatine palp; E) gladius, with cross-sections. Scale bars = A, D) 1 mm; B, C) 0.5 mm; E) 10 mm.

Colour (preserved) as in *O. megaptera*. In single exceptionally well-preserved specimen (ZMH 73899): five transverse chromatophore bands visible in external gelatinous mantle layer overlying the *recti abdominis* photophores; ring of chromatophores around each PVMP deep in overlying gelatinous layer, with shallower chromatophore patch overlying each PVMP; gelatinous layer over PVMPs globular (as in *O. deletron*). Fresh specimens similar but colours more brilliant (pigmented surfaces redder, non-pigmented white); ex-gut-content specimens dulled, more uniform in colour.

Juvenile specimens (ML 38–61 mm, Fig. 30C) as above, with the following exceptions. PVMP diameter ~3.5% ML, spaced ~14% ML apart; tail length 14–19–25% ML. Fins long (68–74–79% ML), very wide (100–115–130% ML); anterior margin of fin at ~9% ML. Head length ~39% ML; eye diameter 16–20–27 % ML; LHP length ~8% HL (~4% ML); MEP length ~8% HL (~3% ML); EP photophore ~14% HL (~5% ML). Arm length 69–96–143% ML. Tentacles entirely lacking.

Biology. Smallest mature specimen examined ML 141 mm (MV F160001, ♂). Females mature between ML 130 and 160 mm; smallest implanted female examined ML 189 mm (NIWA 71847). Implanted spermatangia with short, rounded sperm mass (~2.25 mm long); most frequently implanted along tail and around posterior ventral mantle photophores, also ventrally along head, funnel, and arms, occasionally also laterally, dorsally. Mature eggs ~0.6 mm in diameter.

Relationships between LRL and URL against ML and body mass were best described by power equations (Fig. 35). Relationships fit the data well ($R^2 > 0.8$) despite small sample sizes (LRL: $n = 14$; URL: $n = 8$). Regressions among studies corresponded relatively well across different relationships, likely a result of *O. rugosa* comprising the bulk of specimens used in these studies (Clarke 1980; Lu & Ickeringill 2002).

Remarks. With a known distribution that is nearly circumglobal in the southern hemisphere, *O. rugosa* co-occurs with the most congeners of any *Octopoteuthis* species. This overlap is most pronounced with *O. fenestra* sp. nov. around New Zealand, but *O. rugosa* is also found along the southern limits of the distributions of *O. megaptera*, *O. laticauda* sp. nov., likely *O. sp. IO nov.*, and to a lesser extent with *O. sicula* and *O. leviuncus* sp. nov. Despite this, *O. rugosa* is readily separated from all these species (save *O. leviuncus*) by its paired Arm II buccal connectives, and from *O. leviuncus* by

its two PVMP and prominent accessory claws (for additional aspects of differentiation see Remarks for *O. fenestra* and *O. megaptera*, and Table 4).

Re-examination of the holotype (Fig. 30D) and the one paratype available yielded measurements between 88 and 114% (mean \pm S.E., $99.5 \pm 1.8\%$) of those reported in the original description for *O. rugosa* (Clarke 1980); two paratypes from whale no. 926 and 196 were not located, and were also not included in Stephen's (1985a) review. Such consistency suggests the minor differences were likely a result of continued contraction

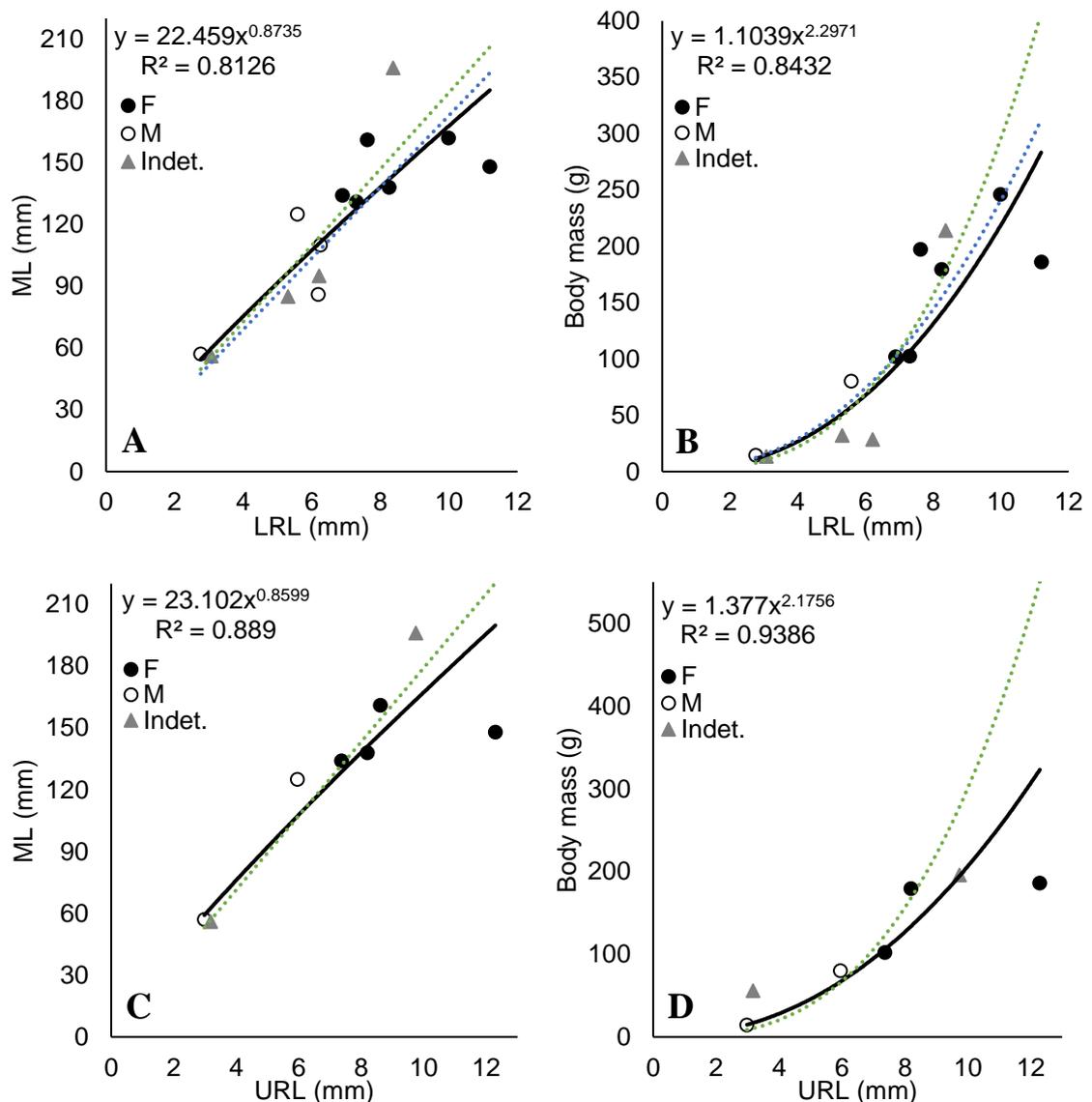


Fig. 35—*Octopoteuthis rugosa*. Regressions of lower rostral length (LRL) against (A) dorsal mantle length (ML) and (B) preserved wet body mass, by sex; upper rostral length (URL) against (C) ML and (D) preserved wet body mass, by sex. Models of best fit (greatest R^2 value) are plotted in black against genus regressions of Clarke (1980; blue), Lu and Ickeringill (2002; green).

over the 30 year period between examinations. Only the holotype measurements are re-reported here; for measurements of the paratypes, see Clarke (1980).

Based on the geographic distributions of *Octopoteuthis* species established herein, *O. 'indica'* Naef, 1923 most likely constitutes a senior synonym of *O. rugosa* given the close proximity of their type localities (*i.e.*, off South Africa). Unfortunately, the type specimen of *O. indica* could not be located during the course of study, while both the holotype and paratype of *O. rugosa* were examined on two separate occasions. At present, *O. rugosa*, a name used to a much greater degree in the literature, is retained for this taxon (see Discussion for treatment of *O. 'indica'*).

Since its description, *O. rugosa* has appeared relatively frequently in the literature. However, these attributions appear to be more contextual than taxonomic: beak identification papers (*e.g.*, Evans & Hindell 2004) and faunal reviews (*e.g.*, Lu 2001; Spencer *et al.* 2009) from the southern hemisphere often included *O. rugosa*, despite a lack of diagnostic criteria for the species and the near-identical beak morphology among small-bodied *Octopoteuthis* species. Furthermore, given that *O. rugosa* co-occurs with other *Octopoteuthis* species throughout its range, no previous publication save Clarke's original description is considered to refer solely, or in discrete parts, to the species herein described as *O. rugosa*.

5.1.2.3. *Octopoteuthis laticauda* sp. nov. (Table 13, Figs 5F, 36–39)

Octopoteuthis nielseni (not Robson, 1948) — Young & Roper (1977): 246–247, Fig. 3;
Young & Harman (1998): Figs 2A, 3G; Carlini & Graves (1999): AF000055;
Lindgren *et al.* (2004): AF000055; Lindgren (2010): AF000055, EU735216.

Type material (3 specimens). **USNM 814611**, Holotype, ♀, ML 216 mm, 11°52.8'N, 144°49.2'W, 100 m, 11/07/1969, RV *Townsend Cromwell*, stn 18, cruise 44, Cobb MWT, Sango Expedition; **USNM 1283023**, Paratype, ♂, ML 169 mm, 21°23.6'N, 158°19.32'W, off Waianae, Oahu Island, Hawaii, 20–30 m, 01/03/1971, RV *Townsend Cromwell*, stn 63, cruise 52, Cobb MWT, P.J. Struhsaker, NMFS-Honolulu Laboratory; **USNM 729746**, Paratype, ♂, ML 73 mm, 21°19.8'N, 156°19.8'W, leeward side of Oahu Island, Hawaii, RV *Kana Keoki*, FIDO VI-66, 3 m IKMWT.

Additional material examined (25 specimens). **NSMT Mo75879**, ♀, ML 162 mm, 36°51.08'N, 141°35.56'E, off Joban, off Hitachi, Ibaraki Prefecture, Japan, 654 m, 11/06/2000, *Wakataka-Marui*, stn 21, trawl; **NSMT Mo85123**, ♀, ML 45 mm, 35°90'N, 135°86'E [*sic*], off Echizen cho, Fukui Prefecture, Sea of Japan, 22/05/2002; **NSMT Mo85041**, ♀, ML 52 mm, 36°06.43'N, 135°43.39'E, off Echizen cho, Fukui Prefecture, Sea of Japan, 290 m, 31/05/2009, *Tanshu-Marui*, stn 105, BTT, T. Kubodera & Umezawa; **NSMT S003-4 DNA 144**, ♀, ML 218 mm, 35°32'N, 142°30'E; **B-Alep-330 Prey #9**, sex indet., ML 30.2 mm, 30°±2.5'N, 160±2.5'W, 23/06/2014, from stomach of *Alepisaurus ferox*, Hawaiian longline fishery; **B-Alep-503 Prey #1**, sex indet., ML 23.5 mm, 30°±2.5'N, 145±2.5'W, 30/07/2014, from stomach of *Alepisaurus ferox*, Hawaiian longline fishery; **USNM 814603**, sex indet., ♀, ML 44, 34 mm, 21°31.8'N, 158°22.2'W, Hawaii, 1006 m, 11/10/1958, RV *Hugh M. Smith*, 47-8, Nanaimo MWT; **USNM 730762**, ♀, ML 66 mm, 21°25.2'N, 158°25.2'W, leeward side of Oahu Island, Hawaii, 0–160 m, 27/02/1971, 71-2-8, 3 m IKMWT, T. Clarke; **USNM 814600**, sex indet., ML 40 mm, 20°58.8'N, 158°28.8'W, Hawaii, 80–121 m, 13/08/1967, RV *Townsend Cromwell*, stn 31, cruise 32, Cobb MWT, Sango Expedition; **USNM 814601**, sex indet., ML 33 mm, 20°58.8'N, 158°12'W, Hawaii, 55–123 m, 15/08/1967, RV *Townsend Cromwell*, stn 37, cruise 32, Cobb MWT, Sango Expedition; **USNM 814608**, ♀, ML 144 mm, 20°58.2'N, 158°33'W, Hawaii, 92–122 m, 25/07/1967, RV *Townsend Cromwell*, stn 28, cruise 32, Cobb MWT, Sango Expedition; **USNM 1468893**, ♂, ML 129 mm, 11°52.8'N, 144°49.2'W, 100 m, 11/07/1969, RV *Townsend Cromwell*, stn 18, cruise 44, Cobb MWT, Sango Expedition; **USNM 814607**, ♂, ML 110 mm, 03°13.2'S,

145°22.8'W, Marquesas Islands, French Polynesia, 150 m, 14/02/1970, RV *Townsend Cromwell*, stn 107, cruise 47, Cobb MWT, Sango Expedition; **AM C.476739**, ♀, ML 134 mm, 05°51'S, 147°20'E, Vitiaz Strait, Papua New Guinea, 110 m, bottom depth 1280 m, 04/11/1969, 1915–2245, FRV *Tagula*, 1-V11/69, 6' IKMWT, R. Eginton; **USNM 814609**, ♂, ML 123 mm, 06°04.2'S, 157°36'W, Line Islands, Kiribati, 140–200 m, 02/02/1966, RV *C.H. Gilbert*, 89-11, Nanaimo MWT; **MV F.159989**, sex indet., ML 5.2 mm, 12°21.9'S, 146°28.9'E, Coral Sea, 1100 m, 30/11/1981, AIMS 1042, 10 m Tucker trawl; **AM C.532747**, ♀, ML 57 mm, 12°36.48'S, 144°43.08'E, Queensland, Australia, 0–200 m, 25/05/1997, 2046 hr, RV *Southern Surveyor*, SS6-97 13-1-1, MIDOC plankton tow, CSIRO; **AM C.532750**, ♂, ML 61 mm, 13°54.9'S, 146°16.5'E, Coral Sea, Queensland, Australia, 0–200 m, 26.99°C at surface, 12/05/1995, 0344–0615, RV *Southern Surveyor*, SS495 stn 16 2-6, MIDOC plankton tow, CSIRO; **AM C.532749**, ♀, ♂, ML 70, 58 mm, 13°54.9'S, 146°16.5'E, Coral Sea, Queensland, Australia, 150–200 m, 26.99°C at surface, 12/05/1995, 0344–0614, RV *Southern Surveyor*, SS495 stn 16 2-6, MIDOC plankton tow, CSIRO; **AM C.476404**, ♂, ML 55 mm, 14°19.68'S, 145°30.6'E, Coral Sea, Queensland, Australia, 100–200 m, 28/05/1997, 0052 hr, RV *Southern Surveyor*, SS6-97 14-1-2, L Net 2, CSIRO, cruise no. 556-97; **NSMT Mo85691**, ♂, ML 24 mm, 19°56.8'S, 153°19'E, 30/11/1975, sample no. SP38; **AM C.380778**, ♂, ML 76 mm, 34°20'S, 151°56'E, 80km E of Port Kembla, 800–2925 m, bottom depth 3650 m, 15/10/1977, 2050–0030, FRV *Kapala*, Engel midwater trawl, J.P. Paxton.

Unlocalised material examined (4 specimens). **NSMT Mo67355**, ♀, ML 184 mm, Tosa Bay, Japan, 250 m, 04/1962, K. Sakai; **NSMT Mo85664**, ♀, ML 225* mm, Pacific coast of Japanese archipelago, surface, 03/01/1972, 05:00, *Soyo-Maru*, stn 209, hand net, Sato; **USNM 1283033**, ♂, ML 117 mm, around Oahu, Hawaii, RV *Kana Keoki*, FIDO-XIV-33; **RV New Horizon**, sex indet., ML 8.1 mm, 26/04/1993.

Distribution (Fig. 36A). Central to western Pacific Ocean, from 37°N–34°S, between 134°E and 160±2.5°W; 0–2925 m.

Diagnosis. Arms moderately long (~82% ML); Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III; arm hooks very broad aborally; anterior fin margin at 9–13% ML; tail long (19–27% ML).

Table 13. Measurements (mm) of *Octopoteuthis laticauda* sp. nov. Mean indices were calculated from specimens ML >45 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	USNM 814611	USNM 1283023	USNM 729746	USNM 729746	USNM 814608	AM C.476739	USNM 814609	USNM 1283033	Mean index	NSMT Mo85123	RV New Horizon
Type status	Holotype	Paratype	Paratype	None	None	None	None	None		None	None
Sex	♀	♂	♂	♀	♀	♀	♂	♂		♀	Indet.
DML	216	169	73	184	144	134	123	117	30	45	8.1
MW	69	58	23	50	57	35	32	31	68	17	3.3
FL	140	108	53	116	100	86	94	81	86	37	4.7
FW	180	144	72	133	140	109	110	98	27	55.5	10.6
HL	68	53	22	47	52	42	44	32	31	17	2
HW	54	33*	26	48	37*	27	36	30	27	13.5	4.7
Side	L	R	R	R	L	L	R	R		R	R
AL I	101*	40*	30*	142	52*	52*	40*	29*		41.5	3*
AL II	95*	68*	27*	176	94*	38*	45*	19*		52.5	4.1
AL III	100* (R)	78*	31*	165	57*	55*	45*	34*		45	3*
AL IV	137 ^r (R)	60*	37*	130	37*	85 ^r	90	52*	72	41	2.8 (L)
AH				30, 31,			NM			*, *, *, *	
AS				31, 31			NM			*, *, *, *	
TL				4, 3, 3+1,							2.3
CL				4							0.6

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

Description (ML 73–225* mm, Figs 36B–39). Mantle conical to weakly goblet shaped; widest at anterior margin, width 26–30–40% ML; weakly muscled; tail thick, long 19–25–27% ML; dorsal anterior margin bluntly pointed medially, ventral margin with slight indentation between mantle components of locking apparatus. Fins moderately long (length 63–68–76% ML), moderately broad (width 72–86–99% ML), greatest width attained at their midpoint (~45–50% ML); anterior fin margin at 9–11–13% ML; width of fin continuation along tail narrow (~2% ML). Paired PVMPs circular, diameter ~1.7% ML; set laterally along posterior ventral mantle, distance between photophores ~11% ML; overlying chromatophore patch diameter ~8% ML. Anterior fin insertion smoothly rounded posteriorly, depth 9–12–14% ML, width 10–13–17% ML.

Head trapezoidal in outline, length 29–31–35 % ML, width 20–27–35% ML, depth 20–25% ML; outer gelatinous layer in one large specimen (NSMT Mo85664, ♀, ML 225* mm) in excellent condition, indented laterally producing 3 pairs of lobes akin to those of *Taningia* (see *Taningia* genus description): dorsal- and ventral-most lobes roughly triangular, ventral largest; lateral smallest, narrow, oblong. LHP triangular, length ~6% HL (~2% ML); MEPs narrowly oblong, level with anterior margin of lens, oriented ~45° to body axis, length ~11% HL (~3.5% ML), width ~2.5% HL (~0.8% ML); EPs crescent shaped, length ~11% HL (~3.3% ML), width ~1.1% HL (~0.3% ML). Eyes large, diameter 52–61–68% HL (16–19–24% ML), with large lenses, diameter 28–33–39% ED. Funnel length 18–21–25% ML; aperture width ~18% of funnel length, level with posterior third of eye; funnel valve tall, broad; funnel groove shallow. Funnel and mantle components of locking apparatus, nuchal cartilage as in *O. megaptera*: funnel component subtriangular, length ~8% ML, maximum width ~5% ML; mantle component obliquely set, conical, length ~8% ML, maximum width ~4% ML; nuchal cartilage oblong, bluntly pointed anteriorly, length ~14% ML, maximum width ~4% ML, set on rhombic cartilaginous pad of equivalent length, width ~7% ML. Buccal connective as in *O. megaptera* excluding rare form of male Arm II; in one mature male specimen, buccal and basal protective membranes greatly developed. Six pores in buccal membrane: one between paired connectives of Arms I, one between Arms II and III ventral to Arm II buccal connective, and one between Arms III and IV. Olfactory papillae short (height ~2.5% HL), elliptical (breadth ~1.2% HL), fleshy knobs without sculpture.

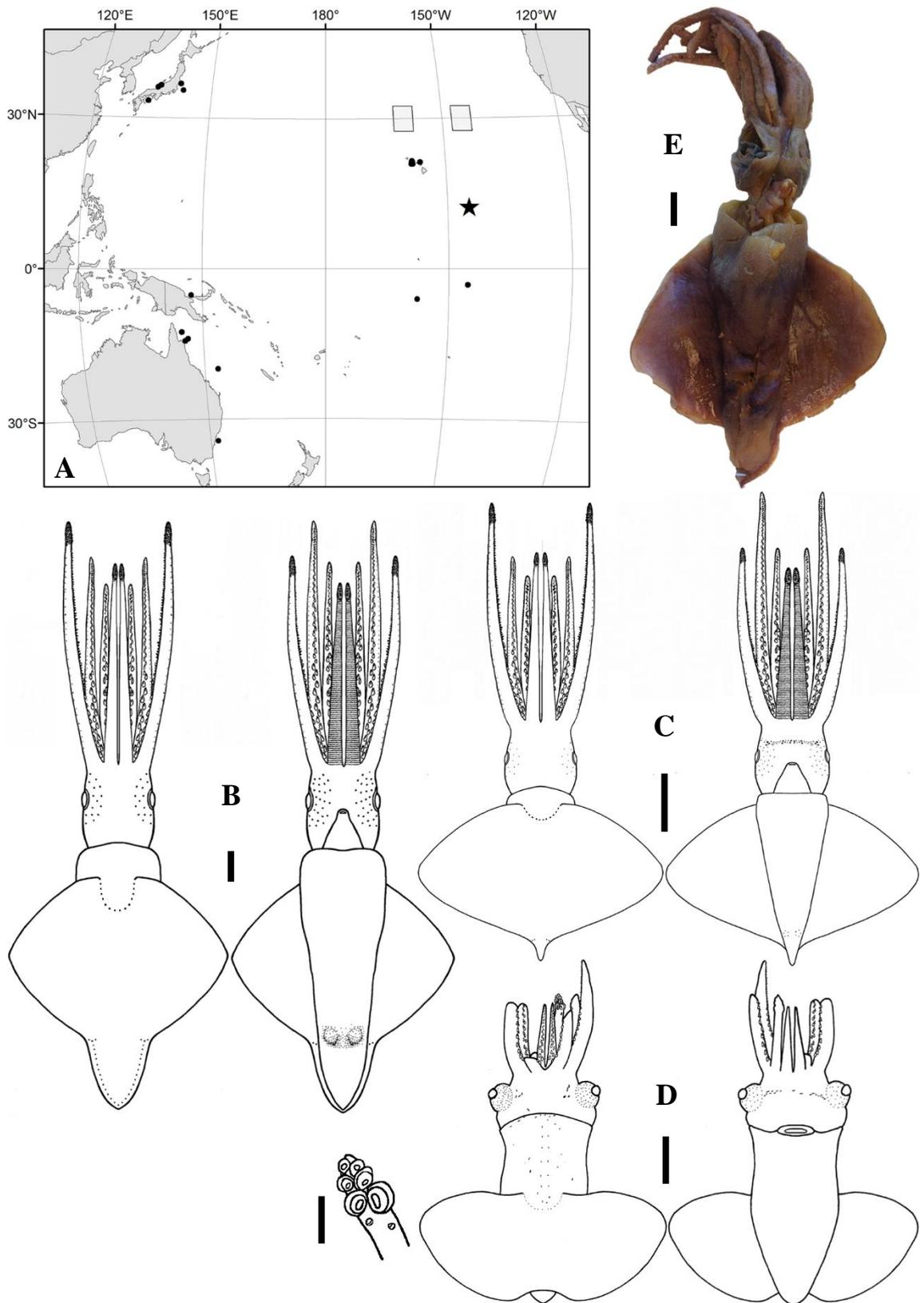


Fig. 36—*Octopoteuthis laticauda* sp. nov. A) Distribution (star indicates type locality); B) adult; C) juvenile (B-Alep-330 Prey #9, sex indet., ML 30.2 mm); D) paralarva, inset tentacle club (RV *New Horizon*, sex indet., ML 8.1 mm); E) USNM 814611, holotype, ♀, ML 216 mm. Scale bars = B, E) 25 mm; C) 10 mm; D) 2 mm, inset 0.5 mm.

Arms slender, length 71–82–97% ML; formula II>III>I>IV; oblong in cross-section, becoming circular distally; with 30–32 pairs of hooks in thick fleshy sheaths, followed by 3–4+1 pairs of suckers distally. Arms narrow gradually to tips, from ~7% AL at base to ~3% at midpoint; arms slightly deeper than wide for almost entire length. Arm-tip photophores occupy distal-most ~7% AL (photophore length ~6% ML); tapering smoothly to blunt tip; arm hooks terminate proximal to photophore, suckers overlies proximal third of photophore. Arm base photophores largest in Arms III (diameter 3.6 mm in ML 216 mm specimen), ~2.5% AL, smallest in Arms II (~75% that of Arm III). Photophore series along ventral Arms III, IV beginning ~12% AL distally from arm-base photophores; comprising dozens of oval to circular photophores, largest basally (diameter 0.7–0.9 mm), decreasing distally; terminating proximal to arm-tip photophore. Arms with gelatinous tissue aborally as in *O. megaptera*.

Arm hooks robust (Fig. 37); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp moderately long, smoothly curved; typically expanded laterally and aborally at junction with base, considerably so in some specimens (Figs 37H–M) imparting an inflated look, few specimens with no such expansion (Figs 37E–G); with no or few shallow lateral ridges; inner angle ~90°; aperture open, broad oval sometimes pointed apically. Accessory claws prominent, slightly curved to straight. Aboral hood absent. Bases broad, crenulated, most prominent laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth) and shorter main cusps. Arm suckers asymmetric, domed.

Tentacles present only in paralarvae (to ML ~8 mm), traces remain in post-larvae (see life stage descriptions below).

Recti abdominis muscles and rectum morphology as in *O. megaptera*; *recti* photophores circular to oblong, at ~30% ML anteriorly; pearly white, raised dorsally; diameter ~2% ML; centred, comprising ~90% of muscle width. Anal flaps of moderate length, ~1% ML. Ventral visceral mesentery pore diameter ~0.5% ML; pore appears as sphincter in membrane. Gills robust; length ~25% ML, with 27 or 28 lamellae.

Lateral profile of lower beak (7.68–10.85 mm LRL, Figs 38A–D) equally long and deep, with distal wing tips extending beyond rostral tip by ~17% baseline; rostral tip with very shallow indentation; jaw edge visible, straight except for slight bend in distal

third of LRL, with short jaw-edge extension; jaw angle 80–90°, slightly obscured by low, rounded wing fold; depth anterior and posterior of jaw angle equal in smallest beak, anterior depth greater than posterior in beaks LRL >~9.5 mm. Hood low over crest, length ~31% baseline. Crest distinct, lateral wall between crest and fold unpigmented; length ~67% baseline; tip free with concave ventral margin; sloped in straight line. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior ~50% of hood length, tapering posteriorly as ventral extension off fold apex; posterior lateral wall

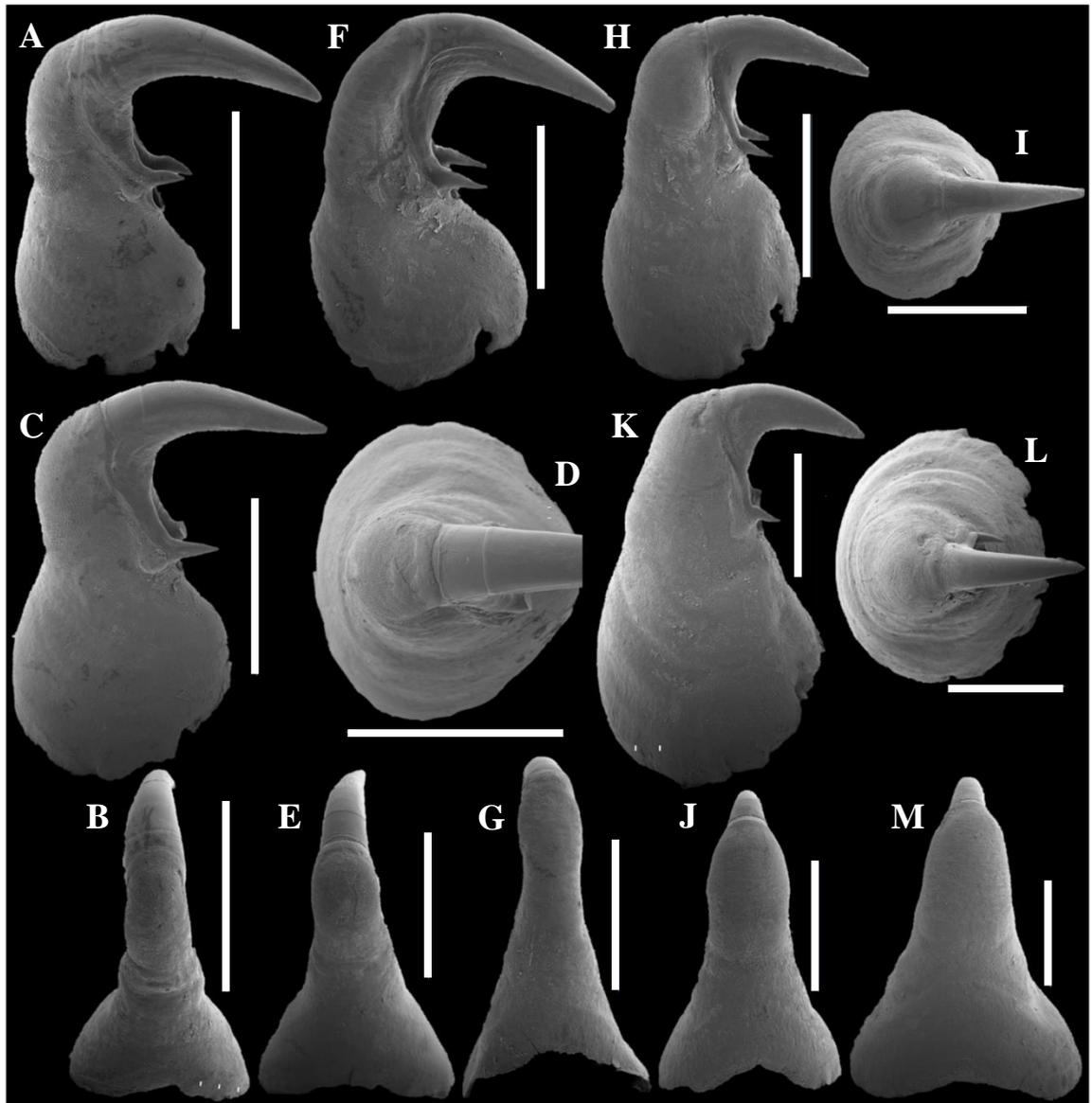


Fig. 37—*Octopoteuthis laticauda* sp. nov. armature. A–E) USNM 1468893, ♂, ML 129 mm; F, G) NSMT Mo67355, ♀, ML 185 mm; H–M) USNM 814611, ♀, ML 216 mm. A, B) 11D hook, Arm III R: (A) lateral profile, (B) aboral; C–E) 4V hook, Arm III R: (C) lateral profile, (D) apical, (E) aboral; F–G) 20V hook, Arm IIR: (F) lateral profile, (G) aboral; H–J) 16D hook, Arm III R: (H) lateral profile, (I) apical, (J) aboral; K–M) 4V hook, Arm III R: (K) lateral profile, (L) apical, (M) aboral. Scale bars = 1 mm.

margin straight; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 213–219–225% that at jaw angle, length ~95% LRL, with cartilaginous pad. Ventral view with very broad, shallow notch in hood; free corners level with inner wing margin. Entire beak excluding wing pigmented in smallest beak examined; beaks >~9.8 mm LRL with fully pigmented wings.

Lateral profile of upper beak (8.71–11.9 mm URL, Figs 38E, F) longer than deep, maximum depth ~46% of length. Rostrum long, ~32% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle 70–80°; low ridge of cartilage present orally along shoulder; oral shoulder margin straight or slightly undulate, ventrally protruding in low ‘tooth’ in beaks <11.2 mm URL. Hood long (length ~74% UBL), moderately tall (~18% UBL); junction of hood and free shoulder slightly concave. Lateral walls approximately rectangular with maximum depth in posterior third, posterior margin straight. Dorsal view with posterior margin of hood straight or slightly concave, posterior margin of crest slightly concave, posterior margin of crest pigmentation concave. Smallest beak examined with dorso-posterior 75% of lateral wall pigmented, ventro-anterior quarter and free shoulder unpigmented; beaks >~11 mm UBL fully pigmented including free shoulder.

Radula (Figs 39A–C) with tricuspid rachidian: mesocone long, conical, straight; lateral cusps moderately long (~40% mesocone height), straight to slightly laterally directed points; base straight. First lateral tooth bicuspid: inner cusp equal to rachidian in height, narrowly triangular; outer cusp ~30% height of inner cusp, straight to slightly laterally directed; base slightly convex. Second lateral tooth simple, narrowly triangular, ~120% height of rachidian. Marginal tooth simple, conical, ~200% height of rachidian. Marginal plate absent. Palatine palp (Fig. 39D) with ~46 triangular to narrowly triangular teeth, each 95–175% rachidian height; teeth shorter, narrower ventro-anteriorly; teeth evenly distributed across palp.

Gladius not examined due to limited material.

Colour (preserved) in adults deep purple to dark pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose

furrows in females; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patches overlying posterior ventral mantle photophores darkest postero-laterally; one specimen (NSMT Mo67355, ♀, ML 184 mm) in excellent condition with more darkly pigmented area on anterior ventral mantle overlying *recti abdominis* photophores. Inner mantle surfaces and viscera unpigmented.

Juvenile specimens (ML 23.5–55 mm, Fig. 36C) differ from above as follows. Mantle width 38–40–44% ML; PVMP diameter ~3.4% ML, spaced ~19% ML apart; tail short (12–18–24% ML). Fins long (73–77–82% ML), very wide (104–122–142% ML); anterior margin of fin at 9–12–16% ML. Head length 38–40–44% ML, width 30–37–

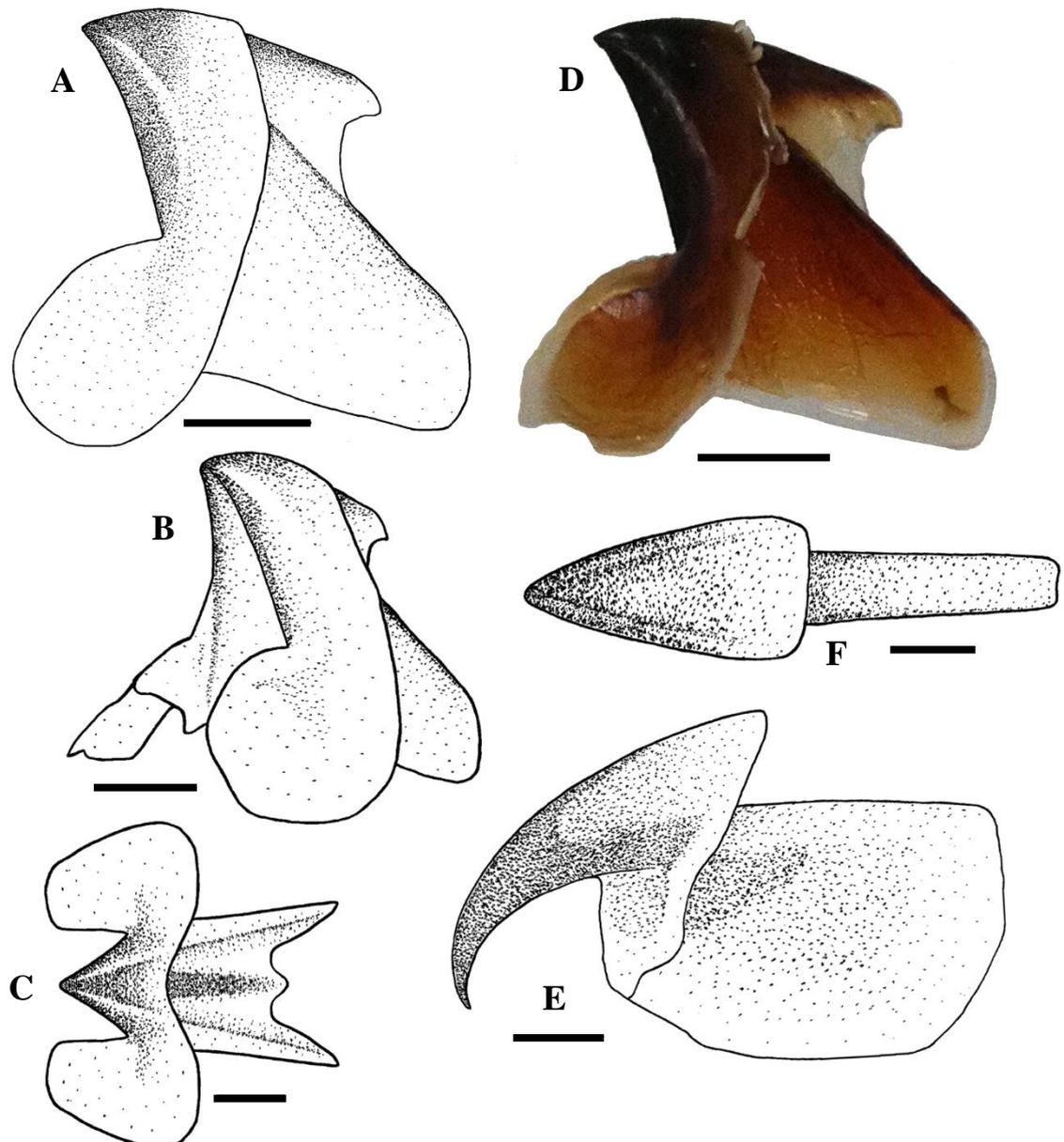


Fig. 38—*Octopoteuthis laticauda* sp. nov. beaks. A–D) NSMT Mo85664, ♀, ML 225* mm, LRL 10.85 mm, URL 11.9 mm; E, F) NSMT S003-4, ♀, ML 218 mm, LRL 9.81 mm, URL 11.19 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

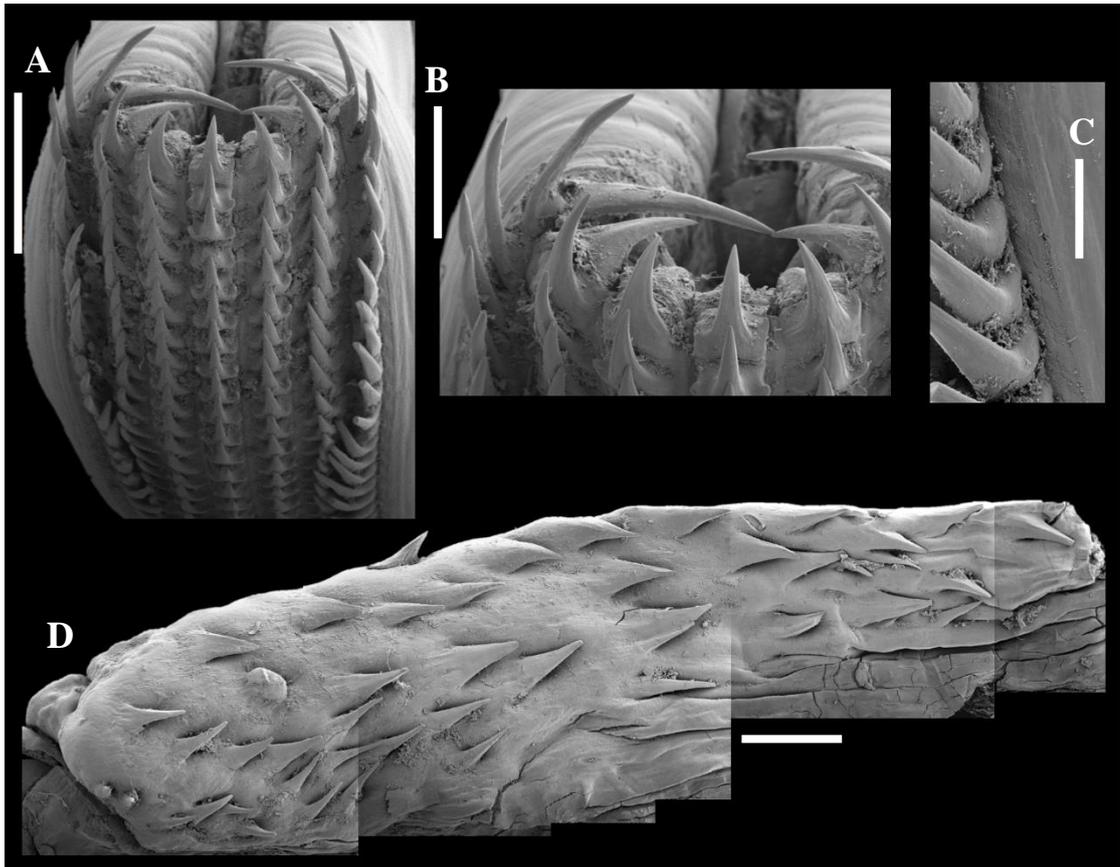


Fig. 39—*Octopoteuthis laticauda* sp. nov. A–D) NSMT Mo85664, ♀, ML 225* mm. A–C) Radula: (A) whole, (B) bending plane, (C) lateral margin; D) palatine palp. Scale bars = A, D) 1 mm; B) 0.5 mm; C) 250 μ m.

43% ML. Arms long (86–106–130% ML). Tentacles entirely lacking, smallest specimens still with very thin, low web between Arms III and IV that sheltered tentacles.

Two paralarval specimens (ML 5.2–8.1 mm, Fig. 36D) as above, with the following exceptions. Fins short (~58% ML), very wide (~131% ML); anterior fin margin at ~45% ML; posterior fin margin concave, mantle extending beyond fins as tail, length ~6% ML. Head short (~25% ML), wide (~58% ML); with band of chromatophores across ventral surface, level with anterior margin of eye, comprising 2 or 3 offset rows of dash-shaped or circular black chromatophores. Eyes sessile, diameter ~15% ML, directed antero-laterally, lenses protruding. Three intact arms: Arm IIR 51% ML, Arms IV shortest (~35% ML); all with two series of fully developed arm hooks. Right tentacle intact, short (~28% ML), possibly in early stages of resorption; base width equivalent to adjacent arms, thickness maintained distally to club. Club length ~8% ML, ~28% TL; with 4 pairs of suckers, carpal pair very small, 2D sucker (first manus sucker) largest, gradually decreasing in size distally; suckers domed.

Etymology. The species is named after the considerable breadth of the tails of the first specimens examined (*laticauda*, “broad tail”), and for the breadth of the ‘back’ of the arm hooks.

Biology. Smallest mature specimen examined ML 123 mm (USNM 814609, ♂). Females mature between ML 140 and 160 mm; smallest implanted female examined ML 184 mm (NSMT Mo67355); some females with rugose furrows along entire anterior mantle circumference, decreasing in length dorsally. Implanted spermatangia with short, rounded sperm mass (~2 mm long); found in rugose furrows along anterior ventral mantle, dorsal and ventral head, medially along tail. Mature eggs ~1.16 mm in diameter, orange, translucent.

Remarks. This species’ distinctive arm hook morphology is most easily visualised in aboral and apical views (Figs 37I, J, L, M) after removal of the encasing sheath. At present, it appears most prominent in females and most specimens demonstrated a broadened aboral surface to some extent. However, it remains somewhat variable among individuals: one large female (NSMT Mo67355, ML 185 mm) bore narrow-backed hooks comparable to those of *O. rugosa*, as did USNM 814609 (♂, ML 123 mm), collected within 18° of latitude of specimens with distinctly broad-backed hooks. While some variability was found in *O. laticauda*, and similarly in *O. sp.* IO nov. (see below), such morphology was not encountered among other species of *Octopoteuthis*. This, combined with strong genetic separation and differences in certain body proportions, supports the designation of a new species.

In the northwest of its distribution, *O. laticauda* co-occurs only with *O. deletron*, from which it is readily distinguishable by its two PVMPs (versus a single PVMP in *O. deletron*). With greater understanding of the full distribution of *O. laticauda* and *O. sp.* IO nov., the possibility exists that specimens may be collected from adjacent waters through the southeast Asian islands. *Octopoteuthis laticauda* can be differentiated from its western relative by the more posterior position of the fins (anterior fin margin at 9–13% ML vs 4–8%).

5.1.2.4. *Octopoteuthis* sp. IO nov. (Table 14, Figs 40–42)

Material examined (15 specimens). **OJMFD9**, ♀, ML 45 mm, 10°56.25'N, 74°18.18'E, 100 m, 00/00/2015, night, coll. K. Sajikumar; **OAMFD1**, sex indet., ML 29.8 mm, 10°28.33'N, 71°19.3'E, 200 m, 21/04/2015, night, coll. K. Sajikumar; **NHMUK 20150465**, 3 sex indet., ML 22, 10, 9.5 mm, 01°29.2'N, 57°59.5'E, western Indian Ocean, 0–88 m, 02/06/1964, stn 5413, RRS *Discovery* Expedition, IKMWT; **NHMUK 20150466**, ♂, ML 31 mm, 00°32.1'N, 58°04'E, western Indian Ocean, 0–100 m, 03/06/1964, stn 5415, RRS *Discovery* Expedition, IKMWT; **NHMUK 20150458**, sex indet., ML 39 mm, ♂, ML 38 mm, 01°25'S, 58°06.9'E, Somali Basin, NE of Seychelles, 0–100 m, 05/06/1964, stn 5420, RRS *Discovery* Expedition, IKMWT; **ZMUC stn 268**, ♂, ML 83 mm, eye and arm sections from second specimen, 03°14'S, 54°28'E, 4046 m, 23/03/1951, Galathea expedition 1950-52, stn 268, TOT; **ZMUC stn 3946II**, ♂, ML 105 mm, 03°26'S, 42°58'E, 03/01/1920, 1900 hr, S-200; **ZMUC stn 3804I**, ♀, ML 47.5 mm, 09°09'S, 114°47'E, 30/08/1929, 2345 hr, E 300; **NSMT Mo85690**, 2 sex indet., ML 37*, 29* mm, 09°15'S, 83°45'E, 28/07/1975, Sample no. CII176; **ZMUC stn 3929I**, ♂, ML 42.6 mm, 12°11'S, 50°18'E, 18/12/1929, 1900 hr, S-200; **MV 65963**, ♂, ML 140 mm, 17°56'S, 118°14'E, off Broome, Western Australia, 600–650 m, 07/02/1990, 0715–0930 hrs, shot 1, FV *Courageous*, trawl, coll. CSIRO & V. Wadley; **MV F67717**, ♂, ML 90 mm, 20°07.8'S, 112°55.1'E, 854–868 m, 23/01/1991, SS0191 3, RV *Southern Surveyor*, trawl, coll. CSIRO & V. Wadley.

Additional genetic samples (1 sample). **OJMFD3**, ♀, ML 116 mm, 10°56.25'N, 74°18.18'E, 100 m, 00/00/2015, night, coll. K. Sajikumar.

Distribution (Fig. 40A). Indian Ocean, 11°N–20°S, 54–113°E; 0–900 m.

Diagnosis. Arms long (~90% ML); Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III; arm hooks broad aborally; anterior margin of fin at 4–8% ML; tail very long (24–29% ML).

Description (ML 83–140 mm, Figs 40B–42). Mantle conical to weakly goblet shaped; widest at anterior margin, width 28–33–38% ML; weakly muscled; tail long 24–27–29% ML; dorsal anterior margin bluntly pointed medially, ventral margin with slight indentation between mantle components of locking apparatus. Fins moderately

Table 14. Measurements (mm) of *Octopoteuthis* sp. IO nov. Mean indices were calculated from specimens ML >48 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	MV F65963	ZMUC stn 3946II	MV F67717	ZMUC stn 268	Mean index	ZMUC stn 3804I	NHMUK 20150458	NHMUK 20150458	NHMUK 20150466	NHMUK 20150465	NHMUK 20150465
Sex	♂	♂	♂	♂		♀	Indet.	♂		Indet.	Indet.
DML	140	105	90	83		47.5	39	38	31	22	10
MW	50	30	34	24	33	14.6	13	14	11	7.5	3.7
FL	104	70	63	57	70	34	27.7	27	23	17.6	7.0
FW	135	88	90	82	95	50	38	39.5	37.5	25.8	13
HL	NM*	26	32	31	33	13.1	12	13	10	7.8	4.0
HW	NM*	23*	26	25*	29	13.9	12	12.5	10	7	4.5
Side	L			L			R	L	L	L	L
AL I	NM*	NM*	NM*	NM*		NM*	12*	24	20	13.2	2.9*
AL II	149 (R)	NM*	NM*	74	98	NM*	10*	27	23*	18	8.0*
AL III	130	NM*	NM*	70	89	NM*	28	20*	23	15.5	6.2 ^r
AL IV	111	NM*	NM*	NM*		NM*	23	22 (R)	18	10.4* (R)	4.1* (R)
AH	31, *, *			*, 30					*, *, *	*, *, *	
AS	*, *, *			*, 4+1					*, *, *	*, *, *	
TL											
CL											

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

long (length 66–70–74% ML), broad (width 83–95–100% ML), greatest width attained at their midpoint (~45–50% ML); anterior fin margin at 4–7–8% ML; fins continue along tail in thin strip. Paired PVMPs circular; set laterally along posterior ventral mantle. Anterior fin insertion smoothly rounded posteriorly, depth 9–12–14% ML, width 10–13–17% ML.

Head square in outline, length 25–33–38% ML, width ~29% ML, depth 20–25% ML. LHP triangular, large, length ~11% HL (~3% ML); MEPs oblong, obliquely set; EPs narrow, crescent shaped, length ~23% ED. Eyes large, diameter ~68% HL (~20% ML), with large lenses, diameter ~31% ED. Funnel length 18–22–28% ML; aperture width ~15% of funnel length, level with posterior margin of lens. Funnel component of locking apparatus as in *O. megaptera*: subtriangular, length ~6% ML. Nuchal cartilage oblong, length ~11% ML. Buccal connectives as in *O. megaptera*, excluding specified modifications in males. Pore ventral to Arm II dorsal connective, between Arms II and III. Olfactory papillae short, elliptical, fleshy knobs without sculpture.

Only two subadult to adult specimens with complete intact arms (marginally more intact among juveniles, see below), comprising only two of each of Arms II and III, and one Arm IV; Arm II length ~98% ML, Arm III length ~89% ML, Arm IV length 79% ML; oblong in cross-section, becoming circular distally; with 30–31 pairs of hooks in thick fleshy sheaths, only arm with fully intact armature with 4+1 pairs of suckers distally. Arms taper gradually to tips. Arm-tip photophores occupy distal-most ~6% AL (photophore length ~5.5% ML); swelling slightly to midpoint, tapering distally to slight bulb at tip; arm hooks terminate proximal to photophore, suckers overlie proximal third of length. Arm-base and series photophores as described above. All arms with low gelatinous aboral keels from base to tip.

Arm hooks robust (Fig. 41); largest in pairs 3–6 of Arms II, decreasing gradually in size distally. Main cusp long, smoothly curved; typically expanded laterally and aborally at junction with base in basal hooks, considerably so in some specimens (Figs 41A–C) imparting an inflated look, few specimens with no such expansion (Figs 41G–I); with no or few shallow lateral ridges; inner angle ~90° in proximal 40–50% of hook pairs, becoming acute (~70°) distally; aperture open, oval. Accessory claws prominent, curved. Aboral hood absent. Bases very broad; crenulated, most prominent laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and

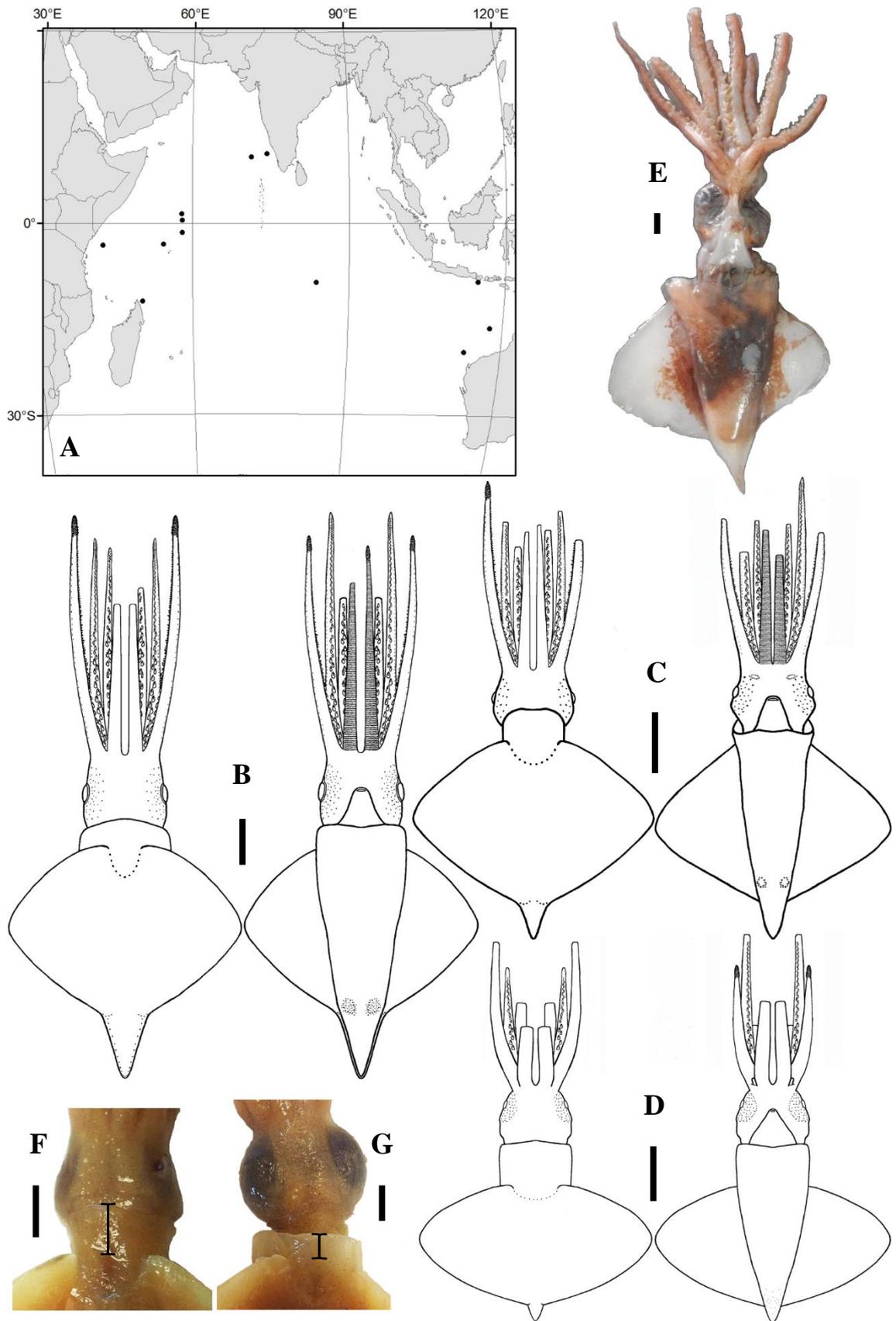


Fig. 40—*Octopoteuthis* sp. IO nov. A) Distribution; B) adult; C) juvenile (NHMUK 20150458, sex indet., ML 38 mm); D) post-larva (NHMUK 20150465, sex indet., ML 10 mm); E) OJMFD3, ♀, ML 116 mm; F) NHMUK 20150458, sex indet., ML 39 mm; G) *O. rugosa*, NHMUK 20160088, ♂, ML 44 mm. Scale bars = B, E) 25 mm; C) 10 mm; D) 3 mm; F, G) 5 mm.

breadth) and shorter main cusps. Arm suckers asymmetric, domed; sucker rings dentate, ultrastructure not examined.

Tentacles absent, traces only remain in post-larvae (see life stage description below).

Recti abdominis muscles and rectum morphology as in *O. megaptera*; *recti* photophores circular to oblong, diameter ~2% ML. Gills robust, with 25 or 26 lamellae.

Lateral profile of lower beak (6.50 mm LRL, Figs 42A–D) equally long and deep, with distal wing tips extending beyond rostral tip by ~18% baseline; rostral tip with shallow to distinct notch indent; jaw edge visible, straight except for very slight bend in distal third of LRL, with short jaw-edge extension; jaw angle 90°, slightly obscured by low, rounded wing fold; depth anterior of jaw angle greater than posterior. Hood low over crest, length ~38% baseline. Crest distinct; length ~72% baseline; tip free with concave ventral margin; sloped in straight line; lateral wall between crest and ridge with triangular pigmented region anteriorly. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior ~50% of hood length; posterior lateral wall margin straight; free corner beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width ~210% that at jaw angle, length ~95% LRL, with cartilaginous pad. Ventral view with very broad, shallow notch in hood; free corners level with inner wing margin. Both beaks examined (from specimens ML 105, 116 mm) fully pigmented, including wings.

Lateral profile of upper beak (6.81 mm URL, Figs 42E, F) longer than deep, maximum depth ~45% of length. Rostrum long, ~39% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~70°; low ridge of cartilage present orally along shoulder; oral shoulder margin concave or slightly undulate, ventrally protruded in low ‘tooth’. Hood long (length ~82% UBL), moderately tall (~15% UBL); junction of hood and free shoulder slightly concave. Lateral walls approximately rectangular with maximum depth in posterior third, posterior margin straight. Dorsal view with posterior margin of hood straight, posterior margin of crest slightly concave, posterior margin of crest pigmentation concave. Both beaks examined (from specimens ML 105, 116 mm) fully pigmented, including free shoulder.

Radula with tricuspid rachidian: mesocone long, conical, straight; lateral cusps moderately long (~30% mesocone height), straight to slightly laterally directed points. First lateral tooth bicuspid: inner cusp equal to rachidian in height, narrowly triangular; outer cusp ~30% height of inner cusp, slightly laterally directed point. Second lateral tooth simple, conical, ~150% height of rachidian. Marginal tooth simple, conical, ~200% height of rachidian. Palatine palp not examined.

Gladius not examined due to scarcity of subadult to adult specimens.

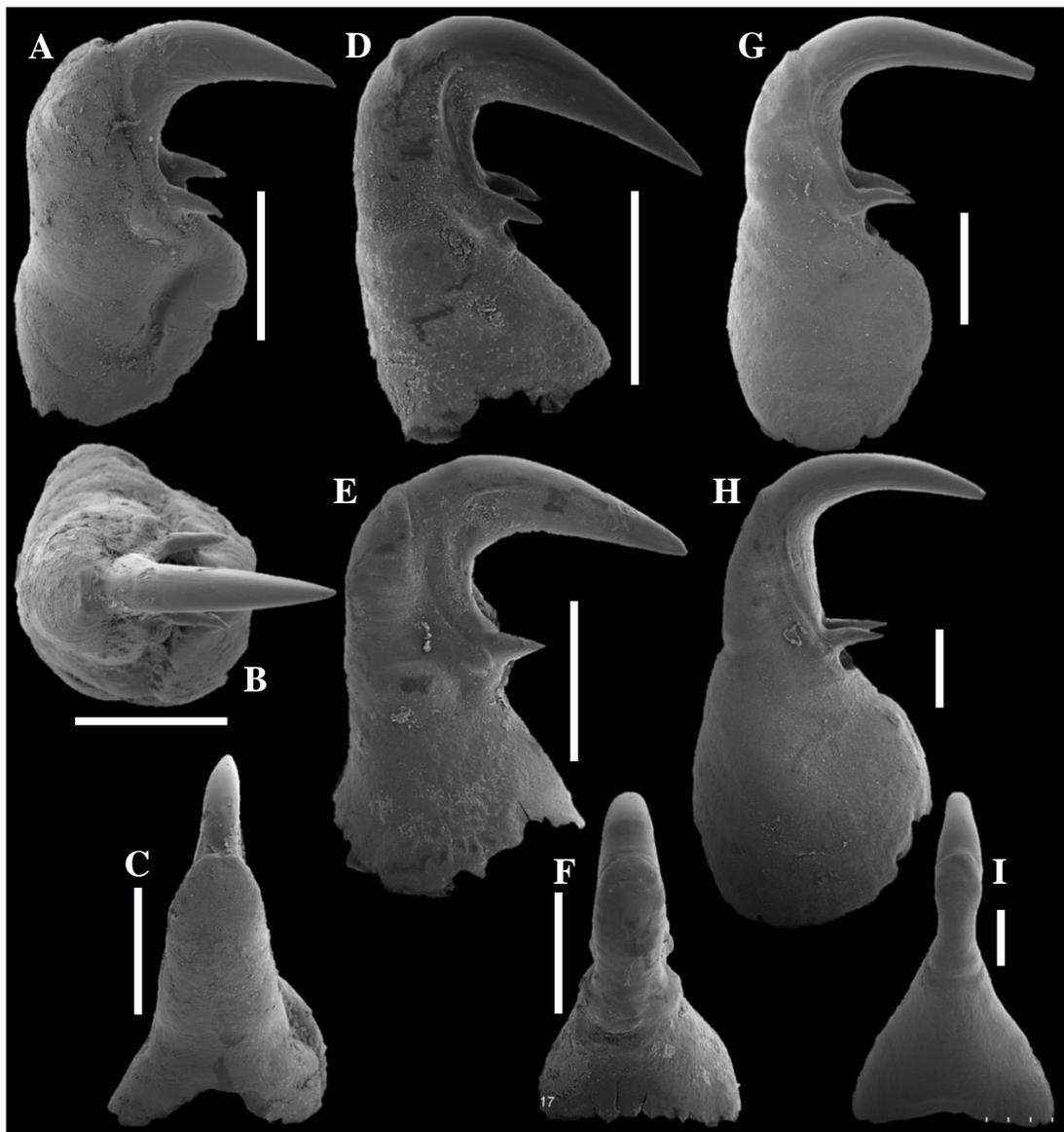


Fig. 41—*Octopoteuthis* sp. IO nov. armature. A–C) OJMFD9, ♀, ML 45 mm; D–F) ZMUC stn 268, ♂, ML 83 mm; G–I) MV F65963, ♂, ML 140 mm. A–C) 4D hook, Arm IIL: (A) lateral profile, (B) apical, (C) aboral; D) 15V, Arm IIR; E, F) 4D hook, Arm IIR: (E) lateral profile, (F) aboral; G) 11D, Arm IIR; H, I) 4D hook, Arm IIR: (H) lateral profile, (I) aboral. Scale bars = 0.5 mm.

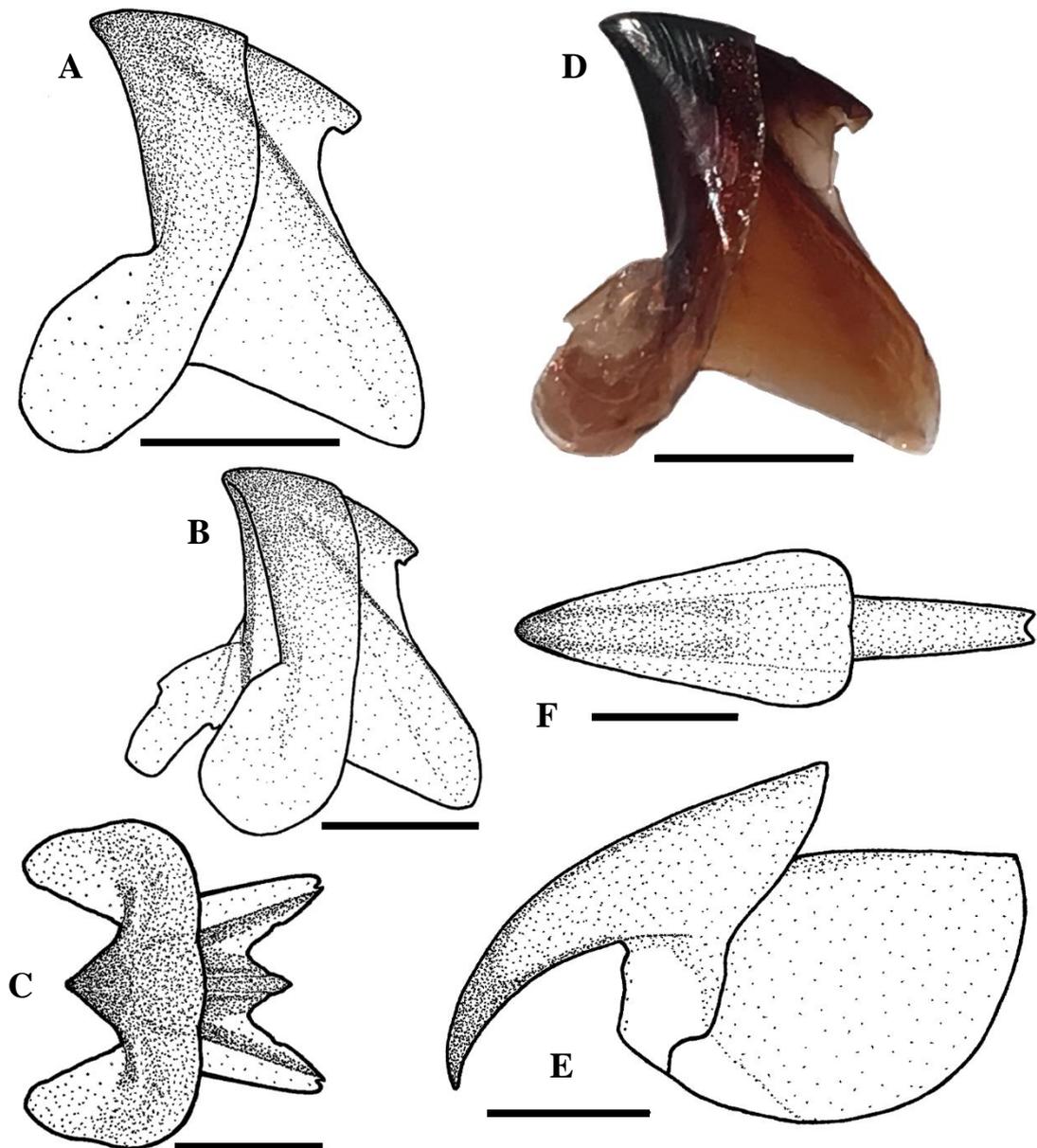


Fig. 42—*Octopoteuthis* sp. IO nov. beaks. A–F) OJMFD3, ♀, ML 116 mm, LRL 6.5 mm, URL 6.81 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

Colour (preserved) in adults deep purple to dark pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose furrows in females; arm tips over photophores dark purple; chromatophore patches overlying posterior ventral mantle photophores darkest postero-laterally. Inner mantle surfaces and viscera unpigmented. Fresh specimens similar but colours more brilliant: pigmentation redder, non-pigmented tissues white or translucent.

Juvenile specimens (ML 31–47.5 mm, Figs 40C, F) as above, with the following exceptions. PVMP diameter ~1.7% ML, spaced ~15% ML apart; tail short (13–19–21%

ML). Fins wide (97–108–121% ML); anterior margin of fin at ~11% ML (Fig. 40F). Head with ventral transverse band of two or three sparse rows of chromatophores, level with anterior eye margin; VHP length ~8% HL (~3% ML); MEP length ~8% HL (~3% ML); EP length ~11% HL (~4% ML). Arms short (58–66–72% ML); arm-tip photophores long (~10% AL, ~7% ML). Tentacles entirely lacking, smallest specimens still with very thin, low web between Arms III and IV that overlaps tentacles. *Recti abdominis* photophores ~3% ML, almost entire width of muscle band, squarish. In NHMUK 20150458 (sex indet., ML 38 mm) immediately anterior to *recti* photophores asymmetric, barbell-shaped iridescent, peachy-pink coloured patch on the ventrum of ink sac; other specimen in lot (sex indet., ML 39 mm) with similar tissue along ventral depressions in ink sac into which *recti* photophores insert.

Post-larval specimens (ML 9.5–22 mm, Fig. 40D) differ from above as follows. Tail very short, length 5–9–11% ML, tip level with posterior margin of fin. Gladius visible through dorsal mantle anterior of fins at ML 9.5–10 mm; vanes visibly expanded anterior to anterior fin insertion. Fins wide, width 117–121–130% ML; anterior fin margin at 15–27–33% ML, greatest in smallest specimens. Head length ~37% ML, width 32–40–45% ML. Eye diameter ~16% ML, antero-laterally oriented. Arms of specimen ML 22 mm 60–82% ML; with two series of fully developed arm hooks. Tentacles reduced to gelatinous, translucent, short nubs (length ~2% ML).

Biology. Smallest mature specimen examined ML 140 mm (MV F65963, ♂). Maturity in females unknown; largest female examined ML 47.5 mm (ZMUC stn 3804I). Implanted spermatangia with short, oblong sperm mass.

Unpublished data suggest males in the Arabian Sea may mature at sizes smaller than those encountered herein: the terminal organ of a specimen ML 71 mm was protruding beyond the anterior mantle margin and had 65 implanted spermatangia along its tail (likely self-implanted), while the protruding organ of a second specimen ML 79 mm contained 165 spermatophores averaging 7 mm in length (K. Sajikumar, pers. comm.). Two males of comparable size examined herein (ML 105, 83 mm) did not have emergent organs although a third specimen of ML 90 mm did, but did not have externally implanted spermatangia nor observable extruded spermatophores; dissection was not undertaken. Sexual maturity at such small size is comparable only with *O. megaptera*, to which it is most closely related (see Genetics).

Remarks. Type material was not designated as available material in best condition was examined years before recognition of this species. Formal description based on newly collected material from the Arabian Sea (with complementary genetic analyses) is planned for the near future.

As in *O. laticauda* sp. nov., this species' arm hook morphology, while characteristic, remains somewhat variable at present. It appears most prominent in females, but most specimens (of both sexes) demonstrated a broadened aboral surface to some degree, although exceptions remain (*e.g.*, MV F65963, ♂, ML 140 mm; Figs 41G–I). This character combined with preliminary but strong genetic separation and differences in certain body proportions support the designation of a new species.

Octopoteuthis sp. IO nov. is most morphologically similar to *O. laticauda* and may, in the future, prove to be regionally sympatric around southeast Asia (see *O. laticauda* Remarks). Overlap is also likely with *O. rugosa* in the southern Indian Ocean. However, juvenile *O.* sp. IO nov. are readily distinguishable from *O. rugosa* by their more posteriorly set fins (anterior fin margin at ~12% compared to ~9% ML, respectively; Fig. 40F, G).

Little taxonomic work has been written on octopoteuthids from the Indian Ocean other than brief survey reports. However, based on geography, two of Chun's (1910) '*Octopodoteuthis*' paralarvae could be attributable to this species: the small larvae from stn 190 (sex indet., ML 1.2 mm; inner sea of West Sumatra; not figured but extant at MfN, Berlin) and stn 215 (sex indet., ML 1.7 mm; Indian North Equatorial Current; Plate XVII, Figs 11, 12; presumed lost).

5.1.3. *deletron* Species Group. With one PVMP overlain by single patch of chromatophores; one photophore dorsally on each *recti abdominis* muscle; one LHP, MEP on each side of head; one photophore at base of each of Arms II–IV; photophore series along ventral brachial nerve of Arms III and IV only. Arm II buccal connectives paired, equal in depth, attaching both dorsally and ventrally. Arms IV with thin densely set transverse pigment bands aborally. Arm hooks without aboral hood on main cusp; basal-most hook pattern VVDD. 2+1 to 11+1 pairs of suckers present at tip of each arm.

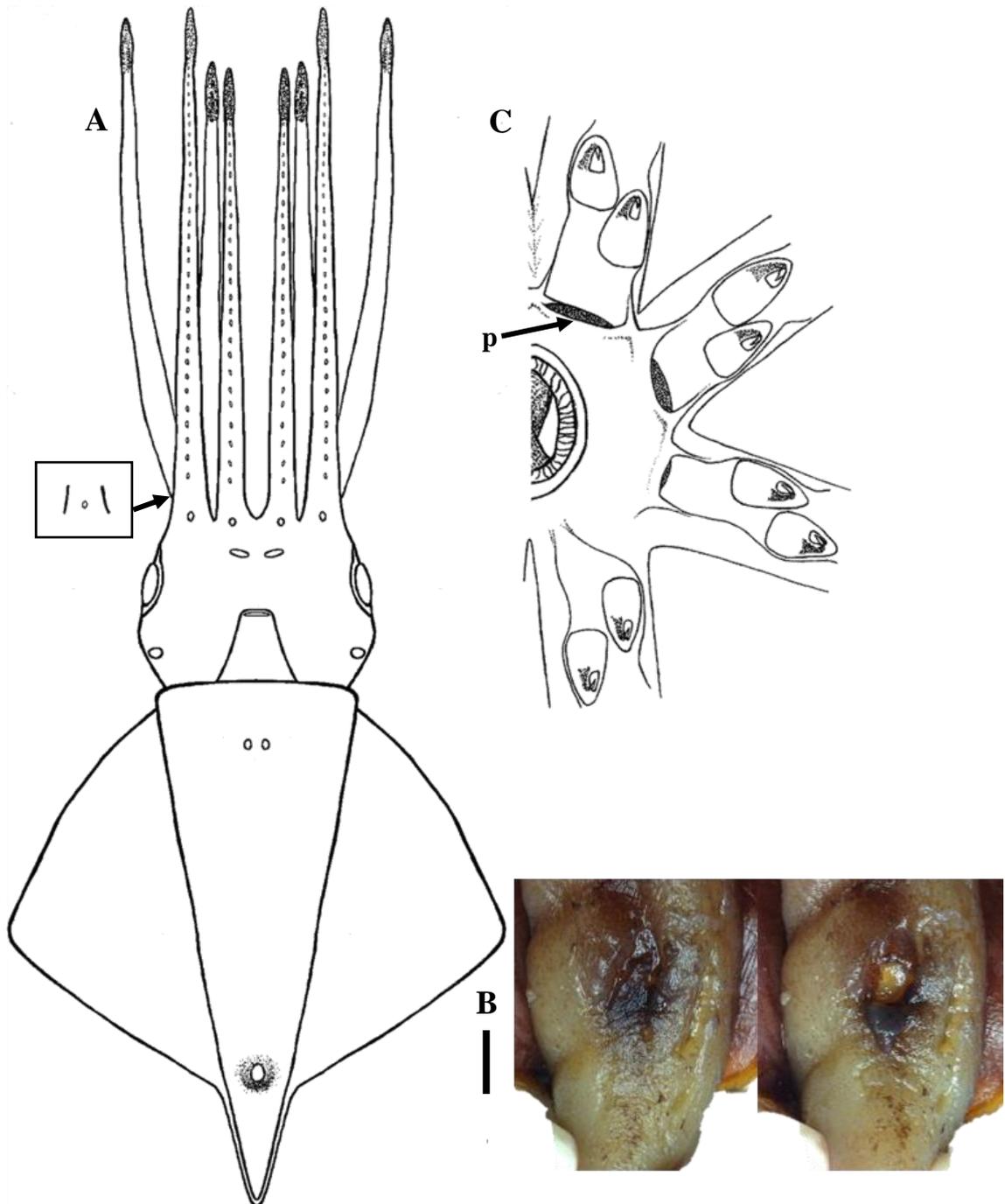


Fig. 43—*deletron* species group general morphology. A) Ventral photophore pattern; B) single chromatophore patch in *O. leviuncus* sp. nov. (NHMUK 20130457, holotype, ♀, ML 186 mm): natural state (left) and dissected revealing single PVMP (right); C) oral surface with paired buccal connectives Arms I–III, pores (p). Scale bar = 10 mm.

5.1.3.1. *Octopoteuthis deletron* Young, 1972 (Tables 15, 16, Figs 5C, G, 6H, 44–51)

Octopoteuthis deletron Young, 1972: 40–43, Table 9, Pl. 10 Figs H–M, Pl. 11, Pl. 12

Figs A–D; Toll (1982): 290–293, Pl. 35 Fig. A; Stephen (1985a): 63–72, Fig 4-12–4-14, Table 4-1; Nesis (1987): 182; Lindgren (2010): AY557541, EU735217.

Octopoteuthis sicula (not Rüppell, 1844) — Percy (1965): Table 1.

Octopodoteuthopsis (not Pfeffer, 1912) — Okutani and McGowan (1969): 21, 23, 24, Fig. 8.

Type material (6 specimens). **SBMNH 34966**, Holotype, ♂, ML 96 mm, 33°15'N, 118°37.02'W, 925 m, 06/07/1963, RV *Velero IV*, stn 8716, MWT, coll. Allan Hancock Foundation; **SBMNH 34967**, Paratype, ♂, ML 155 mm, 33°01'N, 119°04.02'W, 3090 m, 08/20/1963, RV *Velero IV*, stn 8878, MWT, coll. Allan Hancock Foundation; **SBMNH 34968**, Paratype, ♀, ML 141 mm, 32°33'N, 118°04.023'W, 1385 m, 04/14/1966, RV *Velero IV*, stn 11097, MWT, coll. Allan Hancock Foundation; **SBMNH 360102**, 3 paratypes, ♀, ML 30 mm, 2 ♂, ML 28, 28 mm, 33°28'N, 118°19.02'W, 805 m, 09/07/1961, RV *Velero IV*, stn 7414, MWT, coll. F. Ziesenhenne.

Additional material examined (124 specimens). **NSMT Mo67812**, ♂, ML 42.5 mm, 46°14.4'N, 125°10.0'W, Oregon, USA, 200 m, 18/04/1963, 2220-2258, RV *Acona*, AH-45, haul 346, cruise 6304, 6' IKMWT at 4-5 knots, coll. W.G. Percy and Oregon State University; **NSMT Mo67811**, ♂, ML 61* mm, 44°45'N, 125°16'W, Oregon, USA, 1000 m, 24/01/1962, 0910-1140, RV *Acona*, NH-50, haul 102, cruise 6201, 6' IKMWT at 4-5 knots, coll. W.G. Percy and Oregon State University; **USNM 813397**, ♀, ML 73 mm, 44°37.2'N, 162°58.2'W, 17/08/1955, RV *Hugh M. Smith*, 30-82, 3 m IKMWT; **NSMT Mo67813**, sex indet., ML 24 mm, 44°25.4'N, 125°18.1'W, Oregon, USA, 30/08/1963, NH-50, MT-MPS408, IKMWT, coll. W.G. Percy and Oregon State University; **USNM 1283025**, 3 ♀, ♂, sex indet. (head only), ML 79, 73, 63, 59 mm, 41°55.2'N, 124°52.5'W, 27 miles west of Pt. St. George, California, USA, 229 m, 29/08/1967, 67A6-3, MWT, coll. J. Duffy; **NSMT Mo74951**, ♀, ML 180* mm, 41°54.4'N, 144°51.7'E, off Sanriku, Japan, 550 m, 24/07/1996, *Marusada-Maru*, stn 16-1, MWT; **NSMT Mo74950**, ♀, ML 156* mm, 41°48.4'N, 145°06.7'E, off Sanriku, Japan, 650 m, 23/07/1996, *Marusada-Maru*, stn 15-3, MWT; **NSMT Mo71876**, ♀, ML 159 mm, 41°27.7'N, 145°30.5'E, off Sanriku, Japan, 500 m, 22/07/1996, *Marusada-Maru*, stn 14-4, MWT; **NSMT Mo71956**, ♀, ML 195* mm, 41°14.7'N, 143°39.9'E, off Sanriku, Japan, 550 m, 26/07/1996, *Marusada-Maru*, stn 18-4, MWT; **NSMT**

Mo71815, ♂, ML 149 mm, 41°02.6'N, 145°20.9'E, off Sanriku, Japan, 650 m, 21/07/1996, *Marusada-Maru*, stn 13-3, MWT; **NSMT Mo71979**, ♂, ML 144 mm, 41°02.6'N, 144°30.7'E, off Sanriku, Japan, 550 m, 06/07/1996, *Marusada-Maru*, stn 2-1, MWT; **NSMT Mo71852**, 3 ♂, ML 151*, 140, 117 mm, 41°01.5'N, 145°42.2'E, off Sanriku, Japan, 550 m, 22/07/1996, *Marusada-Maru*, stn 14-1, MWT; **NSMT Mo72026**, ♀, ML 183* mm, 41°00.5'N, 145°21.7'E, off Sanriku, Japan, 630 m, 07/07/1996, *Marusada-Maru*, stn 3-3, MWT; **NSMT Mo74949**, ♂, ML 165 mm, 40°59.7'N, 144°34.0'E, off Sanriku, Japan, 650 m, 20/07/1996, *Marusada-Maru*, stn 12-4, MWT; **NSMT Mo71967**, ♀, ML 189 mm, 40°46.0'N, 143°31.3'E, off Sanriku, Japan, 550 m, 27/07/1996, *Marusada-Maru*, stn 19-3, MWT; **NSMT Mo75350**, 2 ♂, ML 161, 137* mm, 40°02.6'N, 143°37.4'E, off Sanriku, Japan, 600 m, 13/07/1996, *Marusada-Maru*, MWT; **NSMT Mo71752**, ♂, ML 158 mm, 40°00.1'N, 145°32.3'E, off Sanriku, Japan, 600 m, 14/07/1996, *Marusada-Maru*, stn 10, MWT; **NSMT Mo74948**, ♂, ML 148 mm, 39°59.6'N, 143°32.6'E, off Sanriku, Japan, 530 m, 14/07/1996, *Marusada-Maru*, stn 9, MWT; **NSMT Mo75352**, ♂, ML 158 mm, 39°00.1'N, 143°29.0'E, off Sanriku, Japan, 550 m, 29/07/1996, *Marusada-Maru*, stn W, MWT; **NSMT Mo75351**, ♀, ML 227 mm, 38°58.4'N, 143°29.3'E, off Sanriku, Japan, 600 m, 30/07/1996, *Marusada-Maru*, stn W, MWT, coll. M. Moku; **NSMT Mo71581**, 2 ♂, ML 179, 145* mm, 37°44.6'N, 142°11'E, off Tohoku, 692 m, 04/06/1999, *Wakataka-Maru*, BTT, coll. D. Kitagawa; **USNM 817565**, ♂, ML 36 mm, 37°39.5'N, 123°12.48'W, California, USA, 32 m, 31/05/1989, RV *David Starr Jordan*, 154-2-111, Stauffer MWT; **NSMT Mo71579**, ♂, ML 161 mm, 37°28.5'N, 142°2.5'E, off Tohoku, 600 m, 22/04/1997, *Tanshu-Maru*, BTT, coll. G. Shinohara; **USNM 817558**, ♂, ML 49 mm, 37°00'N, 123°09.12'W, Davonport, California, USA, 110 m, 22/05/1989, RV *David Starr Jordan*, 777-3-65, Stauffer MWT; **NSMT Mo71580**, sex indet., ML 150 mm, 36°53.5'N, 141°42'E, off Tohoku, 769 m, 19/11/1998, *Wakataka-Maru*, BTT, coll. D. Kitagawa; **USNM 1283019**, 6 ♀, 2 ♂, sex indet., ML 114, 93, 89, 85, 44, 43, 94*, 76, 36 mm, 36°40.2'N, 122°06'W, 8 miles west-northwest of Pt. Pinos, California, USA, 366 m, 65A10-18A, MWT, coll. K. Mais; **USNM 817541**, ♂, ML 130 mm, 36°35.9'N, 123°05.88'W, Monterey Bay, California, USA, 110 m, 24/05/1989, RV *David Starr Jordan*, 666-0-73, Stauffer MWT; **NMNZ M.317511**, ♀, ML 108 mm, 36°32.03'N, 122°30.12'W, Monterey Bay, Monterey Canyon, California, USA, 821 m, 15/11/2014, RV *Western Flyer*, ROV *Doc Ricketts*, stn 692/S1, ROV, coll. K. Bolstad; **ZMH 11204**, sex indet. (head only), HL 22 mm, 35°00'N, 125°45'W, USA, 60–80 m, 11/04/1975, RV *Bonn*, stn 415; **SBMNH 46000**, ♂, ML 41 mm, 34°11.1'N, 120°00'W, Santa Barbara

Channel, off Coal Oil Point, California, USA, 366 m, 04/08/1965, SWAN MS-31--65 2A, SWAN MS-31--65 2A, coll. Bercaw; **ZMH 11209**, ♂, ML 42 mm, 34°00'N, 125°35'W, USA, 360–380 m, 09/04/1975, RV *Bonn*, stn 405; **SBMNH 457099**, ♀, ML 130 mm, 33°51.3'N, 119°55.98'W, Santa Rosa Flats, California, USA, 95 m, 00/10/1980; **SBMNH 457087**, ♂, ML 54 mm, 33°48.78'N, 119°31.98'W, off Anacapa Island, California, USA, 1591 m, 08/03/1967, RV *Velero IV*, stn 11387; **SBMNH 265407**, ♂, ML 39 mm, 33°39.12'N, 118°31.02'W, Channel Islands, California, USA, 23/01/1961, RV *Velero IV*, stn 7273, IKMWT; **SBMNH 265400**, 3 ♀, ML 47, 41, 35 mm, 33°34.28'N, 118°27.1'W, Channel Islands, California, USA, 860 m, 21/11/1962, RV *Velero IV*, stn 8311, IKMWT; **SBMNH 265416**, ♀, ML 39 mm, 33°31.43'N, 118°26.5'W, Channel Islands, California, USA, 865 m, 23/06/1964, RV *Velero IV*, stn 7391, IKMWT, coll. V.O. Maes; **SBMNH 265414**, sex indet., ML 25.5 mm, 33°29'N, 118°20'W, Channel Islands, California, USA, 1690 m, 15/08/1961, RV *Velero IV*, stn 7389, IKMWT, coll. V.O. Maes; **SBMNH 457084**, ♂, ML 40 mm, 33°28.01'N, 118°47.99'W, California, USA, 3380 m, 25/10/1962, RV *Velero IV*, stn 8238; **SBMNH 265395**, ♂, ML 38 mm, 33°27.71'N, 118°52.99'W, Channel Islands, California, USA, 1280 m, 24/06/1964, RV *Velero IV*, stn 9858, IKMWT; **SBMNH 457083**, ♀, ML 84 mm, 33°26.52'N, 118°50.33'W, California, USA, 1244 m, 12/03/1966, RV *Velero IV*, stn 11020; **SBMNH 265415**, ♂, ML 38 mm, 33°25.99'N, 118°51.49'W, Channel Islands, California, USA, 23/06/1964, RV *Velero IV*, stn 9952, IKMWT, coll. V.O. Maes; **SBMNH 457082**, sex indet., ML 32 mm, 33°25.02'N, 118°52.92'W, off Catalina Island, California, USA, 1317 m, 23/08/1963, RV *Velero IV*, stn 8888; **ZMH 12930**, 3 sex indet., ML 88*, 74*, 67* mm, 33°25'N, 121°37'W, USA, 320 m, 17/03/1975, RV *Weser*, stn 360; **SBMNH 265431**, sex indet., ML 19 mm, 33°22.88'N, 118°47.33'W, Channel Islands, California, USA, 1244 m, 23/06/1971, RV *Velero IV*, stn 15780, IKMWT; **SBMNH 265394**, ♀, ML 51 mm, 33°22.01'N, 118°48.25'W, Channel Islands, California, USA, 1289 m, 29/03/1965, RV *Velero IV*, stn 10474, IKMWT; **SBMNH 265412**, ♀, ML 33 mm, 33°20.74'N, 118°46'W, Channel Islands, California, USA, 1271 m, 17/10/1963, RV *Velero IV*, stn 8957, IKMWT, coll. V.O. Maes; **SBMNH 457097**, ♀, ♂, ML 137, 35 mm, 33°20.64'N, 118°45.47'W, off Santa Catalina Island, California, USA, 17/01/1963, RV *Velero IV*, stn 8439; **SBMNH 265402**, ♀, ML 50 mm, 33°19'N, 118°41.33'W, Channel Islands, California, USA, 1271 m, 12/02/1967, RV *Velero IV*, stn 11365, IKMWT; **SBMNH 457094**, ♀, ML 136 mm, 33°18.48'N, 120°50.51'W, off San Nicolas Island, California, USA, 3658 m, 08/05/1968, RV *Velero IV*, stn 12084; **SBMNH 265408**, ♀, ♂, ML 32, 22 mm, 33°18.36'N, 118°35.66'W, Channel Islands,

California, USA, 1207 m, 16/07/1963, RV *Velero IV*, stn 8789, IKMWT, coll. V.O. Maes; **SBMNH 457085**, ♂, ML 43 mm, 33°17.99'N, 117°49.97'W, off Dana Point, California, USA, 640 m, 07/12/1965, RV *Velero IV*, stn 10864; **SBMNH 265413**, 2 ♂, ML 31, 27.5 mm, 33°16.2'N, 118°38.33'W, Channel Islands, California, USA, 1385 m, 23/08/1962, RV *Velero IV*, stn 8116, IKMWT, coll. V.O. Maes; **SBMNH 265403**, ♂, ML 58 mm, 33°15.49'N, 118°33.75'W, Channel Islands, California, USA, 24/05/1963, RV *Velero IV*, stn 8700, IKMWT; **SBMNH 457095**, ♂, ML 133 mm, 33°15.41'N, 120°55.02'W, off San Nicolas Island, California, USA, 2195 m, 20/01/1967, RV *Velero IV*, stn 11298; **SBMNH 265406**, ♂, ML 92 mm, 33°15.41'N, 118°31.39'W, Channel Islands, California, USA, 1289 m, 16/04/1964, RV *Velero IV*, stn 9244, IKMWT, coll. V.O. Maes; **USNM 727460**, sex indet., ♂, ML 38, 29 mm, 33°15'N, 118°31.19'W, Southern, California, USA, 1198–1267 m, 22/08/1962, RV *Velero IV*, 8114, 3 m IKMWT, Allan Hancock Pacific Expedition; **SBMNH 265405**, ♂, ML 61 mm, 33°14.55'N, 118°32.08'W, Channel Islands, California, USA, 1262 m, 30/03/1965, RV *Velero IV*, stn 10479, IKMWT, coll. V.O. Maes; **SBMNH 265391**, 2 ♂, ML 35, 33 mm, 33°13.18'N, 118°34.99'W, Channel Islands, California, USA, 01/09/1964, RV *Velero IV*, stn 9951, IKMWT, coll. V.O. Maes; **SBMNH 457381**, ♂, ML 98 mm, 33°11.88'N, 118°39.30'W, off W end Santa Catalina Island, California, USA, RV *Velero IV*, stn 8298; **SBMNH 457089**, 2 ♂, ML 147, 142 mm, 33°10.98'N, 121°00.18'W, off San Nicolas Island, California, USA, 3658 m, 20/01/1967, RV *Velero IV*, stn 11300; **SBMNH 265392**, ♂, ML 41 mm, 33°09.88'N, 118°29.55'W, Channel Islands, California, USA, 1289 m, 01/09/1964, RV *Velero IV*, stn 8352, IKMWT, coll. V.O. Maes; **SBMNH 457081**, ♂, ML 58 mm, 33°08.99'N, 119°13.01'W, off San Nicolas Island, California, USA, 1792 m, 14/05/1964, RV *Velero IV*, stn 9659; **SBMNH 265404**, ♀, ML 68 mm, 33°08.16'N, 119°13.24'W, Channel Islands, California, USA, 1646 m, 10/06/1965, RV *Velero IV*, stn 11608, IKMWT; **SBMNH 265409**, ♀, ML 47 mm, 33°07.48'N, 118°07.99'W, Channel Islands, California, USA, 1231 m, 10/02/1967, RV *Velero IV*, stn 11352, IKMWT; **SBMNH 265398**, ♂, ML 43 mm, 33°00'N, 119°45'W, Channel Islands, California, USA, 1463 m, 23/07/1968, RV *Velero IV*, stn 12168, IKMWT; **SBMNH 265393**, ♂, ML 45 mm, 32°58.75'N, 119°05.5'W, Channel Islands, California, USA, 1582 m, 27/02/1969, RV *Velero IV*, stn 12729, IKMWT; **SBMNH 265411**, ♂, ML 37 mm, 32°52.41'N, 118°54.21'W, Channel Islands, California, USA, 1737 m, 08/03/1965, RV *Velero IV*, stn 10401, IKMWT, coll. V.O. Maes; **SBMNH 265399**, ♀, ML 45 mm, 32°43.60'N, 118°17.50'W, Channel Islands, California, USA, 1756 m, 26/01/1968, RV *Velero IV*, stn 11879, IKMWT; **SBMNH**

265397, ♂, ML 49 mm, 32°43.16'N, 118°16.75'W, Channel Islands, California, USA, 1509 m, 09/11/1971, RV *Velero IV*, stn 16783, IKMWT; **SBMNH 457091**, ♂, ML 142 mm, 32°41.75'N, 118°16.01'W, San Clemente Island, California, USA, 1829 m, 13/12/1968, RV *Velero IV*, stn 12533; **SBMNH 457096**, ♀, ML 170 mm, 32°40.98'N, 118°15'W, off San Clemente Island, California, USA, 1792 m, 09/11/1971, RV *Velero IV*, stn 16784; **SBMNH 265410**, ♂, ML 37 mm, 32°38.99'N, 118°11.83'W, Channel Islands, California, USA, 1555 m, 27/01/1968, RV *Velero IV*, stn 11884, IKMWT; **SBMNH 265396**, ♂, ML 40* mm, 32°35.50'N, 118°08.91'W, Channel Islands, California, USA, 1737 m, 25/08/1970, RV *Velero IV*, stn 14497, IKMWT; **SBMNH 457086**, 2 ♂, ML 80, 43 mm, 32°34.68'N, 118°08.51'W, off San Clemente Island, California, USA, 1737 m, 20/01/1971, RV *Velero IV*, stn 14925; **SBMNH 265434**, ♂, ML 35 mm, 32°33.91'N, 118°09.41'W, Channel Islands, California, USA, 1555 m, 17/08/1971, RV *Velero IV*, stn 16250, Tucker trawl; **SBMNH 265430**, sex indet., ML 19 mm, 32°33.46'N, 118°10.24'W, Channel Islands, California, USA, 1426 m, 26/07/1968, RV *Velero IV*, stn 12201, IKMWT; **SBMNH 265432**, sex indet., ML 24 mm, 32°30'N, 118°03.16'W, Channel Islands, California, USA, 1701 m, 15/08/1972, RV *Velero IV*, stn 17803, IKMWT; **SBMNH 265429**, sex indet., ML 26 mm, 32°27.83'N, 117°56.66'W, Channel Islands, California, USA, 1682 m, 21/07/1971, RV *Velero IV*, stn 16121, IKMWT; **SBMNH 457090**, ♂, ML 137 mm, 32°27'N, 120°46.98'W, California, USA, 3658 m, 18/10/1966, RV *Velero IV*, stn 11243; **SBMNH 457092**, ♂, ML 122 mm, 32°25.98'N, 119°25.02'W, Cortez Bank, Bishop Rock, California, USA, 1646 m, 14/08/1969, RV *Velero IV*, stn 13295; **SBMNH 457093**, ♀, ML 156 mm, 32°21.96'N, 117°49.91'W, San Clemente Island, California, USA, 1829 m, 10/10/1968, RV *Velero IV*, stn 12390; **SBMNH 265428**, sex indet., ML 24 mm, 32°08.25'N, 117°45.49'W, Islas Coronados, S Los Coronados Light, Baja California Sur, Mexico, 1792 m, 26/07/1967, RV *Velero IV*, stn 11588, IKMWT; **SBMNH 265424**, sex indet., ML 12 mm, 31°48.01'N, 119°47.65'W, Channel Islands, Cortez Bank, Bishop Rock, California, USA, 3566 m, 23/07/1967, RV *Velero IV*, stn 11626, IKMWT; **SBMNH 265419**, sex indet., ML 16.5 mm, 31°45.25'N, 118°46.99'W, Channel Islands, Cortez Bank, Bishop Rock, California, USA, 2048 m, 16/08/1967, RV *Velero IV*, stn 11614, IKMWT; **SBMNH 457098**, ♀, ML 176 mm, 31°45.18'N, 119°45.47'W, Cortez Bank, Bishop Rock, California, USA, 3566 m, 24/07/1968, RV *Velero IV*, stn 12179; **ZMH 11061**, ♀, ML 58 mm, 31°44'N, 121°47'W, México, 80–280 m, 19/04/1975, RV *Weser*, stn 435; **USNM 727461**, ♂, ML 94 mm, 31°40.2'N, 120°06'W, Southern, California, USA, 406 m, 31/07/1966, RV *Velero IV*, 11168, 3 m

IKMWT, Allan Hancock Pacific Expedition; **ZMH 11190**, 3 ♂, ML 136, 111, 103 mm, 31°20'N, 121°10'W, México, 90 m, 18/04/1975, RV *Weser*, stn 430; **SBMNH 265401**, sex indet., ML 48* mm, 31°15.57'N, 117°39.18'W, Baja California [Norte], Mexico, 1920 m, 29/01/1968, RV *Velero IV*, stn 11896, IKMWT; **SBMNH 265418**, 2 sex indet., ML 16, 14 mm, 31°08.5'N, 119°11.28'W, Channel Islands, Cortez Bank, Bishop Rock, California, USA, 3475 m, 25/07/1968, RV *Velero IV*, stn 12190, IKMWT; **SBMNH 457088**, ♂, ML 134 mm, 31°03'N, 119°45'W, off Cortez Bank, Bishop Rock, California, USA, 3566 m, 26/08/1965, RV *Velero IV*, stn 10666; **ZMH 11207**, ♂, ML 110 mm, 30°45'N, 120°30'W, México, 60–150 m, 17/04/1975, RV *Weser*, stn 429; **SBMNH 265427**, sex indet., ML 16 mm, 30°17'N, 118°04.98'W, Baja California [Norte], Mexico, 3703 m, 20/08/1967, RV *Velero IV*, stn 11633, IKMWT.

Unlocalised material examined (14 specimens). **MBARI HJH1**, sex indet., ML 148 mm, Monterey Canyon, no stn; **MBARI HJH2**, sex indet., ML 171 mm, Monterey Canyon, no stn; **PC001**, ♀, ML 46.7 mm, Monterey Canyon, no stn; **PC002**, ♂, ML 37.7 mm, Monterey Canyon, no stn; **PC003**, sex indet., fresh ML 31.6 mm, Monterey Canyon, no stn; **PC004**, sex unknown, fresh ML 36.5* mm, Monterey Canyon, no stn; **NHMUK 20150461**, 2 ♀, sex indet., ML 41, 41, 26 mm, 480 m, Haul #6, IKT; **ZMH 11164**, ♀, 6 ♂, ML 152, 123, 115*, 109*, 104*, 100, 98 mm, Pacific Ocean, 1977, RV *Julius Fock*, stn 695.

Beak only material (74 samples). **OD1–3, 7, 11–49, 51–69, 71–73, 75–83**, ML 28–172 mm, 34°06'–36°38.16'N, 121°12'–123°06.06'W, Monterey Canyon, 2012, trawl, coll. H.J. Hoving.

Distribution (Fig. 44A). North Pacific, 46–29°N, 141°E–117°W, likely further north (see Remarks); 60–1300 m, possibly deeper.

Diagnosis. Arm hooks with accessory claws, aperture rim narrow, rounded.

Description (ML 61–227 mm, Figs 44B–48). Mantle conical to weakly goblet shaped; widest at anterior margin, width 30–36–48% ML; weakly muscled; tail short, blunt, length 7–18–27% ML; dorsal anterior margin slightly produced medially, ventral margin with slight indentation between mantle components of locking cartilage. Fins

Table 15. Measurements (mm) of *Octopoteuthis deletron*. Mean indices were calculated from specimens ML >40 mm with undamaged dimensions, and 'Side' indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	SBMNH 34966	NSMT Mo75351	NSMT Mo71579	ZMH 11164	ZMH 11164	ZMH 11164	SBMNH 265406	SBMNH 265404	SBMNH 265405	Mean index	SBMNH 265416	SBMNH 265413
Type status	Holotype	None	None	None	None	None	None	None	None		None	None
Sex	♂	♀	♂	♂	♀	♂	♂	♀	♂		♀	♂
DML	96	227	161	123	152	92	92	68	61		40	27.5
MW	34	70	51	37	53	31	31	31	29	36	12.9	10.8
FL	74	154	122	88	111	66	66	49	41	72	31	22.5
FW	97	189	142	111	128	93	93	73	71	96	43	35
HL	25	68	43	37	41	31	31	28	21	31	14.2	11
HW	30	37*	41	19*	24*	32	32	26	19	32	11.9	10
Side	R	R	R	L	R	R	R	R	R		R	R
AL I	45*	50*	31*	28*	101*	39*	39*	37*	25*		22*	22.5
AL II	55 ^r	90*	61*	42*	52*	42*	42*	62 ^r	33*		45	23*
AL III	83 (L)	108*	96*	91	50*	41*	41*	28*	30*	80	37	15*
AL IV	77	78*	71*	36*	71*	38*	38*	41*	21*		33	22 (L)
AH	32, 32			*							32, 30, 30	*, *
AS	7+1, 6+1			*							7+1, 5+1, 6+1	*, *

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

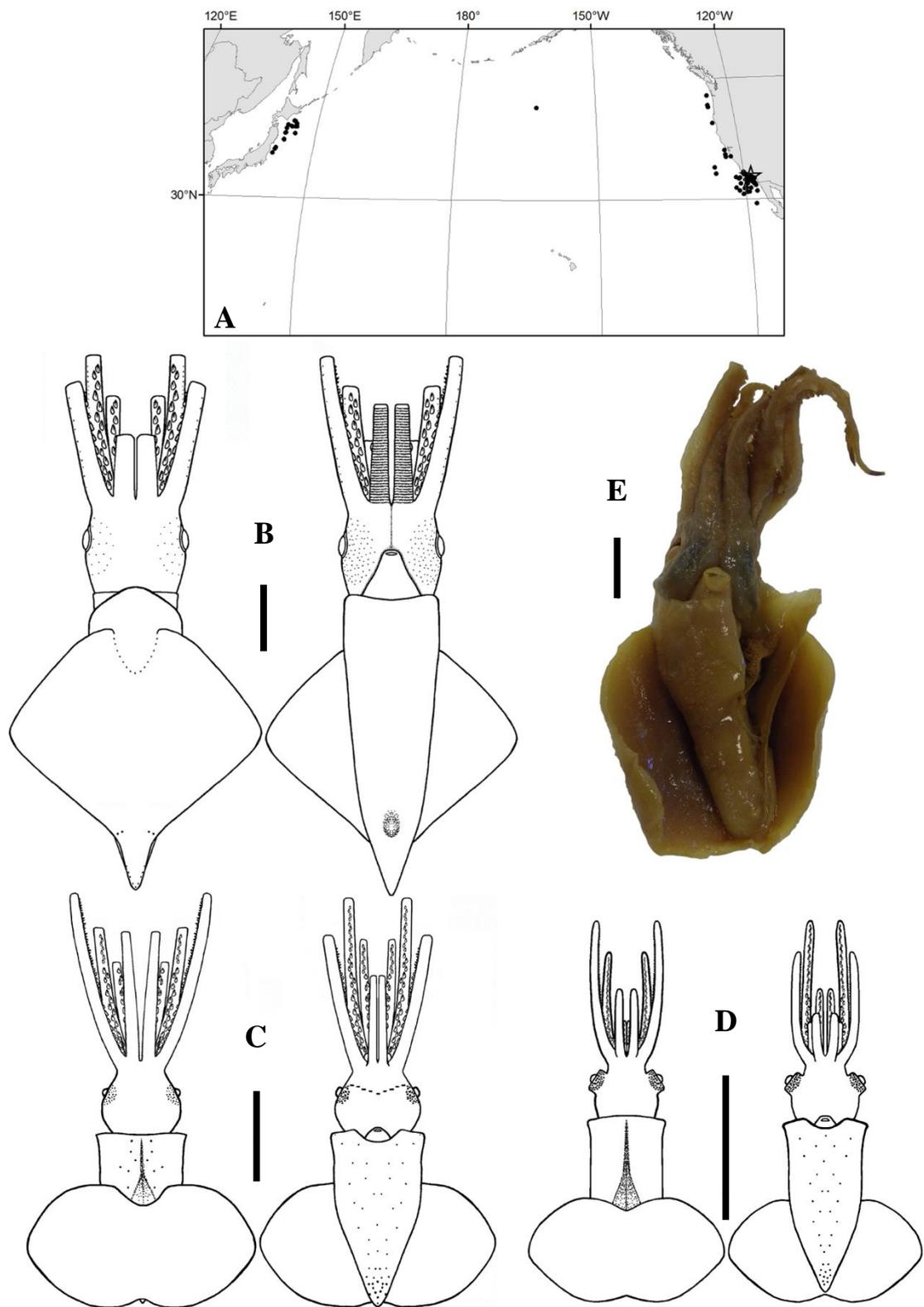


Fig. 44—*Octopoteuthis deletron*. A) Distribution (star indicates type locality); B) adult; C) post-larva (SBMNH 265431, sex indet., ML 19 mm); D) post-larva (SBMNH 265424, sex indet., ML 12 mm); E) SBMNH 34966, holotype, ♂, ML 96 mm (photo by K. Bolstad). Scale bars = B) 50 mm; C, D) 10 mm; E) 20 mm.

large (length 67–72–77% ML), broad (width 83–96–116% ML); anterior margin at 9–15–21% ML; greatest fin width attained at 50–60% ML. Posterior ventral mantle photophore circular, large (diameter ~3% ML); embedded basally in hemisphere of gelatinous tissue which protrudes ventrally, epidermis level with outer gelatinous tissue layer of mantle; hemisphere covered by chromatophore patch, sparsely over surface, more dense around circumference. Anterior fin insertion pointed posteriorly, depth 14–17–21% ML, width 13–20–29% ML.

Head trapezoidal in outline, length 26–31–41% ML, width 26–32–38% ML, depth 20–30% ML. Single triangular photophore present laterally, posterior to each eye (underlying olfactory papilla), length ~7% HL (~2% ML); single oblong photophore on inner surface of each eyelid ventro-medially, level with mid-eye, oriented 45–90° to body axis, length ~10% HL (~3% ML), width ~4% HL (~1.5% ML). Eyes large, diameter 16–23–31% ML, with large lenses, diameter 33% ED. Funnel length 24–30–43% ML, funnel groove shallow; aperture width ~23% of funnel length, level with midpoint of eye; funnel valve tall, broad. Funnel component of locking apparatus subtriangular; groove broadest posteriorly (~80% of cartilage width), narrowing anteriorly to slender channel; medial margin of groove concave creating flat region medial to groove; lateral margin straight, slight flat region anteriorly; length ~12% ML, maximum width ~6% ML. Mantle component of locking apparatus subtriangular; length ~12% ML, maximum width ~7% ML. Nuchal cartilage oblong, pointed anteriorly; with medial groove flanked by ridges all equal in width, flanked by broader grooves pointed antero-medially; length ~15% ML, maximum width ~4% ML, narrowing slightly posteriorly. Buccal connectives of Arms I–III paired (Fig. 43C), Arms IV with weakly paired connectives set closely together, ventrally; in males only, buccal and basal protective membranes greatly developed proximally (Fig. 45D), breadth greatest between Arms I (~50–60% arm base width) decreasing ventrally with no connective between Arms IV. Pores in buccal membrane between paired connectives of Arms I and II, and between Arms II and III; pocket only between Arm III connectives. Olfactory papillae short (length ~3% HL), elliptical (breadth ~5% HL), fleshy knobs without sculpture.

Arms slender, length 59–85–119% ML; formula II>III>IV=I; oblong to circular in cross-section; with 27–38 pairs of hooks in fleshy sheaths followed by 4 to 11+1 pairs of suckers distally. All arms narrow gradually to tips, from width ~6% AL at base to

~3% at midpoint. Arm tip-photophores occupy distal-most ~6% AL (length ~5% ML); outline continues arm tapering until slight bulb at tip; arm hooks terminate proximal to photophore, suckers overlie proximal ~20% of photophore length. Single large, oval photophore embedded deeply in bases of Arms II–IV; length ~2% AL, smaller in Arms II. Photophore series of Arms III, IV beginning ~13% AL distally from arm-base photophores; comprising oval photophores much smaller than base photophores, diameter ~0.5 mm; presumed to extend to arm tip. All arms with low gelatinous aboral keels from base to tip; breadth 40–50% arm depth in proximal 75% arm length, increasing to ~70% in distal 25% arm length.

Arm hooks robust (Fig. 46); largest in pairs 3–6 of Arms II, decreasing gradually in size distally, slight decrease in size proximally. Main cusp long, smoothly curved, tip pointed; smooth laterally or with several shallow lateral ridges; typically maintaining

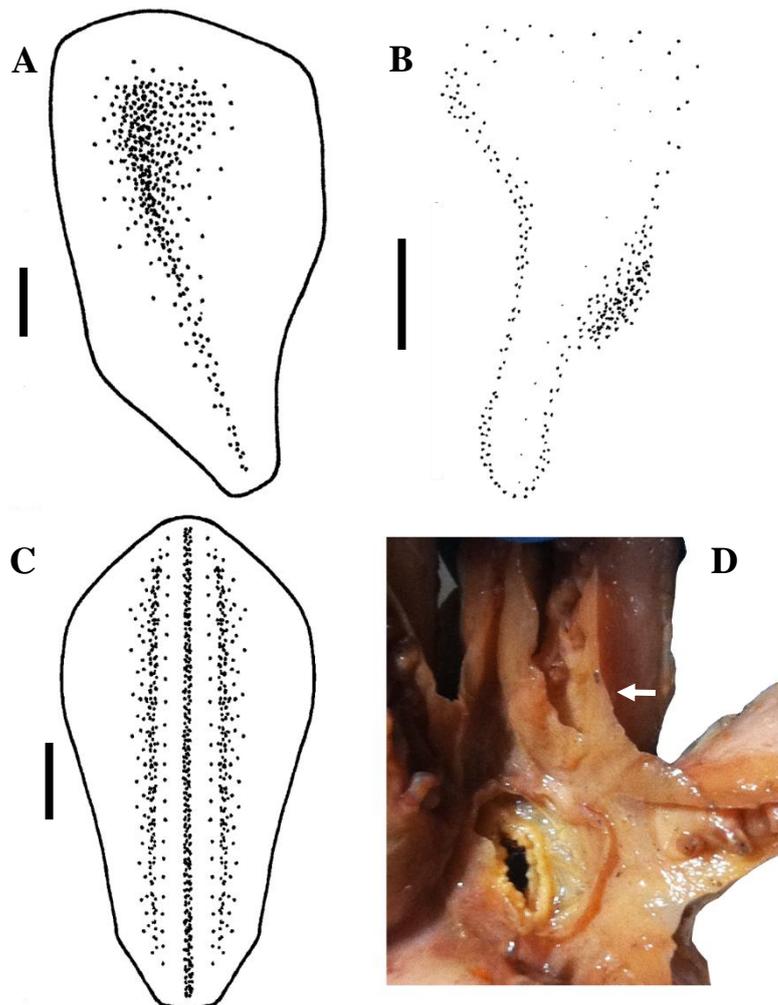


Fig. 45—*Octopoteuthis deletron*. A) SBMNH 457090, ♂, ML 137 mm; B) SBMNH 265406, ♂, ML 92 mm; C, D) NSMT Mo71581, ♂, ML 145* mm. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage; D) male with expanded buccal connectives (arrow). Scale bars = A–C) 2 mm.

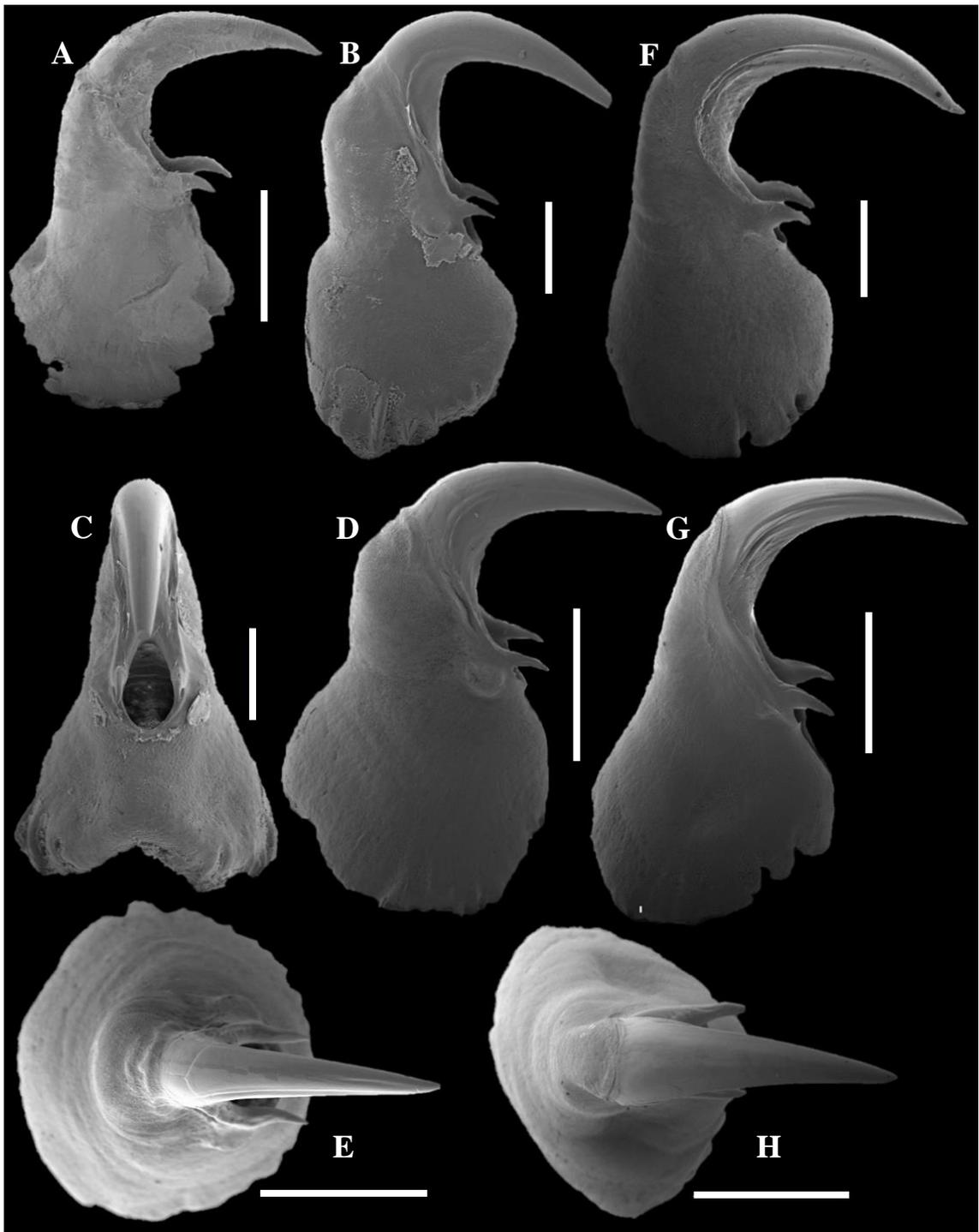


Fig. 46—*Octopoteuthis deletron* armature. A) OD-62, ♀, fresh ML 77 mm; B–E) SBMNH 34966, holotype, ♂, ML 96 mm; F–H) NSMT Mo75351, ♀, ML 227 mm. A) Lateral profile, location unknown; B, C) 15D, Arm III L: (B) lateral profile, (C) oral; D, E) 3D hook, Arm III L: (D) lateral profile, (E) apical; F) 15D, Arm III R; G, H) 7V hook, Arm III R: (G) lateral profile, (H) apical. Scale bars = A, C, E, G) 0.5 mm; B, D) 0.25 mm; F, H) 1 mm.

similar breadth aborally and laterally along junction with base (SBMNH 34699 broad aborally, Figs 46C, E); inner angle $\sim 90^\circ$ in proximal hooks, acute ($\sim 70\text{--}80^\circ$) among distal 50% of pairs; aperture open, broad oval. Accessory claws prominent, curved, pointed. Aboral hood absent. Bases crenulated, most prominent oral-laterally. Proximal

hooks stouter than distal hooks, with relatively larger bases (width and breadth). Arm suckers not examined.

Tentacles absent, only traces remain in post-larvae (see below).

Recti abdominis muscles (Figs 5E, F) as discrete muscle bands straddling rectum anteriorly, posteriorly merging and fusing over rectum; weakly attached to rectum and immediately adjacent tissues dorsally; anteriorly inserting under dorsal component of funnel organ, beyond rectum, posteriorly expanding into thin sheet attaching to ventral surface of visceral mass; single near-circular photophore on dorsal surface of each *recti abdominis* muscle at ~30% ML anteriorly; pearly white, slightly raised dorsally; length ~2% ML, width ~2% ML; nearly centred, comprising ~75% of *recti abdominis* width. Rectum free briefly anteriorly, terminating just inside funnel posterior to dorsal funnel organ concavity; laterally bearing two moderate-length anal flaps, length ~2% ML, ovate, anterior tip pointed, chiral dorso-ventrally. Ventral visceral mesentery pore small, diameter ~0.5% ML; pore appears as sphincter in membrane. Gills robust; length ~25% ML, with 27–28 lamellae.

Lower beak sexually dimorphic by size: beaks and LRLs greater in females than males of equivalent body size. Lateral profile of lower beak (2.43–8.1 mm LRL, Figs 47A–D) slightly longer than deep, with distal wing tips extending beyond rostral tip by 16–22–29% baseline; rostral tip occasionally with slight notch, sometimes worn down; jaw edge visible, straight until slight bend in distal third of LRL, with short jaw extension; jaw angle 85–100°, slightly obscured by low, rounded wing fold; depth anterior to jaw angle greater than posterior. Hood off crest in beaks LRL <~3.5 mm, close to crest in larger beaks; length ~30% baseline; occasionally with shallow hood grooves, originating from rostral notch, overlying lateral wall ridges. Crest distinct, often with some of anterior lateral wall between crest and fold pigmented; length 60–64–68% baseline; tip free with concave notch between crest and lateral wall; sloped in nearly straight line. Lateral wall with straight, narrow, sharp fold, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior 50–60% hood length; posterior lateral wall margin straight; free corner beyond crest tip; lateral wall fold and crest more darkly pigmented than remaining wall, especially anteriorly. Wings broaden distally, greatest width 161–175–192% that at jaw angle, length 84–99–109% LRL, with cartilaginous pad. Ventral view with broad, shallow

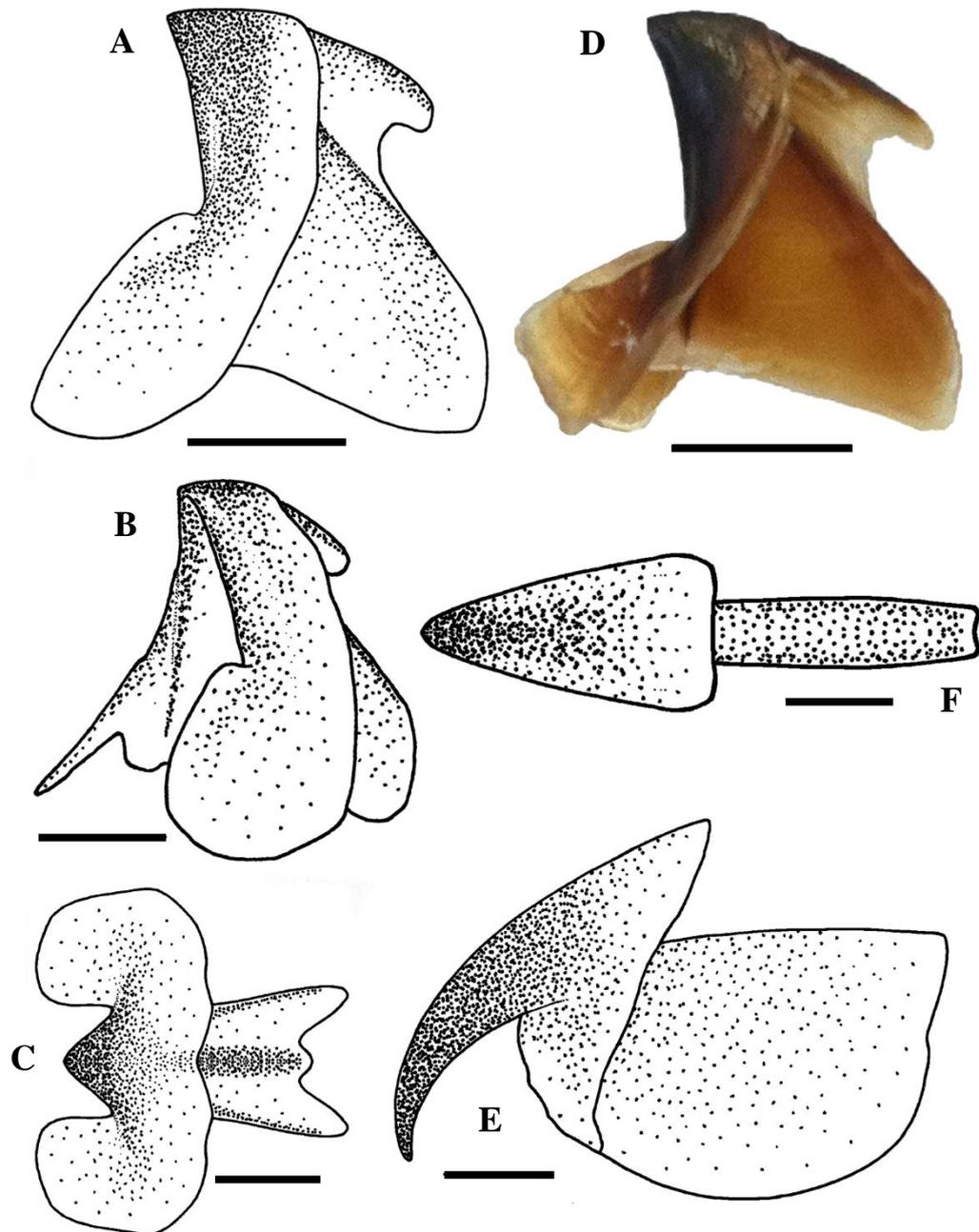


Fig. 47—*Octopoteuthis deletron* beaks. A–C, E, F) NSMT Mo71956, ♀, ML 195* mm, LRL 8.1 mm, URL 8.74 mm; D) OD31, ♀, fresh ML 160 mm, LRL 6.89 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

notch in hood; free corners level with medial margin of wing. Beak pigmentation develops with ontogeny: crest, lateral wall ridges pigmented first; then lateral walls (lightly but fully pigmented by LRL ~2.4 mm); lastly wings, latero-medially (beginning LRL ~5 mm). Ontogenetic pigmentation sexual dimorphic, occurring at smaller sizes in males than females. For males, largest specimen with unpigmented wings LRL 3.69 mm (fresh ML 83 mm); smallest specimen with fully pigmented wings LRL 5.2 mm (fresh ML 88 mm). For females, largest specimen with unpigmented wings LRL 5.82 mm

(fresh ML 120 mm); smallest specimen with fully pigmented wings LRL 5.98 mm (fresh ML 105 mm).

Upper beak sexually dimorphic by size: beaks and URLs greater in females than males of equivalent body size. Lateral profile of upper beak (2.67–8.74 mm URL, Figs 47E, F) longer than deep, maximum depth ~46% UBL. Rostrum very long, ~33% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle 70–80°; low ridge of cartilage present orally along shoulder, decreases with ontogeny; oral shoulder margin slightly scalloped in small beaks, convex in large beaks. Hood long (73–76–79% UBL), moderately tall (~18% UBL); junction of hood and free shoulder very slightly concave. Lateral walls approximately rectangular with maximum depth at midpoint, posterior margin straight or slightly angled. Dorsal view with posterior margin of hood straight to slightly concave, posterior margin of crest and crest pigmentation straight. Lateral wall pigmentation begins along anterior crest, progressing posteriorly until crest fully pigmented; continues ventrally along posterior lateral wall, finally progressing anteriorly to free shoulder along a ~45° to axis of UBL. Crest unpigmented at URL 2.67 mm (fresh ML 50 mm, ♂); isolated faint patch of pigmentation anteriorly along crest at URL 4.18 mm (fresh ML 80 mm, ♀); crest and full height of posterior lateral wall pigmented at URL 6.04 mm (ML 85 mm, sex indet.), free shoulder and anterior lateral wall transparent; crest, lateral wall fully pigmented at URL 9.74 mm, free shoulder unpigmented (fresh ML 196 mm, ♀, largest beak examined).

Radula (Figs 48A–D) with tricuspid rachidian: mesocone moderately long, narrowly triangular, straight; lateral cusps moderately long (~40% mesocone height) straight points; base concave. First lateral tooth bicuspid: inner cusp conical to narrowly triangular, slightly shorter than rachidian; outer cusp moderately long (40–45% height of inner) straight to slightly medially curved point; base straight to slightly concave. Second lateral tooth simple, conical to narrowly triangular, 80–130% height of rachidian. Marginal tooth simple, conical, ~150% height of rachidian. Marginal plate absent. Palatine palp (Fig. 48E) with 21 broad, triangular teeth generally with rounded base, each 80–150% rachidian height, smallest orally; oral end of palp rounded, tooth-bearing surface raised; depth of tooth-bearing surface decreases posteriorly; dorso-anterior margin and surface adentate; teeth sparse, evenly arranged across surface.

Gladius (90*–98* mm GL, Fig. 48F) broad, very thin (<0.1 mm thick), delicate, transparent; greatest width (~11% GL) at ~35% GL; rachis broad, evenly concave; free rachis ~8% GL, pointed anteriorly, smoothly widening posteriorly to maximum width (~2% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden quickly to maximum width, then taper gradually for remainder of length; short conus present (~2% GL), very fragile, into which tissue inserts (the traction of which often results in breakage during dissection). Posterior gladius curved ventrally, with vanes bending ventro-medially in advance of fusion at conus.

Colour (preserved) in adults deep purple to pink over all external body surfaces where epidermis remains intact; overlying gelatinous layer unpigmented except rugose furrows in females; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patch overlying posterior ventral mantle photophore darkest posteriorly. Inner mantle surfaces and viscera unpigmented. Small individuals with distinct, large chromatophores evenly spaced across all external surfaces.

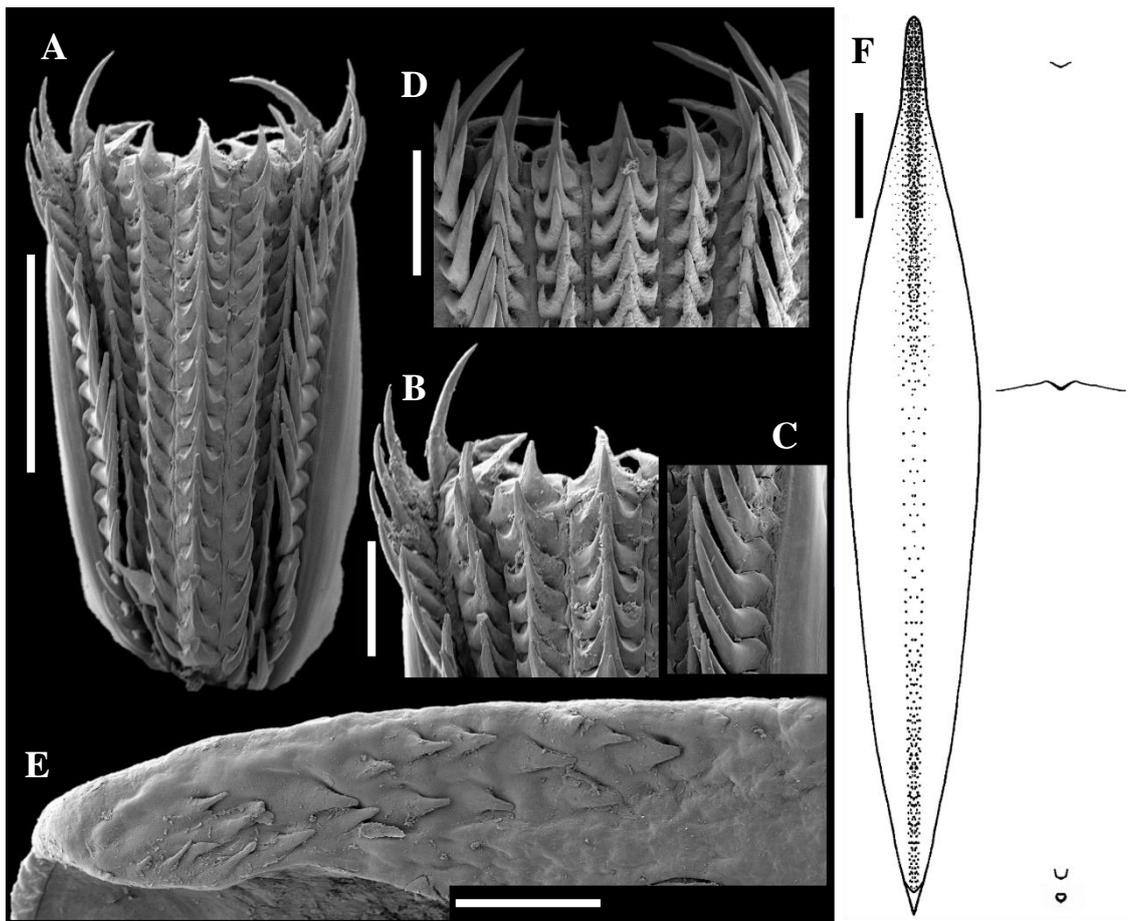


Fig. 48—*Octopoteuthis deletron*. A–C, E) PC001, ♀, ML 46.7 mm; D) OD21, ♀, fresh ML 133 mm; F) USNM 727461, ♂, ML 94 mm, GL 89.56* mm. A–D) Radulae: (A) whole, (B, D) bending plane, (C) marginal surface; E) palatine palp; F) gladius, with cross-sections. Scale bars = A, D, E) 0.5 mm; B, C) 0.2 mm; F) 10 mm.

Juvenile specimens (ML 27.5–54 mm) as above, with the following exceptions. Tail short, length 7–11–14% ML. Fins long (67–80–89% ML), very broad (113–134–170% ML); anterior fin margin at 9–16–19% ML. Head length 31–40–51% ML. Arms long, length 58–85–134% ML. Arm hooks bear small but distinctly formed accessory claws by ML 33 mm (SBMNH 265391). Tentacles entirely lacking.

Post-larval specimens (ML 12–26 mm; Table 16, Figs 44C, D) as above, with the following exceptions. Posterior ventral mantle photophore discernable to ML 24 mm (SBMNH 265432), associated chromatophore pattern and mantle structure allows species identification to ML 12 mm (SBMNH 265424): single central, circular gap in chromatophores; occasionally, circular raising in external gelatinous tissue layer. Without tail; posterior margins of fins extend beyond posterior tip of mantle. Anterior fin margin variable along mantle, occurring at 21–31–43% ML in size class. Gladius clearly visible through dorsal mantle anterior of fins at ML <20 mm; free rachis long, 20–24% ML; vanes expand in association with anterior fin insertion. Fins variable in length (60–71–82% ML), very broad (115–121–132% ML); anterior fin insertion very shallow, broad; posterior fin margins convex. Head length 38–43–47% ML, width 32–40–45% ML; eyes on low stalks in smallest specimens. Posterio-lateral head and inner eye lid photophores not discernable. Arms proximally with suckers or modified suckers: ML 11–12 mm with 3 suckers basally followed by single “hooked” sucker (sucker with single, central, main tooth), then fully formed hooks; ML 16–19 mm with single, domed sucker basally followed by 2 hooked suckers, then fully formed hooks; larger specimens with fully formed hooks basally; arm hooks with slight points or corners in place of fully formed accessory claws. Tentacles atrophying, gelatinous, translucent; short nubs without definition (length ~6% ML) or insubstantial broken stalks; bases 40–50% width of adjacent Arm IV bases. Variable characters within size class due to anterior progression of anterior fin margin with ontogeny: fin length positively correlated with mantle length, inversely with free rachis length and level along mantle of anterior fin margin.

Biology. Smallest mature specimen examined ML 103 mm (ZMH 11190, ♂).

Smallest mature female ML 130 mm (SBMNH 457099): ovary with mature ova, nidamental and oviducal glands developed (length 42% and 15% ML, respectively), heavily implanted with spermatangia. In mature, mated female ML 141 mm (SBMNH 34968, paratype), ovary with mature ova (diameter 1.18–1.43 mm), undeveloped

oocytes (diameter <0.5 mm). Rugose furrows clearly visible by ML 61 mm (USNM 1283025). Possibly sexually dimorphic by size: largest male examined ML 165 mm, 10 specimens >165 mm all female (largest ML 227 mm).

Plots of select morphometrics (Fig. 49) through ontogeny corresponded well with patterns identified in *O. sicula* (Fig. 13) – decreasing FWI, HLI and HWI, consistent FLI – although the nature of those relationships differed (*e.g.*, FWI was best described by a power function in *O. deletron* versus a linear relationship in *O. sicula*). Eye diameter showed a relatively strong decreasing trend through ontogeny that was not found in *O. sicula*, although this may be due to the greater number of *O. deletron* post-larvae. Tail length and the anterior fin margin in *O. deletron* also demonstrated the inverse relationship found in *O. sicula*; however, their point of intersection occurred at a considerably greater size (ML ~90 vs ~30 mm, respectively) and relationships with mantle length were generally less strong ($R^2 = 0.28, 0.40$ compared with 0.34, 0.82, respectively). Adult and juvenile *O. deletron* have taxonomically significant shorter tails and more posteriorly set fins than *O. sicula*.

Table 16. Measurements (mm) of a selection of *Octopoteuthis deletron* post-larval specimens. Mean indices were calculated from specimens with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	SBMNH 265414	SBMNH 265431	SBMNH 265424	Mean index
Sex	Indet.	Indet.	Indet.	
DML	25.5	19	12	
MW	9.1	9.3	5.3	43
FL	21	13.6	7.2	71
FW	29.7	25.1	13.8	121
HL	9.6	8.4	5.6	43
HW	8.2	8	5.4	40
Side	L	L	L	
AL I	12.5*	13.2*	4.6*	
AL II	16.8*	17.1*	9.3*	
AL III	20.2	13.7*	7.1*	
AL IV	15.9 (R)	10.3*	2.7*	
AH	28, 18*			
AS	*, *			
TL	0.2	1.21	2.34*	

* indicates damaged character.

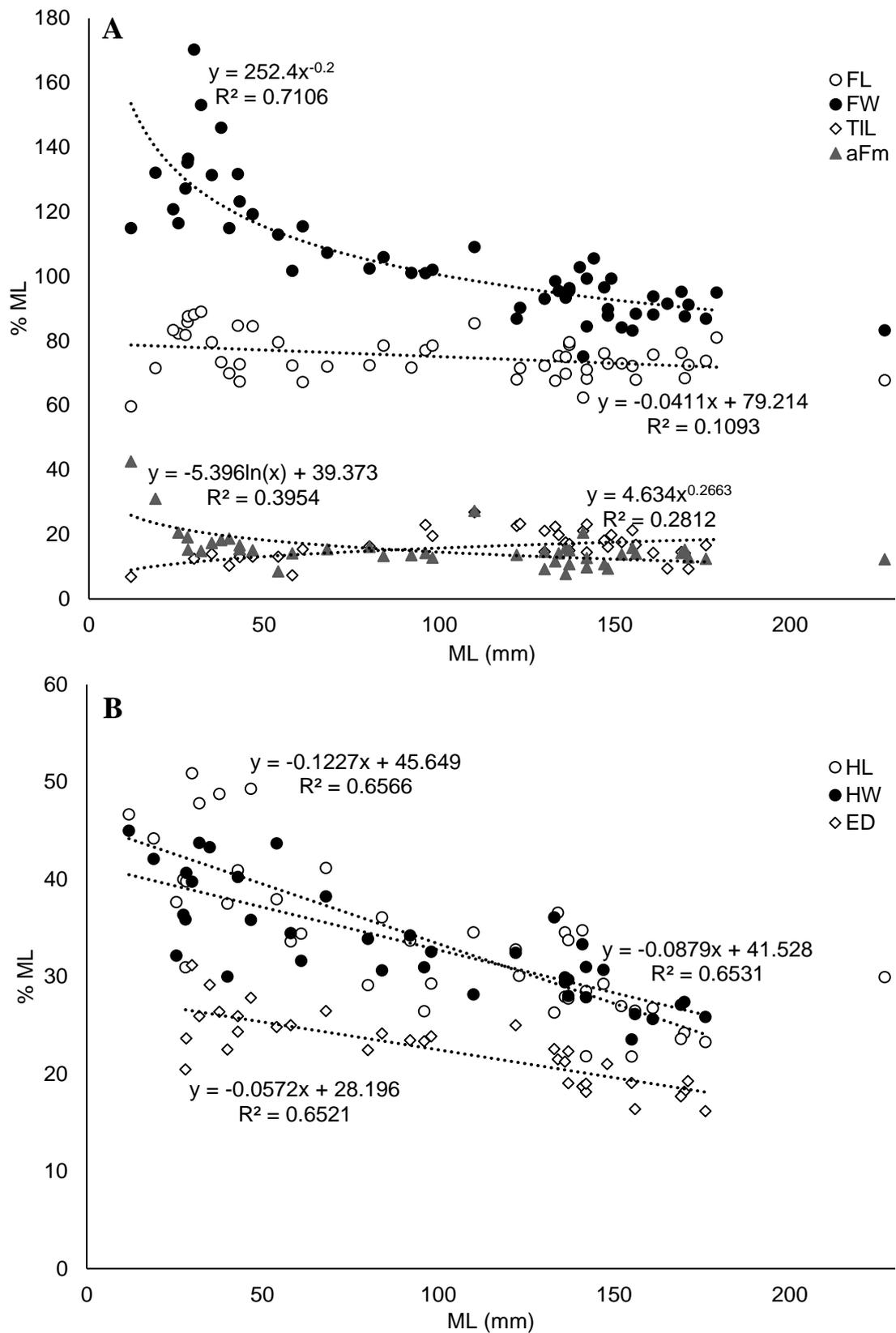


Fig. 49. Selected morphometric indices through ontogeny of *Octopoteuthis deletron*: A) fin length (FL; hollow circles), fin width (FW; solid circles), tail length (TIL; hollow diamonds), level of anterior fin margin (aFm; grey triangles); B) head length (HL; hollow circles), head width (HW; solid circles), eye diameter (ED; hollow diamonds). Regression equations and R^2 values of best fitting models are shown; indices for NSMT Mo75351 (♀, ML 227 mm) were excluded from regression analyses due to the disjunct size of the specimen.

Relationships between LRL and URL against ML and body mass were best described by power equations (Figs 50, 51). Regressions were calculated separately for fresh and preserved measures, but all relationships fit data well ($R^2 > 0.89$). Preserved and fresh regressions diverged at large rostral lengths, possibly due to differences in sample size (preserved, $n = 7$), body size ranges of each sample (largest individuals were preserved), and measuring technique (fresh body measures by H.J. Hoving; beak, preserved measures by J.T. Kelly). Females appear to have greater beak measures than do males of the same ML, although values tended to spread with increasing rostral lengths (most apparent in LRL against ML, least in URL against ML). Previous genus-level regressions generally aligned closely with the present fresh regressions, with the exception of Clarke (1980) in LRL against body mass and the preserved regression of Lu and Ickeringill (2002) for URL against body mass.

Remarks. *Octopoteuthis deletron* was the sole *Octopoteuthis* species encountered in the northeast Pacific, from southern California north to British Columbia. It co-occurs with *O. laticauda* around Japan, but is readily distinguishable by its single PVMP, single overlying chromatophore patch, and paired Arm II buccal connectives compared to the paired PVMP and chromatophore patches, and single dorsal buccal connective on Arms II of *O. laticauda*. Morphologically *O. deletron* most closely resembles *O. leviuncus* sp. nov. (see below), but can be easily distinguished by its prominent accessory claws in all sizes; accessory claws are absent in *O. leviuncus*, which is also exclusively found in the Atlantic.

Re-examination of the type series (excluding Velero 8025, ♀, DML 39 mm, which was unavailable) yielded measurements (excluding ALs) between 76 and 105% (mean \pm S.E. $90.4 \pm 1.4\%$) of those reported in the original description for *O. deletron* (Young 1972). The consistency of the difference between measures suggests it could be a result of continued contraction over the 40 year period between examinations. Some measurements of the holotype reported by Stephen (1985a) during the interim are supportive of this (e.g., DML and FL were intermediate). However, overall, either due to small sample size (five measures, tail length excluded) or differences in measuring style, the mean differences (\pm S.E.) between Stephen's and Young's measurements and those reported herein were not substantially different ($87.8 \pm 2.1\%$ and $88.5 \pm 2.6\%$, respectively). Only the holotype measurements are re-reported here; for measurements of the remainder of the type series, see Young (1972).

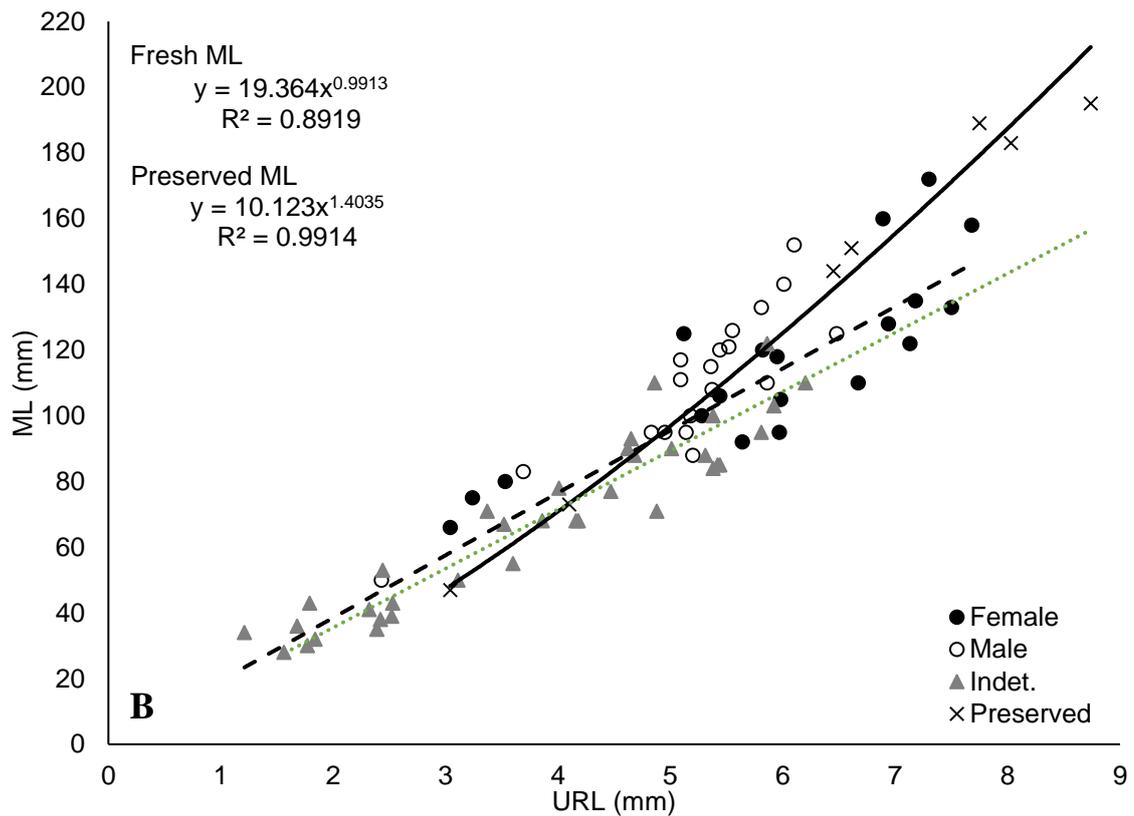
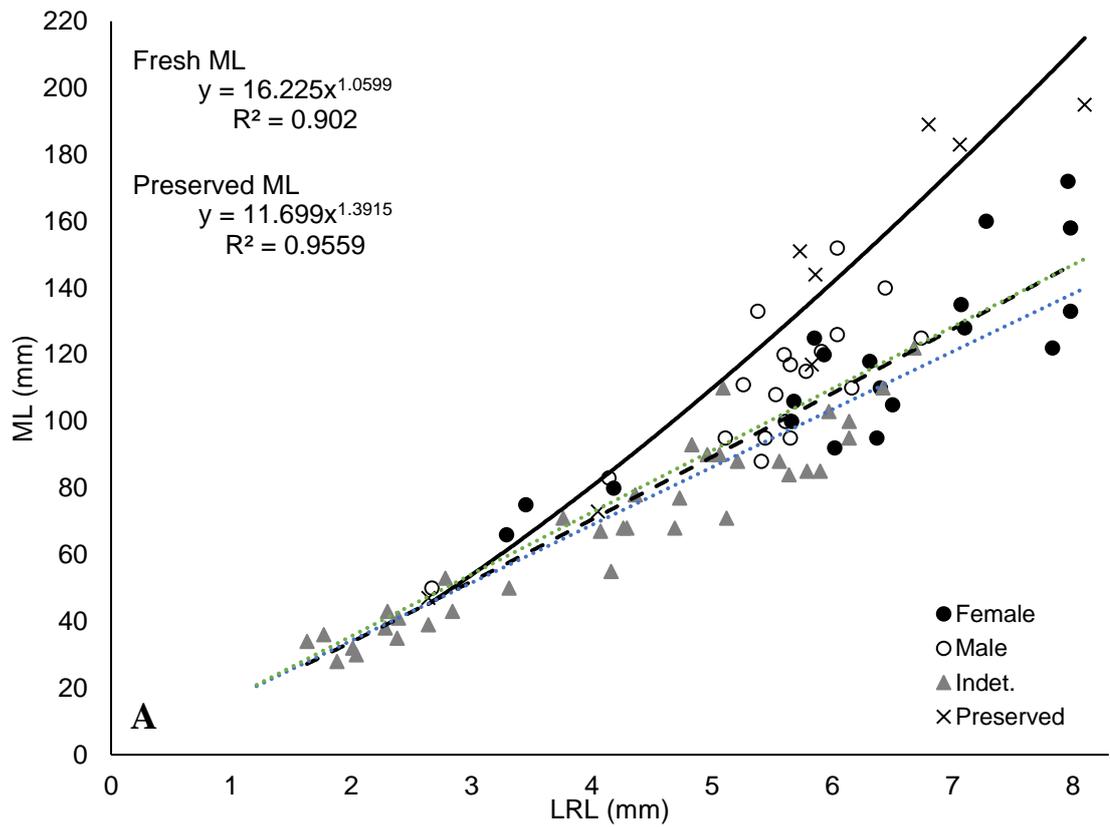


Fig. 50—*Octopoteuthis deletron*. Regressions of (A) lower rostral length (LRL) and (B) upper rostral length (URL) against dorsal mantle length (ML), by sex. Models of best fit (greatest R^2 value) were calculated separately for fresh (all stages combined, $n = 74$, dashed line) and preserved specimens ($n = 8$, solid line), and are plotted in black against genus regressions of Clarke (1980; blue) and Lu and Ickeringill (2002; green).

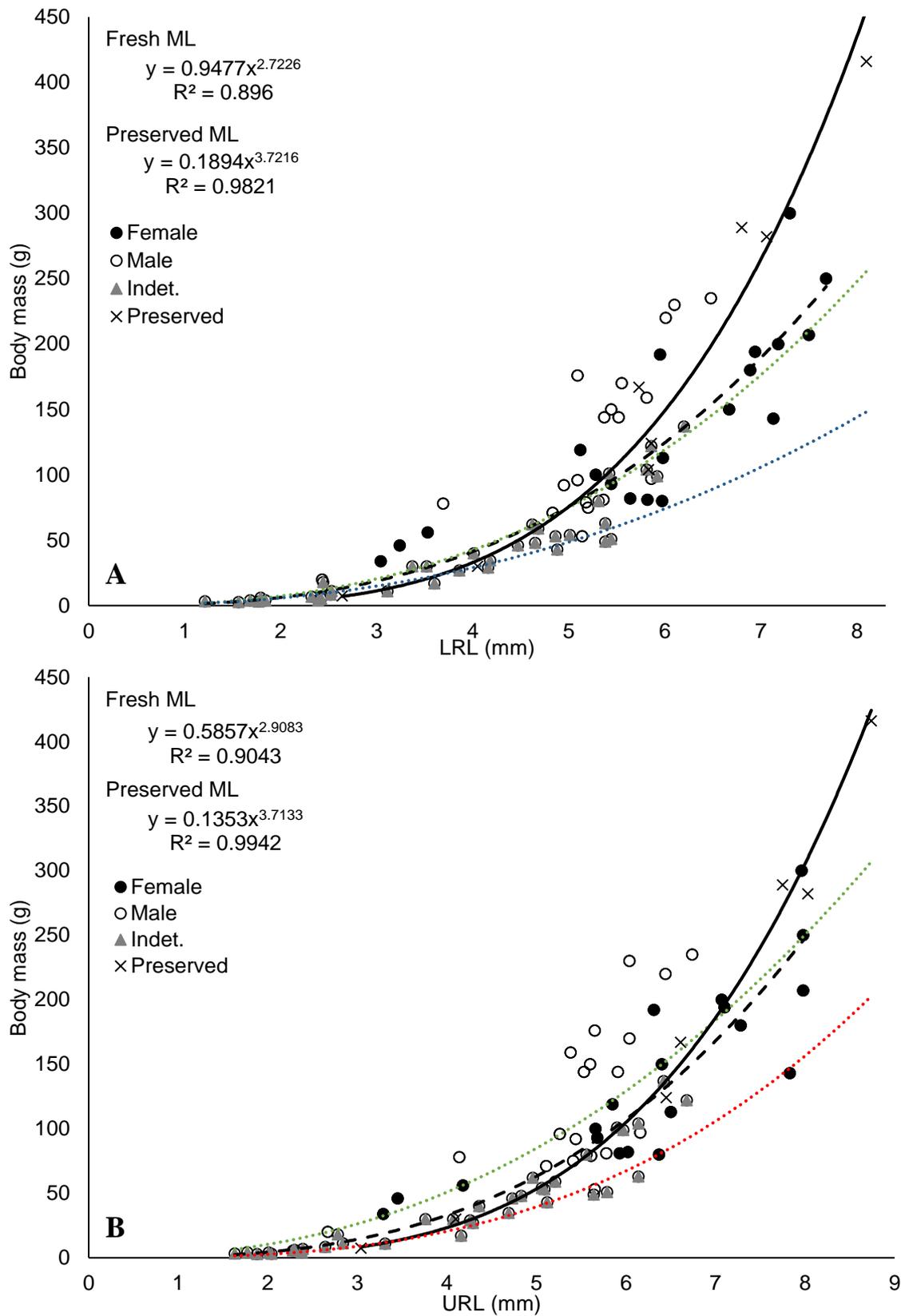


Fig. 51—*Octopoteuthis deletron*. Regressions of (A) lower rostral length (LRL) and (B) upper rostral length (URL) against body mass, by sex. Models of best fit (greatest R^2 value) were calculated separately for fresh (all stages combined, $n = 74$, dashed line) and preserved specimens ($n = 8$, solid line), and are plotted in black against genus regressions of Clarke (1980; blue) and Lu and Ickeringill (2002; green = fresh weight, red = fixed weight).

Okutani *et al.* (1976) and Okutani & Satake (1978) reported 300 specimens of *Octopoteuthis* sp. from Japanese waters with a single posterior ventral mantle photophore. Based on differences in fin dimensions (*i.e.*, $FL \approx ML$, $FWI \approx 130\%$; Okutani *et al.* 1976), they suggested these specimens may represent a new species (also noted by Nesis 1987). This material was obtained from sperm whale stomach contents, and the FLI of $\sim 100\%$ suggests the mantles of these specimens had been impacted by digestive processes. Although no size range was given by Okutani *et al.* (1976), 11 of the 214 specimens reported in Okutani & Satake (1978) ranged between ML 120 and 155 mm. Herein, specimens of *O. deletron* with FL 120–155 mm gave values for FW/FL of 116–122–132% ($n = 8$), compared to FWI of 83–90–95% ML. Furthermore, the specimen imaged in Okutani *et al.* (1976) shows a contracted ventral mantle and affected lateral fin margins (Plate V, Fig. 11–12). Thus, in this study, no characters were found to separate Pacific *Octopoteuthis* specimens with a single posterior ventral mantle photophore. Examined specimens attributable to *O. deletron* from California and Japan overlapped in FWI, with the greatest FWI observed among the Japanese material (106% ML) within the expected range of values for adults and subadults. Small individuals of *O. deletron* (ML 20–43 mm) from the eastern Pacific did achieve FWI of 130%+ as FWI decreased with ontogeny; specimens of such sizes from Japanese waters were not available for examination. Although specimens reported in Okutani *et al.* (1976) and Okutani & Satake (1978) were not examined for this study, they are herein attributed to *O. deletron*.

The illustrations of post-larvae (ML 12–19 mm) included herein, combined with the paralarvae figured by Okutani and McGowan (1969; ML 5.2, 10 mm), juveniles by Young (1972; ML 31–39 mm), and adults (Young 1972; ML 109, 167 mm; herein) yield a full ontogenetic series for *O. deletron*.

The geographic distribution of *O. deletron* along western North America extends further north than documented in Fig. 44A. Specimens housed at the Royal British Columbia Museum (but not examined herein) were collected from 48°20'–52°07'N, including one that genetically matched *O. deletron* sequences in this study. CASIZ contains two unexamined lots of '*O. deletron*' from 55°N. Finally, a further northerly record exists for an *Octopoteuthis* reported from Lynn Canal, Alaska ($\sim 58^\circ\text{N}$), in 2009, which clearly bears a single posterior ventral mantle photophore (images only examined).

5.1.3.2. *Octopoteuthis leviuncus* sp. nov. (Table 17, Figs 43B, 52–55)

Octopoteuthis sp. A Young, 1972: 42, Pl. 12 Figs E, F; Stephen (1985a): 77–80, Fig 4-17; Nesis (1987): 182.

Octopoteuthis sicula (not Rüppell, 1844) — Toll (1982): 293.

Type material (4 specimens). **NHMUK 20130457**, holotype, ♀, ML 186 mm, 32°19.1'N, 29°48.6'W, 304–1400 m, 09/06/1962, stn 10378#26, *Discovery* Expedition, RMT8M; **ZMH 11198**, paratype, ♀, ML 110 mm, 32°31'N, 16°54'W, 900–1000 m, 21/01/1968, RV *Walther Herwig*, stn 6, cruise #23, coll. Schulz; **USNM 885295**, paratype, ♂, ML 169 mm, 10°57'S, 11°21.6'W, 1800–1900 m, 04/07/1971, RV *Walther Herwig*, 459-71, 1600 mesh Engel trawl; **USNM 885294**, paratype, ♂, ML 144 mm, 30°07.2'S, 05°24'E, 308 m, 31/03/1971, RV *Walther Herwig*, 431-II-71, 1600 mesh Engel trawl.

Additional material examined (26). **ZMH 11215**, ♀, sex indet., ML 149*, 44* mm, 33°45'N, 16°00'W, 160–600 m, 10/05/1966, RV *Walther Herwig*, stn 177, cruise #15, coll. Schulz; **USNM 817936**, ♂, ML 73 mm, 33°01.2'N, 39°34.2'W, 27/04/1979, RV *Anton Dohrn*, 330-79, 1600 mesh Engel trawl; **NHMUK 20160095**, ♀, ML 71 mm, 32°40'N, 17°15.8'W, 0–330 m, 29/10/1966, stn 6147, *Discovery* Expedition, EMT; **NHMUK 20160101**, ♀, ML 44.5 mm, 32°34.5'N, 17°17.5'W, 0–245 m, 01-10/03/1962, stn 4843, *Discovery* Expedition, BCMT; **NHMUK 20160103**, sex indet., ML 25 mm, 32°32'N, 17°15'W, 17/10/1986, stn C.86/20, *Challenger* Expedition, RMT, 3 lights, 150W; **NHMUK 20160104**, sex indet., ML 28 mm, 32°23.4'N, 17 21'W, 17/10/1986, stn C.86/22, *Challenger* Expedition, RMT, lights 20W; **NHMUK 20160126**, sex indet., ML 31 mm, 31°58.2'N, 47°18.5'W, 0–1000 m, 04/03/1973, stn 8274, *Discovery* Expedition, RMT8; **USNM 817937**, ♂, ML 138 mm, 31°55.2'N, 47°46.2'W, 26/04/1979, RV *Anton Dohrn*, 323-79, 1600 mesh Engel trawl; **USNM 817935**, ♂, ML 53 mm, 31°10.8'N, 63°31.8'W, Sargasso Sea, 19/04/1979, RV *Anton Dohrn*, 268-79, 1600 mesh Engel trawl; **USNM 817934**, ♀, ML 77 mm, 30°27'N, 66°07.8'W, Sargasso Sea, 15/04/1979, RV *Anton Dohrn*, 256-79, 1600 mesh Engel trawl; **USNM 817941**, ♂, ML 104 mm, 30°27'N, 66°07.8'W, Sargasso Sea, 15/04/1979, RV *Anton Dohrn*, 256-79, 1600 mesh Engel trawl; **ZMH 11206**, sex indet., ML 23* mm, 27°30'N, 18°48'W, 100–500 m, 12/05/1966, RV *Walther Herwig*, stn 179, cruise #15, coll. Schulz; **ZMH 11196**, ♂, ML 98 mm, 23°30'N, 20°08'W, 220–500 m, 13/05/1966, RV *Walther Herwig*, stn

180b, cruise #15, Schulz; **USNM 814605**, ♂, ML 65 mm, 22°06'N, 32°45'W, 0–255 m, 29/11/1970, RV *Atlantis II*, RHB-2090, 3 m IKMWT, coll. R.H. Backus; **ZMH 12998**, ♀, ML 87 mm, 17°36'S, 28°53'W, Brazil, 160–660 m, 23/05/1966, RV *Walther Herwig*, stn 190, cruise #15, coll. Schulz; **USNM 730683**, ♂, ML 142 mm, 18°39'S, 04°16.2'W, 300–310 m, 04/04/1971, RV *Walther Herwig*, 447-II-71, 1600 mesh Engel trawl; **USNM 730684**, ♂, ♀, ML 156, 149 mm, 20°04.2'S, 05°22.2'E, 500–502 m, 31/03/1971, RV *Walther Herwig*, 431-III-71, 1600 mesh Engel trawl; **USNM 885284**, ♂, ML 57 mm, 20°04.2'S, 05°22.2'E, 500–502 m, 31/03/1971, RV *Walther Herwig*, 431-III-71, 1600 mesh Engel trawl; **USNM 1471843**, ♂, ♀, ML 123, 134 mm, 30°07.2'S, 05°24'E, 308 m, 31/03/1971, RV *Walther Herwig*, 431-II-71, 1600 mesh Engel trawl; **ZMH 73900**, ♂, ML 111* mm, 30°09'S, 05°26'W, 100–105 m, 31/03/1971, RV *Walther Herwig*, stn 431, cruise #36, coll. Schulz; **ZMH 10788**, ♀, ML 95 mm, 32°54'S, 50°24'W, Brazil, 170 m, 10/06/1966, RV *Walther Herwig*, stn 221, cruise #15, coll. Schulz; **ZMH 35985**, ♀, ML 95 mm, 35°12'S, 52°41'W, Brazil, 110 m, 12/06/1966, RV *Walther Herwig*, stn 235, cruise #15, coll. Schulz.

Unlocalised material examined (1 specimen). **NHMUK 20150463**, ♂, sex indet., ML 41.5, 30 mm, 00/00/1986, stn 86/27, *Challenger* Expedition.

Distribution (Fig. 52A). Temperate and tropical Atlantic, 33°N–35°S, 66°W–5°E; 0–1900 m.

Diagnosis. Arm hooks without accessory claws, aperture rim laterally expanded, flattened.

Description (ML 67–186 mm, Figs 52B–55). Mantle conical to weakly goblet shaped; widest at anterior margin, width 26–33–46% ML; weakly muscled; tail long, thick, length 18–20–24% ML; dorsal anterior margin smoothly rounded or with weak medial point, ventral margin slightly concave between mantle components of locking apparatus. Fins large (length 66–71–76% ML), broad (width 85–93–112% ML); anterior margin at 6–9–12% ML; greatest fin width attained at their midpoint, ~50% ML; continuing along tail posteriorly in thin strip. Posterior ventral mantle photophore circular, large (diameter ~2.2% ML); embedded basally in hemisphere of gelatinous tissue which protrudes ventrally, epidermis level with outer gelatinous tissue layer of mantle; hemisphere covered by circular chromatophore patch, sparsely over surface,

Table 17. Measurements (mm) of *Octopoteuthis leviuncus* sp. nov. Mean indices were calculated from specimens ML >57 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side).

Specimen ID	NHMUK	USNM	USNM	ZMH	USNM	ZMH	USNM	ZMH	USNM	ZMH	USNM	Mean index	NHMUK	NHMUK
Type status	Holotype	Paratype	Paratype	Paratype	None	None	None	None	None	None	None		None	None
Sex	♀	♂	♂	♀	♀	♂	♂	♀	♂	♀	♂		♂	Indet.
DML	186	169	144	110	149	98	95	149	98	95	73	33	41.5	30
MW	69	49	41	36	44	45	25	44	45	25	24	71	17.5	14.5
FL	131	115	105	77	108	74	63	108	74	63	53	93	28.8	23.5
FW	173	151	121	97	127	96	90	127	96	90	82	35	45.8	39.5
HL	65	46	46	39	54	40	38	54	40	38	31*	32	16.2*	12.6
HW	60	30*	34*	32	29*	36	28	29*	36	28	24*		11*	10.3
Side	L	L	R	L	R	R	L	R	R	L	R		L	L
AL I	154	54*	79*	55*	64*	49*	38*	64*	49*	38*	31*		17*	12*
AL II	182	48*	116*	66*	93*	83 ^r	54*	93*	83 ^r	54*	32*		48*	28*
AL III	156	42*	100*	71*	72*	85 ^r	53*	72*	85 ^r	53*	30*		17*	12*
AL IV	142	37*	94*	44*	37*	57*	43*	37*	57*	43*	25*		16*	17*
AH	29, 35, 44, 27													
AS	2+1, 7+1, 5, 4													

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

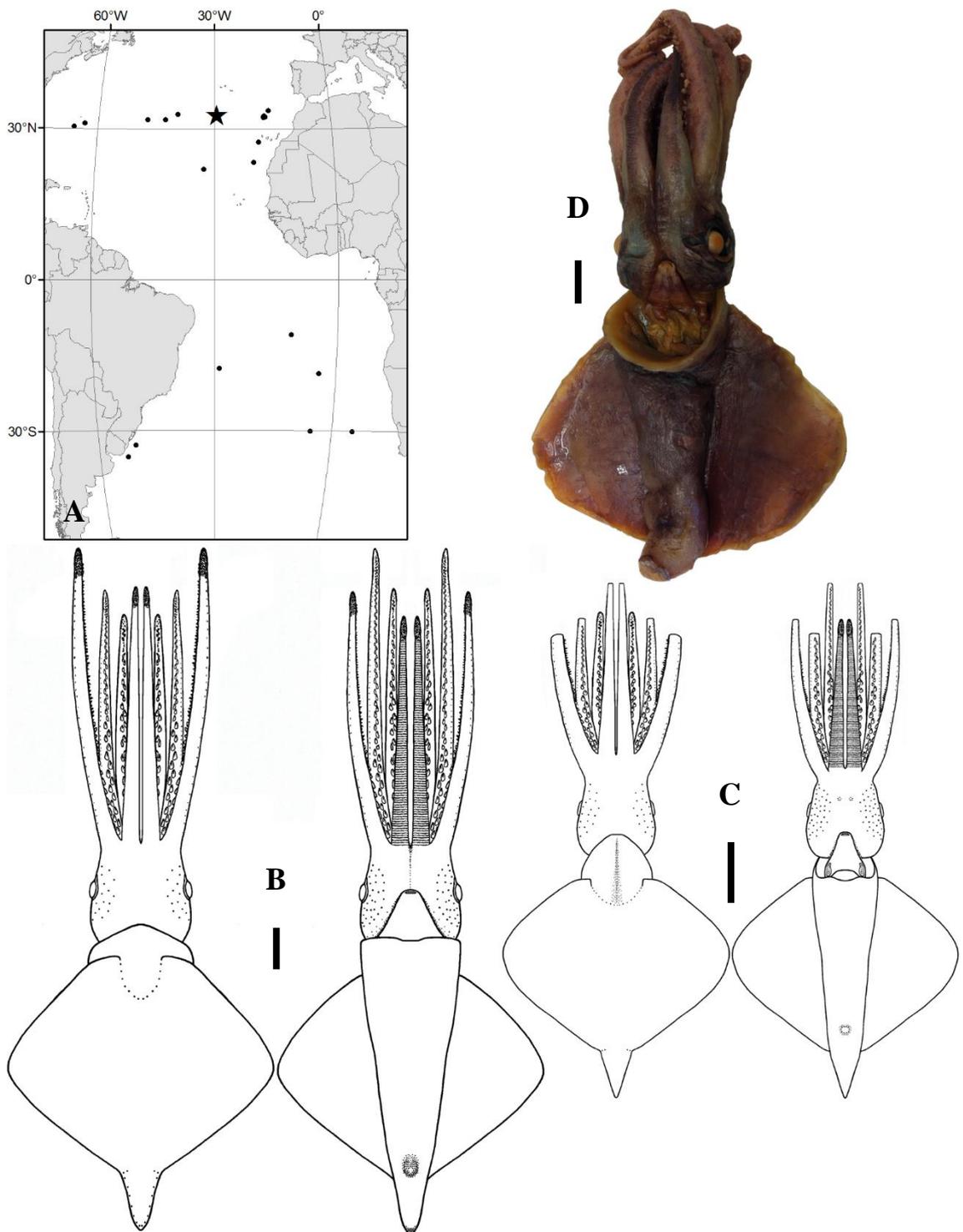


Fig. 52—*Octopoteuthis leviuncus* sp. nov. A) Distribution (star indicates type locality); B) adult; C) juvenile (NHMUK 20160101, ♀, ML 44.5 mm); D) NHMUK 20130457, holotype, ♀, ML 186 mm. Scale bars = B, D) 25 mm; C) 10 mm.

densely around circumference especially postero-laterally. Anterior fin insertion pointed posteriorly, depth ~15% ML, width 11–14–18% ML.

Head trapezoidal in outline, length 27–35–41% ML, width 29–32–37% ML, depth 20–30% ML. LHP length ~6% HL (~2.5% ML); MEP square to oblong, broad, length ~6%

HL (~2.5% ML). Eyes large, diameter 51–57–67% HL (~18% ML), with large lenses, diameter 31% ED. Funnel short (length ~20% ML), funnel groove shallow; aperture width ~14% of funnel length, level with anterior margin of lense; funnel valve tall, broad. Funnel components of locking apparatus as in *O. deletron*: length ~8% ML, maximum width ~4% ML. Mantle component obliquely set, broadly triangular posteriorly, narrowing antero-medially to slender ridge along anterior half; surrounded by narrow groove laterally and anteriorly; length ~7% ML, width ~4% ML. Nuchal cartilage oblong to slightly spatulate, length ~12% ML, greatest width (~5% ML) just anterior of midpoint; smoothly rounded anteriorly, bluntly pointed posteriorly; dorsal sculpture as in previous *Octopoteuthis* species. Buccal connectives and pores as in *O. deletron* (Fig. 43C) but without the increased membrane depth observed in *O. deletron* males. Olfactory papillae short, elliptical, fleshy knobs without sculpture.

Seven intact, non-regenerating arms among available subadult to adult specimens, comprising two complete Arms I, three Arms II, and one of each of Arms III, IV. Arms slender; Arms I length ~101% ML, Arms II length 98–132–149% ML, Arm III length 84% ML, Arm IV length 76% ML. Trapezoidal to circular in cross-section; with 27–44 pairs of hooks followed by 2+1 to 7+1 pairs of suckers distally based on single specimen with intact series; hooks enclosed in fleshy sheaths. All arms narrow gradually to tips, from width ~7% AL (depth ~9% AL) at base to ~4% at midpoint (depth ~5% AL). Arm-tip photophores occupy distal-most ~5% AL (length ~6% ML); shape consistent with tapering of arm, until slight bulb at tip; arm hooks terminate proximal to photophore, suckers overlies proximal third of length. Arms III and IV base photophores larger than in Arms II. Photophore series along ventral Arms III, IV beginning after slight gap distal to base photophores. Gelatinous tissue along aboral arms often produced into low keels from base to tip, increasing distally relative to arm depth.

Arm hooks stout, robust (Fig. 53); largest in pairs 3–6 of Arms II, decreasing gradually in size distally, slight decrease in size proximally. Cusp moderately long, smoothly curved, pointed; smooth laterally; typically maintaining similar breadth aborally and laterally along junction with base; inner angle acute in all hooks: generally ~80° in proximal hooks, decreasing distally (~60–80°); aperture very broad, open, ovoid. Accessory claws absent; aperture rim expanded laterally, flat, evenly smooth. Aboral hood absent. Bases crenulated, most prominent oral-laterally. Proximal hooks stouter

than distal hooks, with relatively larger bases (width and breadth). Arm suckers not examined.

Tentacles absent from all examined material.

Recti abdominis muscles and rectum morphology as in *O. deletron*. *Recti* photophores squarish, at ~30% ML anteriorly; length ~2% ML, comprising full width of muscle width (~2% ML). Anal flaps short, ~1.3% ML. Ventral visceral mesentery pore small, diameter 0.5 mm (~0.3% ML). Gills robust; length 20–25% ML, with 24–27 lamellae.

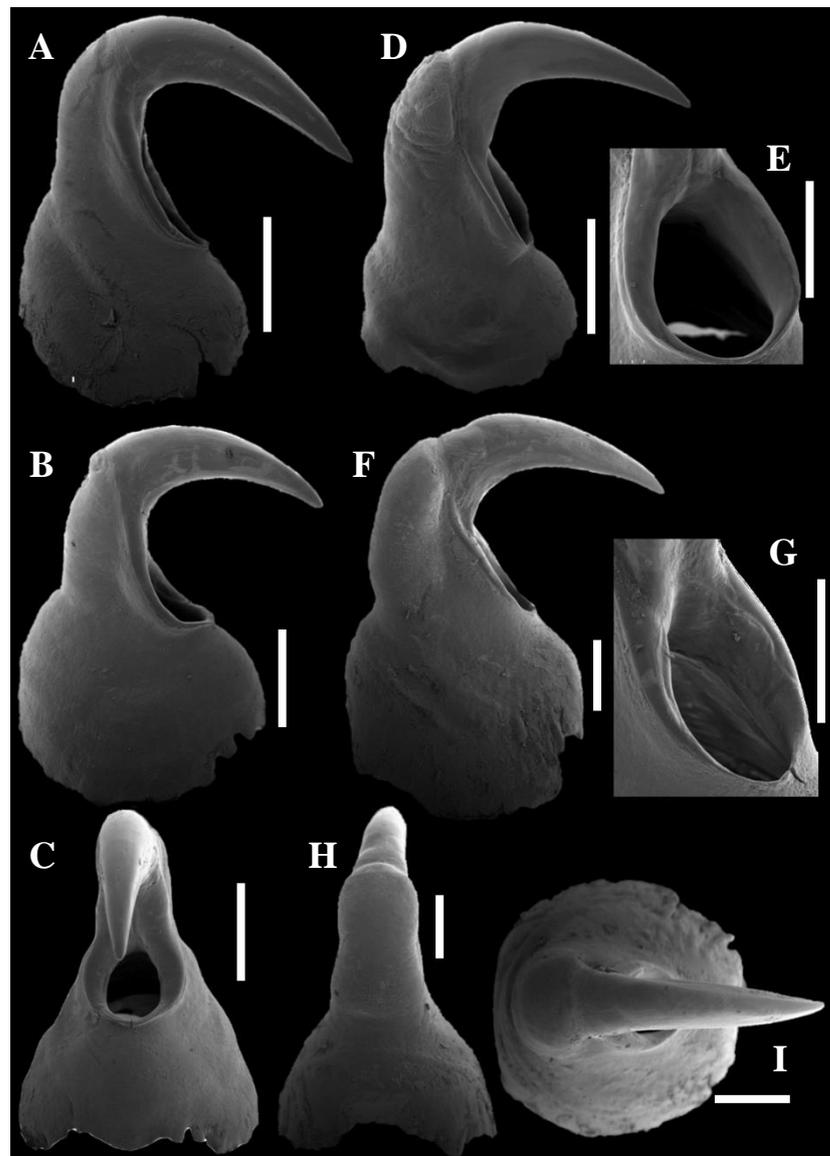


Fig. 53—*Octopoteuthis leviuncus* sp. nov. armature. A–C) USNM 885294, paratype, ♂, ML 144 mm; D–I) NHMUK 20130457, holotype, ♀, ML 186 mm. A) 22V, Arm IIIR; B, C) 4V, Arm IIIR: (B) lateral profile, (C) oral; D, E) 25D hook, Arm IIII: (D) lateral profile, (E) oblique aperture; F–I) 4V, Arm IIII: (F) lateral profile, (G) oblique aperture, (H) aboral, (I) apical. Scale bars = A–D, F–I) 0.5 mm; E) 300 μ m.

Lateral profile of lower beak (6.27–10.05 mm LRL, Figs 54A–D) slightly longer than deep, with distal wing tips extending beyond rostral tip by ~19% baseline; rostral tip occasionally with shallow notch, sometimes worn down; jaw edge visible, straight until slight bend in distal third of LRL, with short jaw extension; jaw angle 85–100°, slightly obscured by low, rounded wing fold; depth anterior to jaw angle greater than posterior in largest beak, equivalent in smallest beak. Hood very close to crest; hood length ~32% baseline; with shallow hood grooves overlying lateral wall ridges, broadening posteriorly. Crest distinct; length ~68% baseline; sloped in nearly straight line; tip free with concave notch between crest and lateral wall; lateral wall between crest and ridge fully pigmented. Lateral wall with slightly curved, narrow, sharp fold, produced laterally in cross-section, not increasing in breadth posteriorly; produced into shelf along anterior 50% hood length; posterior lateral wall margin straight; free corner beyond crest tip; crest, lateral wall fold (and distinct band directly dorsal to fold) more darkly pigmented than remaining wall, especially anteriorly. Wings broaden distally, greatest width ~180% that at jaw angle, length ~110% LRL, with cartilaginous pad. Ventral view with broad, shallow notch in hood; free corners level with medial margin of wing. Beak fully pigmented excluding wings at LRL 6.27 mm (ML ~100 mm); wings fully pigmented in beak LRL 10.05 mm (ML ~160 mm).

Lateral profile of upper beak (7.29–11.07 mm URL, Figs 54E, F) longer than deep, maximum depth ~44% UBL. Rostrum very long, ~36% UBL, curved ventrally, with distinct long jaw-edge extension; jaw angle ~80°; low ridge of cartilage present orally along shoulder, margin slightly scalloped. Hood long (~75% UBL), moderately tall (~18% UBL); junction of hood and free shoulder slightly concave. Lateral walls approximately rectangular with maximum depth in posterior third; posterior margin slightly angled. Dorsal view with posterior margin of hood, crest, and crest pigmentation straight. Crest and dorso-posterior ~60% of lateral wall pigmented at URL 7.29 mm (ML ~100 mm), ventro-anterior third and free shoulder unpigmented; lateral wall fully pigmented, free should ~50% pigmented at URL 11.07 mm (ML ~160 mm).

Radula (Figs 55A–C) with tricuspid rachidian: mesocone moderately long, very narrowly triangular; lateral cusps long (45–50% mesocone height) straight points; base concave. First lateral tooth bicuspid: inner cusp conical to very narrowly triangular, equivalent in height to rachidian, curved slightly medially; outer cusp long (45–50% height of inner) straight to slightly medially curved point; base slightly concave. Second

lateral tooth simple, conical, ~130% height of rachidian, curved slightly medially. Marginal tooth simple, conical, ~180% height of rachidian, straight. Marginal plate absent. Palatine palp (Figs 55D, E) with 40–51 long, narrowly triangular teeth, each 60–150% rachidian height; narrower anteriorly; oral and dorso-anterior margin and surface adentate, followed posteriorly by small region of greater tooth density, teeth evenly arranged posteriorly along surface. General palp morphology as in *O. deletron*.

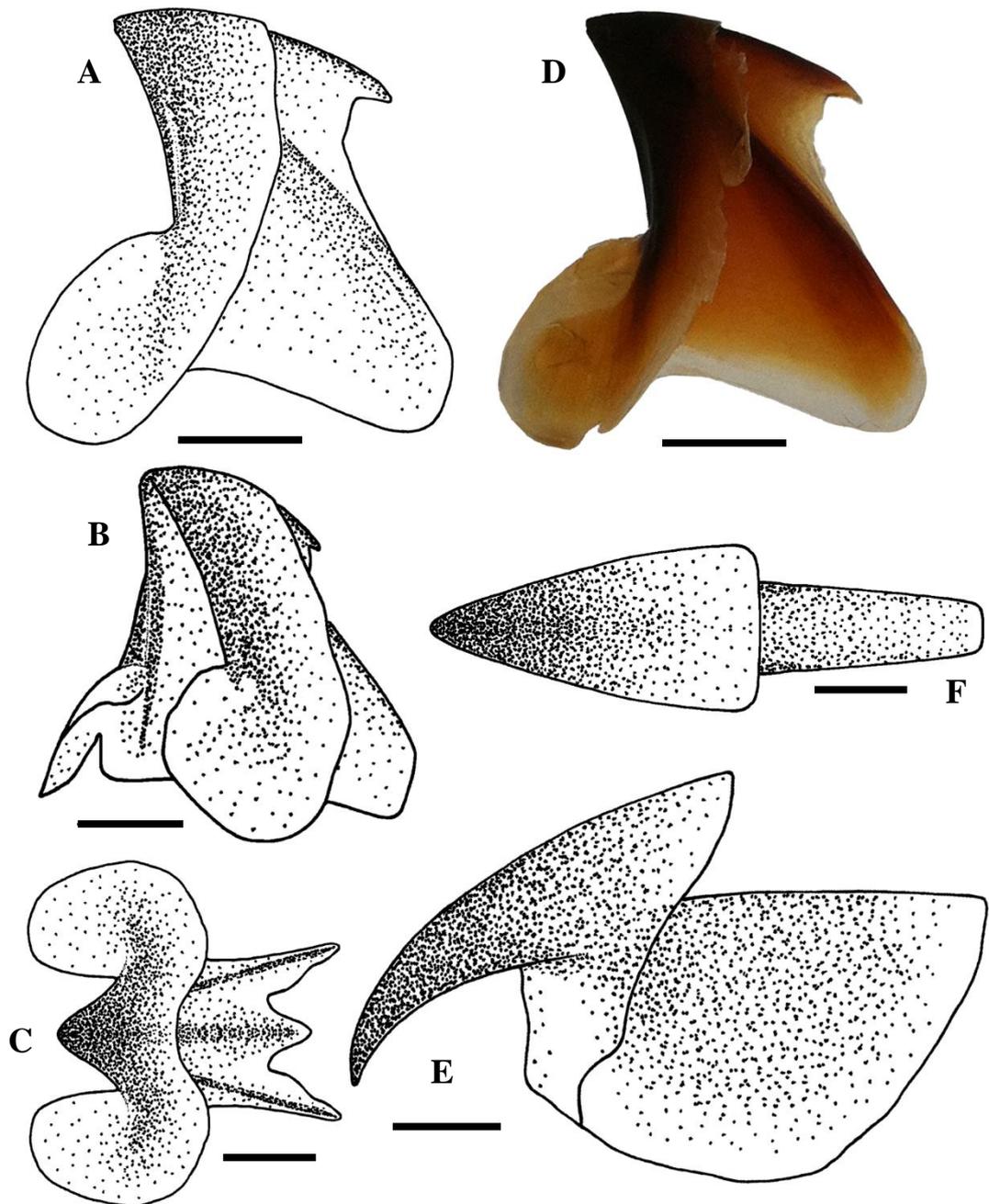


Fig. 54—*Octopoteuthis leviuncus* sp. nov. beaks. A–F) ZMH 11215, ♀, ML 149* mm, LRL 10.05 mm, URL 11.07 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 5 mm.

Gladius (154–171* mm GL, Fig. 55F) broad, very thin (<0.1 mm thick), delicate, transparent; greatest width (~11% GL) at ~33% GL; rachis broad, evenly concave; free rachis ~10% GL, pointed anteriorly, smoothly widening posteriorly to maximum width (~2.5% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden quickly to maximum width, then taper gradually for remainder of length; short conus present (~1.5% GL), very fragile, into which tissue inserts (the traction of which often results in breakage during dissection). Posterior gladius curved ventrally, with vanes bending ventro-medially in advance of fusion at conus.

Colour (preserved) in adults deep purple to pink over all external body surfaces where epidermis remains intact; holotype (NHMUK 20130457) with pigmented region on ventral anterior mantle, over *recti abdominis* photophores; arm tips over photophores dark purple; posterior tail tip darkly pigmented; chromatophore patch overlying PVMP darkest posteriorly, laterally; overlying gelatinous layer unpigmented except rugose furrows in females. Inner mantle surfaces and viscera unpigmented.

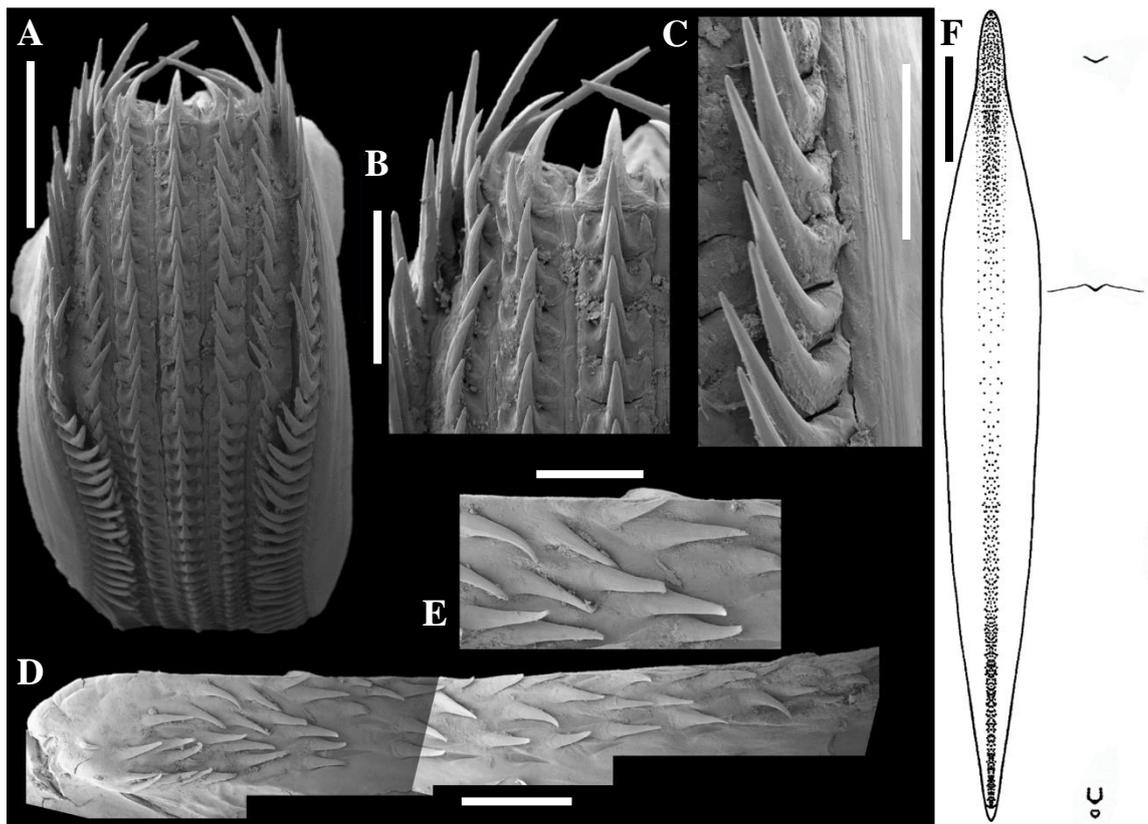


Fig. 55—*Octopoteuthis leviuncus* sp. nov. A–F) USNM 730684, ♂, ML 156 mm. A–C) Radula: (A) whole, (B) bending plane, (C) lateral margin; D, E) palatine palp; F) gladius with cross-sections. Scale bars = A, D) 1 mm; B, E) 0.5 mm; C) 0.4 mm; F) 20 mm.

Juvenile specimens (ML 28–57 mm, Fig. 52B) as above, with the following exceptions. Tail moderately long, length 7–16–23% ML; single PVMP discernible in specimens ML 25, 28 mm, diameter ~3% ML; MEPs visible in specimen ML 41.5 mm. Fins broad, width 94–116–146% ML; more posteriorly set than in adults, anterior fin margin at ~14% ML. Two specimens with total of 3 intact, non-regenerating arms; Arm I length 65% ML, Arms IV length ~60% ML. Arm hooks on single specimen (ML 31 mm) possibly with low accessory claws, all others without any trace of claws along aperture. Tentacles lacking macroscopically from all material, smallest specimens were not examined under dissecting scope.

Etymology. The name *leviuncus* (from Latin *levis* = smooth, smoothed and *uncus* = hook) is given to this species due to its characteristic arm hooks which lack accessory claws.

Biology. Smallest mature specimen examined ML 156 mm (USNM 730684, ♂), only individual with implanted spermatangia among examined material (presumably self-implanted). Females mature between ML 77 and 149 mm; largest female examined (ML 186 mm) staged as maturing, assessed before ‘resting’ stage characterised.

Remarks. *Octopoteuthis leviuncus* sp. nov. co-occurs in the Atlantic with both *O. sicula* and *O. megaptera*, but is readily distinguished from both of these paired PVMP species by its single PVMP and paired Arm II buccal connectives. While morphologically most similar to *O. deletron* of the Pacific, *O. leviuncus* can be differentiated by the absence of accessory claws on the arm hooks, and their very broad aperture and laterally expanded rim.

5.1.4. “Giant” Species Group. Adults ML >300 mm. Without photophores other than at arm tips. Head small (length, width ~23–27% ML). Arm II buccal connective dorsal, ventral protective membrane attaches basally to Arm III. Arms IV without transverse pigment bands. Arms without distal suckers, hook series extend to tips. Arm hooks with aboral hood on main cusp; accessory claws prominent. External gelatinous tissue firm.

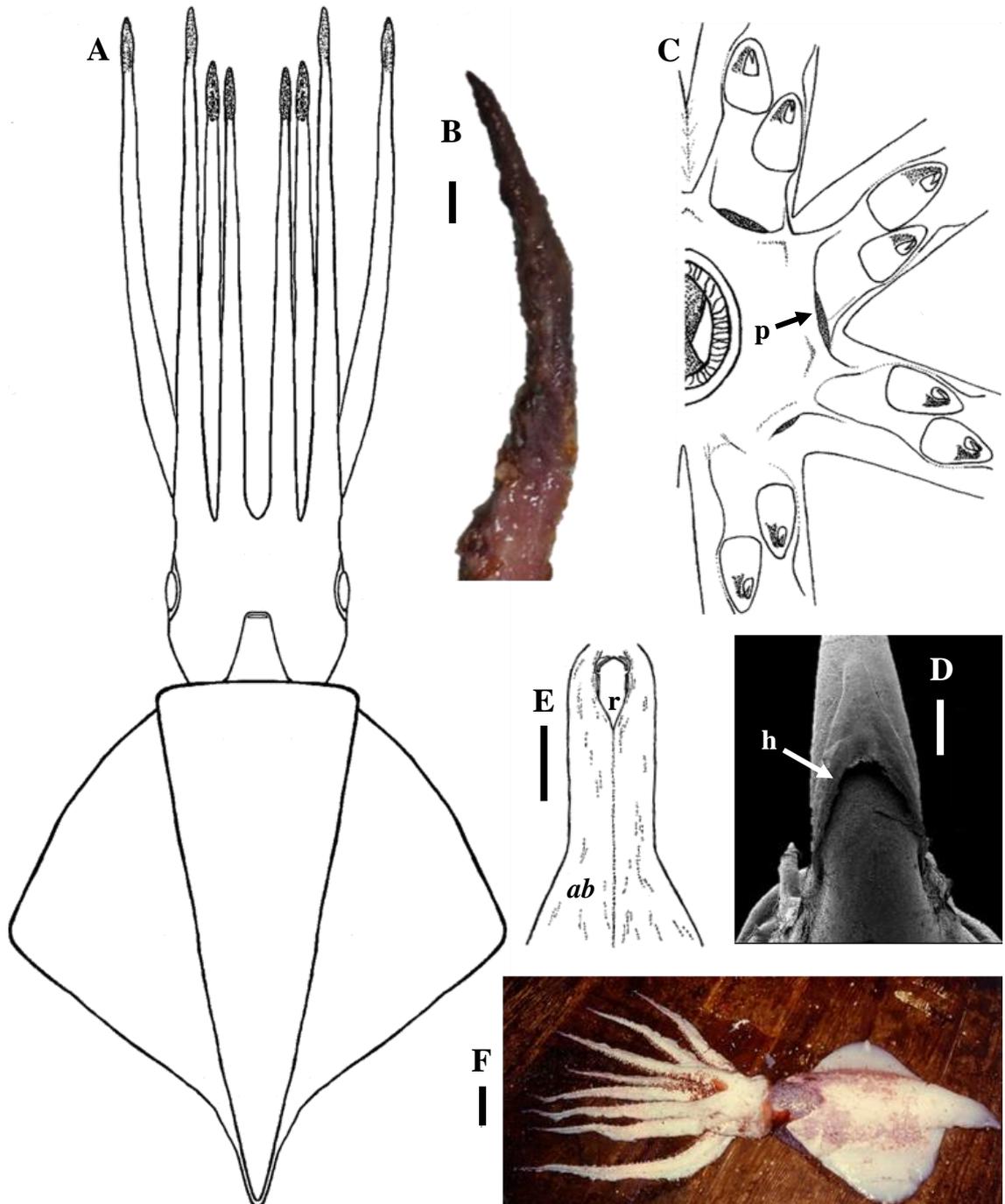


Fig. 56—“Giant” species group general morphology. A) Ventral morphology, arm-tip photophores only; B) arm-tip photophore, *O. sp.* Giant Pacific (AUT OG1, holotype, ♂, ML 372 mm); C) oral surface with single dorsal buccal connective Arm II, pore (p); D) aboral hood (h), *O. sp.* Giant Pacific (NMNZ M.174307, ♀, ML 472 mm; 17th pair arm hook, Arm IIL); E) *recti abdominis* muscles (*ab*) and rectum (*r*), *O. sp.* Giant Atlantic (NHMUK 20150459, ♂, ML 47 mm); F) unexamined fresh specimen, *O. sp.* Giant Pacific (1983, FV Arrow, trip 1, set 78). Scale bars = B, E) 5 mm; D) 0.5 mm; F) 10 cm.

5.1.4.1. *Octopoteuthis* sp. Giant Pacific nov. (Table 18, Figs 5H right, 6I, 56B, D, F, 57–61)

Octopoteuthis sp. ‘Giant’ Gomez-Villota, 2007: 142, Fig. 88.

Type material (1 specimen). **AUT OG1**, holotype, ♂, ML 372 mm, unlocalised near Port Davey, Tasmania, 26/08/2002.

Additional material examined (5 specimens). **USNM 1283041**, ♀, ML 148 mm, 21°25'N, 158°25'W, 1130 m, 10/08/1977, RV *Kana Keoki*, NORPAX Equatorial Expedition, stn 77-8-6, IKMWT, coll. University of Hawaii; **NMNZ M.174307**, ♀, ML 472 mm, 35°00'S, 165°00'E, 940 m, 00/04/2004, FV *Atlantic Elizabeth*, trawl, coll. L. Elkington; **NMNZ M.90005**, ♂, ML 409 mm, 40°08.1'S, 167°57.7'E, 914–963 m, 13/05/1987, FV *Poong San I*, coll. R. Connell & M. Ensor; **NIWA Z10746** (beaks: NIWA 23751; tissue sample: NIWA 84512), ♀, ML 552 mm, 42°36'S, 170°20.15'E, 360 m, 10/08/2000, FV *Tomi Maru*, MFish SOP trip 1379/86, 1379/12, NZOI Z10746, tow 12, coll. K. Brady & Y. Guskov.

Unlocalised material examined (1 specimen). **MV F189415**, sex indet., ML 305 mm, unlocalised [southern Australia], 31/03/1992, FV *Karagach*, shot 10.

Comparative material (1 lot of 2 lower beaks). **NHMUK20160143**, sex indet. (2 lower beaks), LRL 20.10*, 18.03* mm, Donkergat.

Distribution (Fig. 57A). Tasman Sea and off southern Australia, single specimen from Hawaiian waters; 360–1130 m.

Diagnosis. Basal-most hook pattern VVDD; arms very long, 91–142% ML.

Description (ML 148–552 mm, Figs 57B–61). Mantle conical to weakly goblet shaped; widest at anterior margin, width 37–40–44% ML; weakly muscled; tail thick, of moderate length, 15–18–22% ML; dorsal anterior margin bluntly produced medially, ventral margin with slight indentation between mantle components of locking cartilage; external gelatinous tissue firm. Fins large (length 77–81–85% ML), broad (width 87–99–108% ML); anterior margin at 2–5–10% ML; greatest fin width attained at ~50% ML; width of fin continuation along tail ~3% ML. Without photophores in posterior

Table 18. Measurements (mm) of *Octopoteuthis* sp. Giant Pacific nov. Mean indices were calculated from specimens with undamaged dimensions (excluding NIWA Z10746, see Remarks), and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side).

Specimen ID	AUT OG1	NMNZ M.174307	NMNZ M.90005	NMNZ M.90005	MV F189415	USNM 1283041	Mean index	NIWA Z10746
Type status	Holotype	None	None	None	None	None		None
Sex	♂	♀	♂	Indet.	♀	♀		♀
DML	358	472	409	305	148	552		552
MW	137	198	150	135	57	237	40	237
FL	304	379	340	240	114	360	81	360
FW	357	409	385	319	160	384	99	384
HL	98	128	97	75	36	117	25	117
HW	85*	est. 110	114	75*	40	105	27	105
Side	L	L	R	L	L	R		R
AL I	415	395*	429	405	139 ^r	587	118	587
AL II	449	431	350*	423	80*	523	118	523
AL III	414	206*	346 ^r	382	154 ^r	380*	120	380*
AL IV	377	400*	315*	252*	142 ^r	10*		10*
AH	34, 32, 35, 37	35	35+1	*, *, *		*, *, *		*, *, *

* indicates damaged character, ^r indicates regenerating feature, not used to calculate indices.

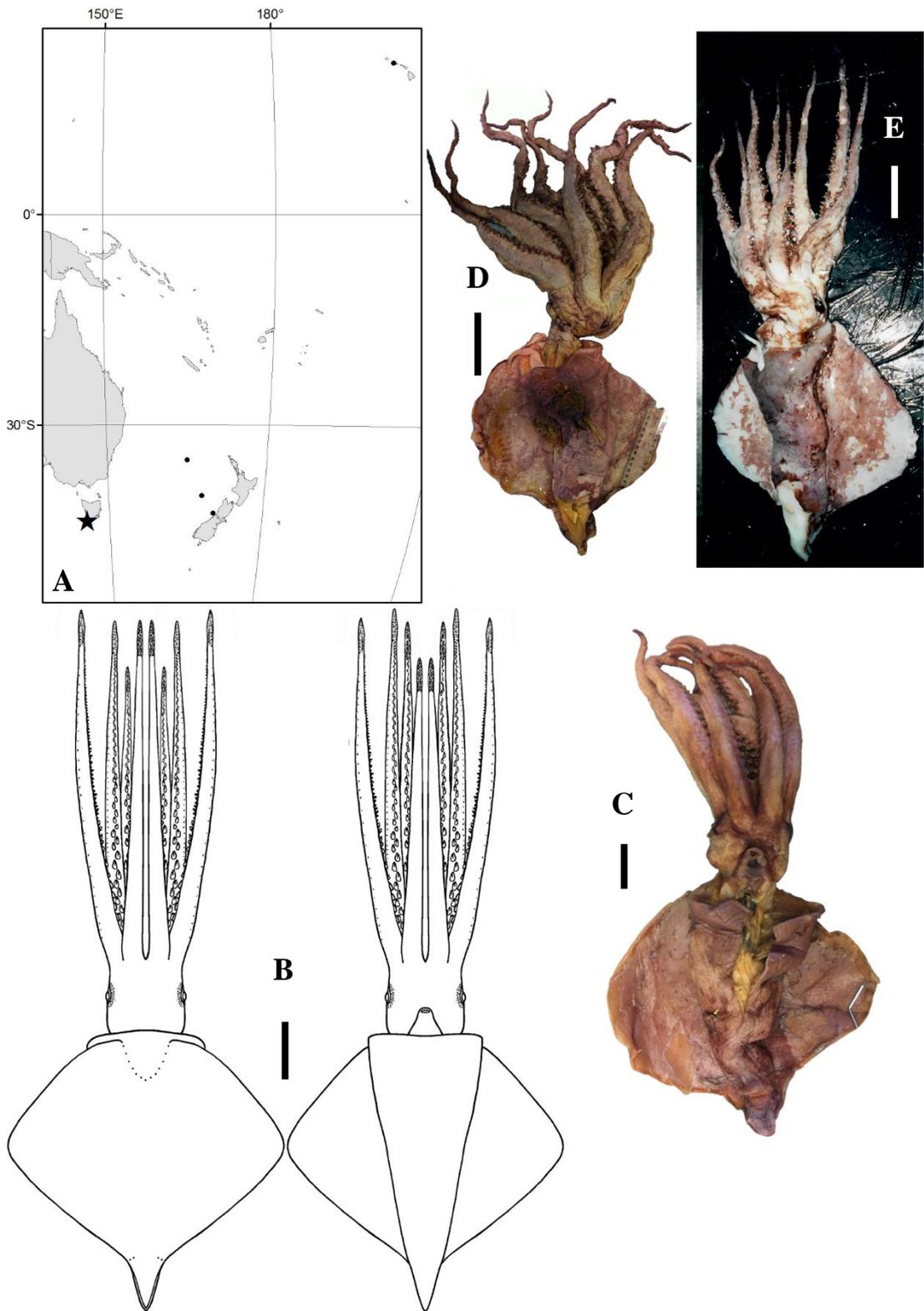


Fig. 57—*Octopoteuthis* sp. Giant Pacific nov. A) Distribution (solid star indicates type locality); B) adult; C) subadult (USNM 1283041, ♀, ML 148 mm); D, E) AUT OG1, holotype, ♂, ML 372 mm: (D) preserved, (E) fresh. Scale bars = B, D, E) 100 mm; C) 25 mm.

ventral mantle. Anterior fin insertion blunt, smoothly rounded posteriorly; depth ~14% ML, width 11–15–20% ML.

Head square in outline, short (length ~25% ML), narrow (width ~27% ML), depth ~20% ML. Eyes small, diameter 6–10–18% ML, with small lenses, diameter 13–20–38% ED. Funnel length 16–20–24% ML, funnel groove shallow; aperture width 15–23–37% funnel length, level with posterior margin of eye. Funnel organ not examined. Funnel component of locking apparatus length ~9% ML, maximum width ~4% ML; degraded in all Australasian specimens; in Hawaiian specimen ovoid, narrow, broadest posteriorly, with slender medial groove narrowing anteriorly (Fig. 58A). Mantle component of locking apparatus low oblique ridge (Fig. 58B); length ~8% ML, maximum width ~3% ML. Nuchal cartilage spatulate, slightly pointed anteriorly (Fig. 58C); broad medial ridge with slender medial groove, flanked by shallow grooves broadest anteriorly; length ~13% ML, maximum width ~5% ML. Buccal connectives paired on Arms I, dorsal taller than ventral; Arms II with broad dorsal connective only, ventral protective membrane attaches basally to Arm III; Arms III and IV with broad ventral connective, fused for 30–50% arm width. External gelatinous tissue firm. Six pores in buccal membrane: one between connectives of Arms I, large one between Arms II and III, small one between Arms III and IV. Olfactory papillae short, elliptical.

Arms robust, very long, length 91–117–142% ML; formula II>III=I>IV; trapezoidal in cross-section; with 32 to 37 pairs of hooks in thick fleshy sheaths; without suckers distally. Arms taper gradually to tips, from ~7% AL at base to ~3% at midpoint. Arm-tip photophores occupy distal-most ~7% AL (photophore length ~8% ML); photophore continuous with arm tapering, distally tapering smoothly to tip, without bulb; up to four pairs of hooks overlie photophore proximally. Arm-base, series photophores absent. All arms with low, firm gelatinous aboral keels from base to tip; breadth 30–60% arm depth. Arms IV without aboral pigmented banding.

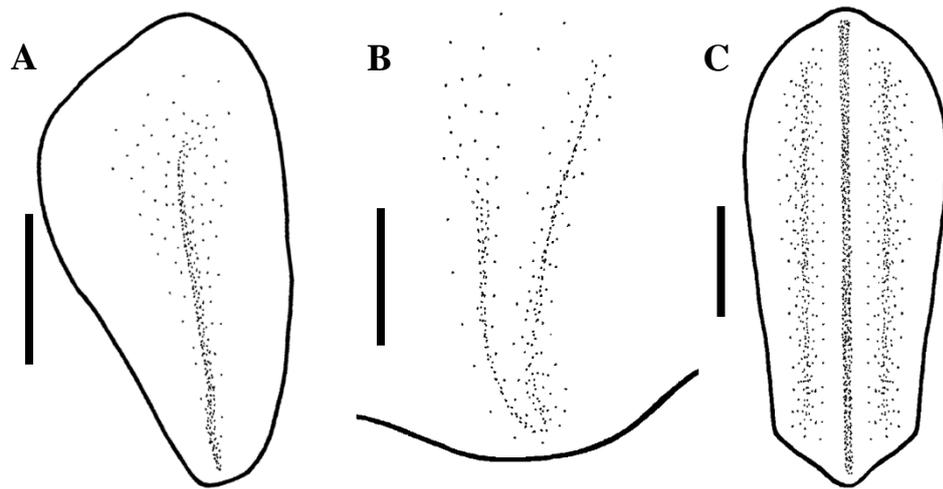


Fig. 58—*Octopoteuthis* sp. Giant Pacific nov. A–C) USNM 1283041, ♀, ML 148 mm. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage. Scale bars = 5 mm.

Arm hooks broad, robust (Fig. 59); largest in pairs 4–6 of Arms I and II, decreasing gradually in size distally, slight decrease in size proximally. Main cusp long, smoothly curved, pointed; often with single prominent ridge along lateral surface; aboral breadth consistent along junction with base, broadening basally; inner angle $\sim 90^\circ$, oral surface of cusp rounded, less angular than in small-bodied *Octopoteuthis*; aperture exceptionally broad, open, ovoid to broadly oblong. Accessory claws prominent, curved. Hooks with aboral hood into which tissue from sheath inserts; hood apical, aboral on main cusp; basal margin of hood concave to ‘V’ shaped; hood formed from medial fusion of lateral processes. Hook base crenulated, most prominent oral-laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth). Arm suckers absent.

Tentacles absent from all material examined (likely lost during post-larval stages as in other *Octopoteuthis* spp.).

Without bioluminescent structure associated with ink sac area. *Recti abdominis* muscles difficult to separate, fused medially for most of length leaving only short anterior section of rectum visible; posteriorly expanding, attaching to ventral surface of visceral mass. Anal flaps long, length $\sim 1\%$ ML, thin; lanceolate, tapering smoothly to fine tip. Ventral visceral mesentery pore diameter $\sim 1\%$ ML. Gills robust; length 13–23–27% ML, with 27–32 lamellae.

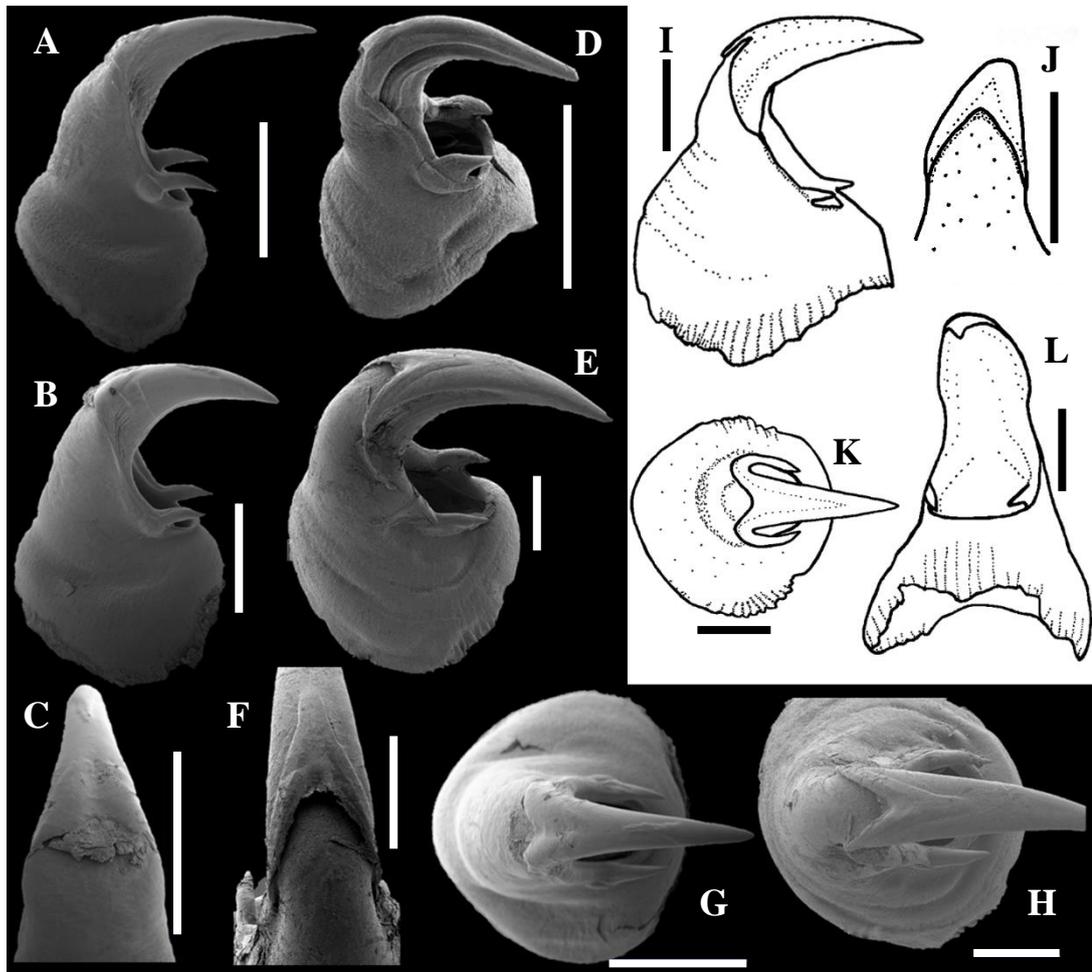


Fig. 59—*Octopoteuthis* sp. Giant Pacific nov. armature. A–C, G) USNM 1283041, ♀, ML 148 mm; D–F, H–L) NMNZ M.174307, ♀, ML 472 mm. A) 17D hook, Arm III; B, C, G) 4D hook, Arm III: (B) lateral profile, (C) aboral, (G) apical; D) est. 29V hook, Arm III; E, F, H) hook from 17th pair, Arm III: (E) lateral profile, (F) aboral, (H) apical; I–L) 3V hook, Arm III: (I) lateral profile, (J) aboral, (K) apical, (L) oral. Scale bars = A–H) 1 mm; I–L) 5 mm.

Lateral profile of lower beak (18.11–23.33 mm LRL; Figs 60A–D) slightly deeper than long, with distal wing tips extending beyond rostral tip by ~12% baseline; rostral tip sometimes with deep notch and distinct tip; jaw edge visible, straight until slight bend at distal ~20% of LRL, with short jaw-edge extension; jaw angle typically 90–95°, obscured slightly by low, rounded wing fold; depth anterior to jaw angle greater than posterior. Hood off crest, length 28–31–35% baseline, with shallow hood groove beginning at rostral notch and continuing in line with lateral wall fold. Crest discrete, lateral wall between crest and fold fully pigmented at all sizes; length 59–62–65% baseline; tip free, with concave notch between free tip and lateral wall ridge; sloped in straight line. Lateral wall with straight, narrow, sharp folds, produced laterally in cross-section, only slightly increasing in breadth posteriorly; produced into shelf along anterior 50% of hood length; posterior lateral wall margin straight; free corner beyond

crest tip; crest, lateral wall fold (and distinct band directly dorsal to fold) more darkly pigmented than remaining wall, especially anteriorly. Wings broaden distally, greatest width 195–208–232% that at jaw angle, length 77–91–107% LRL, with cartilaginous pad. Ventral view with broad notch in hood; free corners level with medial ~20% of wing breadth. All beaks examined with fully pigmented lateral walls and wings.

Lateral profile of upper beak (18.95–24.87 mm URL; Figs 60E, F) longer than deep, maximum depth 44–48–50% of length. Rostrum long, 30–34–36% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~80°; very low ridge of cartilage present along shoulder, particularly dorsally; oral shoulder margin straight. Hood long (length ~79% UBL), tall (height ~21% UBL); junction of hood and free shoulder slightly concave. Lateral walls approximately rectangular, maximum depth in posterior ~25%, posterior margin straight; with oblique groove in anterior midsection, deepest level with posterior hood margin, becoming shallower posteriorly until indistinguishable; often also with short ridge in dorsoposterior quarter, similar orientation and breadth as groove. Dorsal view with posterior margin of hood concave, posterior margin of crest and crest pigmentation straight. All beaks examined with fully pigmented lateral walls and free shoulders.

Radula (Fig. 61A–D) variable in morphology among specimens. Rachidian tricuspid: mesocone moderately long, thinly conical to narrowly triangular, straight; lateral cusps as low nubs (~20% mesocone height) to moderately long points (~45% mesocone height), slightly laterally directed; base concave. First lateral tooth bicuspid: inner cusp thinly conical or narrowly triangular, slightly shorter than rachidian in height, straight, slightly medially directed; outer cusp as low nub (~20% height of inner) or moderately long (45% height of inner) point; straight; base concave. Second lateral tooth simple, conical or narrowly triangular, 100–130% height of rachidian. Marginal tooth simple, conical or narrowly triangular, 120–130% height of rachidian. Marginal plate absent; single specimen with series of low nubs lateral to marginal tooth series (Fig. 61D). Palatine palp (Fig. 61E) with 55 triangular teeth, broad basally but narrowing quickly; each 50–160% rachidian height, smallest orally; depth of tooth-bearing surface decreases posteriorly; oral end of palp rounded, recessed relative to majority of tooth-bearing length; three irregular rows of small thin teeth along oral slope up to tooth-bearing surface; teeth of consistent size and shape, arranged evenly along surface, in roughly three series.

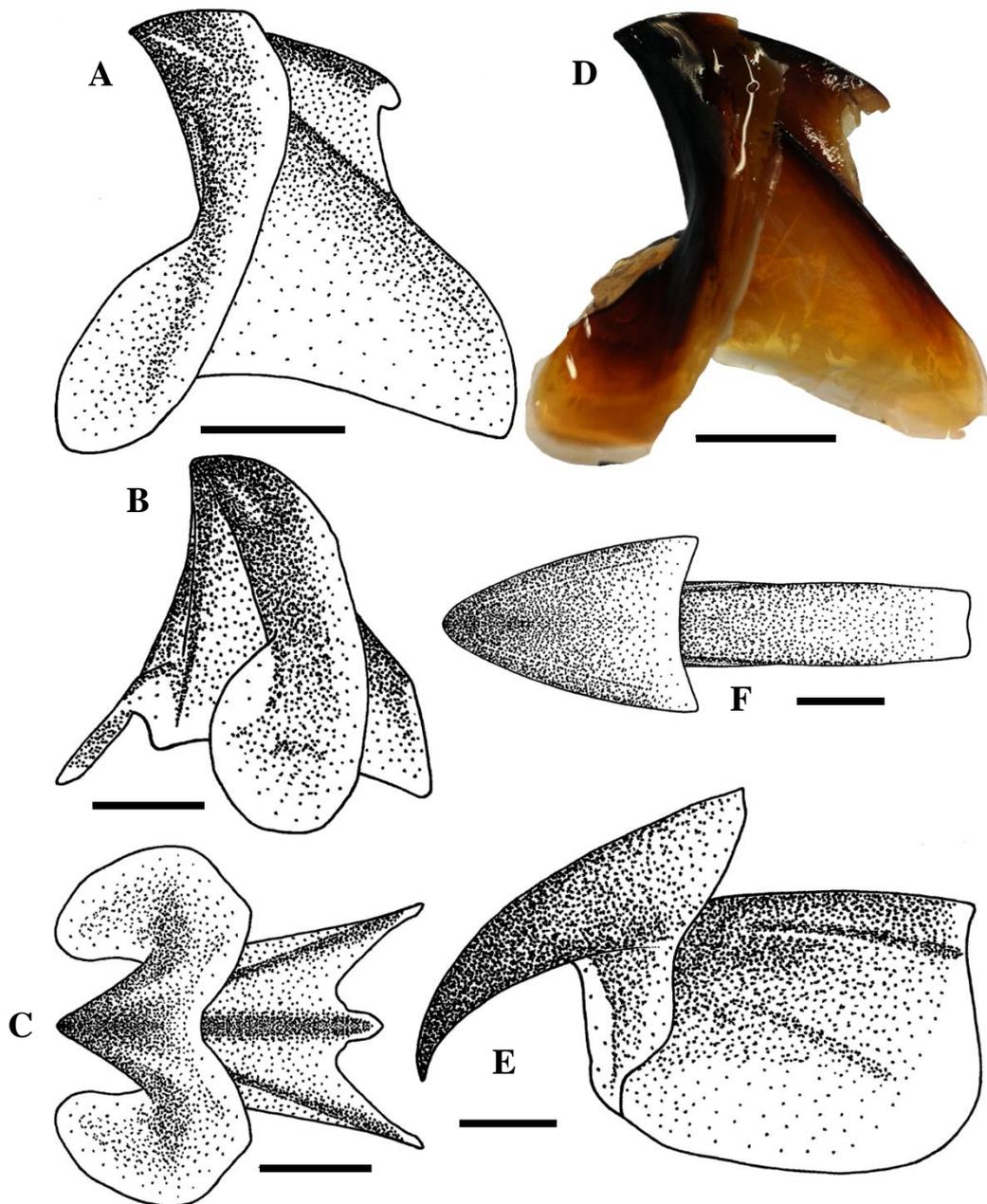


Fig. 60—*Octopoteuthis* sp. Giant Pacific nov. beaks. A–C, E, F) NMNZ M.174307, ♀, ML 472 mm, LRL 23.33 mm, URL 24.87 mm; D) NMNZ M. 90005, ♂, ML 409 mm, LRL 20.18 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = 10 mm.

Single partial gladius examined (Fig. 61F), missing free rachis and anterior portion; remaining gladius length 409* mm; vanes thin, transparent, delicate; rachis narrow, width ~2 mm; maximum width of remaining portion 36 mm, gradually tapering posteriorly; conus present, length 19 mm.

Colour (preserved) deep purple, maroon, or pink over all external body surfaces where epidermis remains intact; arm tips over photophores dark purple; external gelatinous

layer of arms and ventral mantle pigmented. Inner mantle surface pigmented anteriorly in large individuals. Fresh specimens similar but colours more brilliant (pigmented surfaces red, purple; non-pigmented white).

Biology. Smallest mature specimen examined ML 358 mm (AUT OG1, ♂). Smallest mature female examined (NMNZ M.174307, ML 472 mm) mated, nidamental and oviducal glands paired, bilobed. Spermatangia with oblong sperm mass (4.9–6.0 mm long) tapered at both ends, with long (~11 mm), thread-like aboral extensions; implanted in rugose furrows ventral and lateral mantle, lateral head, Arms II and III left aborally, and dorsally in anterior fin insertion; sperm mass implanted deeply in tissue, extensions protruding out through skin. Matured ova in ovary large, diameter 1.77–2.87 mm (NIWA Z10746, ML 552 mm).

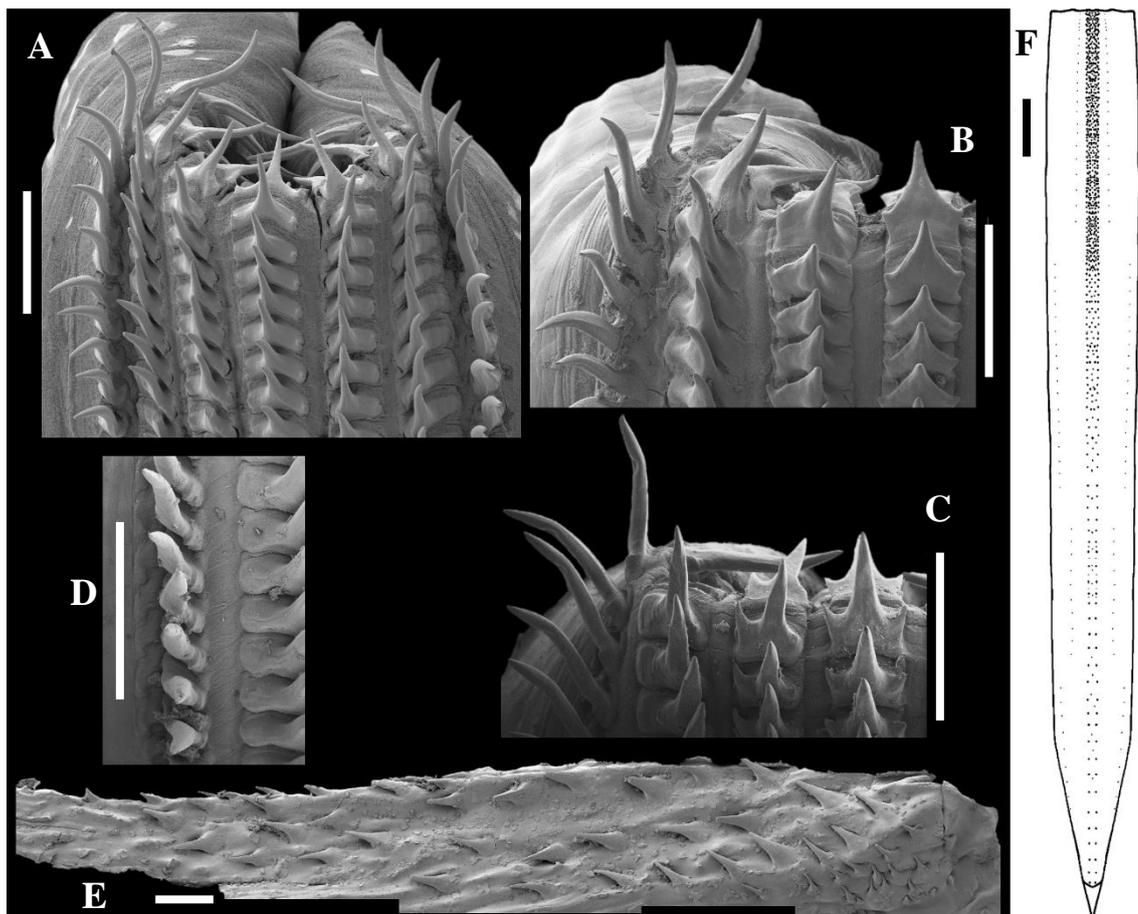


Fig. 61—*Octopoteuthis* sp. Giant Pacific nov. A) NIWA Z10746, ♀, ML 552 mm; B, F) NMNZ M.174307, ♀, ML 472 mm, GL 409* mm; C, D) MV F.189415, sex indet., ML 305 mm; E) NMNZ M.90005, ♂, ML 409 mm. A–D) Radulae: (A–C) bending plane, (D) lateral margin; E) palatine palp; F) gladius, anterior portion damaged. Scale bars = A–E) 1 mm; F) 25 mm.

Values of LRL, URL, ML, and body mass ($n = 6$) were pooled with those of *O. sp. Giant Atlantic nov.* to calculate combined regressions from greater sample size (see Biology *O. sp. Giant Atlantic nov.*, Fig. 67).

Remarks. Specimens of *O. sp. Giant Pacific nov.* differ considerably from all small-bodied *Octopoteuthis* species in several consistent, taxonomically significant ways: body photophores absent (Table 4), all arm hooks with aboral hood, arms without distal suckers, *recti abdominis* muscles fused medially, and proportionally smaller heads. However, in addition to their considerably greater adult size, the trait that most readily separates *O. sp. Giant Pacific nov.* is their tendency to retain complete arms: of 132 specimens and 1056 potential arms of *O. rugosa* and *O. fenestra sp. nov.* from New Zealand waters, only 39 were non-truncated (4%). Conversely, all Australasian *Octopoteuthis sp. Giant Pacific nov.* specimens retained at least one complete arm, and among the five specimens 23 arms (58%) were intact.

The diagnostic character separating the two Giant species described herein is novel: basal-most arm hook pattern (alternatively, the arm hook series more proximally set). In all previously described species of *Octopoteuthis*, the basal-most hook on Arms I through IV was VVDD on both sides. This was also true for all Australasian *O. sp. Giant Pacific nov.*, with one exception: AUT OG1, left side VVDD, right side possibly VVDV but damaged. Conversely, all specimens of *O. sp. Giant Atlantic nov.* had the pattern VVDV on both sides. The specimen from Hawaii (USNM 1283041), in excellent condition, was intermediate between these two states (left VVDD, right side VVDV). It is here tentatively attributed to *O. sp. Giant Pacific nov.* primarily based on locality, although the possibility remains that this specimen may represent a third Giant species.

Arm-tip photophores remain the only confirmed photophores present in this species. Australasian specimens were generally in moderate to poor condition as relates to photophore location (e.g., holotype and paratype both sustained damage to PVMP region). However, the Hawaiian specimen and those from the Atlantic (see below) are in better condition and lacked all photophores otherwise found in the genus (e.g., ventral mantle, head, and arm photophores excluding those at the arm tips).

Fin and arm length indices of NIWA Z10746 differed considerably from other specimens, generally 12–37% less (mean 24%) than the mean index of the other specimens. All relevant taxonomic characters were consistent among all specimens reported herein, and the difference in these proportions is considered most likely an artifact of preservation history, or possibly size. As such, fin and arm measurements for NIWA Z10746 were not used in mean calculations for *O. sp. Giant Pacific nov.*, and its measurements reported separately in Table 18.

Two additional references, both reporting on sperm whale stomach contents from Australian waters, likely refer to beaks attributable to *O. sp. Giant NZ*: the largest beaks (LRL 13.0–14.5 mm) from Albany of Clarke (1980), and the largest beaks (LRL >15.0 mm) as well as three smaller beaks (LRL 10.5–15.0 mm) with unpigmented wings from whales in the Tasman Sea, reported in Clarke and MacLeod (1982).

One lot of 2 ‘giant’ *Octopoteuthis* beaks from Donkergat (west coast of South Africa; NHMUK 20160143) could not be morphologically attributed to either ‘giant’ *Octopoteuthis* species; however, to afford it some attribution, it is included under Comparative Material for both. Recognised distributions for both species are incomplete, but given the distribution patterns among other *Octopoteuthis* spp., the lot’s locality could be attributable to *O. sp. Giant Pacific nov.* should the species prove to have a southern circumglobal distribution as in *O. rugosa*, or to *O. sp. Giant Atlantic nov.* (see below) if that species proves to have an Atlantic-wide distribution as in *O. sicula*.

5.1.4.2. *Octopoteuthis* sp. Giant Atlantic nov. (Table 19, Figs 56E, 62–66)

Octopoteuthis sp. B Clarke and MacLeod, 1976: 741; =‘giant *Octopoteuthis*’ Clarke, 1986: Fig. 58B; =*Octopoteuthis* sp. G Clarke *et al.*, 1993: 75, Fig. 3C.

Type material (1 specimen). **USNM 1283027**, holotype, ♂, ML 246 mm, 14°10.8'N, 18°28.2'W, Senegal, 2000 m, 18/07/1974, RV *Anton Dohrn*, AD 11/74, Gate Expedition, A.D. 1974, stn 1.

Additional material examined (3 specimens). **USNM 730685**, ♀, ML 452 mm, 65°00'N, 30°00'W, east coast of Greenland, 1973, Polar Arctic Collection, RV *Walther Herwig*, 1600 mesh Engel trawl; **NHMUK 20130455**, ♀, ML 467 mm, 59°30'N, 17°05'W, trawl, “Swanella,” “Giant,” Lowestoft; **NHMUK 20150459**, ♂, ML 47 mm, 37°34.9'N, 25°34.1'W, Azores Islands, 0–515 m, 18/10/1966, RRS *Discovery* Expedition, stn 6118, EMT.

Unlocalised material examined (1 specimen). **NHMUK 20130456**, sex indet. (arm crown), LRL 14.25 mm, Iceland, 22/09/1977, I-337-77.

Comparative material (6 lots totaling 18 lower beaks). **NHMUK 20160141**, sex indet. (5 lower beaks), LRL 21.28, 20.33, 20.28, 19.66, 18.98, Azores, 17/11/1981; **NHMUK 20160142**, sex indet. (5 lower beaks), LRL 20.95, 19.40, 18.94, 18.74, 18.39 mm, Azores; **NHMUK 20160144**, sex indet. (single lower beak), LRL 18.31 mm, Azores; **NHMUK 20160145**, sex indet. (single lower beak), LRL 14.10* mm, Azores; **NHMUK 20160146**, sex indet. (4 lower beaks), LRL 18.82*, 17.12*, 16.78*, 11.98 mm, Azores; **NHMUK 20160143**, sex indet. (2 lower beaks), LRL 20.10*, 18.03* mm, Donkergat.

Distribution (Fig. 62A). Eastern north Atlantic, from off Cape Verde to Icelandic waters; 0–2000 m.

Diagnosis. Basal-most hook pattern VVDV; arms long, 85–105% ML.

Description (ML 246–467 mm, Figs 62B–66). Mantle conical to weakly goblet shaped; widest at anterior margin, width 30–38–46% ML; weakly muscled, reduced dorsally along fusion with fin to membrane ventral of gladius; tail pointed, long, ~22% ML;

dorsal anterior margin smoothly rounded or slightly concave, ventral margin slightly indented between mantle components of locking cartilage; external gelatinous tissue firm. Fins large (73–81–87% ML), broad (width 90–94–101% ML); anterior margin at ~5% ML; greatest fin width attained at ~50% their width (~40% ML); fins continue along tail in narrow strip. Without photophores in posterior ventral mantle. Anterior fin insertion blunt, smoothly rounded posteriorly; depth ~16% ML, width ~10% ML.

Head square in outline, short (length ~26% ML), narrow (width ~24% ML), depth ~20% ML. Eyes small, diameter ~36% HL (~9% ML), with small lenses, diameter ~34% ED. Funnel small, narrow, length ~65% HL (~17% ML); funnel groove shallow; aperture width ~23% of funnel length, level with posterior margin of eye. Funnel organ not examined. Funnel component of locking apparatus length ~7% ML, maximum width ~4% ML; degraded, subtriangular, with groove narrowing anteriorly (Fig. 63A). Mantle component of locking apparatus low, slightly sinusoidal oblique ridge (Fig. 63B); length ~7% ML, maximum width ~1.5% ML. Nuchal cartilage spatulate, becoming increasingly rounded anteriorly through ontogeny (Fig. 63C, D); broad medial ridge with thin medial groove, flanked by shallow grooves broadest anteriorly;

Table 19. Measurements (mm) of *Octopoteuthis* sp. Giant Atlantic nov. Mean indices were calculated from specimens ML >47 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	USNM 1283027	NHMUK 20130455	USNM 730685	Mean index	NHMUK 20150459
Type status	Holotype	None	None		None
Sex	♂	♀	♀		♂
DML	246	467	452		47
MW	75	215	170	38	25
FL	205	407	330	81	39
FW	223	472	408	94	74
HL	64	135	105	26	18.6
HW	60	120*	103	24	17.6
Side	L	R	R		L
AL I	209	251*	383*		29*(R)
AL II	246(R)	491	418*	103	40*
AL III	203*	448	342*		41*
AL IV	191*	319*	327*		30*
AH	34, 33	*, *			
TL					3.3

* indicates damaged character, not used to calculate indices.

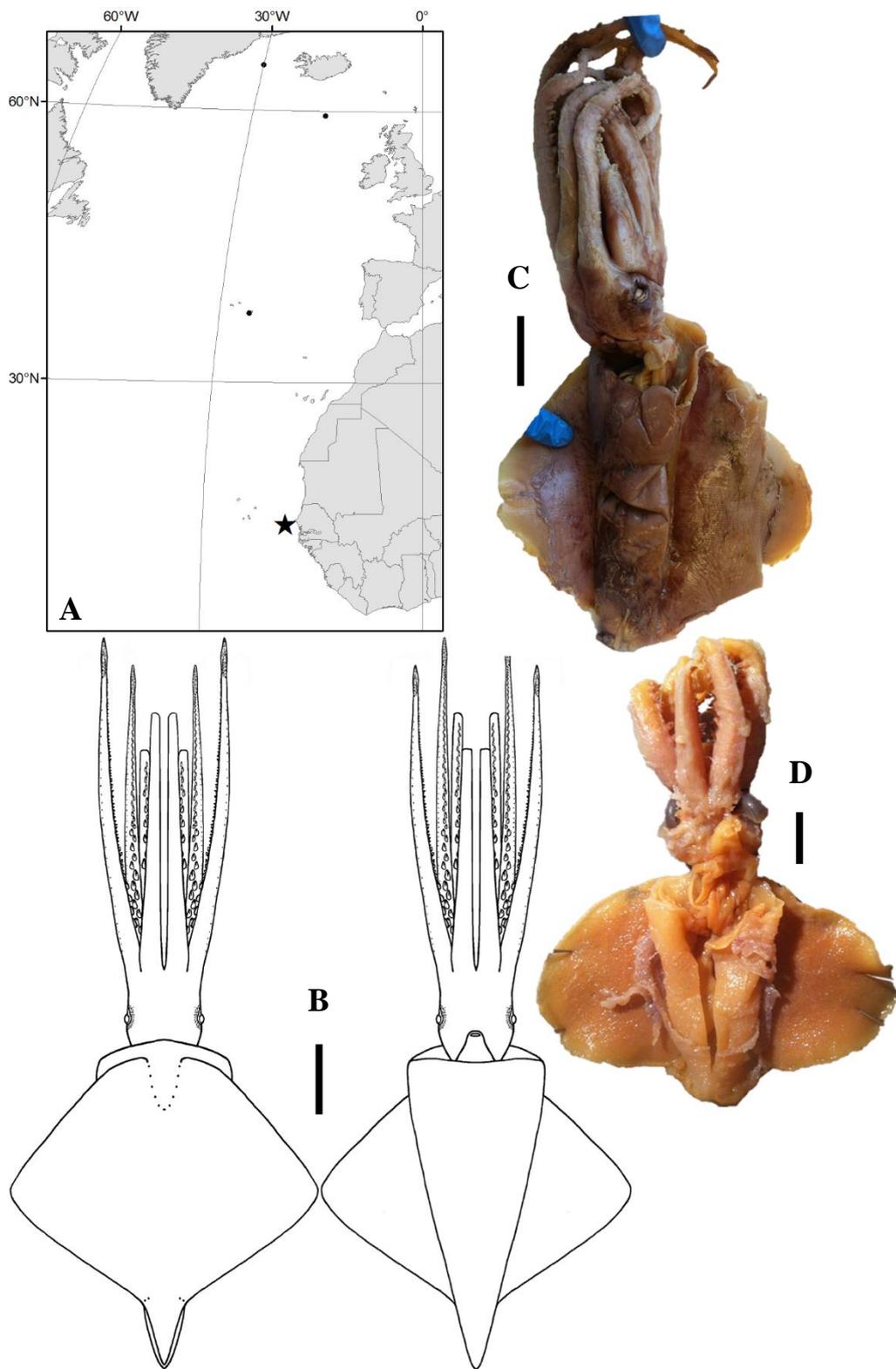


Fig. 62—*Octopoteuthis* sp. Giant Atlantic nov. A) Distribution (star indicates type locality); B) adult; C) subadult (USNM 1283027, holotype, ♂, ML 246 mm); D) post-larva (NHMUK 20150459, ♂, ML 47 mm). Scale bars = B) 100 mm; C) 50 mm; D) 10 mm.

length ~11% ML, maximum width ~5% ML. Buccal connectives paired on Arms I, occasionally dorsal taller than ventral; Arms II with broad dorsal connective only, ventral protective membrane attaches basally to Arm III; Arms III and IV with broad ventral connective. Six pores in buccal membrane: one between connectives of Arms I, large one between Arms II and III, small one between Arms III and IV. Olfactory papillae short (height ~4% HL), elliptical (diameter ~3% HL). External gelatinous tissue firm.

Two adults with four intact arms, comprising one Arm I, two Arms II, one Arm III; robust, Arm I length 85% ML, Arms II length ~103% ML, Arm III length 96% ML; trapezoidal in cross-section; with 32 to 35 pairs of hooks in thick fleshy sheaths; without suckers distally. Arms taper gradually to tips, from ~7% AL at base (depth ~8% AL) to

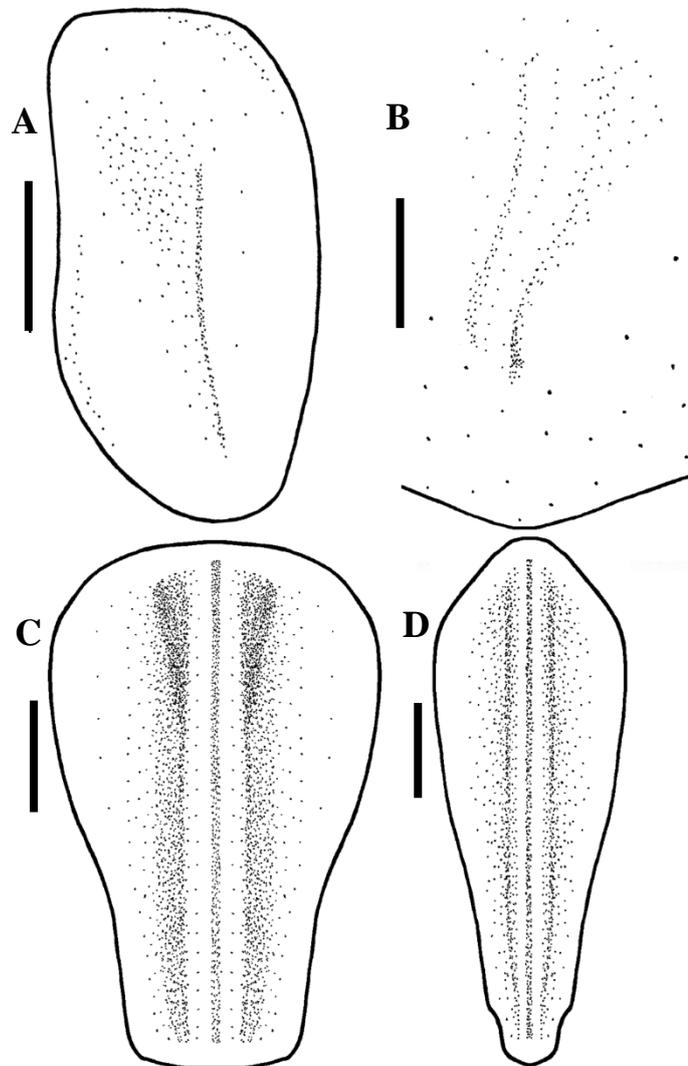


Fig. 63—*Octopoteuthis* sp. Giant Atlantic nov. A–C) USNM 730685, ♀, ML 452 mm; D) USNM 1283027, ♂, ML 246* mm. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C, D) nuchal cartilages. Scale bars = A–C) 10 mm; D) 5 mm.

~4% at midpoint (depth ~4% AL). Arm-tip photophores occupy distal-most ~8% AL (photophore length ~8% ML); photophore continuous tapering of arm, distally tapering smoothly to tip, without bulb. Without arm base or arm series photophores. All arms with low, firm gelatinous aboral keels from base to tip; depth ~50% arm depth at base, ~30% arm depth at midpoint. Arms IV without aboral pigmented banding.

Arm hooks robust (Fig. 64); largest in pairs 4–6 of Arms I and II, decreasing gradually in size distally, slight decrease in size proximally. Main cusp long, smoothly curved; typically with single dominant ridge along lateral surface; maintain aboral breadth along junction with base, broadening basally; inner angle 90–100°; aperture broad, open, oval. Accessory claws very prominent, curved. Hooks with aboral hood into which tissue from sheath inserts; hood apical, aboral on main cusp; basal margin of hood concave. Hook base crenulated, most prominent oral-laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (width and breadth). Arm suckers absent.

Tentacles absent, traces remain in post-larvae (see below).

Without bioluminescent structure associated with ink sac area. *Recti abdominis* muscles and rectum morphology as in *O. sp. Giant Pacific* nov. (Fig. 56E). Anal flap length ~0.8% ML. Ventral visceral mesentery pore diameter ~0.5% ML. Gills robust; length ~20% ML, with 27–33 lamellae.

Lateral profile of lower beak (14.25–20.91 mm LRL; Figs 65A–D) slightly deeper than long, with distal wing tips extending beyond rostral tip by ~22% baseline; rostral tip without notch; jaw edge visible, straight until slight bend at distal ~20% of LRL, with short jaw-edge extension; jaw angle 90°, obscured by low, rounded wing fold; depth anterior to jaw equal to or greater than posterior. Hood off crest, length ~29% baseline, with shallow hood groove in line with underlying lateral wall fold. Crest discrete, lateral wall between crest and fold fully pigmented at all sizes; length ~59% baseline; tip free, with concave notch between free tip and lateral wall ridge; sloped in straight line. Lateral wall with straight, narrow, rounded folds, produced laterally in cross-section, only slightly increasing in breadth posteriorly; produced into shelf along anterior ~50% of hood length; posterior lateral wall margin straight; free corner beyond crest tip; crest, lateral wall fold (and distinct band directly dorsal to fold) more darkly pigmented than

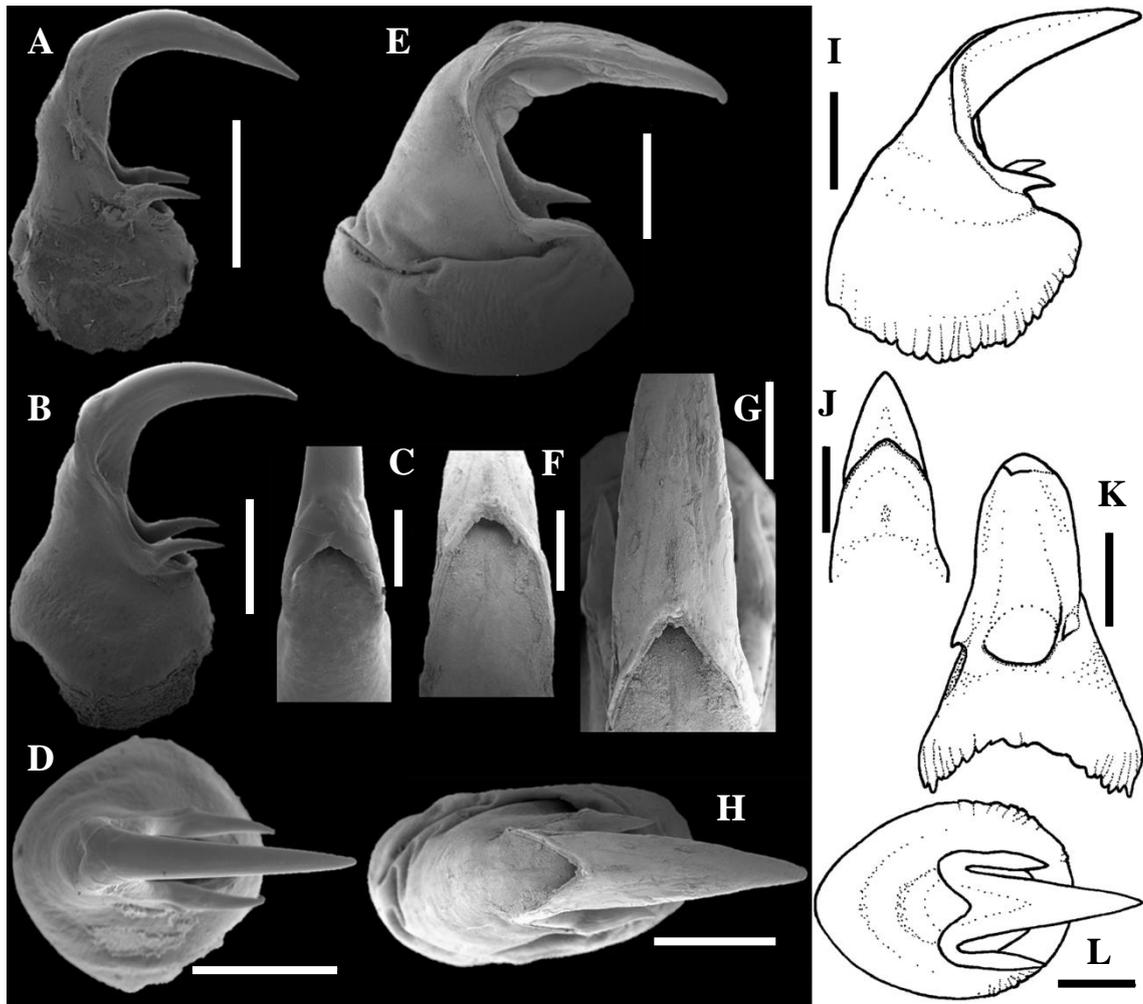


Fig. 64—*Octopoteuthis* sp. Giant Atlantic nov. armature. A–D) NHMUK 20150459, ♂, ML 47 mm; E–H) NHMUK 20130455, ♀, ML 467 mm; I–L) USNM 730685, ♀, ML 452 mm. A) 11D hook, Arm IIII; B–D) 4V hook, Arm IIL: (B) lateral profile, (C) aboral, (D) apical; E–H) 12V hook, Arm IIL: (E) lateral profile, (F) aboral, (G, H) apical); I–L) 5D hook, Arm IR: (I) lateral profile, (J) aboral, (K) oral, (L) apical. Scale bars = A, B, D) 0.5 mm; C) 0.2 mm; E, H–L) 2 mm; F, G) 1 mm.

remaining wall, especially anteriorly. Wings broaden distally, greatest width ~228% that at jaw angle, length ~91% LRL, with substantial cartilaginous pad. Ventral view with broad, ‘V’-shaped notch in hood; free corners level with medial ~20% of wing breadth. Wings of smallest beak (LRL 14.25 mm) incompletely pigmented, with small lateral patches only (Fig. 65D); largest beak (LRL 20.91 mm) with continuous pigmentation laterally along wing to distal and dorsal margin, region underlying cartilaginous pad not pigmented.

Lateral profile of upper beak (15.53–20.70 mm URL; Figs 65E, F) longer than deep, maximum depth ~47% of length. Rostrum long, ~40% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~80°; ridge of cartilage present along shoulder;

oral shoulder margin, weakly scalloped. Hood long (length ~80% UBL), moderately tall (height ~19% UBL); junction of hood and free shoulder slightly concave. Lateral walls rectangular, maximum depth in posterior quarter, posterior margin straight; lateral surface smooth. Dorsal view with posterior margin of hood straight, posterior margin of crest and crest pigmentation straight to very slightly concave. Smallest beak (URL 15.51 mm) with dorso-posterior half pigmented, antero-ventral half and free shoulder unpigmented; largest beak (URL 20.70 mm) lateral walls fully pigmented, free shoulder incompletely pigmented.

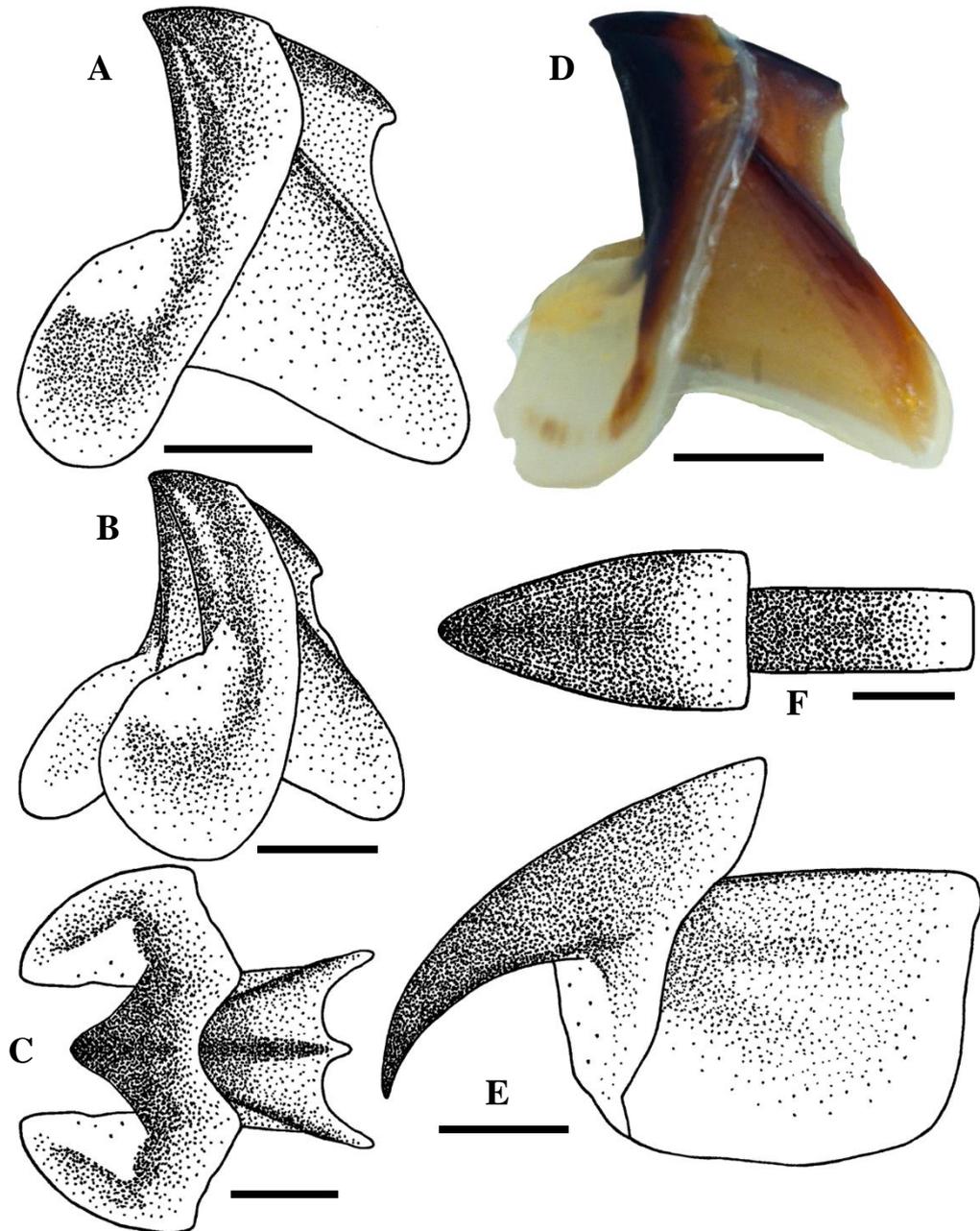


Fig. 65—*Octopoteuthis* sp. Giant Atlantic nov. A–C, E, F) USNM 730685, ♀, ML 452 mm, LRL 20.91 mm, URL 20.70 mm; D) NHMUK 20130456, sex indet., LRL 14.25 mm. A–D) lower beak: (A, D) lateral profile, (B) oblique profile, (C) ventral view; E, F) upper beak: (E) lateral profile, (F) dorsal view. Scale bars = A–F) 10 mm.

Radula (Fig. 66A–C) with tricuspid rachidian: mesocone moderately long, broadly triangular, straight; lateral cusps as broad corners (~40% mesocone height); base concave. First lateral tooth bicuspid: inner cusp broadly triangular, equivalent in height to rachidian, straight, slightly medially directed; outer cusp as low point (~40% height of inner); straight; base concave. Second lateral tooth simple, triangular, ~110% height of rachidian. Marginal tooth simple, narrowly triangular, ~160% height of rachidian. Marginal plate absent, series of very low short ridges lateral to marginal tooth series. Palatine palp (Fig. 66D) with 70 triangular teeth, conical to narrowly triangular; each 100–160% rachidian height, smallest orally and posteriorly; oral end of palp rounded, recessed relative to majority of tooth-bearing length; small thin teeth along oral slope up to tooth-bearing surface; teeth of consistent size and shape, arranged evenly along surface, in roughly five series.

Gladius unexamined due to scarcity of specimens.

Colour (preserved) purple, maroon, or pink over all external body surfaces where epidermis remains intact; circumference of eye lid, arm tips over photophores, tail tip dark purple; external gelatinous layer of arms and ventral mantle pigmented. Inner mantle surface pigmented along anterior margin in large individuals.

Single post-larval specimen (ML 47 mm, Fig. 62D) as above, with the following exceptions. Mantle conical, width 53% ML; tail broad, short, length 20% ML. Fins very broad, width 157% ML; anterior fin margin at 7% ML; breadth of fin continuation along tail 6% ML. Head length 40% ML, width 37% ML; eyes large, 49% HL (19% ML). Funnel long, length 31% ML; funnel component of locking apparatus length 12% ML, width 6% ML; mantle component length 11% ML, width 2% ML; nuchal cartilage length 17% ML, width 6% ML, on cartilaginous pad equivalent in length, width 14% ML. Arm hooks thinner in appearance than in adults (Fig. 64A–D), with longer accessory claws relative to adults; hook hood visible. Tentacles atrophying, length 7% ML; tentacle bases thin, width 7% thickness of adjacent Arm III base, tissue insubstantial; without distinct structure, no clubs or suckers intact; blunt terminally, only slight taper at distal tip, with sparse chromatophores.

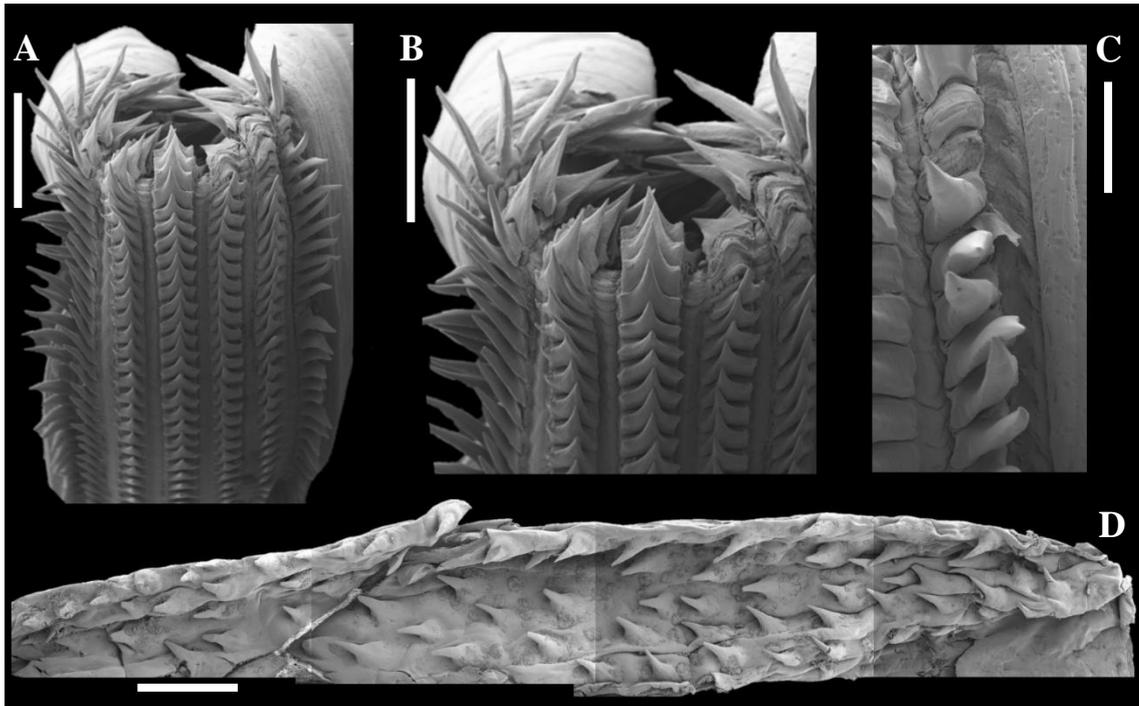


Fig. 65—*Octopoteuthis* sp. Giant Atlantic nov. A–D) NHMUK 20130455, ♀, ML 467 mm. A–C) Radula: (A) whole, (B) bending plane, (C) lateral margin; D) palatine palp. Scale bars = A, D) 2 mm; B) 1 mm; C) 0.5 mm.

Biology. No mature specimens among available material. Largest male (USNM 1283027, ML 246* mm) maturing, largest female (NHMUL 20130455, ML 467 mm) missing viscera. Second large female (USNM 730685, ♀, ML 452 mm) either maturing or resting: nidamental gland length 16% ML, width 2%; oviducal glands extend 4% ML anterior to gill artery, width 1% ML; ovary length 3% ML, width 1.5% ML, composed of single central core with short lateral strings of oocytes. No specimens with implanted spermtangia.

Values of LRL, URL, ML, and body mass ($n = 4$) were pooled with those of *O.* sp. Giant Pacific nov. ($n = 6$) to calculate combined regressions from a greater sample size. Relationships were best described by exponential equations for LRL values, and power equations for URL against ML and body mass (Fig. 67). Relationships for LRL values fit the data well ($R^2 > 0.8$), while those for URL had poor fit ($R^2 < 0.5$), likely a result of the small sample size ($n = 5$). Previous genus regressions consistently underestimated body size for all relationships (Clarke 1980; Lu & Ickeringill 2002).

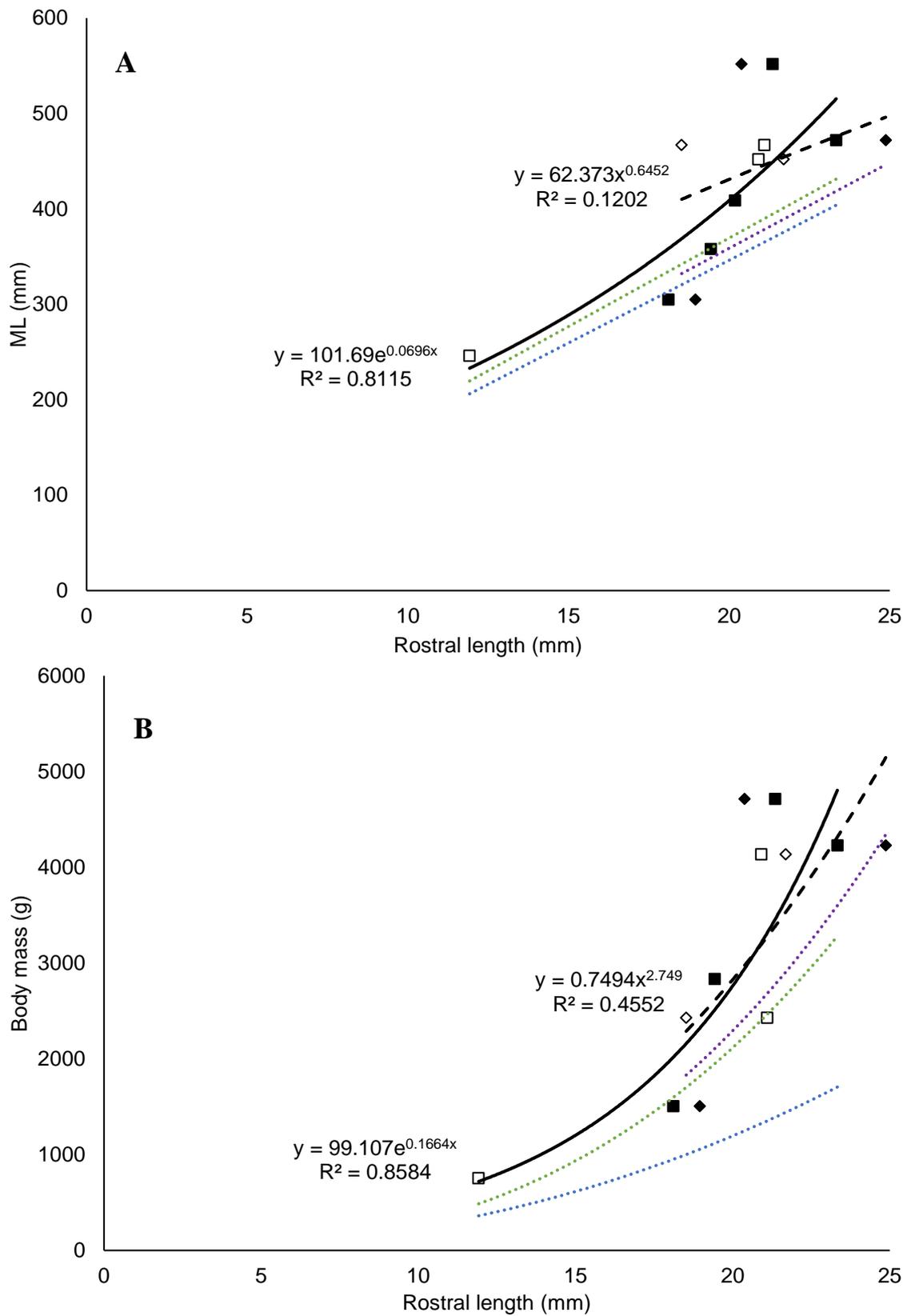


Fig. 67—Pooled regressions for *Octopoteuthis* sp. Giant Pacific nov. (solid) and *O.* sp. Giant Atlantic nov. (hollow) specimens, of lower (LRL; squares) and upper rostral length (URL; diamonds) against (A) dorsal mantle length (ML) and (B) body mass. Models of best fit (greatest R^2 value) are plotted in black (LRL: solid, URL: dashed) against genus regressions of Clarke (1980; LRL: blue) and Lu and Ickeringill (2002; LRL: green, URL: purple).

Remarks. *Octopoteuthis* sp. Giant Atlantic nov. is most similar morphologically to *O.* sp. Giant Pacific nov., being similarly different from all small-bodied *Octopoteuthis* species as described previously (see *O.* sp. Giant Pacific nov. Remarks). Although novel, the diagnostic character (basal-most arm hook pattern) separating the two Giant species was otherwise remarkably constant among octopoteuthids (as VVDD), and did not vary among specimens from different life stages, sexes, species, species groups, or genera (outside the two possible exceptions mentioned for *O.* sp. Giant Pacific nov.). Thus, the clear distinction in basal arm hook pattern observed in Giant *Octopoteuthis* specimens from the Atlantic is considered of sufficient taxonomic significance to support the designation of a new species. Preliminary examinations of other oegopsid families (Mastigoteuthidae, Pholidoteuthidae) identified considerable variability in this character within species and even individuals (left side vs right side), and its taxonomic importance outside the Octopoteuthidae requires further work.

The two available lower beaks of *O.* sp. Giant Atlantic nov. were generally shorter than those of *O.* sp. Giant Pacific nov. (whose lateral walls extend further postero-ventrally) and had broader wings with greater intact cartilaginous pads. The lower beak of NHMUK 20130455 (ML 467 mm) could not be located during this study, but it appears to have similarly long lateral walls as in *O.* sp. Giant Pacific nov., as well as has the broad wings and substantial intact cartilaginous pads observed here for *O.* sp. Giant Atlantic nov. (as imaged in Clarke 1986). The latter character is noteworthy as it tends to decrease in prominence through ontogeny in octopoteuthids, and beaks from large adults (ML >450 mm) of both species were available. Thus, wing morphology may prove useful in separating these closely related species, although current sample sizes are too low. Alternatively, *O.* sp. Giant Atlantic nov. may achieve greater sizes or have a slower development than *O.* sp. Giant Pacific nov.; specimens of *O.* sp. Giant Atlantic nov. are known from higher latitudes than *O.* sp. Giant Pacific nov.

Subadult and adult specimens of *O.* sp. Giant Atlantic nov. were also characterised by a dense, opaque (whitish) outer gelatinous layer (with the exception of NHMUK 20130455) compared to the insubstantial translucent layer found on even large specimens of small-bodied *Octopoteuthis* species. Specimens of *O.* sp. Giant Pacific nov. from Australasia did not present in such a manner, although the specimen from Hawaii retained an intact, dense gelatinous layer comparable to those of *O.* sp. Giant Atlantic nov. This could be an artifact of collection or preservation history: specimens

of both species that retained a dense gelatinous layer were housed at the USNM, while those at other institutions (NHMUK, NIWA, NMNZ, MV) did not.

The presence of the species in high north Atlantic waters, around Iceland, established by one whole specimen and one arm crown, is further supported by the report of 67 large (LRL 12–24 mm) lower beaks recovered from five sperm whales caught off Iceland (Clarke & MacLeod 1976). These beaks (not examined herein) had minimal or no pigmentation on wings, or the wings were missing (inferred to have been unpigmented and quickly digested) and matched the morphology of NHMUK 20130455. The species presence in the Azores, established by NHMUK 20150459, is additionally supported by 16 lower beaks of ‘giant’ *Octopoteuthis* morphology recovered from whale stomachs and reported previously as *Octopoteuthis* sp. G (Clarke *et al.* 1993). These lots were geographically attributed to *O.* sp. Giant Atlantic nov., and were, thus, included under Comparative Material. A single lot of two ‘giant’ beaks from Donkergat (west coast South Africa; NHMUK 20160143) was also included as Comparative Material (see Remarks, *O.* sp. Giant Pacific nov.).

If truly an *Octopoteuthis*, the large specimen (NMSZ 1999158.105, sex unknown, ML 368 mm) reported by Collins *et al.* (2001) from the Rockall Trough, northwest of Ireland, likely constitutes a sixth specimen of this species.

5.2. *Taningia* Joubin, 1931

Type species. *Taningia danae*, Joubin, 1931, by monotypy.

Diagnosis. Arms II terminating in a single, large, lidded photophore (Fig. 68A–C); arm length 25–58% ML, Arms II shortest (6–7% ML shorter than next shortest arm pair); buccal connectives single, broad, formula DDVV (Fig. 68D); mantle cartilage broad, blunt anteriorly.

Description. Large-bodied squids (maximum observed ML 1310* mm in *T. danae*) with low gelatinous keel along posterior ventral mantle midline. Fins rhombic, length 65–85% ML, width 80–110% ML; greatest width attained at ~40% ML; anterior fin margins slightly convex, posterior margins straight to slightly concave. Arms robust, trapezoidal in cross-section narrowing orally; Arms II and III generally shorter than I and IV. Arm hooks with aboral hood on main cusp (Fig. 68E); accessory claws present on hooks along at least distal half of arm length; basal-most hook pattern VVDD (Fig. 68D). Hook series extend to tip (no distal suckers), in all post-larval stages. Tentacles completely lost by ML 60 mm. Large specimens with seven fleshy nuchal pads extending posteriorly from head between eye orbit and buccal collar (Fig. 68E, F); largest rectangular, positioned along dorsal mid-line; three smaller spatulate pads present along each side of head, decreasing in size ventrally, with ventral-most pad on each side adjacent to funnel. Lower beak depth between jaw angle and baseline greater than or equal to half of overall depth.

Remarks. This genus has been considered monotypic and cosmopolitan since its description, with any large squid bearing the characteristic Arm II photophores attributed to *T. danae*. However, the present morphologic and genetic review has identified four additional species, at least some of which appear to have more discrete geographic distributions. At present, *T. fimbria* sp. nov. (circumglobal between 30° and 50°S) and *T. rubea* sp. nov. (from the western north Pacific) can be reliably differentiated from *T. danae* (see descriptions below); however, additional examinations and material remain necessary to morphologically and geographically characterise *Taningia* spp. IV and V.

In *Taningia* species, the arm hook hood is more developed than among Giant *Octopoteuthis* species. It begins lower on the aboral main cusp, and its basal margin is typically a single smooth surface (Fig. 68E). In Giant *Octopoteuthis* species, the hood is produced by the fusion of two separate lateral flanges, resulting in a more apical position, a more distinct 'V' shape, and often with visible ridges along the apical cusp surface (*e.g.*, Fig. 59H).

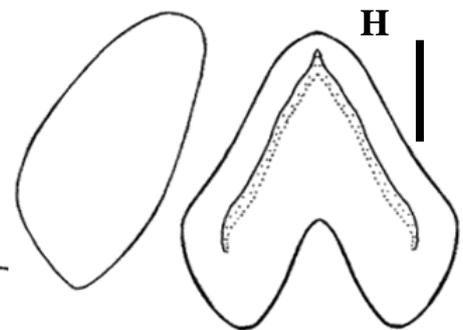
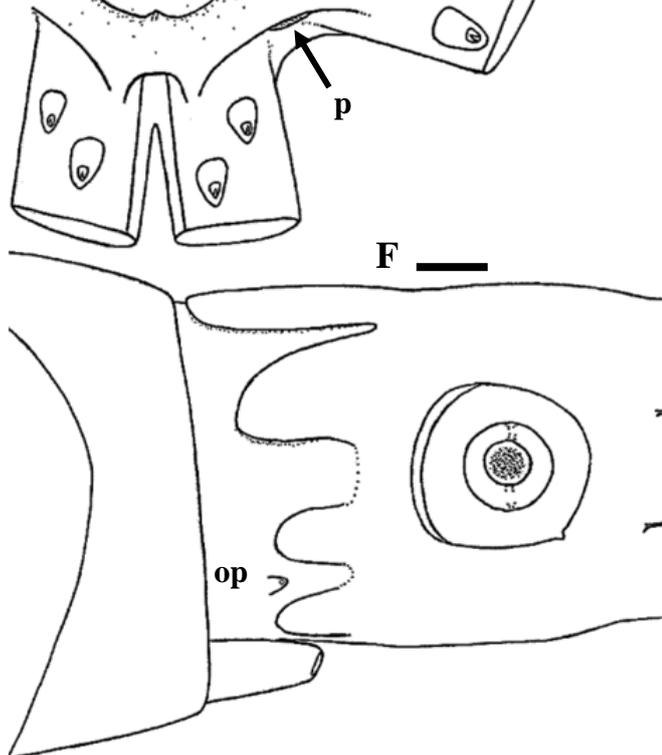
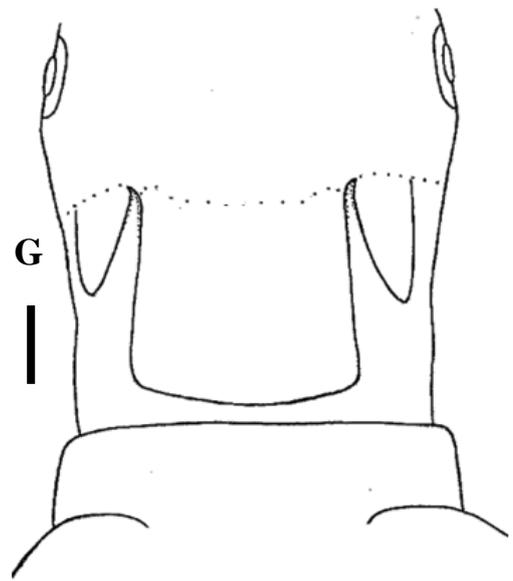
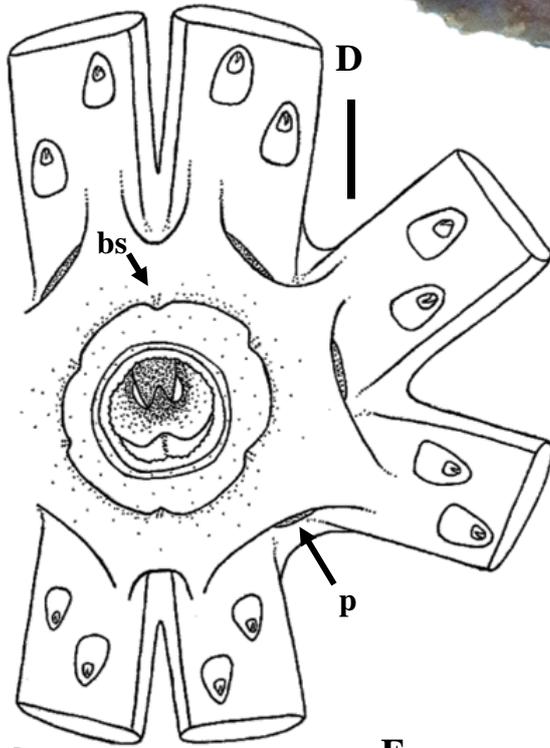
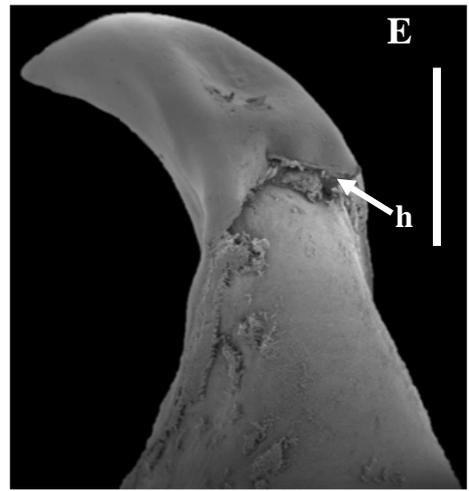
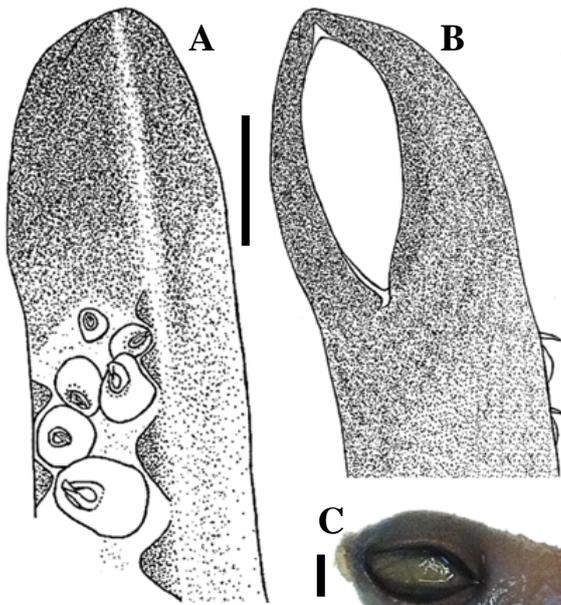
The nuchal pads described above are equivalent to the “nuchal lobes” of Clarke (1967); however, he counted only six in total (the 3 lateral pairs) and made no mention of the large dorsal pad.

Joubin (1931) dedicated his new genus to Vedel Tåning, an assistant to Professor Schmidt at Carlsberg Laboratory, Copenhagen. Roper and Vecchione (1993) raised the issue of Joubin’s incorrect transliteration of Tåning to *Taningia*, the proper transliteration of “å” being “aa” (resulting in *Taaningia*). They considered the repeated use of the incorrect spelling evidence of Joubin’s intent, and not an inadvertent error, and retained his original spelling in accordance with Article 32 of the International Code of Zoological Nomenclature. This decision is supported herein.

Table 20. Taxonomically significant indices for *Taningia* species, by life stage (subadult to adult ML >~110 mm, post-larva ML <~60 mm). Post-larval *T. fimbria* and adult *T. sp. IV* were not available during this study.

Taxon, life stage	Arm length	Tail length	Fin width
<i>T. danae</i>			
Adult	25–38–46% ML	7–11–15% ML	100–105–113% ML
Post-larva	30–41–51% ML; V ≈ D	5–10–16% ML	119–144–171% ML
<i>T. fimbria</i>			
Adult	26–41–56% ML	14–20–25% ML	75–83–91% ML
<i>T. rubea</i>			
Adult	26–34–40% ML	~17% ML	80–83–90% ML
Post-larva	60–70% ML; V ≈ D	Unknown	172–188–214% ML
<i>T. sp. IV</i>			
Post-larva	40–53–67%; V > D	~10% ML	166, 210% ML

Fig. 68 (following page)—*Taningia* general morphology. A, B) *T. danae*, NIWA 92142, ♀, fresh ML 900 mm; C) *T. danae*, NHMUK 20160098, ♀, ML 138 mm; D) *T. fimbria* sp. nov., NIWA 71439, ♂, ML 296* mm; E) *T. danae*, NIWA 76658, ♂, ML 260 mm; F, G) *T. fimbria* sp. nov., NIWA 71438, paratype, ♀, ML 730 mm; H) *T. danae*, NMNZ M.67249, ♀, ML 48 mm. A–C) Arm II photophore: (A) oral view, (B, C) dorso-lateral view; D) oral surface illustrating buccal connective and basal hook pattern, pores (p), buccal supports (bs) as established for *T. danae* and *T. fimbria* sp. nov. (unverified in other spp.); E) aboral hood (h) of 4V hook, Arm IVR; F, G) nuchal pads: (F) lateral view with olfactory papilla (op), (G) dorsal view; H) funnel organ. Scale bars = A, B) 20 mm; C) 2 mm; D) 10 mm; E) 1 mm; F, G) 20 mm; H) 2 mm.



5.2.1. *Taningia danae* Joubin, 1931 (Tables 20, 21, 25, Figs 3D, 69A–C, E, H, 70–74)
Cucioeteuthis unguiculata (not Molina, 1782) — Joubin (1898): 150–158, Fig. 1, (1900):
 51–57, Pl. 10 Figs 11, 12, Pl. 13 Figs 1, 2, Pl. 14 Fig. 6, Pl. 15 Figs 11–13;
 Clarke (1956): 258, Pl. 2 Figs 3, 6, 7; Rees & Maul (1956): 265; Clarke (1962a):
 175–177, Fig. 2.
Architeuthis sp. (not Steenstrup, 1857) — Joubin (1900): Pl. 14 Fig. 2.
Octopoteuthis (not Rüppell, 1844) — Chun (1910): 144–145 (specimen from station
 271), Pl. 17 Figs 1, 2, 7, 8, 10.
Cucioeteuthis (not Steenstrup, 1882) — Clarke (1962b): Pl. 17 Figs A–C.
Octopodoteuthis persica Naef, 1923: 337.
Taningia danae Joubin, 1931: 181–185, Figs 11–16; Clarke (1967) (*partim*): Table 1
 (specimens 1, 2, 13, 14 only), Figs 2 (specimens 1, 14 only), 3–6 (not 6B), 8A,
 8D, 10, 11A; Vecchione & Roper (1993): 444, Figs 1–3; Lu & Ickeringill
 (2002): Fig. 34; Escáñez & Perales-Raya (2017): 56–57, Figs 1–3, Table 1.
 Not *Taningia danae* Clarke (1967; specimens 4, 8, 10) (= *T. fimbria* sp. nov.); Watanabe
et al. (2006), Kubodera (2007), Kubodera *et al.* (2007) (= *T. rubea* sp. nov.).

Type material (1 specimen). **ZMUC CEP-90**, Holotype, sex indet., ML 38 mm,
 14°52'N, 28°04'W, 300 m, 05/11/1921, RV *Dana*, stn 1161.

Additional material examined (56 specimens). **USNM 1100340**, ♀, ML 58 mm,
 39°55.62'N, 67°25.22'W, Bear Seamount, off Massachusetts, USA, 04/12/2000, RV
Delaware II, stn 9, cruise 11, Bear Seamount Expedition; **NHMUK 20160098**, ♀, ML
 138 mm, 37°35.5'N, 25°22'W, Azores, 0–400 m, 17/10/1966, RRS *Discovery*, stn 6117,
 EMT; **NHMUK 20160129**, sex indet., ML 41 mm, 37°04.8'N, 19°34.1'W, NE Atlantic,
 70–300 m, 08/06/1984, RRS *Discovery*, stn 11130#1, RMT 8 CCE; **USNM 815476**, sex
 indet., ML 48 mm, 34°48'N, 20°36'W, Madeira Islands, 225–230 m, 24/06/1969, RV
Atlantis II, RHB-1914, 3 m IKMWT, R.H. Backus; **NHMUK 20150464**, ♂, ML 58
 mm, 34°17.5'N, 7°59.4'W, eastern central Atlantic, 0–1180 m, 17/11/1966, RRS
Discovery, stn 6184, 1 KMT; **USNM 817210**, sex indet., ML 20.7 mm, 33°06'N,
 17°46.2'W, Madeira Islands, 160–170 m, 22/06/1969, RV *Atlantis II*, RHB-1903, 3 m
 IKMWT, R.H. Backus; **USNM 728849**, sex indet., ML 24 mm, 32°16.8'N, 64°16.8'W,
 Ocean Acre Area (OAA), Bermuda, 0–600 m, 24/08/1971, RV *Delaware II*, stn 85-N,
 cruise 12, 1400 Engel trawl, USNOAP; **USNM 728039**, sex indet., ML 13.5 mm,
 32°10.2'N, 63°58.8'W, Bermuda (OAA), 282–298m, 04/06/1972, RV *Sands*, stn 2-C,

cruise 14, 3 m IKMWT, USNOAP; **USNM 726981**, sex NM, ML NM, 32°04.2'N, 64°15'W, Bermuda (OAA), 0–180 m, 17/03/1970, RV *Sands*, stn 3-N, cruise 9, 3 m IKMWT, USNOAP; **USNM 726984**, sex indet., ML 13.8 mm, 32°00'N, 64°22.8'W, Bermuda (OAA), 175 m, 04/09/1968, RV *Sands*, stn 5-C, cruise 4, 3 m IKMWT, USNOAP; **USNM 726980**, sex indet., ML 8.9 mm, 31°55.8'N, 64°25.2'W, Bermuda (OAA), 55 m, 03/06/1970, RV *Sands*, stn 9-A, cruise 10, 3 m IKMWT, USNOAP; **USNM 726982**, 3 specimens, sex NM, ML NM, 31°54'N, 64°16.8'W, Bermuda (OAA), 0–140 m, 17/03/1970, RV *Sands*, stn 5-N, cruise 9, 3 m IKMWT, USNOAP; **NHMUK 20160128**, sex indet., ML 17.4 mm, 29°58.1'N, 23°00.9'W, eastern central Atlantic, 205–300 m, 03/04/1972, RRS *Discovery*, stn 7856#21, RMT; **USNM 1179460**, sex indet., ML 37* mm, 28°36.54'N, 87°56.04'W, eastern Gulf of Mexico, off Louisiana, USA, 27/02/2010, 2210–2350 m, RV *Pisces*, stn 24, SWAPS, cruise 2, Aleutian wing trawl, NOAA, MMS Collections, BOEM-SWAPS/2010/PC/T24; **USNM 1179378**, 3 arm pieces, 27°33.15'N, 86°46.74'W, eastern Gulf of Mexico, 23/02/2010, 3135–3180 m, RV *Pisces*, stn 16, SWAPS, cruise 2, Aleutian wing trawl, NOAA, MMS Collections, BOEM-SWAPS/2010/PC/T16; **USNM 1179761**, ♂, ML 58* mm, 26°46.61'N, 91°04.01'W, off Louisiana, 11/08/2011, RV *Gordon Gunter*, stn 22, cruise GG0903, SWAPS, 174 ft MWT, NOAA-NMFS-SEFSC-Mississippi Laboratories, MMS Collections, MMS-SWAPS/2009/GG/022; **ZMH 11169**, sex indet., ML 83 mm, 26°20'N, 19°21'W, 200–220 m, 22/01/1968, RV *Walther Herwig I*, stn 8, cruise 23, Schulz; **USNM 885291**, ♀, ML 79 mm, 17°24'N, 22°57'W, 293–305 m, 17/04/1971, RV *Walther Herwig*, 498-II-71, 1600 mesh Engel trawl; **USNM 816681**, ♀, ML 115 mm, 10°52.2'N, 22°09'W, 592–608 m, 15/04/1971, RV *Walther Herwig*, 490-II-71, 1600 mesh Engel trawl; **USNM 885297**, ♀, ML 68 mm, 10°49.8'N, 22°07'48"W, 100–111 m, 15/04/1971, RV *Walther Herwig*, 490-I-71, 1600 mesh Engel trawl; **ZMH 11167**, sex indet., ML 72* mm, 10°46'N, 23°54'W, 200–300 m, 16/05/1966, RV *Walther Herwig*, stn 182, cruise 15, Schulz; **ZMUC stn 3894I**, ♀, ML 31.7 mm, 6°38.5'N, 92°44'E, 600 m, 07/11/1929, 04:00, stn 3894I, S. 200; **NHMUK 20160127**, sex indet., ML 27.4 mm, 2°43.5'S, 00°56.5'W, eastern central Atlantic, 125–175 m, 16/08/1927, RRS *Discovery*, stn 285, N 450; **NSMT Mo85683**, sex indet., ML 33* mm, 8°06'S, 88°41'E, 25/07/1975, sample no. CI 139; **NSMT Mo85685**, 1 head, HL 13* mm, 8°27.5'S, 87°05.3'E, 04/08/1975, sample no. CI 74~81; **NSMT Mo85686**, 1 head, HL 16* mm, 9°06.4'S, 84°00'E, 27/07/1975, sample no. CI 114; **NSMT Mo85684**, 1 head, HL 15* mm, 9°18'S, 55°53'E, 23/10/1975, sample no. WI 164; **NSMT Mo85687**, 1 head, HL 19* mm, 9°21'S, 81°42'E, 06/08/1975, sample no. CI 111; **USNM 816680**,

♂, ML 109 mm, 10°57'S, 11°19.8'W, 1800–1900 m, 07/04/1971, RV *Walther Herwig*, 459-71, 1600 mesh Engel trawl; **ZMH 11188**, ♂, ML 213* mm, 28°40'S, 47°12'W, S Brazil, 850 m, 13/03/1968, RV *Walther Herwig I*, stn 121, cruise 23, Schulz; **MV F160011**, sex indet. (arm crown only), LRL 11.70 mm, 28°51'S, 102°46.8'E, Western Australia, Indian Ocean, 20/10/1992, FV *Shoei Maru 52*; **NMNZ M.305062**, ♀, ML 1310* mm, 34°34'S, 175°16'E, 32 km N of Knights Terraces, NE of Poor Knights Islands, North Island, New Zealand, 31/01/2012, G. James; **NMNZ M.174308**, ♀, ML 1074* mm, 35°00'S, 165°00'E, New Zealand, 940 m, 00/04/2004, FV *Atlantic Elizabeth*, trawl, L. Elkington; **MV F160003**, sex indet., ML 5.7 mm, 35°13'S, 152°16'E, Tasman Sea, New South Wales, Australia, 194.1 m, 00/02/1980, SP02/80 15, trawl; **NIWA 71442**, ♀ (head only), HL 235 mm, 37°26'S, 168°45'E, 998 m, 11/03/2000, 1331/66, Z10242; **MV F80327**, '♀', 'ML 1260 mm', 38°37'S, 141°24'E, off Portland, Victoria, Australia, 393 m, 14/04/1989, FV *Craigmin*, G. Canute; **ZMH 73901**, ♀, ML 59 mm, 38°39.03'S, 52°09'W, Argentina, 05/01/1971, RV *Walther Herwig*, stn 350, cruise 36, Schulz; **NIWA 76658**, ♂, ML 260 mm, 38°49.53'S, 178°34.33'E, 756 m, 25/03/2010, TAN1003/61, BTT; **NMNZ M.067249**, ♀, ML 48 mm, 39°07.7'S, 178°57.2'E, SE of Gisborne, North Island, New Zealand, 200 m, bottom depth 1700 m, 13/01/1980, RV *James Cook*, J01/53/80, MWT; **USNM 817411**, ♀, ML 31 mm, 39°15'S, 179°34.8'W, North Island, New Zealand, 2178–2489 m, 30/11/1964, RV *Eltanin*, stn 1402, cruise 15, 3 m IKMWT, University of Southern California, USAP project; **NIWA 76663**, ♂, fresh ML 199 mm, 39°24.9'S, 178°27.53'E, 1265 m, 25/03/2010, TAN1003/57, BTT; **NIWA 84374**, ♀, ML 31.5 mm, 40°05'S, 179°20'W, 20–100 m over 3367 m, 01/02/1998, RV *Tangaroa*, TAN9802/133, Z9301 B12, FMMWT, NIWA; **USNM 885296**, ♀, ML 22 mm, 40°18'S, 39°04.2'W, 760–800 m, 08/03/1971, RV *Walther Herwig*, 363-III-71, 1600 mesh Engel trawl; **NIWA TRIP1795/81**, ♀, ML 395* mm, 40°53'S, 171°09'E, 08/08/2003, TRIP1795/81, SOP & J. Houston; **NMNZ M.118403**, sex indet. (head only), HL 130 mm, 41°05'S, 170°48'E, NW of Cape Foulwind, South Island, New Zealand, 355–510 m, 01/08/1994, FV *Nikon Karpenko*, coll. S. Tong; **NMNZ M.127087**, ♀ (head only), HL NM, 42°13.7'S, 170°26.3'E, W of Punakaiki, South Island, New Zealand, 516 m, 31/07/1990, FV *Akebono Maru 77*, 414/88, G. Williams & A. Freeman; **NIWA 62693** (beaks: NIWA 23753), ♂, ML 550 mm, 42°18'S, 170°18'E, 02/02/2000, 702–920 m, 19/07/1999, 0808–1200 hr, TRIP1248/16, MWT, SOP; **NIWA 23750**, '♂' (beaks only), LRL 17.14 mm, 42°25.08'S, 170°28.03'E; **NIWA 75790**, sex indet. (head only), fresh HL 170 mm, 42°30'S, 170°24'E, 497–550 m, 06/07/2008, 1027–1620 hr, TRIP2659/43, MWT, SOP

& Marli; **NMNZ M.183012**, ♂ (head only), HL 143* mm, 42°33.6'S, 170°24.6'E, New Zealand, 500–550 m, 08/08/2005, FV *Ivan Golubets*, 2126/153, R. Cropp; **NMNZ M.118355**, ♀ (head only), HL 134* mm, 43°07.8'S, 174°15.7'W, off Chatham Islands, New Zealand, 799 m, 12/07/1994, RV *Tangaroa*, TAN9406/299; **NMNZ M.318205**, ♀, ML 882 mm, 43°53.9'S, 175°39.2'E, E of Banks Peninsula, 474 m, 27/06/2001, 1520/92, Z10865, SOP; **NMNZ M.127086**, ♂, ML 680* mm, 44°07.3'S, 177°47.2'W, Chatham Rise, New Zealand, 480 m, 03/01/1992, RV *Tangaroa*, TAN9106/37; **NIWA 95932**, sex indet. (beaks only), LRL 18.48 mm, 46°37.2'S, 166°26.4'E, 809–815 m, 17/12/2006, TAN0617/80, BTT, NIWA; **NMNZ M.306360**, ♀, fresh ML 815* mm, 47°36.7'S, 166°26.4'E, S of Stewart Island, New Zealand, 257 m, 10/04/2011, TRIP3394/18, MWT, SOP & C. Couchman; **NMNZ M.274771**, ♀ (head only), HL NM, 49°00.5'S, 166°33.2'E, S of The Snares, New Zealand, 581–624 m, 16/12/2003, FV *Tomu Maru 86*, 1835/85, S. Artieu.

Unlocalised material examined (18 specimens). **NHMUK 20160120**, ♂, HL 206 mm, Horta, Azores, 1949, from 2nd stomach of male sperm whale, 9.9 m, 'sp. 1 whale 51', MRC Acc. No. 122; **NHMUK 20160105**, sex indet. (arm section only), length 235 mm, taken from Fuchal Bay, Madeira, 12 m, 27/08/1926, 16:00; **USNM 1179543**, ♂, ML 148* mm, Gulf of Mexico, 30/01/2010, RV *Pisces*, stn 01-test, SWAPS, cruise 1, MWT, NOAA, MMS Collections, BOEM-SWAPS/2010/PC/T01-test; **USNM 1179529**, ♂, ML 115* mm, Gulf of Mexico, 04/02/2010, RV *Pisces*, stn 54, SWAPS, cruise 1, MWT, NOAA, MMS Collections, BOEM-SWAPS/2010/PC/T54; **USNM 575748**, sex indet., ML 19.6 mm, St. Helena Island, James Bay, 17/06/1964, A. Loveridge; **NHMUK 20160110**, sex indet. (head only), HL 85 mm, Durban, 1963, unlabelled head 2254; **NHMUK 20160114**, sex indet. (head only), HL 86 mm, off coast of South Africa, MRC Acc. No. 106; **NIWA 92142**, ♀, fresh ML 900 mm, Cook Strait, New Zealand, Sealords & T. Harrison; **ZMH 11726**, ♀, ML 200 mm, Patagonia, Argentina; **NHMUK 20160115**, sex indet. (head only), HL 175 mm, MRC Acc. No. 112, '284'; **NHMUK 20160121**, sex indet. (head only), HL 135 mm, MRC Acc. No. 126; **NHMUK 20160116**, sex indet. (head only), HL 127 mm, MRC Acc. No. 81, 'ex. shower room'; **NHMUK 20160112**, sex indet. (head only), HL 124 mm, MRC Acc. No. 104; **NHMUK 20160108**, sex indet. (head only), HL 90 mm, A2510, MRC Acc. No. 50; **NHMUK 20160107**, sex indet. (arm only), AL 320 mm, 18/09/1964, from stomach of sperm whale, 446 A64, MRC Acc. No. 48; **NHMUK 20160122**, ♀ (arm crown only), LRL 19.96 mm, from stomach of sperm whale, 45'0", '488 A65', MRC Acc. No. 119;

NHMUK 20160119, sex indet. (arm crown only), LRL 16.58 mm, '68 A66'; **NHMUK 20150462**, sex indet., ML 13.6* mm, 06/10/1975, RRS *Challenger*, stn C.75/42, RMT 8+7.

Additional genetic samples (3 samples). **MNCN 239**, '♀', 'ML 1320 mm', 43°52.53'N, 05°18.73'W, Cantabrian Sea, Luarca, Asturias, Spain, 30/10/2000, ~400–600 m, *Boer*; **BAMZ 2012 280 017**, sex unknown, ML unknown, ~10 nm SW of Bermuda, near Challenger Bank, floating on surface, 25/04/2011; **TMAG E24300**, sex unknown, ML unknown, unlocalised Tasman Sea, SE coast of Australia, offshore, 00/05/2002, CSIRO.

Distribution (Fig. 69A). Cosmopolitan in temperate to tropical waters apparently excluding western North Pacific; presence in eastern Pacific uncertain (see Discussion); 0–2500 m.

Diagnosis. Single large bioluminescent patch on ventral surface of ink-sac; proximal arm hooks without accessory claws in specimens ML >150 mm; funnel component of locking apparatus blunt anteriorly; lower beak free corners spaced widely apart, posterior lateral wall margin straight, depth between jaw angle and baseline greater than half overall depth; fin width 100–113% ML; arm length 25–46% ML; Arms II with 12–14 pairs of hooks; skin and funnel aperture smooth; basal-most hooks on Arms I in males not enlarged.

Description (ML 115–1310* mm, Figs 69B–74). Mantle conical to weakly goblet-shaped; widest at anterior margin, width 25–31–35% ML; weakly muscled, dorsally reduced to thin mesentery between gladius and fin; gelatinous outer tissue layer present ventrally; tail short, blunt, length 7–11–15% ML. Fin length 63–80–86% ML, width exceptionally broad (100–105–113% ML). Anterior fin insertion depth ~14% ML, width ~19% ML.

Head square to trapezoidal, length 23–28–32% ML, width 20–26–33% ML, depth ~20% ML. Eyes large, diameter 7–13–23% ML, with large lenses, diameter ~32% ED; single shallow dorsal and ventral indentation in iris; individuals ML <180 mm with slender, crescent-shaped sheet of lustrous, copper-coloured tissue along ventral eye (Fig. 70A), potentially photogenic, becoming less obvious with ontogeny. Funnel length

Table 21. Measurements (mm) of *Taningia danae*. Mean indices were calculated from specimens ML >48 mm with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows. Additional specimens can be found in Tables 22, 25.

Specimen ID	ZMUC CEP-90	NMNZ M.305062	NMNZ M.318205	NIWA 62693	NIWA TRIP1795/81	ZMH 11726	USNM 816681	Mean index	USNM 815476	MV F160003
Type status	Holotype	None	None	None	None	None	None		None	None
Sex	Indet.	♀	♀	♂	♀	♀	♀		Indet.	Indet.
DML	37.5	1310*	882	550	395*	200	115	31	48	5.7
MW	15.6	475	235	194	202	63	36	80	23.1	3.0
FL	32.6	1025*	560	475	336	169	97	105	36.5	5.3
FW	48.1	1040	880	556	570	145*	130	28	57	10.1
HL	13.5	240*	202	148	88	64	33	26	17	3.3
HW	17.3	220*	185	110	78	65	36		20.5	3.4
Side	L	L	L	L	R	R	L		R	R
AL I	12.7	338*	292 (R)	246	198	78	46	39	16.1	1.4
AL II	13.5	325*	220	204	165	62	44	33	14.2	1.7*
AL III	14.9 (R)	386*	304	232	186	89	45	40	15.5	1.8
AL IV	13.9	314*	302	249	197	91	45*	42	16.5	1.2
AH	20, 13+1, 26, 24		31, 11+1, 27, 27*	30, 12+1, 28, 31	31, 12+1, 30, 30	31, 12, 25, 24	29, 12+1, 29		NM	NM
TL	4.8*								4.33	2.3
CL									1.33	0.8
CS									*	3

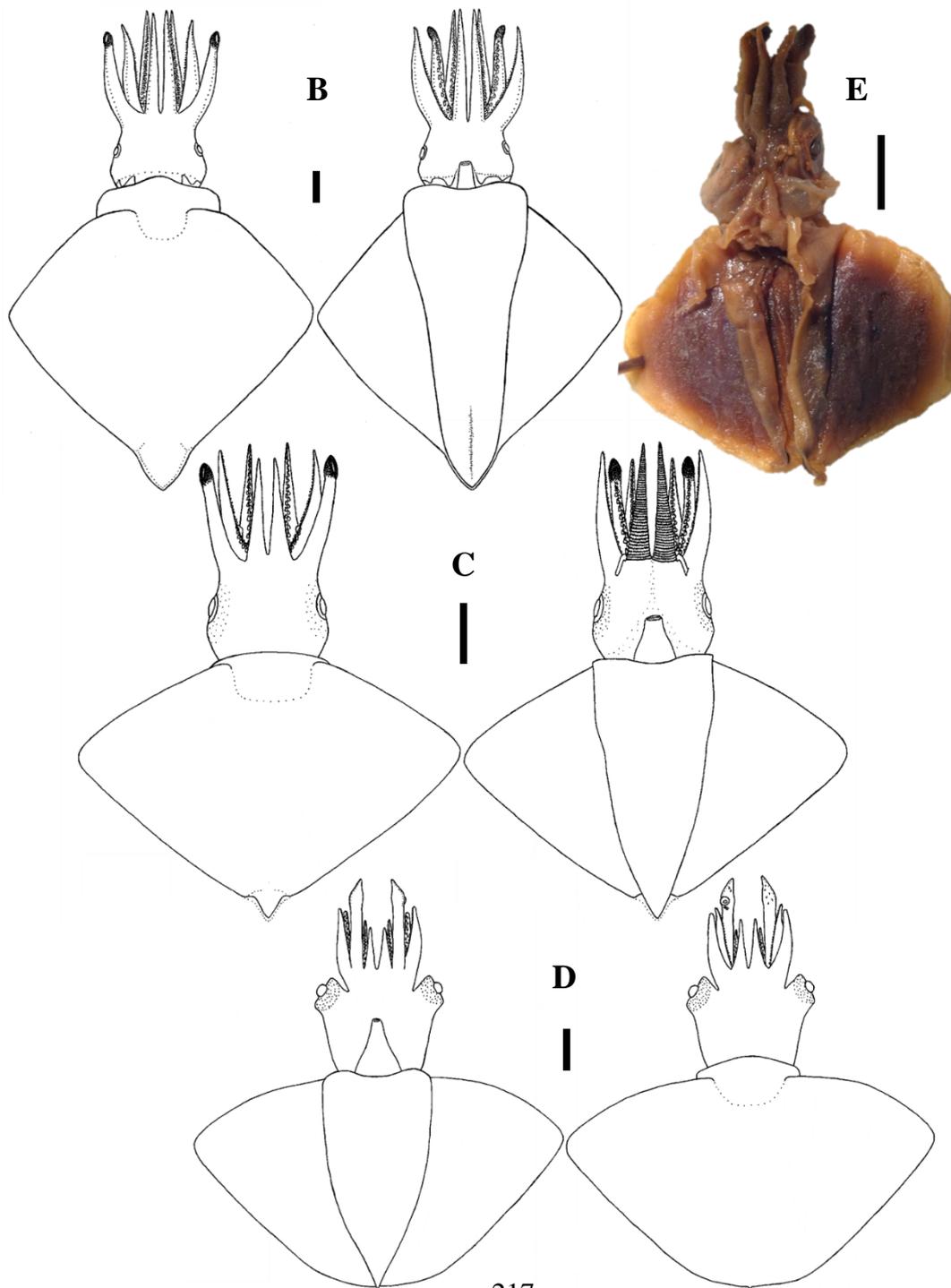
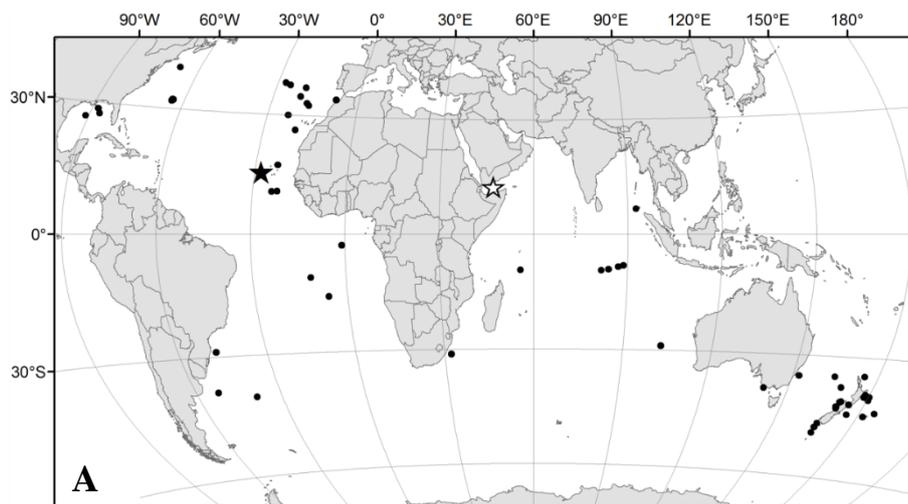
* indicates damaged character, not used to calculate indices.

~28% ML; aperture margin smooth, width ~22% funnel length, anteriorly level with mid- to anterior eye; funnel groove shallow, set between ventral-most nuchal pads; funnel valve tall, broad. Dorsal funnel organ cordiform with anterior tip and lateral edges free; ventral components 'D'-shaped, flat (Fig. 68H). Funnel component of locking apparatus with broad (~50% cartilage width), simple, straight groove displaced laterally on cartilage, ending bluntly antero-medially (Figs 70B, D); length ~10% ML, maximum width ~4% ML. Mantle component blunt raised ridge, height greatest antero-medially (Figs 70C, E); length ~8% ML, width ~5% ML; set posteriorly from mantle margin by ~5% ML. Nuchal cartilage oblong, becoming spatulate in largest specimens (Figs 70F, G); with strong medial ridge with superficial medial indentation, flanked by deep grooves, pointed anteriorly; length ~11% ML, maximum width ~5% ML. Olfactory papilla located laterally on head between two ventral-most nuchal pads; tall, length ~4% HL; triangular; with free, rounded tip with large terminal pore, diameter ~1.5% HL, orientated laterally when papilla collapsed against head. Six pores in buccal membrane: one ventral to base of each of Arms I and II, one between Arms III and IV.

Arms stocky, short, length 25–38–46% ML; formula IV=I>III>II; Arms I, III and IV each with 29–35 pairs of hooks in fleshy sheaths, Arms II with 12–14 pairs. Arm bases fleshy; Arms I, III and IV narrow rapidly to tips, their diameter diminishing from ~13% arm length at base to ~9% at midpoint; Arms II narrow only slightly before terminal photophores, except in large males where arm width swells around hook pairs 8–9 (Fig. 71A). Arm II photophore length ~6% ML (~18% AL II), maximum width ~4% ML, possibly smaller in large males. All arms with low gelatinous aboral keels from base to tip; breadth 40–50% arm depth in proximal 75% arm length, increasing to 100% in distal 25% arm length. Arms IV with pronounced transverse pigmented bands on aboral arm surface; bands present within and underlying gelatinous keels (Figs 71C); present over at least proximal ~60% arm length; proximal-most band depth ~1% of arm length, becoming narrower and more densely set distally.

Arm hooks stout, robust; largest in pairs 3–6 of Arms II (excluding large males); basal-most pair on Arms I smaller than second pair. Hook series generally decrease gradually

Fig. 69 (following page)—*Taningia danae*. A) distribution (solid star indicates type locality, empty star indicates locality of junior synonym '*Octopodoteuthis persica*' Naef, 1923); B) adult; C) post-larva; D) paralarva, MV F160003, sex indet., ML 5.7 mm, paralarva; E) ZMUC CEP-90, holotype, sex indet., ML 38 mm. Scale bars = B) 100 mm; C, E) 10 mm; D) 1 mm.



in size distally; hooks on Arms II maintain large proximal size until distal-most two pairs, then decrease rapidly and terminate proximal to photophores (Fig. 71B); in large males only, Arm II hooks increase in size distally with pairs 6–10 very large (pairs 8–9 largest; hook base breadth 220% that of basal hook), distal hooks decrease in size, very rapidly among terminal two pairs. Accessory claws disappear from proximal hooks with ontogeny: all hooks with accessory claws at ML <175 mm (Figs 71D, E); proximal-most pair only without claws at fresh ML 199 mm; proximal 13–16 pairs without claws at ML 260–550 mm (Figs 71F, G); proximal 20–22 pairs without claws at ML >900 mm (Figs 71H, I). Hood low on main cusp; basal margin flat to slightly concave; tissue inserts under hood from inner hook sheath surface (Figs 71J, K). Hook bases crenulated, most prominent laterally; main cusp low off base, smoothly curved, inner angle obtuse to slightly acute; accessory claws (when present) pointed, variably curved; aperture broad (Fig. 71L). Proximal hooks stouter than distal hooks, with relatively larger bases (length and breadth) and slightly shorter main cusps; proximal hooks of largest specimens squat, without neck, aboral surface of main cusp and base forming continuous curve.

Tentacles absent, traces remain in post-larvae, fully intact only in paralarvae (see life stage descriptions below).

Single ovate bioluminescent patch on ventral surface of ink-sac (Figs 72A, B), positioned ~20% ML posteriorly from anterior mantle margin; length ~5% ML, width ~3% ML (7.45 x 4.17 mm at ML 153 mm); iridescent to peach-coloured; with sparse streaks extending radially and anteriorly an additional ~3% ML; overlain medially by rectum, laterally by *recti abdominis* sheet; all associated structures become less conspicuous with ontogeny. *Recti abdominis* muscles indiscrete; strongly fused medially, creating thickened sheet of tissue; anteriorly attached at concavity of funnel organ dorsal component, posteriorly expanding into thinner sheet attached to ventral surface of visceral mass. Short free section of rectum emerges between fusion of *recti abdominis* muscles, terminating in posterior quarter of funnel component of locking apparatus; in large specimens, fused rectum-*recti* complex protrudes longitudinally from viscera. Anal flaps short, positioned laterally; length ~1.3% ML; ovate, anterior tip pointed, chiral dorso-ventrally. Ventral visceral mesentery pore diameter ~1% ML. Gills robust, length ~27% ML, with 38–44 lamellae.

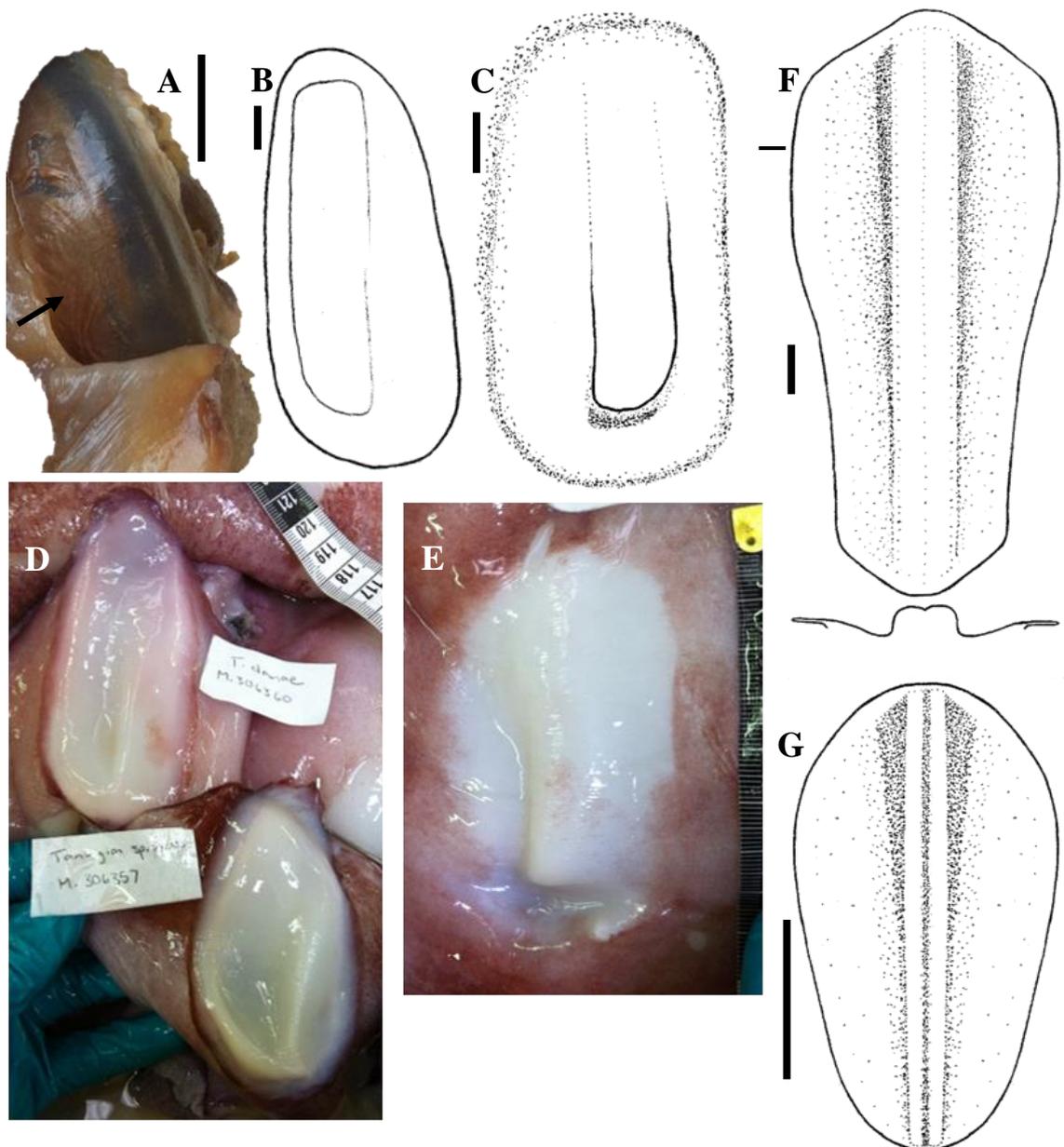


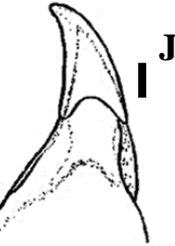
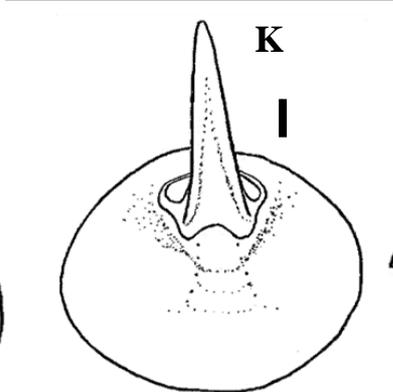
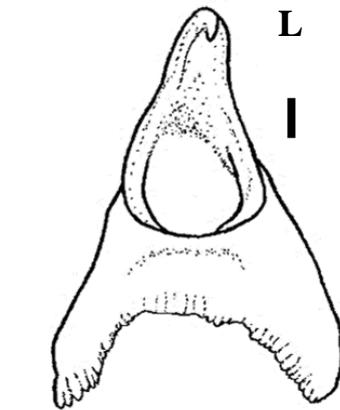
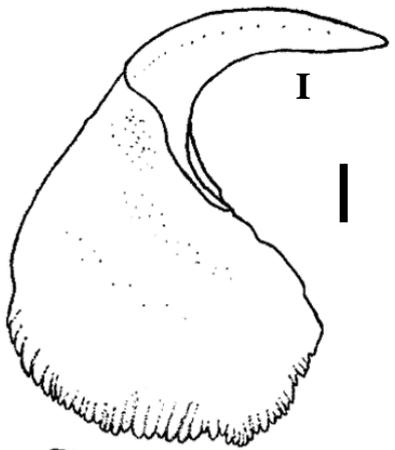
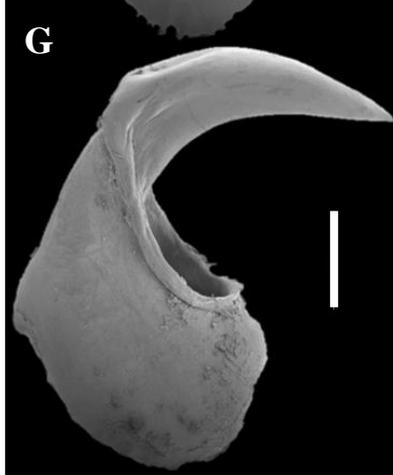
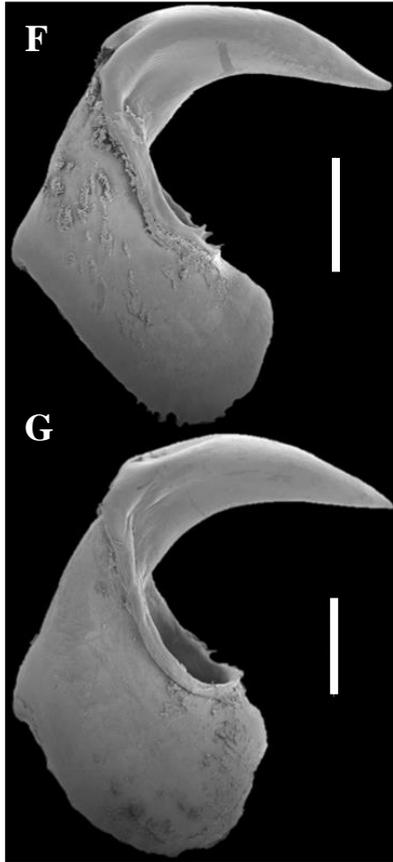
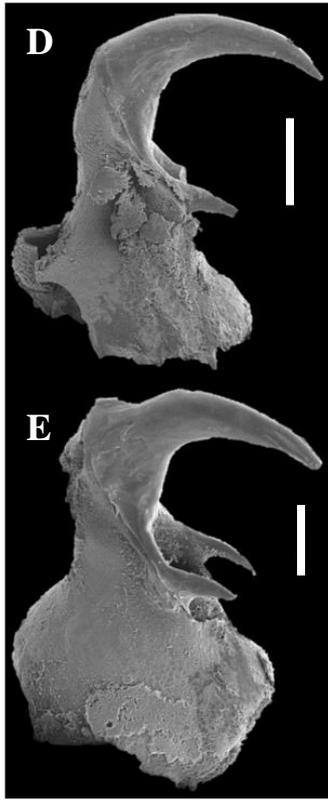
Fig. 70—*Taningia danae*. A) USNM 885291, ♀, ML 79 mm; B–D[top], E) NMNZ M.306360, ♀, fresh ML 815* mm; D[bottom]) *T. fimbria* sp. nov., NMNZ M.306357, ♀, fresh ML 970 mm; F) NMNZ M.174308, ♀, ML 1074* mm; G) ZMH 11188, ♂, ML 213* mm. A) ventral view of left eye with sheet of lustrous, copper-coloured, potentially photogenic tissue (arrow); B) funnel component of locking apparatus; C) mantle component of locking apparatus; D) funnel components from similar-sized, large, fresh specimens of *T. danae* (top) and *T. fimbria* sp. nov. (bottom) from New Zealand waters; E) mantle component of same fresh *T. danae* specimen; F, G) nuchal cartilage: (F) large adult, with cross-section (bar), (G) juvenile to subadult. Scale bars = A) 5 mm; B, C, F, G) 10 mm.

Lateral profile of lower beak (7.59–20.92 mm LRL, Figs 72D–G) slightly longer than deep, with distal wing tips extending beyond rostral tip 22–29–35% baseline; rostrum with distinct tip distal to shallow notch, tip eroded in largest specimens; jaw edge visible, slightly concave, with short jaw-edge extension; jaw angle 100–110°, slightly obscured laterally by low, rounded wing fold; depth between jaw angle and baseline

greater than half overall depth. Hood high off crest, length 25–28–34% baseline. Crest discrete, lateral wall between crest and fold fully pigmented; length 46–56–61% baseline; tip free, with concave notch between crest and lateral wall; sloped steeply in nearly straight line. Lateral wall with curved, rounded folds, produced dorso-laterally in cross-section, doubling in breadth posteriorly; produced into shelf along anterior 40% of hood length; posterior lateral wall margin straight; free corner well beyond crest tip; lateral wall fold (especially anteriorly), crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 149–164–180% that at jaw angle, length 122–129–137% LRL, with cartilaginous pad. Ventral view with broad notch in hood; free corners widely spaced, in line with middle of wing breadth. Wing entirely unpigmented at LRL ~7.5 mm, remainder of beak pigmented excluding posterior lateral wall near free corner; beak fully pigmented including wing at LRL ~18–19 mm.

Lateral profile of upper beak (8.29–18.18 mm URL, Figs 72H, I) longer than deep, maximum depth ~46% of length. Rostrum very short, ~30% of length, strongly curved ventrally, with distinct jaw-edge extension; jaw angle ~60°; low ridge of cartilage present along shoulder, most visible after free shoulder fully pigmented, dorsal cartilage decreases with ontogeny; oral shoulder margin convex. Hood long (length ~76% UBL), tall (height ~22% UBL); junction of hood and free shoulder very slightly concave. Lateral walls trapezoidal to triangular, deepest posteriorly, posterior margin straight to slightly angled. Dorsal view with posterior margin of hood straight; posterior margin of crest and crest pigmentation concave. Lateral wall pigmentation progresses first along crest, from anterior to posterior, then laterally along wall from anterior to posterior. Crest pigmented dorsally at URL ~7 mm, free shoulder and remaining lateral wall transparent; free shoulder fully pigmented at URL ~17 mm, anterior lateral wall fully pigmented, posterior ~65% pigmented; beak fully pigmented at URL ~18.5 mm.

Fig. 71 (following page)—*Taningia danae* arm and armature morphology. A) NMNZ M.127086, ♂, ML 680* mm; B) NMNZ M.318205, ♀, ML 882 mm; C) NIWA 92142, ♀, fresh ML 900 mm; D, E) ZMUC CEP-90, holotype, sex indet., ML 38 mm; F, G) NIWA 76658, ♂, ML 260 mm; H–L) NMNZ M.174308, ♀, ML 1074* mm. A, B) oral surface of Arm II, greatest width at bar: (A) male, (B) female; C) Arm IV ventral pigment bands underlying epidermis, fresh adult specimen; D) 14D hook, Arm IIIR; E) 5V hook, Arm IIIR; F) 13D hook, Arm IVR; G) 4V hook, Arm IVR; H) 21D hook, Arm IIIR with accessory claws (arrow); I–L) 4V hook, Arm IIIR: (I) lateral profile, (J) aboral, (K) apical, (L) oral. Scale bars = A, B) 15 mm; C) 5 mm; D, E) 100 μm; F–L) 1 mm.



Radula (Fig. 73A) with tricuspid rachidian; mesocone long, triangular, broad basally, base concave; lateral cusps ~40% mesocone height, slightly laterally directed. First lateral tooth bicuspid, slightly shorter than rachidian, base concave; inner cusp broadly triangular, straight to slightly medially directed; outer cusp ~40% height of inner cusp, straight or slightly laterally directed. Second lateral tooth simple, broadly triangular, slightly longer than rachidian. Marginal tooth narrowly triangular, ~170% height of rachidian. Marginal plate present. Outer surface of all teeth slightly raised. Palatine palp (Fig. 73B) with ~55 robust triangular teeth, each 70–215% rachidian height; more densely set along dorsal margin and in anterior 20% of length, regularly arranged along remainder of oral surface.

Gladius (324–910* mm GL, Fig. 73C) broad and thin (~0.1 mm thick in specimen GL 324 mm), frail, transparent; greatest width (~12% GL) at 25–30% GL; free rachis ~13% GL, pointed anteriorly, broadening posterior to maximum width (~4% GL) at posterior terminus, poorly demarcated from vanes; vanes broaden quickly to maximum width, then taper gradually for remainder of GL; conus short, ~6% GL, into which tissue inserts (the traction of which often results in breakage during dissection); rachis broad, evenly concave. Smallest specimen (NIWA 76658, GL 324 mm) with irregular calcium-like deposits along length.

Colour (preserved) deep purple over all external body surfaces where outer-most gelatinous tissue layer intact, darkest (nearly black) over Arm II photophores. Ventral mantle surface maroon beneath gelatinous layer, other surfaces pale purple.

Chromatophores present on dorsal head, over all external funnel surfaces and within groove. Arms darkest aborally, chromatophores present aborally underneath gelatinous layer, arms maroon orally. Anterior funnel retractor muscles, *recti abdominis* muscle sheet, inner mantle and funnel surfaces, olfactory papillae, and funnel valve pigmented light purple in larger specimens; iris with darker purple pigmentation; mantle component of locking apparatus, funnel organ components, and anal flaps unpigmented. Fresh specimens similar but colours more brilliant, unpigmented areas pure white (*e.g.*, components of locking apparatus, Figs 70D, E).

Post-larval specimens (ML 31.5–59 mm, Figs 69C, E). Mantle conical to weakly goblet shaped. Fins large (length 76–88–98% ML), very broad (width 119–144–171% ML). Head length 35–39–47% ML, width 43–47–54% ML. Eyes very large, diameter ~26%

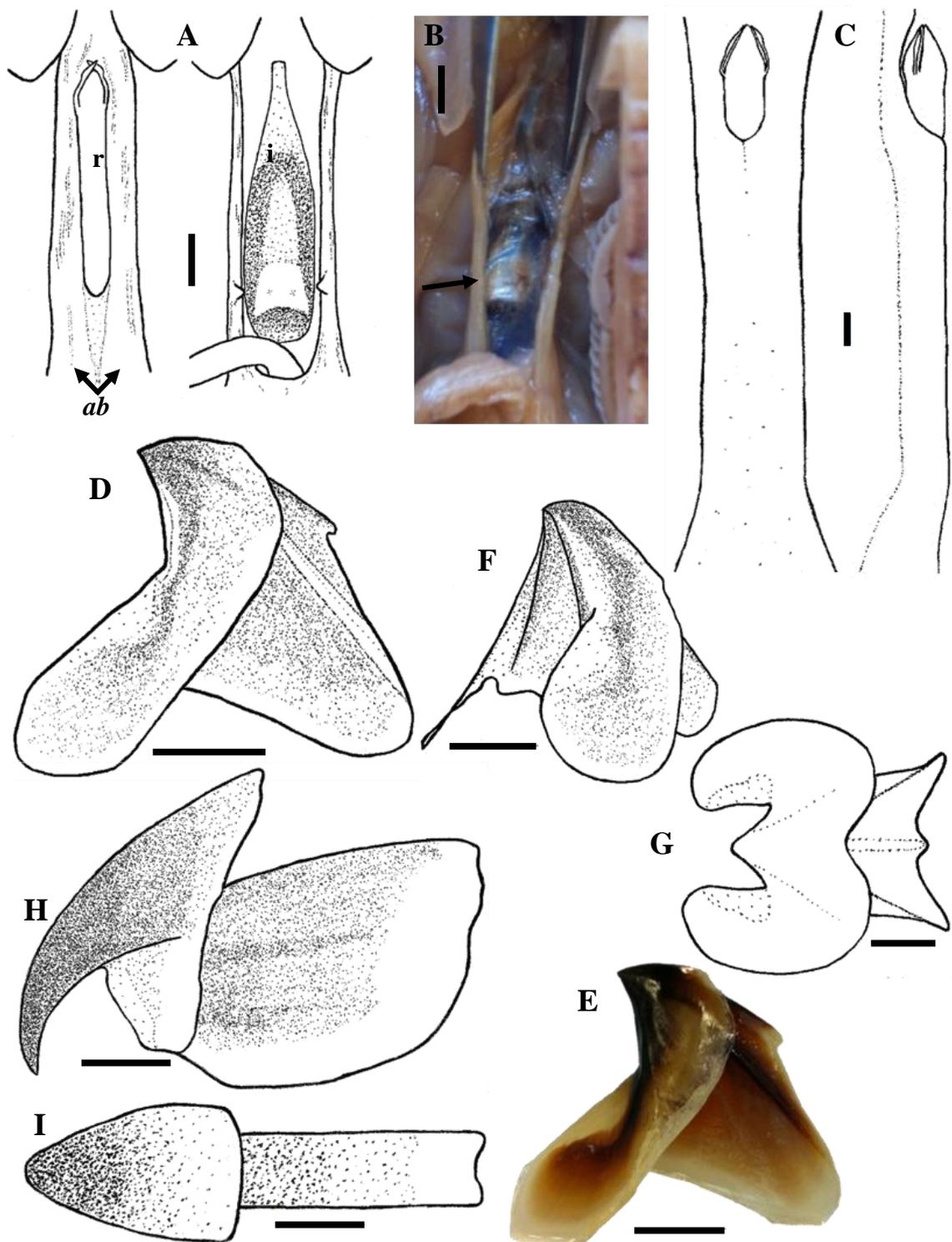


Fig. 72—*Taningia danae*. A) NMNZ M.67249, ♀, ML 48* mm; B) USNM 816681, ♀, ML 115 mm; C) NIWA 62693, ♂, ML 550 mm; D–I) NIWA 75790, sex indet., fresh HL 170 mm. A) *recti abdominis* muscles (*ab*) and rectum (*r*) in post-larva: natural state (left), dissected (right) revealing ventral photogenic patch on ink sac (*i*) and dorsal *recti abdominis* swellings; B) ventral photogenic patch (arrow); C) *recti abdominis* muscles and rectum in adult: ventral view (left), lateral profile (right); D–G) lower beak: (D, E) lateral profile, (F) oblique profile, (G) ventral view (pigmentation not indicated); H, I) upper beak: (H) lateral profile, (I) dorsal view. Scale bars = A) 2 mm; B) 4 mm; C–I) 10 mm.

ML, with large lenses, diameter ~49% ED; ventral photogenic patch prominent. Arm length 30–41–51% ML, with ventral arms slightly longer than dorsal arms, Arms II shortest; Arms IV with ventral transverse pigment bands. Arm II photophore length ~8% ML, ~18% AL II. Hooks present to arm tip; all hooks with accessory claws. Tentacles atrophying, few complete, length ~25% ML (~60% AL); tentacle bases thin, width ~20% thickness of adjacent arms, tissue insubstantial. Club length ~7% ML (~27% TL); ovate, slightly expanded proximally, tapering quickly to distal point (Fig. 73D); low dorsal keel along length of club; 4 pairs of lowly stalked suckers (6 intact on single club): proximal-most carpal-like and very small, second pair ~450% diameter of proximal-most pair, sucker aperture ~60% sucker diameter, offset basally giving sucker ring a domed appearance. Club sucker infundibular ring with very short, slightly tapered teeth along entire circumference (Figs 73E, F); papillated ring comprising singular central and peripheral rings of low, interlocking, irregular polygonal pads; rim composed of short, regular, closely spaced teeth, concave in cross-section, square at tips. Bioluminescent patch on ventrum of ink sac large, length ~10% ML, width ~6% ML (5.1 x 2.5 mm in specimen ML 48 mm); composed primarily of distinct, trapezoidal depression containing two small pits; iridescence greatest in depression, particularly posteriorly, but extends anteriorly in diffuse triangle overlying rectum. *Recti abdominis* muscles discrete, weakly fused medially level with nub projecting dorsally from each muscle; nubs insert into pits in depression. Rectum lies along slight longitudinal indent in depression; anterior-most tip of ink sac strongly attached to rectum dorsally.

Single paralarval specimen (ML 5.7 mm, Fig. 69D). Fin length 93% ML, width 178% ML. Head length 57% ML, width 60% ML; eyes on low stalks, directed anterio-laterally; lenses protruding. Arms with two series of domed suckers instead of hooks; length 20–30% ML, lateral two arm pairs longest, Arms IV shortest; Arm II damaged, photophores absent. Tentacles longer than arms, ~40% ML; bases thicker, ~115% thickness of adjacent arms; tentacles maintain thickness to club. Clubs ~14% ML, ~30% TL; 4 pairs of stalked suckers (3 intact on single club); proximal-most pair very small, dorsally offset; second pair 400% diameter of proximal-most pair, sucker aperture ~60% sucker diameter, offset basally giving sucker ring a domed appearance; sucker ring dentition indiscernible.

Biology. Smallest mature specimen examined ML 550 mm (NIWA 62693, ♂). Females appear to begin maturation between ML 200 and 400 mm; smallest spawned female observed was ML 882 mm (NMNZ M.318205). Implanted spermatangia short, broad (18 x 4.5 mm, *in situ*); one found in outer gelatinous tissue of dorsal mantle, five in right lateral mantle (NMNZ M.305062, ML 1310* mm).

Relationships were best described by power equations for LRL values, and exponential equations for URL against ML and body mass (Fig. 74). Relationships fit the data very well ($R^2 > 0.8$), despite the small sample size ($n = 5$). Single previous genus regression only available for LRL, which differed considerably from that calculated herein for ML, but was nearly identical for body mass (Clarke 1980).

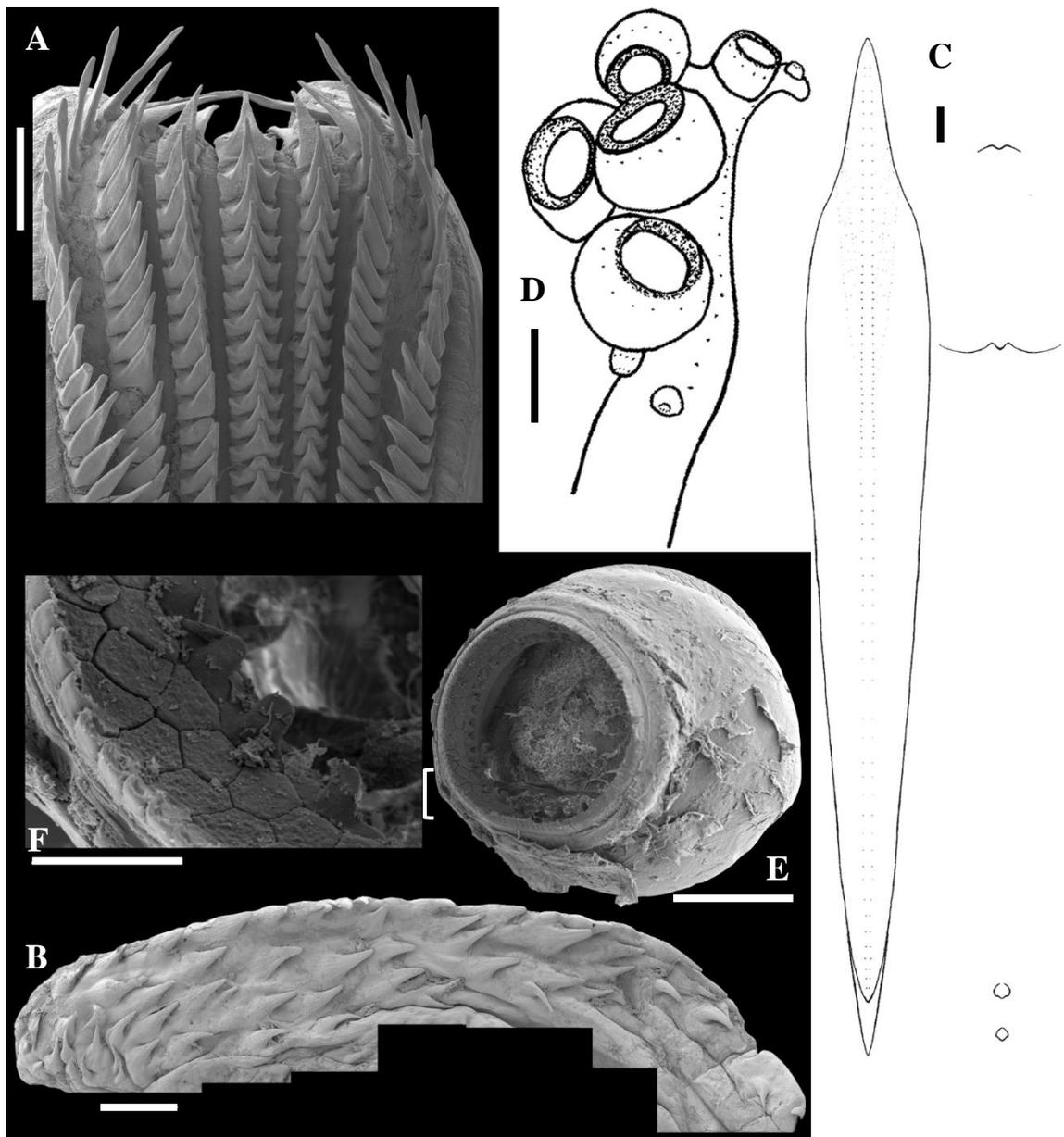


Fig. 73—*Taningia danae*. A) Radula, NIWA 75790, sex indet., fresh HL 170 mm; B) palatine palp, NIWA 23750, ‘♂’, LRL 17.14 mm; C) gladius, with cross-sections; D, E)

ZMUC stn 3894I, ♀, ML 31.7 mm: (D) tentacle club, dorsal view, (E, F) 1V manus sucker, left tentacle. Scale bars = A) 1 mm; B) 2 mm; C) 20 mm; D) 0.6 mm; E) 200 μ m; F) 50 μ m.

Two large females specimens (NMNZ M.306360, fresh ML 815* mm, 19 268 g fresh; NIWA 92142, fresh ML 900 mm, 24 258 g fresh) which could not be accessioned whole were dissected to determine proportional composition of body tissues. Fins comprised the greatest mass (~61% of body mass) for both individuals, followed by the head+arms (23%), and mantle (14%). Viscera comprised ~4% of total mass, the greatest allocation of which was to the reproductive system (~46% of visceral mass), followed by cardiovascular (~32%) and digestive (~22%) systems. The single largest organ was the gills (~29% of visceral mass), followed by reproductive organs: nidamental glands (~15%), oviducal glands+oviducts (~16%), and ovary (~14%); neither female was

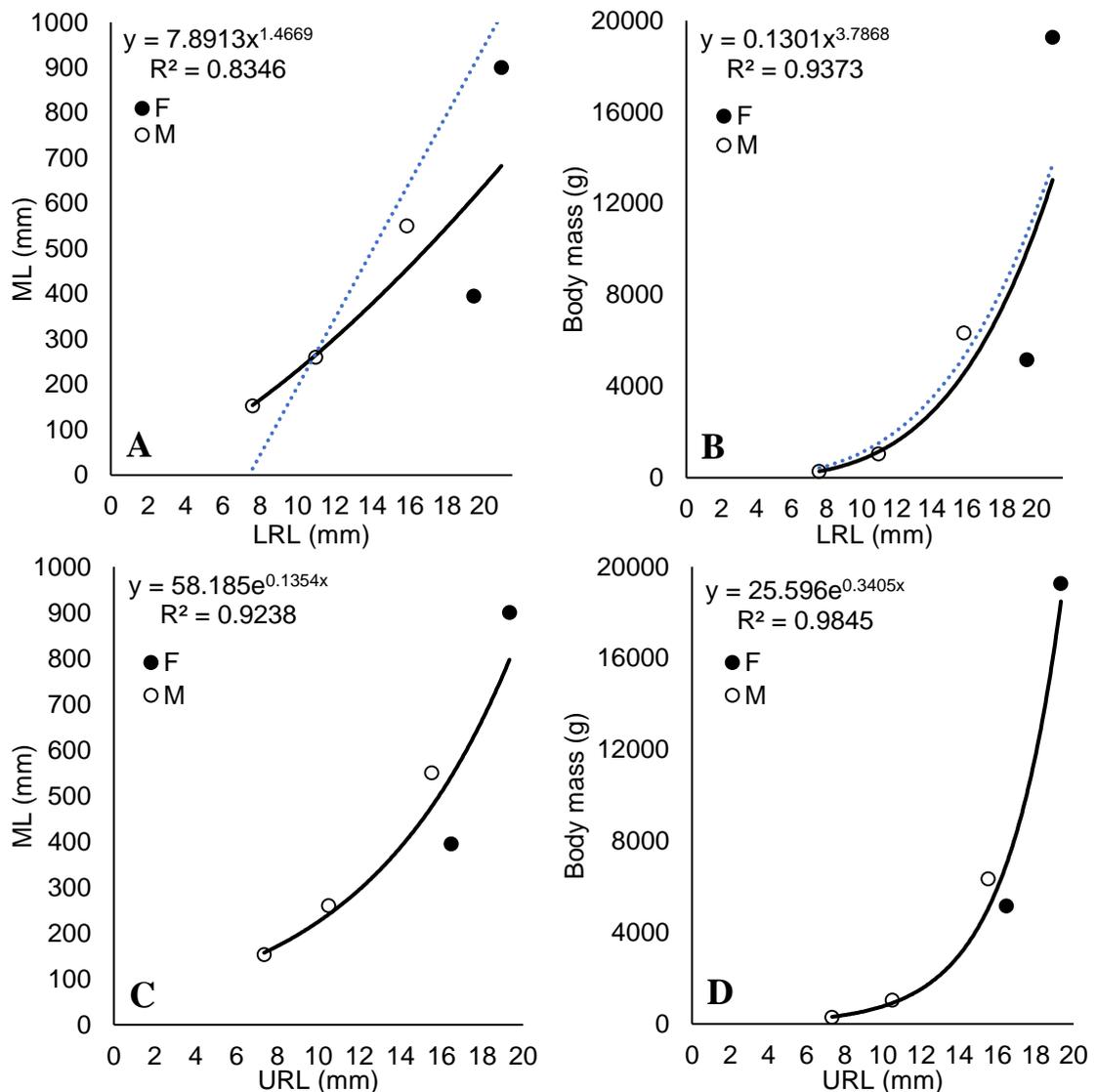


Fig. 74—*Taningia danae*. Regressions of lower rostral length (LRL) against (A) dorsal mantle length (ML) and (B) preserved wet body mass, by sex; upper rostral length

(URL) against (C) ML and (D) preserved wet body mass, by sex. Models of best fit (greatest R^2 value) are plotted (solid) against genus regressions of Clarke (1980; dotted).

considered mature or near spawning condition. Specimens had sustained damage and some tissues (*e.g.*, digestive gland, ovary) are likely underrepresented here; despite this, proportional trends were consistent between specimens.

Remarks. *Taningia danae* is herein recognised from the Atlantic, Indian, and, at least, southwest Pacific Oceans. In addition to specific pairwise differences in various characters (*e.g.*, lower beak morphology between *T. danae* and *T. fimbria*), adult *T. danae* can generally be separated from congeners by their wider fins and short, blunt tails; post-larval *T. danae* tend to have shorter arms than other species.

The sexual dimorphism in Arm II morphology described herein (Figs 71A, B) was established in NMNZ M.127086 (ML 680* mm, HL 215 mm), the largest of only two sexually mature males available during this study (a third is described in González *et al.* 2003). This unique arm morphology was demonstrable in two additional head-only specimens (NHMUK 20160120, HL 206; NMNZ M.183012, HL 143* mm) but not evident among five larger whole female specimens (ML 815*–1310*, HL 202–269 mm).

The ink sac photophore was first observed by Roper & Vecchione (1993) as two organs on either side of the intestine. This is an effect of the opaque rectum medially overlying the single large photogenic patch, seemingly dividing it into ‘two photophores’ unless fully dissected with rectum held aside. In all specimens attributed to *T. danae*, only a single large photogenic patch was observed. The lustrous, coppery strips of tissue along the ventral ocular surface of small (ML <180 mm) specimens are very similar morphologically to the ink sac photophore. They also match the location of two silvery patches along the ventral eyeball visible in a photograph of a live specimen in an aquarium (Vecchione *et al.* 2010), which have an identical presentation as the illuminated ink sac photophore therein. It is therefore with some certainty that these patches are herein considered to be photogenic, and whose ontogenetic decrease in prominence may be attributable to a decrease in functionality on the substantially larger adults.

A single *Taningia* specimen (PC10-01-B0630-2888-MTB251-SN) collected from the Gulf of Mexico was found to differ genetically from other Atlantic *T. danae* samples (see Genetics). This specimen was not available for examination, and other specimens from the Gulf were not found to differ morphologically from Atlantic specimens of *T. danae* (Table 22), although comparisons were not made between known genetically different specimens. Immediately prior to drafting this thesis, a specimen from the central tropical Atlantic (ZMH 79906) was found to group with PC10-01-B0630-2888-MTB251-SN (herein designated *Taningia* sp. V, see below for collection data), calling into question the specific identity of all Atlantic *T. danae*. As a provisional resolution to this issue, figures and illustrations were based upon genetically established *T. danae* *s.s.* or specimens from Australasia as much as possible. The synonymy given above does not differentiate between *T. danae* and *T. sp. V*, but lists references potentially referring to either or both (but not any of the other three *Taningia* species designated herein).

Previous works (*e.g.*, Clarke 1967; Roper & Vecchione 1993) have given similar accounts of the history of ‘*C. unguiculata*’ (Molina, 1782) and ‘*E. hartingii*’ Verrill, 1880 and its relation to *T. danae*, and have gone as far as to synonymise certain specimens previously attributed to ‘*C. unguiculata*’ with *T. danae* (see above synonymy). When considering the species as a whole, Clarke (1967) chose to reserve the name ‘*C. unguiculata*’ for the specimen originally referred to by Banks and Molina (as did Steenstrup [1882]), with the surviving buccal bulb of Owen retaining ‘*E. cookii*’. Roper & Vecchione (1993) considered ‘*Cucioteuthis*’ and associated species *nomina dubia*. Herein, ‘*C. unguiculata*’ and ‘*E. hartingii*’ are both maintained as *species inquirenda*, a result of the discovery of new supportive information allying Owen’s bulb to the original specimen, and pending examinations of both specimens in person. For full treatment of these taxa see Discussion.

Table 22. Measurements (mm) of *Taningia* specimens from the Gulf of Mexico (GOM), with similarly sized specimens of *T. danae* and *T. fimbria* sp. nov. (other comparably sized specimens are reported in Table 25). Mean indices were calculated for GOM specimens using damaged ML measures. ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side).

Specimen ID	USNM 1179543	USNM 1179529	USNM 1179761	USNM 1179460	Mean Index	USNM 816680	USNM 885291	ZMH 73901	Mean Index	USNM 817618
Species Type status	sp. None	sp. None	sp. None	sp. None		<i>danae</i> None	<i>danae</i> None	<i>danae</i> None		<i>fimbria</i> Paratype
Locality	GOM	GOM	GOM	GOM		SC trop. Atlantic	Cape Verde	Argentina		Argentina
Sex	♂	♂	♂	Indet.		♂	♀	♀		♀
DML	148*	115*	58*	37*	45	109	79	59	38	121
MW	69	45	30	15	85	23	32	32	87	49
FL	120	86	58	31	145	96	69	51	124	99
FW	164	128	95	72	42	120	100	79	36	132
HL	47	40	32	17	36	35	27	25	40	32
HW	45	44	23	13*		39	32	26		45
Side	R	R	R	L		R	R	NM		L
AL I	43*	58	36	21	56	47	38	24*	46	45
AL II	61	47	28	22*	43	40	35	22	39	38
AL III	68	52	31	22*	48	43	37	25*	43	44
AL IV	75	56	31	22	51	42	37	25*	43	47
AH	*, 14+1, 28, 29	*, 13+1, *, *	*, 13+1, *, *	*, 13+1, *, *		29, 15, 31, 30	NM, 13+1, NM, NM	NM		28, 13+1, 28, 29
TL			2.5 (L)	8	13			1.4	0.8	
CL			*	2	5			*		
CS			*	*				*		

* indicates damaged character, not used to calculate indices.

5.2.2. *Taningia fimbria* sp. nov. (Tables 22, 23, Figs 68D, F, G, 70D (bottom), 75–79)
Taningia danae (not Joubin, 1931) — Clarke (1967) (*partim*): Table 1 (specimens 4, 8,
10 only), Figs 2 (specimen 4 only), 7, 8C, 8E, (1980) (*partim*): 168, Table 30;
Hoving *et al.* (2010): Table 1 (specimens 8–10), Figs 4, 5.

Type material (5 specimens). **NIWA 95882**, Holotype, ♂, ML 305* mm, 49°14.35'S, 167°44.38'E, 736 m, 08/12/2002, TAN0219/64, BTT, coll. NIWA; **USNM 817618**, Paratype, ♀, ML 121 mm, 39°19.2'S, 48°01.8'W, 0–200 m over 2000 m, 06/03/1971, 2053–0021 hr, RV *Walther Herwig*, 354-II-71, 1600 mesh Engel trawl; **NIWA 71439**, Paratype, ♂, ML 296* mm, 48°36.43'S, 174°59.22'E, 801 m, 26/11/2000, RV *Tangaroa*, TAN0012/02, Z10851; **NIWA TAN1117/59**, Paratype, ♂, ML 282* mm, 49°12.77'S, 168°29.27'E, 673–695 m, 12/11/2011, RV *Tangaroa*, TAN1117/59; **NIWA 71438**, Paratype, ♀, ML 730 mm, unlocalised [New Zealand region].

Additional material examined (21 specimens). **USNM 1157196**, ♂, ML 300* mm, 36°49.2'S, 12°16.8'W, Tristan Da Cunha, 1750–2000 m, 17/03/1971, RV *Walther Herwig*, stn 395-71, 1600 mesh Engel trawl; **NIWA 71443**, ♀ (head only), HL 175 mm, 37°08.8'S, 177°17.3'E, 698 m, 06/04/2000, Z10241, 1343/12; **NMNZ M.174782**, sex indet. (head and fins only), FL 520 mm, 39°00'S, 178°00'E, off Mahia Peninsula, New Zealand, 900 m, 05/05/2004; **NIWA 71441**, ♂, ML 435* mm, 39°25.87'S, 178°24.02'E, 950 m, 02/07/2001, TAN0109/12, Z10872; **NMNZ M.306357**, ♀, fresh ML 970 mm, 42°36'S, 169°54'E, New Zealand, 686–731 m, 20/06/2011, 3331/17, BTT, coll. SOP; **NIWA 71667**, ♂, ML 355* mm, 42°46.48'S, 179°40.37'E, 1142–1146 m, 17/07/2002, TAN0208/119, Z11138, BTT; **NIWA 71440** (spermatophores: NIWA 71849), ♂, ML 364* mm, 42°54.63'S, 179°57.67'E, 723 m, 29/06/1999, AEX9901/34, Z9788; **MV F16403**, sex indet. (buccal bulb, arm section only), LRL 18.37 mm, 43°20'S, 145°55'E, 24 km SW of Port Davey, Tasmania, 768 m, 29/05/1954, coll. CSIRO Division of Fisheries; **NMNZ M.299013**, ♀, ML 555* mm, 44°08.5'S, 174°33'W, off Chatham Islands, New Zealand, 967 m, 09/01/2008, FV *San Waitaki*, stn 2551/269; **NMNZ M.290281**, sex indet. (arm only), AL 328 mm, 44°37.7'S, 177°37.4'W, Chatham Rise, New Zealand, 1000–1284 m, 11/05/2006, FV *San Waitaki*, stn 2247/62, coll. R. Cropp & R. Fraser; **NIWA 95933**, sex indet. (beaks only), LRL 11.00 mm, 48°02.4'S, 169°56.4'E, 887–891 m, 03/12/2006, TAN0617/23, BTT, coll. NIWA; **NIWA 71848**, ♂, ML 253* mm, 48°31.32'S, 171°44.53'E, 944 m, 21/11/2001, RV *Tangaroa*, TAN0118/02, Z10959; **NIWA 60454**, ♂, ML 215* mm, 49°06'S, 168°42'E, 727–745

m, 23/10/2009, TRIP2954/69, BTT, coll. SOP; **NIWA 84704**, sex indet. (beaks only), LRL 10.14 mm, 49°06.92'S, 167°46.37'E, 657 m, 20/12/2000, RV *Tangaroa*, TAN0012/106, Z10747; **NIWA 61959**, ♀, ML 240* mm, 49°12'S, 168°36'E, 700 m, 19/03/2010, MFish SOP TRIP3075/79, BTT, coll. SOP; **NIWA 66003**, ♂, ML 177 mm, 49°12'S, 168°36'E, 713 m, 08/03/2010, TRIP3075/52, BTT, coll. SOP & M. Dee; **NMNZ M.117554**, ♂, ML 285* mm, 49°51.2'S, 168°00.1'E, NE of Auckland Islands, New Zealand, 550 m, 03/10/1992, RV *Tangaroa*, TAN9209/60.

Unlocalised material examined (9 specimens). **NMNZ M.274772**, ♀, ML 884 mm, New Zealand; **NMNZ M.287285**, sex indet (buccal bulb, Arm II only), LRL 17.99 mm, New Zealand; **NHMUK 20160124**, ♀, ML 655 mm, 03/08/1965, unlabelled squid, ex. shower room, from stomach of male sperm whale, 50', MRC Acc. No. 79; **NHMUK 20160117**, ♀, ML 505 mm, A2514; **NHMUK 20160123**, ♀, ML 450 mm, Saldanha, 1963, brass label: 2270, MRC Acc. No. 79; **NHMUK 20160113**, ♂, ML 312 mm, Durban, 1964, A2515, MRC Acc. No. 142; **NHMUK 20160109**, ♀ (head only), HL 153 mm, 25/08/1965, unlabelled squid D3228, from stomach of male sperm whale, 44', MRC Acc. No. 185; **NHMUK 20160111**, ♀ (head only), HL 93 mm, Durban, 1963, 2262; **MV F159950**, ♀ (arm hooks and fragments of skin only), ML unknown, from female *Taningia* held at "Queen Victoria Museum, Launceston, Tasmania".

Additional genetic sample (1 sample). **NIWA TAN1412/36**, ♀, ML unknown, 49°34.3'S, 170°23.9'E, Campbell Plateau, 555 m, 07/12/2014, RV *Tangaroa*, TAN1412/36.

Distribution (Fig. 75A). Southern hemisphere between 30° and 50°S; 550–2000 m.

Diagnosis. Lanceolate projections along funnel aperture; papillate dermal tubercles on fin, head, and mantle; single photophore on dorsal surface of each recti abdominis muscle; all arm hooks with accessory claws; proximal-most hook on Arms I approximately twice the size of next hook in sexually mature males (Fig. 77A); funnel component of locking apparatus pointed anteriorly, constricting antero-medially; lower beak free corners narrowly spaced, posterior lateral wall margin concave, depth between jaw angle and baseline greater than half overall depth; fin width 76–91% ML; arm length 34–58% ML; Arms II with 12–14 pairs of hooks.

Table 23. Measurements (mm) of *Taningia fimbria* sp. nov. (USNM 817618 reported in Table 22). For specimens missing tails, an estimated DML (EML) was attained by dividing the measured DML by 0.80 (see Materials and Methods). Mean indices were calculated from specimens with undamaged or estimated dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	NIWA 95882	NIWA 71438	NIWA 71439	TAN1117 /59	NMNZ M.274772	NIWA 71441	NIWA 71667	NMNZ M.117554	NIWA 60454	NIWA 66003	Mean index
Type status	Holotype ♂	Paratype ♀	Paratype ♂	Paratype ♂	None ♀	None ♂	None ♂	None ♂	None ♂	None	None
Sex	♂	♀	♂	♂	♀	♂	♂	♂	♂	♂	♂
DML	305†	730	296†	282†	884	435†	355*	285*	215*	177†	
EML	381		370	352		544				221	
MW	65	300	105	107	305	110*	135	109	82.5	63	30
FL	271	535	282	264	650	345	341	241	205	169	73
FW	320	618	316	320	672	410	452	310	242	194	83
HL	96	205	91	102*	190	135	145	134	39*	57	25
HW	62	120*	71	63*	225	105	80*	80	48	38	19
Side	L	L	L	L	R	L	L	L	R	L	
AL I	161	322	165	215*	294	171*	259	195	130	113	44
AL II	126	255	133	134	233	211	245	180	114	88	36
AL III	145	291 (R)	148	218*	319	260	285	215	129	103	41
AL IV	160	304	165	130*	321 (L)	272	335 (R)	168*	131	123	45
AH	28, 13, 28, 29	*, 13, *, *	30, 12, 28, 29	13	35, 14, 32, 36	13, 31, 31	30, 13, 30, 33	31, 13, 32	NM, 13, NM, 30, 32		

* indicates damaged character, not used to calculate indices. † indicates specimen missing tail.

Description (ML 212–970 mm, Figs 75B–79). Mantle goblet shaped; widest at anterior margin, width 17–30–41% ML; weakly muscled; tail pointed, very long, length 14–20–25% ML. Fin length 63–73–76% ML, width 75–83–91% ML. Anterior fin insertion with lateral and posterior margins of attachment site straight; depth ~11% ML, width 10–15–22% ML. Small, papillate epidermal tubercles present over dorsal fin and tail surfaces (Figs 76A–D), around anterior mantle margin, dorsal and lateral head (including dorso-medial nuchal pad), and funnel; absent from arm and ventral fin and mantle surfaces; tubercles to ~1 mm in diameter typically bearing 4–6 papillae, smaller tubercles with 1–2 papillae; set in densities of 32–70/cm².

Head square to trapezoidal, length 21–25–28% ML, width 16–19–25% ML, depth ~20% ML. Eyes ~8% ML, with large lenses, ~30% ED; two peach- to orange-brown-coloured semicircular rings around lens separated by mid-eye indentations dorsally and ventrally; without potentially photogenic tissue ventrally. Funnel length 16–21–30% ML; funnel groove shallow, set between ventral-most nuchal pads; funnel valve tall, broad; aperture width 11–18–25% funnel length, level with mid- to anterior eye; with 30–50 narrow lanceolate projections extending from raised triangular ridges along inner surface just proximal to aperture margin (Figs 76E–I), occasionally two projections borne from single ridge, visible in specimens ML >240 mm, length ~0.3% funnel length in specimens ML <500 mm, ~2.5% funnel length in specimens ML >700 mm; in large specimens, projections considerably thickened, ovate, fleshy, pointed distally. Funnel component of locking apparatus with very broad (~70% of cartilage width), simple groove (Figs 76J, 70D); lateral margin tapering quickly antero-medially, terminating in distinct antero-medial point; length ~7% ML, maximum width ~4% ML. Mantle component triangular, raised pad, tapering antero-medially (Fig. 76K); bordered by depression, deepest anteriorly; length ~8% ML, width ~4% ML; set posteriorly from mantle margin ~5% ML. Nuchal cartilage irregular in smallest specimen, oblong to spatulate in adult specimens (Figs 76L–N); with strong medial ridge with superficial medial indentation, flanked by deep grooves, pointed anteriorly; length ~8% ML, maximum width ~4% ML. Olfactory papilla located laterally on head between two ventral-most nuchal pads. Six pores in buccal membrane: one at base of each of Arms I and II ventrally, one between Arms III and IV.

Arms slender, of moderate length, 26–41–56% ML; formula VI=I>III>II; Arms I, III and IV each with 28–36 pairs of hooks in fleshy sheaths, Arms II with 12–14 pairs. Arm

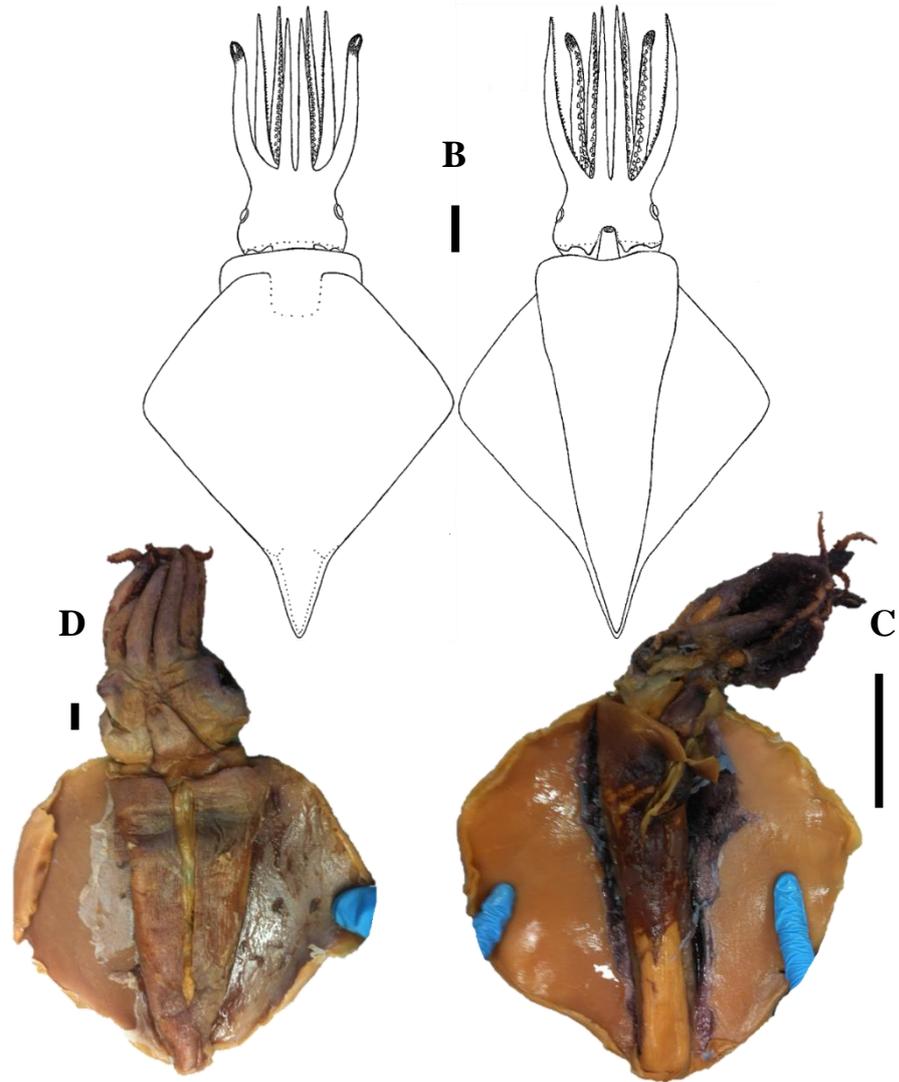
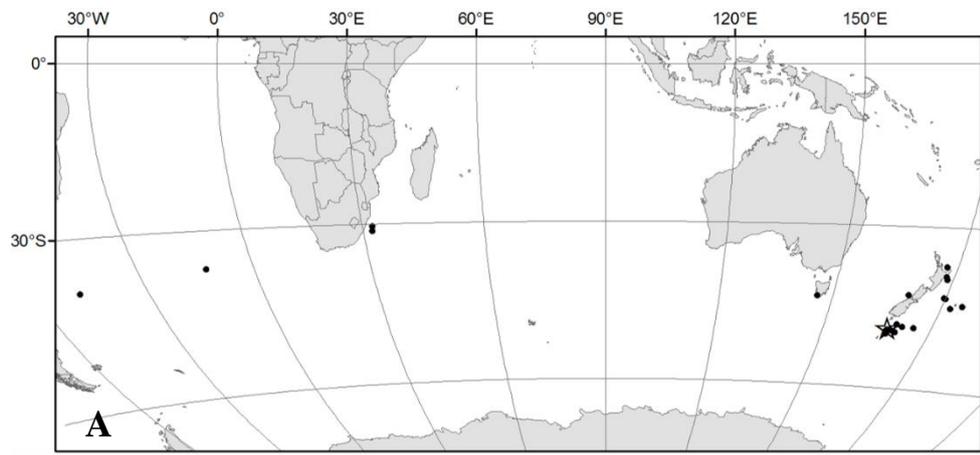


Fig. 75—*Taningia fimbria* sp. nov. A) distribution (star indicates type locality); B) adult; C) NIWA 95882, holotype, ♂, ML 305* mm; D) USNM 817618, paratype, ♀, ML 121 mm. Scale bars = B, C) 100 mm; D) 10 mm.

bases fleshy; Arms I, III and IV narrowing gradually to thin tips, their thickness from ~10% arm length at base to ~6% at midpoint; Arms II narrow only slightly before terminal photophore; bases of Arms I enlarged and hardened in sexually mature males, ~125% thickness of other arms, thereafter decreasing rapidly, matching other arms by 25% of arm length. Arm II photophore length ~5% ML (12–15–18% AL II), maximum width ~4% ML. All arms with low gelatinous aboral keels from base to tip. Arms IV without apparent ventral transverse pigment bands.

Arm hooks stout, robust; in females, largest in pairs 3–6 of Arms II. In males, proximal-most of Arm I ventral series largest (*i.e.*, 1V hook, approximately twice breadth and mass of 1D; Figs 77A–E); main cusp short, upright, inner angle acute; accessory claws broad, pointed but less clearly defined; base exceptionally broad. Hooks decrease gradually in size distally on all arms; hooks on Arms II terminate proximal to photophores. Prominent accessory claws present on all hooks, sharply pointed, variably curved (Figs 77F–K). Main cusp low off base, smoothly curved, inner angle right to slightly acute; aperture broad. Hood low on main cusp (Figs 77K–N); basal margin flat to slightly concave; tissue inserts under hood from inner hook sheath surface. Bases crenulated, most prominent laterally. Proximal hooks stouter than distal hooks, with relatively larger bases (length and breadth) and shorter main cusps.

Tentacles absent from all material examined (likely lost during post-larval stages as in *T. danae*).

Single low, elliptic swelling present on dorsal surface of each *recti abdominis* muscle, positioned ~20% ML posteriorly from anterior mantle margin, possibly photogenic (Figs 78A); diameter 1.8–2.0 mm in specimens ML 258*–437* mm (~0.5% ML); weakly attached dorsally to iridescent red patch of similar size and shape on ventral mesentery of ink sac. *Recti abdominis* muscles two discrete longitudinal bands parallel and adjacent to rectum; occasionally slightly overlie rectum but do not cover it nor contact each other across it; weakly attached to dorsal and lateral tissues; anteriorly attached at concavity of dorsal component of funnel organ; laterally expanded posteriorly, attaching to ventral surface of visceral mass. Rectum discrete, clearly visible between *recti abdominis* muscles; terminates in posterior quarter of funnel component of locking cartilage. Anal flaps short, positioned laterally; length ~0.8% ML; ovate, anterior tip pointed, chiral dorso-ventrally. Ventral visceral mesentery pore

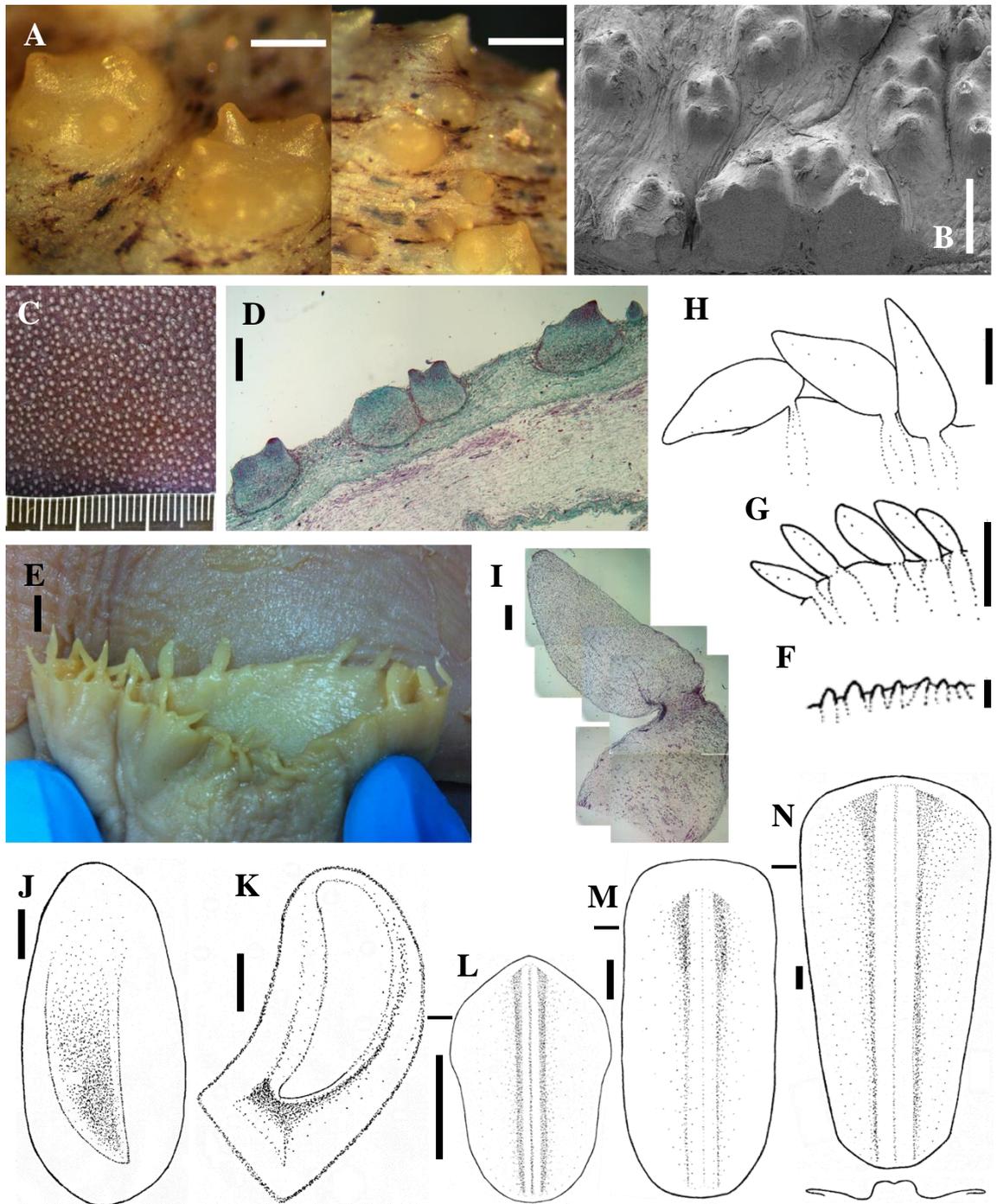


Fig. 76—*Taningia fimbria* sp. nov. A, B, D, H, I) MV F159950, ♀, ML unknown; C, N) NMNZ M.306357, ♀, fresh ML 970 mm; E, J, M) NIWA 71438, paratype, ♀, ML 730 mm; F) NMNZ M.117554, ♂, ML 285* mm; G) NHMUK 20160109, ♀, HL 153 mm; K) NMNZ M.274772, ♀, ML 884 mm; L) USNM 1157196, ♂, ML 300* mm. A–D) Epidermal tubercles: (A) with multiple (left) and single (right) papillae at 40× magnification, (B) ultrastructure including cross-section; (C) density in ~30 mm² section along dorsal fin; (D) section stained with Mallory's trichrome at 2.5× magnification; E–I) funnel aperture projections: (E) *in situ*, (F–H) detailed ontogenetic series, (I) section stained with Mallory's trichrome at 2.5× magnification; J) funnel component of locking apparatus; K) mantle component of locking apparatus; L–N) nuchal cartilage through ontogeny. Scale bars = A) 0.3 mm; B, D) 0.5 mm; E, G, H) 5 mm; F, I) 1 mm; J–N) 10 mm.

diameter ~0.5% ML. Gills robust; length 19–24–29% ML, with 35–40 lamellae.

Lateral profile of lower beak (8.26–18.55 mm LRL, Figs 78B–D) slightly longer than deep, with distal wing tips extending beyond rostral tip by 18–26–31% baseline; rostrum with distinct tip, distal to shallow notch, tip eroded in largest specimens; jaw edge visible, slightly concave; jaw angle obtuse, slightly obscured laterally by low, rounded wing fold, with short jaw-edge extension; depth between jaw angle and baseline greater than half overall depth. Hood high off crest, length 31–38–44% baseline. Crest discrete, lateral wall between crest and fold fully pigmented; length 48–57–63% baseline; tip free, with concave notch between crest and lateral wall; sloped steeply in nearly straight line. Lateral wall with curved, rounded fold, produced dorso-laterally in cross-section, doubling in breadth posteriorly; produced into shelf along anterior 30–40% of hood length; posterior lateral wall margin concave; free corner far beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width 148–154–162% that at jaw angle, length 113–130–142 % LRL, with cartilaginous pad. Ventral view with broad notch in hood; free corners narrowly spaced, in line with inner wing margin. Wing entirely unpigmented at LRL ~9 mm, remainder of beak pigmented excluding lateral wall posteriorly near free corner; beak fully pigmented LRL 10–11 mm.

Lateral profile of upper beak (8.83–16.55 mm URL, Figs 78E, F) longer than deep, maximum depth 44–46–54% length. Rostrum short, ~30% length, with distinct jaw-edge extension; jaw angle ~60°; low ridge of cartilage present along shoulder, most visible after free shoulder fully pigmented; oral shoulder margin convex; dorsal cartilage decreases with ontogeny. Hood long (length 69–71–76% UBL), tall (height ~19% UBL); junction of hood and free shoulder slightly concave. Lateral walls trapezoidal to triangular, deepest posteriorly, posterior margin straight to slightly angled. Dorsal view with posterior margin of crest and crest pigmentation straight to slightly concave. Lateral wall pigmentation progresses first along crest, from anterior to posterior, then laterally along wall from anterior to posterior. Crest pigmented dorsally at URL ~9 mm, free shoulder and remaining lateral wall transparent; free shoulder fully pigmented at URL ~13 mm, anterior lateral wall fully pigmented, posterior ~75% pigmented; beak fully pigmented at URL ~16.5 mm.

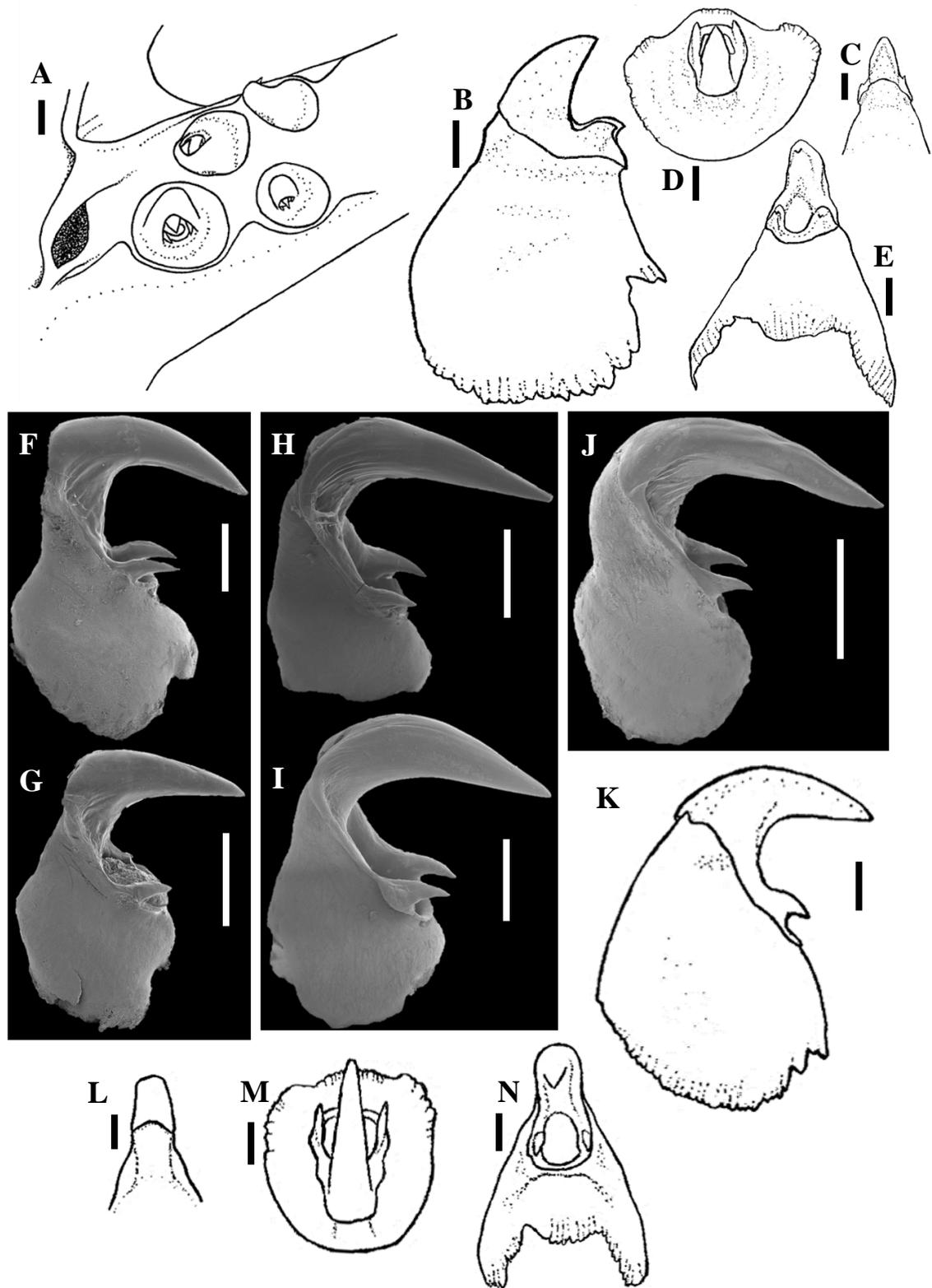


Fig. 77—*Taningia fimbria* sp. nov. arm and armature morphology. A) NMNZ M.117554, ♂, ML 285* mm; B–E) NIWA 71440, ♂, ML 364* mm; F, G) USNM 817618, paratype, ♀, ML 121 mm; H, I) NIWA 61959, ♀, ML 240* mm; J–N) NIWA 71441, ♂, ML 435* mm. A) Enlarged basal hook *in situ*, Arm IR; B–E) 1V hook (♂), Arm IVR: (B) lateral profile, (C) aboral, (D) apical, (E) oral; F) 16D hook, Arm IIIR; G) 3D hook, Arm IIIR; H) 26V hook, Arm IIIR; I) 3D hook, Arm IIIR; J) 21V hook, Arm IVL; K–N) 3D hook, Arm IVL: (K) lateral profile, (L) aboral, (M) apical, (N) oral. Scale bars = A) 5 mm; B–E) 2 mm; F) 0.25 mm; G, H) 0.5 mm; I–N) 1 mm.

Radula (Fig. 78G) with tricuspid rachidian, mesocone long, conical to slightly triangular, base concave; lateral cusps ~30% mesocone height, slightly laterally directed. First lateral tooth bicuspid, slightly shorter than rachidian, base concave; inner cusp conical to slightly triangular, slightly medially directed; outer cusp ~40% height of inner cusp, slightly laterally directed. Second lateral tooth simple, triangular, slightly longer than rachidian. Marginal tooth narrowly triangular, ~150% height of rachidian. Marginal plate present. Palatine palp (Fig. 78H) with 45–50 robust triangular teeth, each 65–125% rachidian height; most densely set in ventro-anterior 20% of length, anterior oral surface and dorso-anterior margin adentate, regularly arranged along remainder of oral surface.

Gladius unexamined to-date.

Colour (preserved) deep purple over all external body surfaces where outer-most gelatinous tissue layer intact, darkest over Arm II photophores; epidermal tubercles pale, unpigmented; ventral mantle surface maroon beneath gelatinous layer, other surfaces pale purple. Chromatophores present on dorsal head, over all external funnel surfaces and within groove. Arms darkest aborally, chromatophores present aborally underneath gelatinous layer, orally arms more maroon. Anterior funnel retractor muscles and inner mantle surface pigmented light purple in larger specimens, mantle component of locking cartilage and anal flaps unpigmented. Inner funnel surface evenly, lightly pigmented. Fresh specimens similar but colours more brilliant, unpigmented areas pure white (*e.g.*, Figs 70D bottom, 76C).

Etymology. This species is named for the fringe (= *fimbria*) of lanceolate projections along the funnel aperture.

Biology. Smallest mature specimen examined EML 342 mm (NMNZ M.117554, ♂, ML 285* mm). Females appear to start mating around ML 320–440 mm, based on two implanted head-only specimens (NHMUK 20160111, HL 93 mm; NHMUK 20160109, HL 153 mm); smallest whole mated female ML 655 mm (NHMUK 20160124). Implanted spermatangia described previously but misidentified as *T. danae* (Hoving *et al.* 2010, Figs 4 [=NHMUK 20160111], 5 [=NHMUK 20160124]; see Remarks below). Smallest specimen examined (ML 121 mm, Table 22) without any remnants of

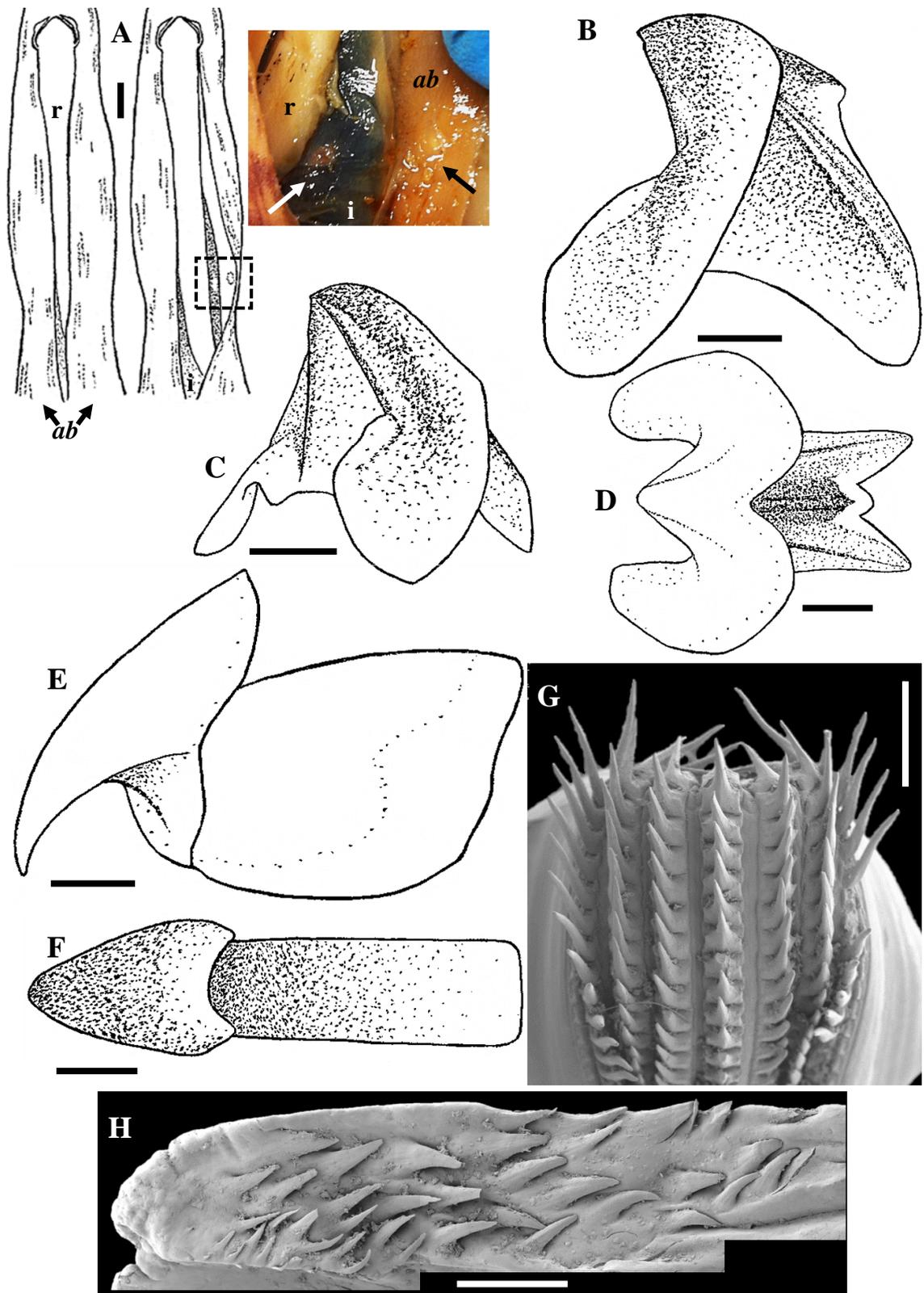


Fig. 78—*Taningia fimbria* sp. nov. A) NIWA 71439, paratype, ♂, ML 296* mm; B, D) NIWA 71667, ♂, ML 355* mm; C, E, F) NMNZ M.117554, ♂, ML 285* mm; G, H) NIWA 71441, ♂, ML 435* mm. A) *recti abdominis* muscles (*ab*) and rectum (*r*): natural state (left), right side dissected (right) revealing low dorsal *recti abdominis* swelling (insert, black arrow) and red iridescent patch (insert, white arrow) on ventral ink sac (*i*); B–D) lower beak: (B) lateral profile, (C) oblique profile, (D) ventral view (hood, wing pigmentation not detailed); E, F) upper beak: (E) lateral profile, (F) dorsal view; G) radula; H) palatine palp. Scale bars = A–F) 5 mm; G) 1 mm; H) 2 mm.

tentacles, therefore not post-larval; generally with greater mantle, fin, and head proportions, and smaller arm proportions than above.

Relationships were best described by power equations, except for a linear relationship between LRL and ML (Fig. 79). Goodness of fit varied somewhat, but most relationships fit the data well ($R^2 > 0.75$) despite relatively small sample sizes ($n = 6-10$). Single previous genus regression only available for LRL relationships, underestimated both measures of body size (Clarke 1980).

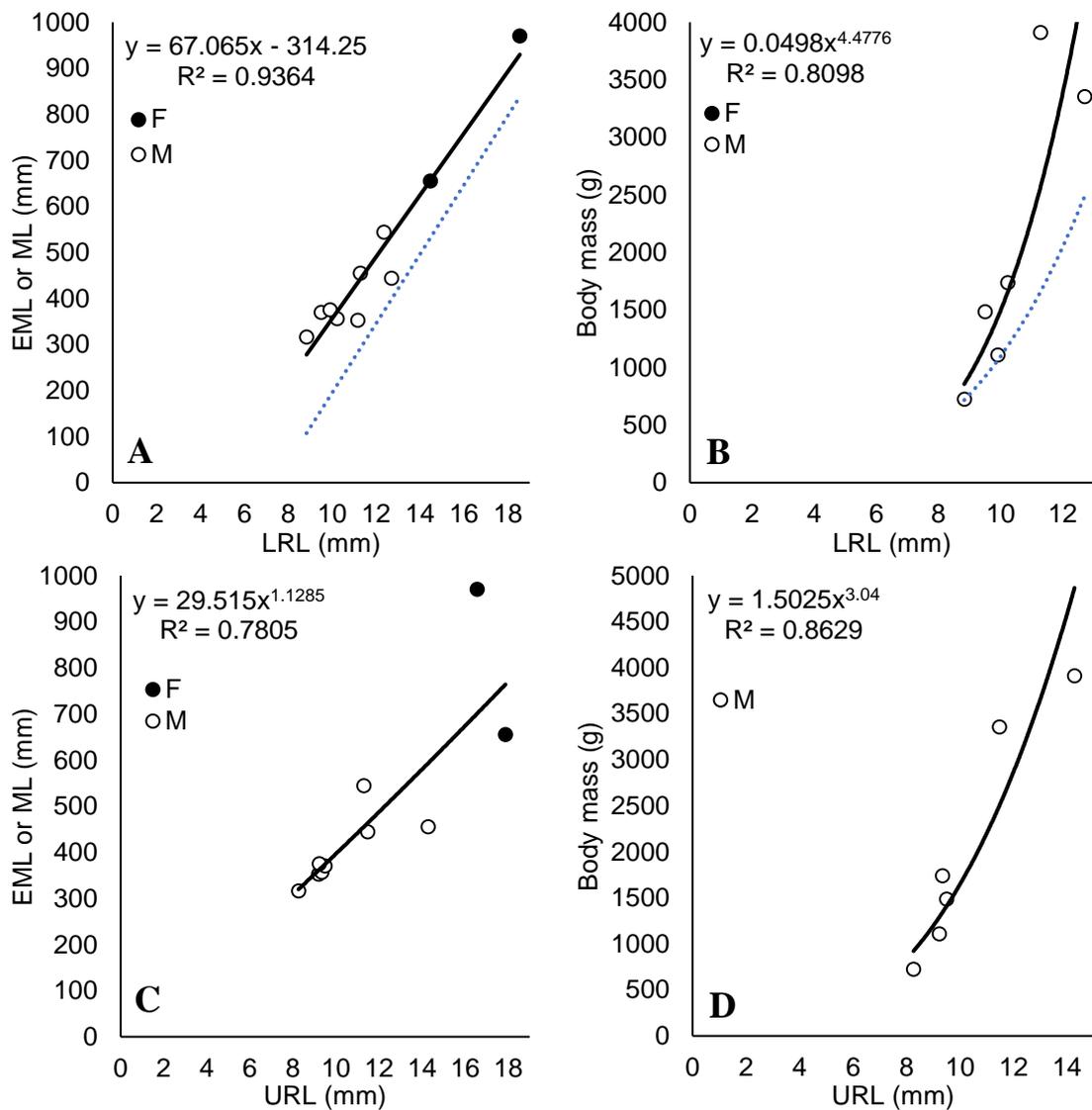


Fig. 79—*Taningia fimbria* sp. nov. Regressions of lower rostral length (LRL) against (A) dorsal mantle length (ML) and (B) preserved wet body mass, by sex; upper rostral length (URL) against (C) ML and (D) preserved wet body mass, by sex. Models of best fit (greatest R^2 value) are plotted in black against genus regressions of Clarke (1980; blue).

Remarks. For specimens of sufficient condition and size (ML >250 mm), *T. fimbria* is most readily separated from congeners by the lanceolate projections along the funnel aperture, the presence of epidermal tubercles, and, in males, the unusual morphology of Arms I and their basal hooks. In smaller or poorer-quality specimens, the most reliable characters separating it from co-occurring *T. danae* are differences in *recti abdominis* muscle and associated structures and the presence of accessory claws on proximal arm hooks in specimens ML >153 mm.

Clarke (1967) provided the first thorough description of the still relatively new species *T. danae* Joubin, 1931. Unfortunately, this work was clouded by the inclusion of at least three specimens of *T. fimbria* sp. nov. (specimens 4, 8 and 10). Similarly, all six specimens given in Table 30 of Clarke (1980) now appear attributable to *T. fimbria* sp. nov. However, Clarke noted the variable morphology of his specimens, and described many of the features now recognised to characterise *T. fimbria*: lanceolate projections along the funnel aperture, epidermal tubercles (which Clarke postulated might be a result of some parasite or disease), enlarged basal-most hook of Arms I (here recognised as sex-specific to males), and variable tail length.

However, contrary to Clarke (1967), the epidermal tubercles were herein recognised as endogenous structures. Histological sections revealed them to comprise dense, cellular connective tissue with thick collagen fibres and chondrocytes distally (Fig 76D); additionally, adjacent surface epithelial fibres encase the outer surface of the tubercles, embedding them in the epidermis. Thus far, material of sufficient condition to preserve their superficial nature has comprised only large female specimens, and additional specimens from the literature herein attributed to *T. fimbria* sp. nov. were either female or sex indeterminate individuals. While unquestionably species-specific, this character may additionally prove to be sex-specific. Finally, the presence of tubercles in *T. fimbria* sp. nov. provides the first conclusive morphologic character uniting the three families of the lepidoteuthid families clade: epidermal sculpture (see Discussion).

The funnel projections were also found histologically to be inherent structures of *T. fimbria* sp. nov., comprised of cellular, loose connective tissue (Fig. 76I). The funnel fringe is, to the author's knowledge, unique among cephalopods, and funnel aperture sculpture in general unreported; somewhat similar sculpture has been observed around the dorso-anterior mantle margin of *Sepioloidea lineolata*. The function of the funnel

fringe in *T. fimbria* sp. nov. could not be established, although the presence of muscle fibres at the attachment point suggests some kind of active role, most plausibly in the manipulation of reproductive products (*e.g.*, egg masses, oviducal or nidamental secretions) or ink (*e.g.*, Bush & Robison 2007).

Some of the specimens reported as *T. danae* by Hoving *et al.* (2010) were re-examined and found to belong to *T. fimbria* sp. nov. Among the examined material of *T. danae* *s.s.*, no such insemination-related incisions, as described therein, were found. Given the sex-specific Arm I modifications in male *T. fimbria* sp. nov., the enlarged basal hooks may be used to make these incisions for spermatangium implantation; the expanded bases of Arms I may be involved in powering the action of the basal hooks or in securing purchase on the female. All life stages of *T. danae* *s.s.* lack such hook alterations, and, in fact, mature males have different sex-specific armature modifications along Arms II.

5.2.3. *Taningia rubea* sp. nov. (Table 24, Figs 80–83)

Taningia danae (not Joubin, 1931) — Watanabe *et al.* (2006): Table 1; Kubodera (2007): Fig. 20; Kubodera *et al.* (2007): Figs 3, 4, Video clips 1–3.

Type material (4 specimens). **NSMT DYMO 1195**, Holotype, ♀, ML 540 mm, 36°05.7'N, 158°02.4'E, 2007, from stomach of sperm whale, 07NP-002; **NSMT Mo75355**, Paratype, sex indet., ML 53* mm, 39°01.6'N, 143°30.4'E, off Sanriku, Japan, 550 m, 30/07/1996, *Marusada-Maru*, stn W, MWT; **NSMT DYMO 1196**, Paratype, ♂, ML 480 mm, 38°21.6'N, 157°11.9'E, 2007, from stomach of sperm whale, 07NP-003; **NSMT DYMO 1114**, Paratype, ♀, ML 495* mm, 35°32'N, 142°30'E, 28/05/2001, from stomach of sperm whale, JARPN-II, S003-01.

Additional material examined (12 specimens). **NSMT Mo76347**, DYMO 1106, ♀, ML 610* mm, 42°00'N, 172°00'E, central north Pacific, 30/07/1995, *Wakatori-Maru*, coll. H. Tanaka; **NSMT Mo85593** (DNA 389), ♀, ML 830 mm, 40°08.93'N, 165°00.53'W, 30/06/2009, *Seikai-Maru*, stn 91, survey for Pacific saury; **NSMT Mo72082**, sex indet., ML 28 mm, 40°01'N, 143°50.3'E, off Sanriku, Japan, 530 m, 13/07/1996, *Marusada-Maru*, stn 8-4, MWT; **NSMT Mo75353**, 2 sex indet., ML 31*, 34 mm, 39°04.1'N, 143°31.9'E, off Sanriku, Japan, 25 m, 29/07/1996, *Marusada-Maru*, stn W, MWT; **NSMT Mo75354**, sex indet., ML 46* mm, 39°02.2'N, 143°29.7'E, off Sanriku, Japan, 450 m, 29/07/1996, *Marusada-Maru*, stn W, MWT; **NSMT Mo75880**, sex indet., ML 45* mm, 38°25.02'N, 142°04.12'E, off Sendai, Miyagi Prefecture, Japan, 450 m, 14/10/2001, *Wakataka-Maru*, haul E450, BTT; **NSMT Mo71582**, ♂, ML 50 mm, 36°53.4'N, 141°44.7'E, off Tohoku, Japan, 896 m, 17/10/1998, *Wakataka-Maru*, haul G-900, BTT; **NSMT DYMO 1194**, ♀, ML 628 mm, 36°05.7'N, 158°02.4'E, 2007, from stomach of sperm whale, 07NP-S002; **NSMT unaccessioned piece of mantle**, sex indet., 26°56'N, 142°21'E, floating at surface near 6 sperm whales, 07/10/1995, coll. Tsutusi & Ogasawara Whale Watching Association.

Unlocalised material examined (1 specimen). **NSMT Mo85689**, sex indet., ML 27 mm, possibly from between Shimizu and Ogasawara Islands, 31/05/1972, sample no. 258, from stomach of *Alepisaurus*, coll. Kubota & Tokai University.

Distribution (Fig. 80A). Northwestern Pacific, 42–27°N, 141°E–165°W; 25–900 m.

Table 24. Measurements (mm) of *Taningia rubea* sp. nov. Mean indices were calculated from specimens ML >53* mm with undamaged dimensions, and 'Side' indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	NSMT DYMO 1195	NSMT DYMO 1114	NSMT DYMO 1196	NSMT Mo75355	NSMT Unaccsioned	NSMT DYMO 1194	NSMT Mo76347	NSMT Mo71582	Mean index
Type status	Holotype	Paratype	Paratype	Paratype	None	None	None	None	
Sex	♀	♀	♂	Indet.	♀	♀	♀	♂	
DML	540	495*	480	53*	830	628	610*	50	30
MW	180	144	132	29*	230	195	227	23	83
FL	436	474	375	51	710	560	267	40	83
FW	484	457	384	84	668	520	590	96	83
HL	107*	161	129*	27	175	106*	185	23	21
HW	85	137	85	21	148	90*	88	23	17
Side	L	R	L	L		R	L	L	
AL I	188	109*	168	31*	318	252	332	36	37
AL II	158	136	124	27	243	180	215	30	28
AL III	198	133*	163	33	255*	238	312	32*	36
AL IV	189	155*	165	37	245	223	274	40 (R)	34
AH	NM, 10+1, NM, NM	10+1	NM, 10+1, NM, NM	10+1, *, *	NM, 10+1, NM	NM, 11, NM, NM	NM, 10+1, NM, NM	est. 25, 11+1, est. 26	
TL				0.6					

* indicates damaged character, not used to calculate indices.

Diagnosis. Arms II with 10 to 11+1 pairs of hooks; single large bioluminescent patch on ventral surface of ink sac; funnel component of locking apparatus blunt anteriorly; lower beak free corners spaced widely apart, posterior lateral wall margin concave, jaw angle positioned at midpoint of beak depth; fin width 80–90% ML; arm length 26–40% ML; skin and funnel aperture smooth; basal-most hooks on Arms I in males not enlarged.

Description (ML 480–830 mm, Figs 80B–83). Mantle conical to narrowly triangular, widest at anterior margin, width 28–30–33% ML; weakly muscled; tail pointed, long, length ~17% ML; dorsal and ventral anterior margins flat. Fin length 78–83–89% ML, width 80–83–90% ML; greatest fin width attained at ~45% ML; width of fin continuation along tail ~3% ML. Anterior fin insertion curved, blunt posteriorly.

Head square to trapezoidal, length ~21% ML, width ~17% ML, depth ~15% ML. Eyes ~8% ML. Funnel length ~21% ML, funnel groove shallow; aperture level with posterior third of eye. Funnel component of locking apparatus with very broad (~70% cartilage width), simple groove (Fig. 81A); groove tapers medially in anterior 20% of length to blunt point, lateral margin more strongly angled than medial; length ~8% ML, maximum width ~3% ML. Mantle component obliquely set raised oblong pad, bluntly pointed anterior medially (Fig. 81B); distinct squarish depression anterior to tip; length ~8% ML, width ~2% ML. Nuchal cartilage oblong, narrowing slightly anteriorly, with two lateral grooves (Fig. 81C). Olfactory papilla located laterally between two ventral-most nuchal pads; short, broad, fleshy round masses with central, shallow, broad pit.

Arms stocky, short, length 26–34–40%; formula I=IV=III>II or I=III>IV>II; Arms I, III, IV with at least 24 pairs of hooks in thick fleshy sheaths, Arms II with 10 to 11+1 pairs (Fig. 81D). Arm bases fleshy; Arms I, III and IV narrowing rapidly to tips, Arms II narrow only slightly before terminal photophores. Arm II photophore length ~5% ML (14–19–21% AL II). All arms with low gelatinous aboral keels from base to tip. Arms IV with pronounced transverse pigmented bands aborally, underlying epidermis, only visible via incision (Fig. 81E); bands present through depth of gelatinous keels, along at least proximal 80% arm length; bands become narrower and more densely set distally.

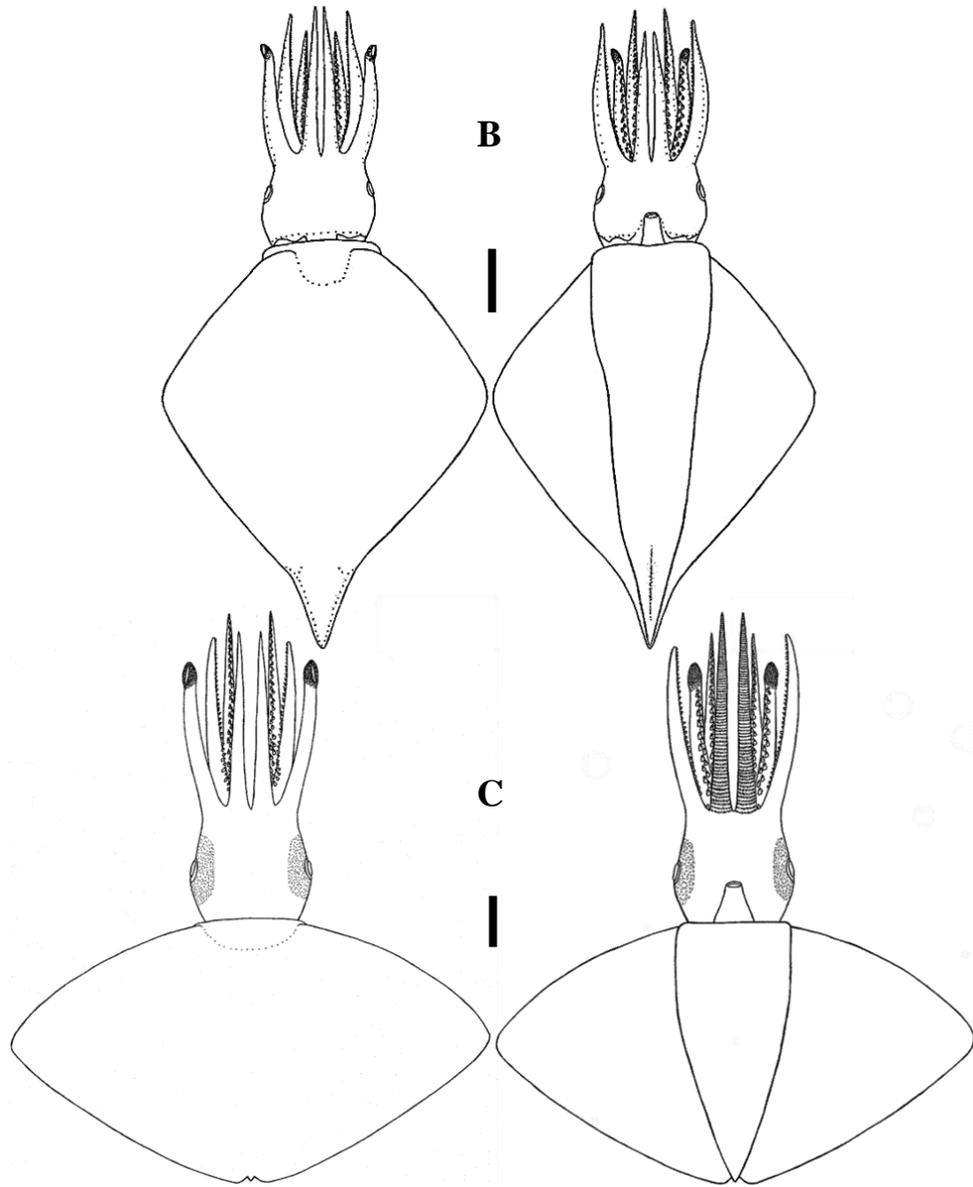
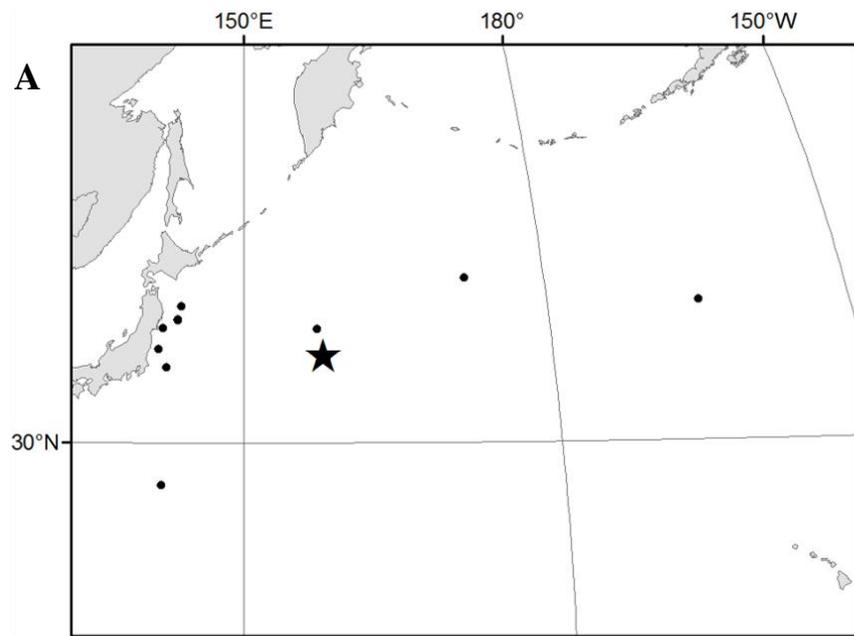


Fig. 80—*Taningia rubea* sp. nov. A) distribution (star indicates type locality); B) adult; C) post-larva. Scale bars = B) 100 mm; C) 10 mm.

Arm hooks stout, robust; in both sexes, largest in pairs 3–5 of Arms II; basal-most pair on Arms I smaller than second pair. Hook series generally decreasing gradually in size distally; hooks on Arms II maintain larger size proximally, with distal-most 3 or 4 hooks decreasing rapidly in size; hooks terminate proximal to photophore. Presence of accessory claws in adults and subadults remains uncertain due to condition (see Remarks). Remainder of description based on single post-larval hook (Fig. 81F–I): main cusp smoothly curved, inner angle slightly acute, aperture broad; accessory claws prominent, slightly curved to distal points; hood low on main cusp, basal margin slightly concave, tissue inserts under hood; bases crenulated, most prominent laterally.

Tentacles absent above ML ~55 mm, traces remain in post-larvae (see below).

Ink-sac photophore structure unknown in adults (see Post-larval section below). *Recti abdominis* muscles indiscrete; strongly fused medially into thickened sheet of tissue across rectum; posteriorly expanding into thinner sheet attached to ventral surface of visceral mass. Short free section of rectum emerges between fusion of *recti abdominis* muscles; in large specimens, fused rectum–*recti* complex protrudes ventrally from viscera. Anal flaps short, positioned laterally; ovate, anterior tip pointed, chiral dorso-ventrally. Gills robust; very large (length ~30% ML), broad (width ~7% ML); with 40–42 lamellae.

Lateral profile of lower beak (3.02, 17.86 mm LRL, Figs 82A–C) slightly longer than deep, with distal wing tips extending beyond rostral tip by ~27% baseline; rostral tip pointed, with slight step; jaw edge visible, slightly concave for length increasing at distal ~20% LRL, with short jaw-edge extension; jaw angle 90° in small beak (LRL ~3 mm), expanding to 110° in large beaks (LRL 14–17 mm), obscured slightly by low, rounded wing fold; depth anterior from jaw angle equal to posterior. Hood high off crest, length ~32% baseline. Crest discrete, lateral wall between crest and fold fully pigmented; length ~64% baseline; tip free with concave notch between crest and lateral wall; sloping in straight or slightly curved line distally. Lateral wall with slightly curved, rounded folds increasing in breadth slightly posteriorly; produced into shelf along anterior ~30% of hood length; posterior lateral wall curved; free corner just beyond crest tip; lateral wall fold (especially anteriorly) and crest more darkly pigmented than remaining wall. Wings broaden distally, greatest width ~153% that at jaw angle, length ~133% LRL, with narrow cartilaginous pad. Ventral view with broad

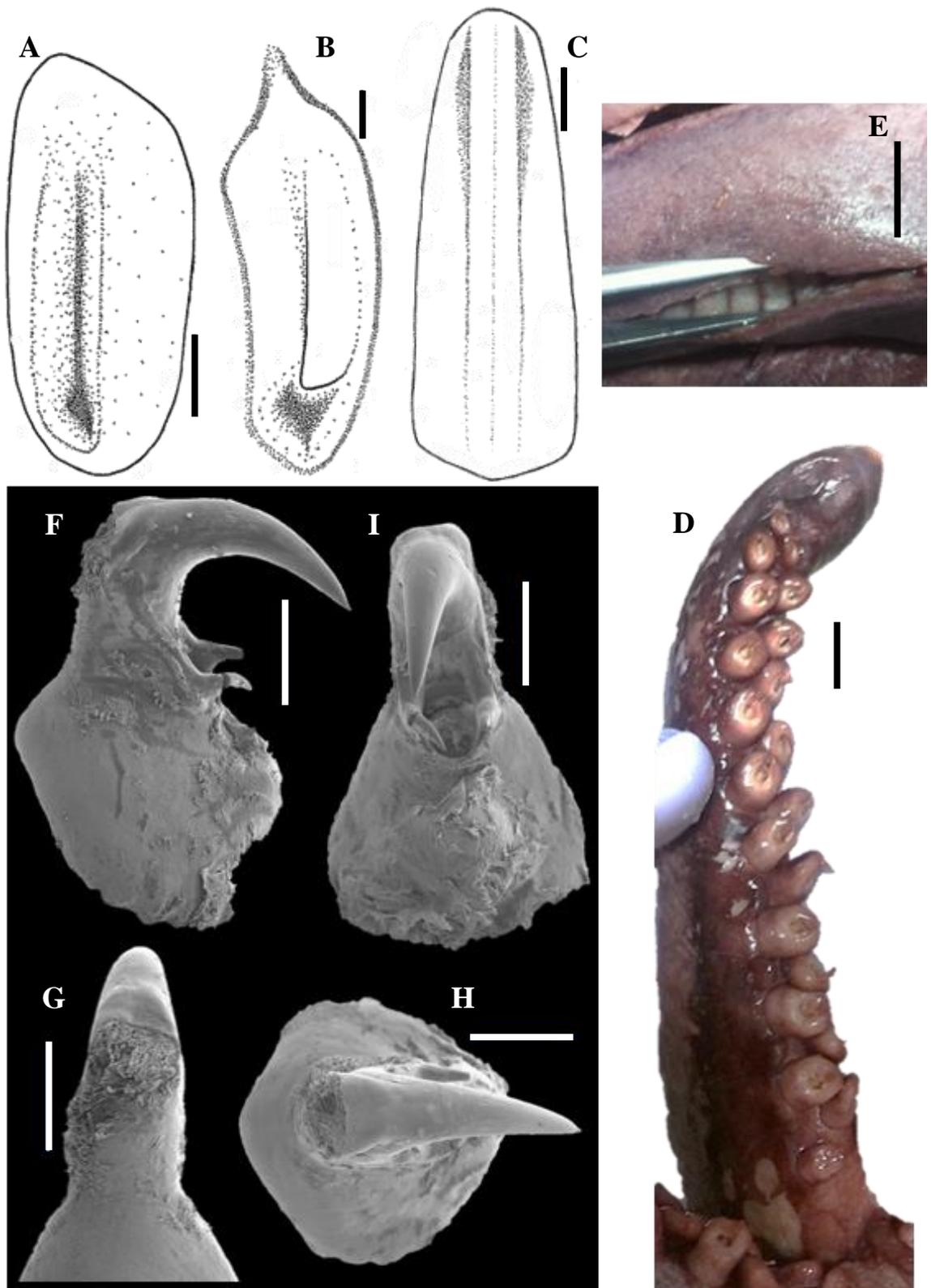


Fig. 81—*Taningia rubea* sp. nov. A, D) NMST DYMO 1114, paratype, ♀, ML 495* mm; B) NMST unaccessioned piece of mantle, sex indet.; C) NSMT Mo76347, ♀, ML 610* mm; E) NSMT DYMO 1195, holotype, ♀, ML 540 mm; F–I) NMST Mo75355, paratype, sex indet., ML 53* mm. A) funnel component of locking apparatus; B) mantle component of locking apparatus; C) nuchal cartilage; D) Arm IIR with 10+1 pairs of hooks; E) Arm IV incised to show aboral pigment bands in adult; F–I) 7D hook, Arm III: (F) lateral profile, (G) aboral, (H) apical, (I) oral. Scale bars = A–E) 10 mm; F–I) 0.25 mm.

notch in hood; free corners level with medial ~20% wing breadth in small beaks (LRL ~3 mm), expanding to midpoint of wing breadth in large beaks (LRL ~17 mm). Wings unpigmented at LRL ~3 mm, remainder of beak pigmented; start of pigmentation along lateral margin of wing at LRL ~14 mm; wing pigmented for entire length excluding patch near cartilaginous pad at LRL ~17–18 mm.

Lateral profile of upper beak (3.49, 19.24 mm URL, Figs 82D, E) twice as long as deep. Rostrum short, ~32% UBL, curved ventrally, with distinct jaw-edge extension; jaw angle ~70°; ridge of cartilage present along shoulder, broadest dorsally; oral shoulder margin with two weak scallops. Hood long (length ~78% UBL), tall (height ~23% UBL); junction of hood and free shoulder very slightly concave. Lateral walls approximately rectangular in small beaks (URL ~3.5 mm), with posterior margin nearly straight; large beaks (URL 16–19 mm) trapezoidal, with angled anterior and posterior margins; deepest at midpoint of UBL; occasionally with slightly indented oblique crease in ventral third, most prominent posteriorly. Dorsal view with posterior margin of hood straight, posterior margin of crest concave, posterior margin of crest pigmentation convex. Lateral wall pigmentation begins at anterior crest, darkening postero-ventrally with ontogeny. Slight pigmentation along anterior ~20% of crest at URL ~3.5 mm, free shoulder and remaining lateral wall transparent; dorso-anterior third of lateral wall pigmented by URL ~16 mm, free shoulder transparent; dorso-anterior ~60% of lateral wall pigmented by URL ~19 mm, dorsal third of free shoulder pigmented.

Radula, palatine palp, and gladius morphology unexamined.

Colour (preserved) deep purple over all external body surfaces where outer-most gelatinous layer of tissue intact, darkest over Arm II photophores; ventral mantle surface maroon beneath gelatinous layer. Arms pigmented around whole circumference, orally maroon, aborally overlying and occluding Arm IV transverse pigment bands; arm hook sheaths pigmented externally excluding basal surface. Funnel pigmented to posterior margin of locking cartilage, lightening posteriorly; with three unique strips of discrete, dark pigmentation in single specimen (NSMT DYMO 1114): single strip around circumference of aperture, pair of longitudinal strips along ventral surface (Fig. 83A). Inner mantle surface excluding mantle component of locking cartilage, anterior funnel

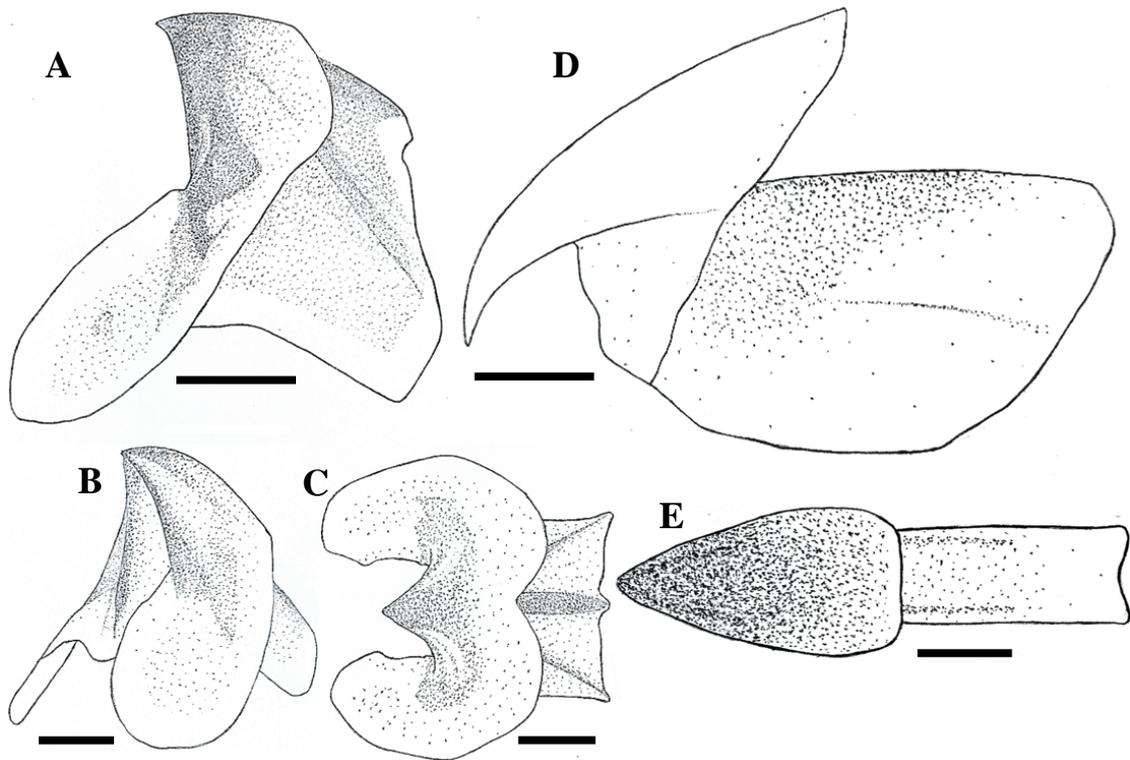


Fig. 82—*Taningia rubea* sp. nov. beaks. A–C) NSMT Mo85593 (DNA 389), ♀, ML 830 mm; D, E) NMST DYMO 1114, paratype, ♀, ML 495* mm. A–C) lower beak: (A) lateral profile, (B) oblique profile, (C) ventral view; D, E) upper beak: (D) lateral profile, (E) dorsal view. Scale bars = 10 mm.

retractor muscles, *recti abdominis* muscle sheet, and olfactory papillae pigmented light purple in large specimens; anal flaps darkly pigmented in specimens ML >495* mm (Fig. 83B). Post-larval specimens with distinct, large chromatophores evenly spaced across all external surfaces, particularly prominent on ventral mantle.

Post-larval specimens (ML 27.4–53* mm, Fig. 80C). Mantle triangular, maximum width ~46% ML. Fins together form short, exceptionally wide rhombus; length 80–91–97% ML, width 172–188–214% ML; with anterior and posterior margins convex. Head large (length, width ~46% ML). Eyes very large, diameter ~27% ML; ventrally with thin, crescent shaped sheet of lustrous, copper-coloured tissue, potentially photogenic (Fig. 83C); lens ~27% ED. Arms long, ~60–70% ML, with ventral arms slightly longer than dorsal, Arms II shortest; Arms IV with visible ventral transverse pigment bands. Arm II photophore length ~16% ML, ~27% AL II. Arm hooks comprise entire armature series (no suckers distally or proximally); all hooks with fully developed accessory claws. Tentacles atrophying, broken or reduced to very short, thin translucent gelatinous nubs. Single bioluminescent patch on ventral surface of ink sac; large, ovate, lustrous, copper coloured; overlain by rectum and *recti abdominis* muscles. *Recti abdominis*

muscles attached medially but division visible; each with single, opaque dorsal swelling at mid-photophore-patch (Fig. 83D). Anal flaps unpigmented.

Etymology. This species is named for the vivid red (=rubea) colour of the animals in life (see Remarks).

Biology. Smallest mature specimen examined ML 480 mm (NSMT DYMO 1196, ♂). Smallest mature female ML 495* mm (NSMT DYMO 1114, resting).

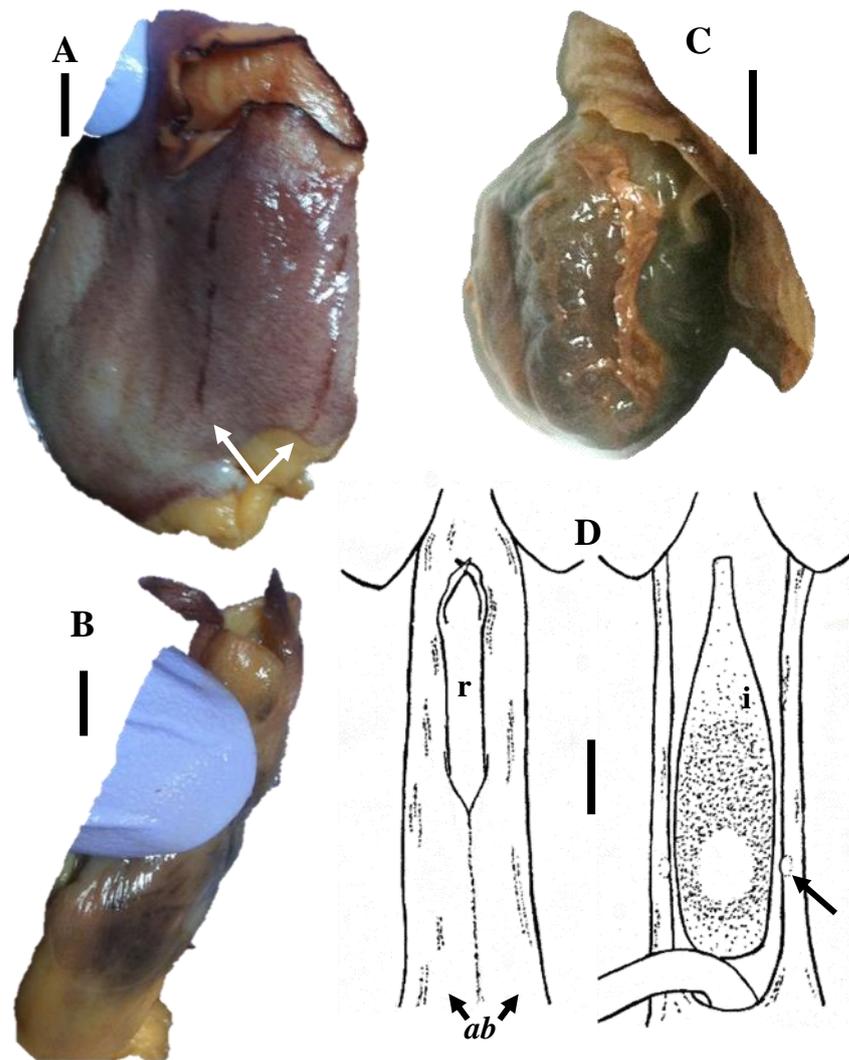


Fig. 83—*Taningia rubea* sp. nov. A, B) NSMT DYMO 1114, paratype, ♀, ML 495* mm; C) NMST Mo75355, paratype, sex indet., ML 53* mm. A) ventral view of funnel with aperture and paired longitudinal pigment bands (arrows); B) rectum with pigmented anal flaps; C) ventral view of left eye with lustrous, potentially photogenic tissue (arrow); D) *recti abdominis* muscles (*ab*) and rectum (*r*): natural state (left), separated (right) revealing ventral photogenic patch on ink sac (*i*) and dorsal *recti abdominis* swellings (arrow). Scale bar = A, B) 5 mm; C, D) 2 mm.

Remarks. *Taningia rubea* sp. nov. is readily separated from congeners by the low hook count on Arms II, a character consistent across the whole size range of specimens examined herein. Amongst the morphologic differences between *T. danae* and *T. fimbria* sp. nov. (see Remarks on those taxa), *T. rubea* sp. nov. shares some characters with each: its shorter arms, ventral Arm IV pigment bands, and rectum-*recti* complex morphology resemble *T. danae*, while narrower fins and a longer tail length align it with *T. fimbria* sp. nov.

All specimens ML >480 mm (excluding NSMT Mo76347 and NSMT Mo85593) were recovered from stomach contents. Thus, the condition of some features on these specimens is exceptionally well preserved compared to trawl-caught specimens. Noteworthy pigmentation characters of the funnel and anal flaps, not yet observed in other *Taningia* spp., were first identified from such specimens. While one of each of these characters was also observed on each of the trawl-caught specimens – NSMT Mo76347 bore pigmented anal flaps but had a damaged funnel aperture, NSMT Mo85593 had a darkly pigmented funnel aperture but damaged anal flaps – they were not raised to diagnostic status given the infrequent presence in specimens of *T. rubea* sp. nov. and the insufficient number of comparable specimens of other species of *Taningia*. However, it appears from a few specimens of *T. danae* and *T. fimbria* sp. nov. that, while the inner funnel surface of both species is lightly pigmented, a distinct band around the aperture is lacking as are darkly pigmented anal flaps. Lastly, also likely due to their collection history, the arm hooks of all *T. rubea* specimens ML >480 mm were softened or degraded beyond use for description.

Based on their geography, the following previous reports of *T. 'danae'* from around Japan are likely attributable to *T. rubea* sp. nov.: a specimen taken from the stomach of an *Alepisaurus ferox* (Okutani & Kubota 1976); six large specimens recovered from sperm whales off Joban District, Japan (Okutani *et al.* 1976), but not the 16 specimens collected from the EASTROPAC survey also mentioned therein (see *Taningia* sp. IV Comparative Material, Remarks); eight small specimens collected from the stomachs of sperm whales of Honshu, Japan (Okutani & Satake 1978); and seven specimens trawled from the Kuroshio Extension (Shevtsov *et al.* 2013). Similarly, video footage of wild *T. 'danae'* off the Chichijima Islands reported by Kubodera *et al.* (2007), as well as a specimen imaged in Kubodera (2007; Fig. 20a), show the long, thin tail of *T. rubea* sp. nov. References to *Taningia 'danae'* in Okutani's (1973) "Guide and keys to squid in

Japan” are likely also referable to *T. rubea* sp. nov. Unfortunately, none of the above specimens were available for examination during the present study and their published descriptions were insufficiently detailed, precluding them from formal synonymy.

5.2.4. *Taningia* sp. IV (Table 25, Fig. 84)

Material examined (2 specimens). **B-Alep-667 Prey #1**, ♂, ML 47 mm, 30°±2.5°N, 140±2.5°W, from stomach of *Alepisaurus ferox*, Hawaiian longline fishery; **B-Alep-344 Prey #1**, sex indet., est. ML 26 mm, 30°±2.5°N, 170±2.5°W, 10/06/2014, from stomach of *Alepisaurus ferox*, Hawaiian longline fishery.

Comparative material (19 specimens). **USNM 730681**, ♀, ML 59 mm, 41°07.8'N, 172°22.2'W, 04/08/1955, RV *Hugh M. Smith*, stn 30-48, 3 m IKMWT; **ZMUC stn 726**, NM, ML 206 mm, 5°49'N, 78°52'W, Gulf of Panama, 3800 m, 13/05/1952, 1110–1240, Galathea Expedition 1950-52, stn 726, HOT; **SBMNH 49330**, sex indet., ML 19.7 mm, 5°24'N, 82°30'W, 1000 m, 18/06/1973, RV *Velero IV*, stn 19097, IKMWT, R. Pieper; **NSMT Mo61897**, ♀, ML 41 mm, ♂, ML 40.5 mm, 01°58.7'N, 85°11.1'W, west off Ecuador, 11/02/1981, from stomach of bigeye tuna, ♂, 168 cm, 114 kg, Shirasawa, JAMARC, temperature at surface 27.0°C, temperature at 100 m 14.7°C; **NSMT Mo61935**, 2 ♀, ML 47.5, 45 mm, 2 ♂, ML 36.5, 31 mm, 01°18.3'S, 84°46.7'W, west off Ecuador, 02/02/1981, from stomach of bigeye tuna, ♀, 99 cm, 21 kg, Shirasawa, JAMARC, temperature at surface 22.2°C, temperature at 100 m 15.1°C; **NSMT Mo61900**, 4 sex indet., ML 38, 26.5, 23.5, 22* mm, 01°18.3'S, 84°46.7'W, west off Ecuador, 02/02/1981, from stomach of bigeye tuna, ♂, 129 cm, 44 kg, Shirasawa, JAMARC, temperature at surface 22.2°C, temperature at 100 m 15.1°C; **NSMT Mo61898**, ♂, ML 36* mm, 01°25.1'S, 95°32.8'W, west off Ecuador, 24/01/1981, from stomach of bigeye tuna, ♀, 98 cm, 22 kg, Shirasawa, JAMARC, temperature at surface 23.7°C, temperature at 100 m 13.2°C; **NSMT Mo61899**, ♂, ML 36 mm, 01°42'S, 95°59.3'W, west off Ecuador, 23/01/1981, from stomach of bigeye tuna, ♀, 146 cm, 68 kg, Shirasawa, JAMARC, temperature at surface 24.1°C, temperature at 100 m 13.2°C; **NSMT Mo85688**, 2 ♂, ML 45, 39 mm, 2 sex indet., ML 43.5, 38* mm, 07°17.6'S, 106°36'W, 01/03/1980, Sample no. EP.B.

Distribution (Fig. 84A). Temperate northeastern Pacific.

Description (ML 26–47 mm, Fig. 84B). Post-larval specimens with conical mantles; widest at anterior margin, width ~40% ML; tail pointed, short, length ~10% ML. Fin length ~90% ML, width very broad (~190% ML); greatest fin width attained at ~55% ML. Anterior fin insertion curved.

Head length ~45% ML, width ~50% ML. Eyes large, diameter ~25% ML; ventrally with thin, crescent-shaped sheet of lustrous, copper- to maroon-coloured tissue, possibly photogenic; lens diameter ~40% ED. Funnel length ~35% ML. Funnel component of locking apparatus unknown (degraded); mantle component length ~10% ML, width ~3% ML. Maximum nuchal cartilage width ~7% ML.

Arms long, 40–53–67% ML, with ventral arms slightly longer than dorsal. Arm hooks present to arm tips, Arms I, III, IV with 25–27 pairs of hooks, Arms II with 12+1 or 13 pairs. Arms robust, Arms I, III and IV taper gradually to tips, Arms II narrow slightly before terminal photophores. Arm II photophore length ~10% ML (~13% AL II). Arms IV without obvious transverse pigment bands. Low gelatinous aboral keels present on at least Arms III.

Table 25. Measurements (mm) of *Taningia* sp. IV from Hawaii, with similar-sized specimens of *T. danae* (for additional comparably sized specimens see Table 22). Mean indices were calculated from specimens with undamaged dimensions, and ‘Side’ indicates the side of the animal used for brachial crown measurements (*i.e.*, the more complete side), with exceptions noted in specific rows.

Specimen ID	B-Alep-667 #1	B-Alep-344 #6	Mean Index	NMNZ M.67249	ZMUC stn 3894I	USNM 728849	Mean Index
Species	sp. IV	sp. IV		<i>danae</i>	<i>danae</i>	<i>danae</i>	
Locality	Hawaii	Hawaii		New Zealand	off NW Sumatra	Bermuda	
Sex	♂	Indet.		♀	♀	Indet.	
DML	47	est. 26		48	31.7	24	
MW	20	*	43	25.7	17.6	10.7	51
FL	41	24.1	90	47	29	21.5	93
FW	78	54.5	188	82	53	41	170
HL	21	12.5	46	17	11.6	9.7	37
HW	19	14.8	49	26	14.3	10.3	47
Side	R	L		L	R	R	
AL I	22	11.7	46	24	14.2	8	43
AL II	19	12.9	45	21	12.8	10.5	43
AL III	25	17.5	60	23 (R)	14.3	9	44
AL IV	26	17 (R)	60	24.5	16.2	8	45
AH	25, 13, 26, 27	16*, 12+1, 14*, 17*		13*, 13, 20*, 12*	*, 13, *, *	NM, NM, NM, NM	
TL	6.5	11.41 (R)	29	4.23*	7.8	4.95* (L)	
CL	1.14	2.32 (R)	6	*	2.1	*	
CS	*	4		*	4	*	

* indicates damaged character, not used to calculate indices.

Arm hooks robust but degraded; at least basal arm hooks with accessory claws.

Tentacles atrophying, thinner and shorter than adjacent arms, tissue insubstantial; in larger specimen, tentacle length 14% ML, without any club definition or intact suckers, distal tip darkly pigmented; in smaller specimen, both tentacles intact, length 44% ML, clubs with 4 pairs of domed suckers, degraded.

Large, circular, coppery bioluminescent patch on ventrum of ink sac, iridescence extending anteriorly and posteriorly of central patch. *Recti abdominis* muscles thin, straddling rectum, with round opaque masses level with the middle of the circular patch. Rectum free for whole length.

Beaks, radula, palatine palps, and gladius were not examined given scarcity and frailty of specimens.

Ventral surfaces, where skin intact, generally with large circular chromatophores of red to purple colouration, pale yellow interstitially. Arm II photophores very darkly pigmented.

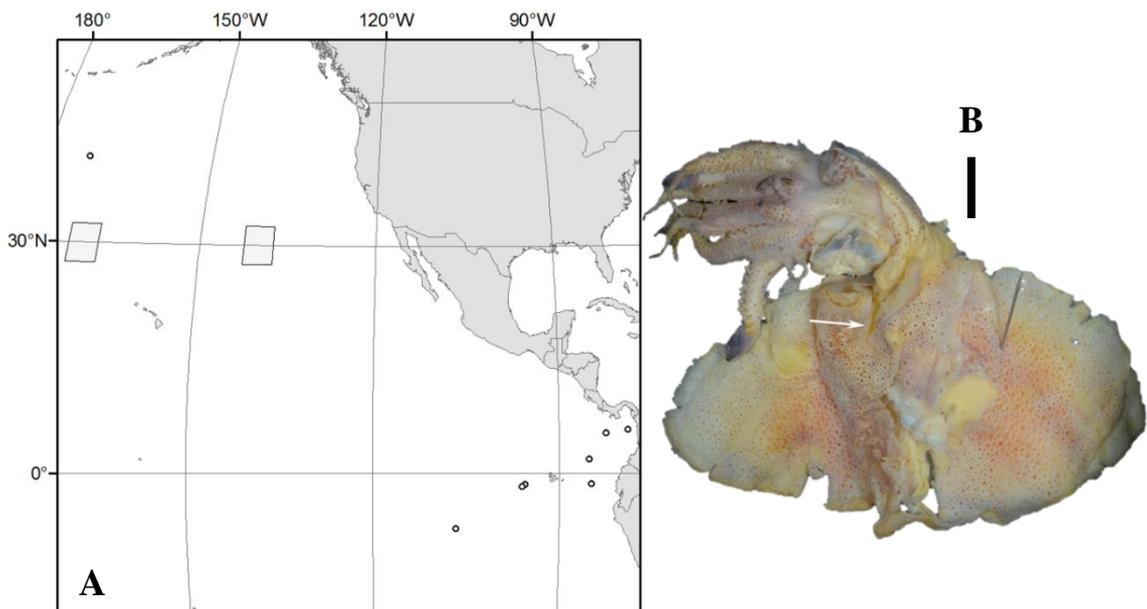


Fig. 84—*Taningia* sp. IV. A) distribution (grey boxes indicates Material Examined, empty circles indicate Comparative Material); B) B-Alep-667 Prey #1, ♂, ML 47 mm (photo by R. Young). Scale bar = 10 mm.

Remarks. This species was identified by strong consistent genetic separation from other recognised species of *Taningia* (see Genetics, Discussion). However, only weak morphologic characters support this designation at present: *Taningia* sp. IV is provisionally distinguished from post-larval *T. danae* by a greater ALI and from post-larval *T. rubea* by having >12 hook pairs on Arms II. The ventral arms in *Taningia* sp. IV are also proportionally longer (compared with the dorsal arms) than in *T. danae* and *T. rubea* (where dorsal and ventral arms are near-equal in length). However, these differences are based on few specimens, none in very good condition, with differing collection histories (*i.e.*, ex-gut-content versus trawl-caught), which renders relying on these characters as diagnostic premature. Additionally, no comparable specimens of *T. fimbria* were available. *Taningia* sp. IV is described above, since specimens of known morphology and genetics were available, but type material is not yet designated due to the poor condition of currently available material, its limited size range, and the lack of strong diagnostic characters for the species.

Nineteen *Taningia* specimens from the eastern Pacific were listed under Comparative Material as their collection locality placed them within the potential range of *Taningia* sp. IV and, given the poor morphologic separation between *Taningia* sp. IV and *T. danae* (their previous designation), they could not be confidently attributed to either. *Taningia rubea* sp. nov. was excluded from consideration due to the substantial geographic separation between it and these lots, with the exception of USNM 730681 (but which had 12 pairs of hooks on Arm IIR). Similar to *Taningia* sp. V, the recognition of *Taningia* sp. IV calls into question the presence of *T. danae* *s.s.* in the north Pacific. Unfortunately, the majority of these specimens could not be re-examined with the timeframe of this study. Their distributions were plotted with those of *Taningia* sp. IV (Fig. 84, hollow circles)

5.2.5. *Taningia* sp. V (Fig. 85)

Genetic samples (2 specimens). **PC10-01-B0630-2888-MTB251-SN**, sex unknown, size unknown, 28°32.07'N, 88°29.06'W, 30/06/2011, 0521–0754 hr, 0–750 m, RV *Pisces*, stn B251, cruise 10, IH trawl; **ZMH 79906**, ♀, ML NM, 02°34.45'N, 25°13.92'W, 29/03/2015, 460 m, RV *Walther Herwig III*, stn 324, cruise 383, coll. Fock.

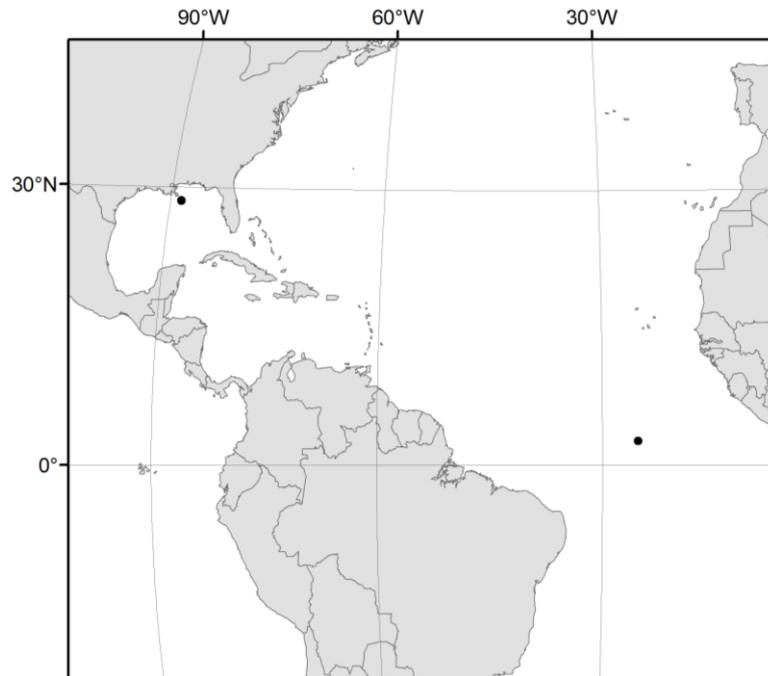


Fig. 85—*Taningia* sp. V. Distribution.

Remarks. Like *Taningia* sp. IV, this species was also identified by consistent genetic separation from other recognised species of *Taningia* (see Genetics). At present, neither specimen has been available for thorough examination, although ZMH 79906 was viewed briefly and does belong to *Taningia*.

6. GENETICS

Bidirectional sequences were successfully obtained from 126 of 128 tissue samples, with sequences from 7 additional specimens either mined from GenBank or provided by colleagues (Table 1). COI sequences were 658 bp, did not contain stop codons or indels, and comprised 133 individuals from 13 of the 16 taxa recognised herein. Two samples (NSMT S003-4 and NSMT DYMO 1114) failed to amplify; however, NSMT had previously obtained COI sequences from these individuals which matched other NSMT sequences for '*O. megaptera*' and '*T. danae*', respectively (herein, these specimens and genetic groupings were identified as *O. laticauda* sp. nov. and *T. rubea* sp. nov., respectively). 16S rRNA sequences were 513–520 bp, contained indels, and comprised 51 specimens from 12 taxa; *cyt b* sequences were 604–606 bp, did not contain indels or stop codons, and comprised 42 individuals from 11 taxa.

Nine octopoteuthid taxa were sequenced for the first time herein, including seven new species described in this work. No samples or sequences were obtained for *O. nielsenii*, *O. leviuncus* sp. nov., or *O.* sp. Giant Atlantic nov.; however, at least one species per species group and genus was sequenced. AT content was greater than GC content in all gene regions sequenced, being the greatest in *cyt b* and the least in COI (Table 26).

All species where multiple individuals were sequenced formed distinct groups on all phylogenies (Figs 86–90). The two species represented by single sequences (*O.* sp. Giant Pacific nov. and *O.* sp. IO nov.) were distinctly separated from other species in the phylogenies in which they were included (Fig. 86, 87, 90). Bootstrap support was high for all species clusters in all phylogenies, with the lowest value being 78% for *O. megaptera* in the 16S rRNA phylogeny (Fig. 87). All other species clusters had >83% bootstrap support, and mean bootstrap values for each species across all phylogenies ranged from 87.3 to 99.4%. However, in three instances sequences belonging to the same species grouped together but did not resolve into a single branch and, therefore, had no associated bootstrap value: *O. rugosa* and *Taningia* sp. V in the 16S rRNA phylogeny (Fig. 87), *T. danae* in the *cyt b* phylogeny (Fig. 88). For COI, mean and maximum intraspecific variation ranged from 0.0–0.15–0.43% and 0.0–0.41–1.08%, respectively (Table 27), and for all gene regions, the greatest mean intraspecific difference was 0.62% (Table 28). The greatest mean intraspecific variation for all gene regions was observed in *O. megaptera*, and the most variable gene region was *cyt b*.

The bPTP analysis supported the majority of genetic groupings across the three gene regions examined. All 13 available taxa for COI were supported, although posterior probability values ranged widely, from 0.13–0.54–1.0 (Fig. 91). Eight of twelve potential clusters were recognised among 16S rRNA sequences, with *Taningia* sp. IV and V not distinguished from *T. danae*, and *O. rugosa* split into six separate taxa (although all were positioned closely together); within the *T. danae*+*Taningia* spp. cluster, the two *Taningia* sp. IV sequences grouped together with posterior probability of 0.26 (Fig. 92). Ten of eleven potential groupings were supported from *cyt b* sequences, including *Taningia* sp. IV and V; however, *T. danae* was divided into three taxa (Fig. 93).

Genetic support was found for both *Octopoteuthis* species groups with multiple species sequenced (*sicula* and *megaptera* groups), and for the now polytypic *Taningia*. A sister-taxon relationship between *O. sicula* and *O. fenestra* sp. nov., constituting all available sequences of the *sicula* species group, was very strongly supported by both the strict and inclusive multigene phylogenies (bootstrap support 94% and 93%, respectively). The *megaptera* species group, comprising three species in the strict phylogeny and four in the inclusive, was moderately supported (bootstrap support 72% and 75%,

Table 26. Sequence composition of three mitochondrial gene regions for specimens of the Octopoteuthidae analysed in this study.

Base %	COI	16S rRNA	<i>cyt b</i>
G	15.33	19.07	19.91
C	22.25	10.01	11.41
A	28.20	33.64	22.75
T	34.23	37.27	45.93

Table 27. Estimated percent distance between COI sequences for 11 octopoteuthid species with >1 available sequence (excludes *O. sp. Giant Pacific* nov., *O. sp. IO* nov.).

Species	Mean intraspecific % distance	Max intraspecific % pairwise distance	<i>N</i>
<i>O. sicula</i>	0.07	0.31	17
<i>O. fenestra</i>	0.13	0.46	16
<i>O. megaptera</i>	0.43	0.77	6
<i>O. rugosa</i>	0.40	0.78	8
<i>O. laticauda</i>	0.17	0.46	7
<i>O. deletron</i>	0.06	0.62	54
<i>T. danae</i>	0.39	1.08	10
<i>T. fimbria</i>	0	0	3
<i>T. rubea</i>	0	0	3
<i>T. sp. IV</i>	0	0	2
<i>T. sp. V</i>	0	0	2

respectively), within which a strongly supported (bootstrap support 89%) sister-taxon relationship was found between *O. megaptera* and *O. sp. IO nov.* in the inclusive phylogeny (the only multigene phylogeny in which *O. sp. IO nov.* was included). *Taningia*, comprising all five taxa in both multigene phylogenies, was strongly supported in the strict phylogeny (bootstrap support 96%) but only weakly in the inclusive phylogeny (bootstrap support 69%); however, both recovered *T. fimbria* sp. nov. as basal in the genus. Very strong bootstrap support (99% in both multigene phylogenies) was found for a sister relationship between *Taningia* sp. IV and V, with *T. danae* as the next closest congener in a moderately supported clade (bootstrap support 76% and 74% in the strict and inclusive phylogenies, respectively). The range of minimum pairwise differences between species groups and genera at COI (12.26–18.64%; Table 29) was similar to the range of maximum pairwise differences within groups (8.73–17.91%; Table 30). Pairwise distances of octopoteuthid COI sequences from the outgroup (*Pholidoteuthis* sp.) were 19.31–22.39–24.89%.

For all three loci, maximum intraspecific differences were smaller than the minimum interspecific differences (Table 28). COI had the highest mean and maximum interspecific difference, more than twice those of 16S rRNA, but only slightly greater than *cyt b*. The *Octopoteuthis* species with the smallest mean interspecific difference at COI were *O. sp. IO nov.* and *O. megaptera* at 5.90%. Within *Taningia*, *Taningia* sp. IV

Table 28. Mean (\pm standard deviation), minimum and maximum of mean intraspecific and interspecific percent distances among the Octopoteuthidae for COI, 16S rRNA, and *cyt b*.

Gene region	Min	Mean	Max
Intraspecific			
COI	0	0.15	0.43
16S rRNA	0	0.09	0.43
<i>cyt b</i>	0	0.36	0.62
Interspecific			
COI	3.04	16.91	25.18
16S rRNA	1.39	6.16	9.65
<i>cyt b</i>	3.85	15.02	22.14

Table 29. Minimum between-species-group (s.g.) and -genus pairwise distances for COI. Two species groups (*deletron* s.g. and Giant s.g.) were only represented by a single species each.

	<i>sicula</i> s.g.	<i>Taningia</i>	sp. Giant	<i>deletron</i>
<i>megaptera</i> s.g.	14.09	18.64	13.98	12.60
<i>deletron</i>	12.26	15.68	13.36	
sp. Giant	14.78	17.02		
<i>Taningia</i>	16.49			

and V had the smallest mean interspecific difference at 3.04%; each were 7.67% and 7.88% different from *T. danae*, respectively, the next closest species. The smallest pairwise difference at COI between species of *Octopoteuthis* and *Taningia* was 15.68% between *O. deletron* and *T. danae* (Table 29). The greatest pairwise percent difference between species of *Octopoteuthis* was 18.79% (between *O. deletron* and *O. megaptera*), and 17.91% between species of *Taningia* (between *T. fimbria* sp. nov. and *Taningia* sp. IV; Table 30). The maximum pairwise difference between sequences of *Octopoteuthis* and *Taningia* was 25.47%, between *Taningia* sp. IV and *O. megaptera*; this was also the greatest difference between any two octopoteuthid sequences.

Table 30. Maximum within-species-group (s.g.) and -genus pairwise distances for COI, of *N* pairwise comparisons. Two species groups (*deletron* s.g. and Giant s.g.) were represented by a single species each, and *O. sp. Giant Pacific nov.* by a single sequence; the maximum intraspecific pairwise distance for *O. deletron* is given in Table 27.

Species group	Max	<i>N</i>
<i>sicula</i> s.g.	12.66	528
<i>megaptera</i> s.g.	8.73	231
<i>Octopoteuthis</i>	18.79	5995
<i>Taningia</i>	17.91	190

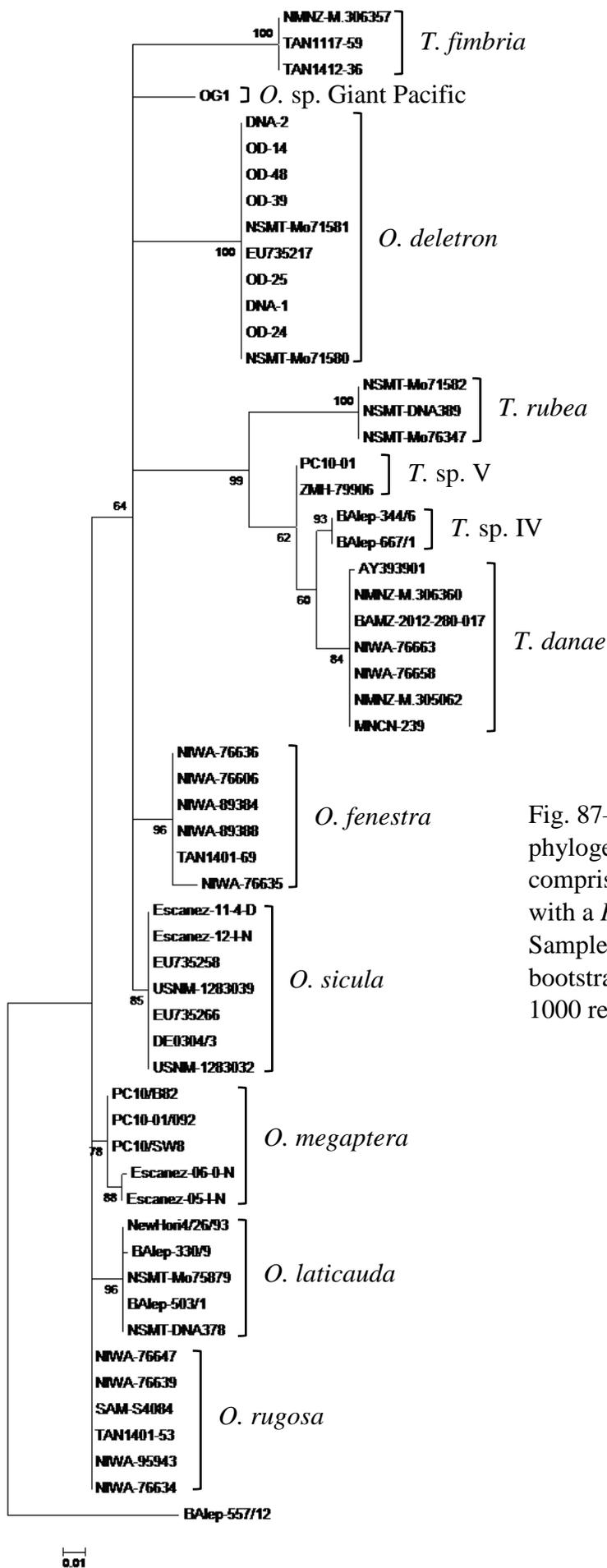


Fig. 87—Maximum-likelihood phylogeny of 51 16S rRNA sequences, comprising 12 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Sample names correspond to Table 1; bootstrap support values are based on 1000 replicates.

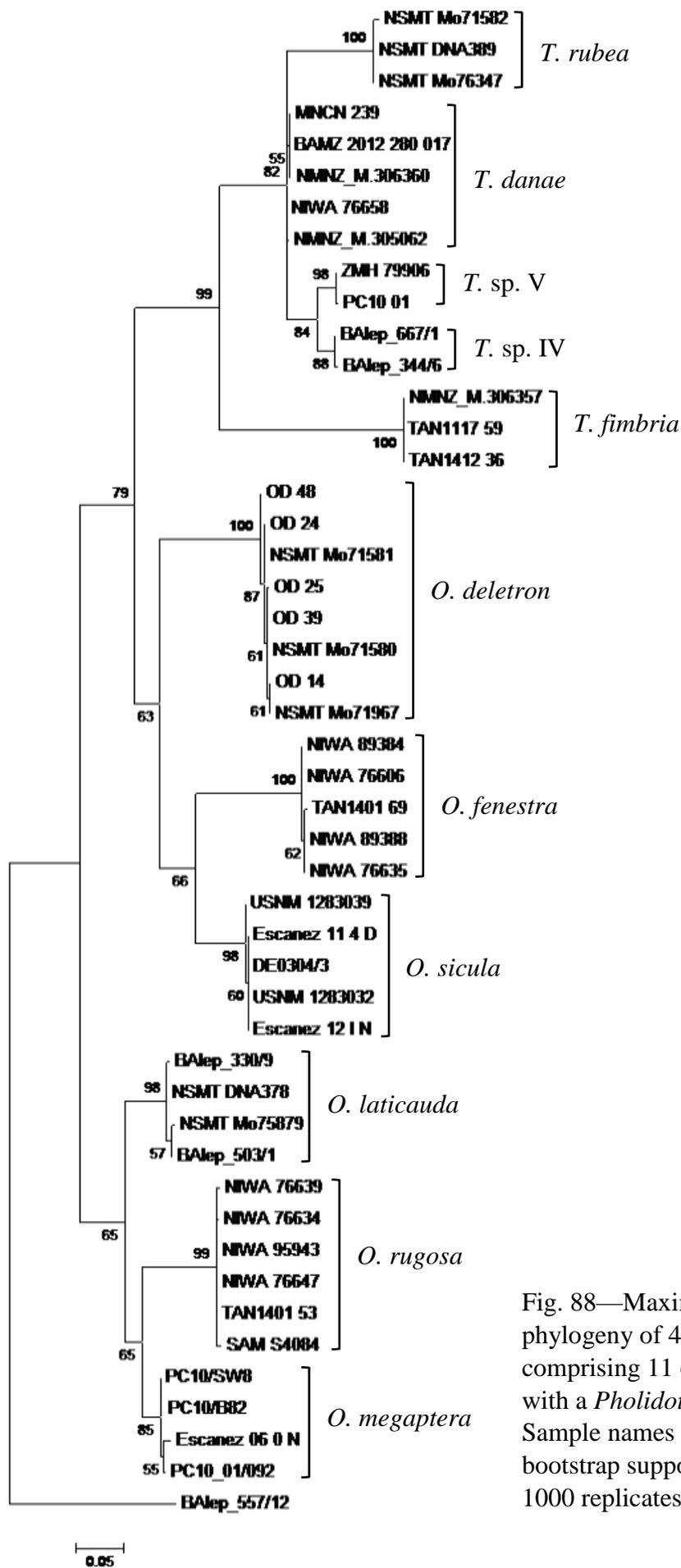


Fig. 88—Maximum-likelihood phylogeny of 42 *cyt b* sequences, comprising 11 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Sample names correspond to Table 1; bootstrap support values are based on 1000 replicates.

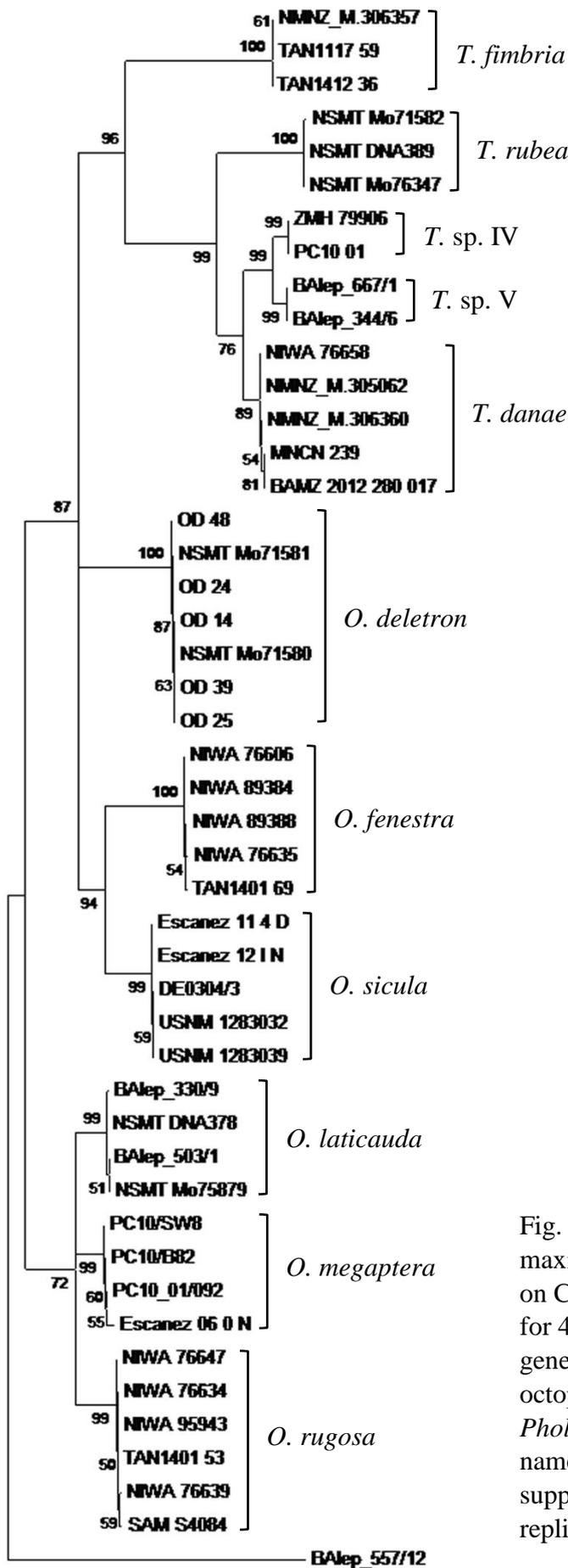


Fig. 89—Strict multigene phylogeny: maximum-likelihood phylogeny based on COI, 16S rRNA, and *cyt b* sequences for 42 individuals for which all three genes were sequenced, comprising 11 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Samples names correspond to Table 1; bootstrap support values are based on 1000 replicates.

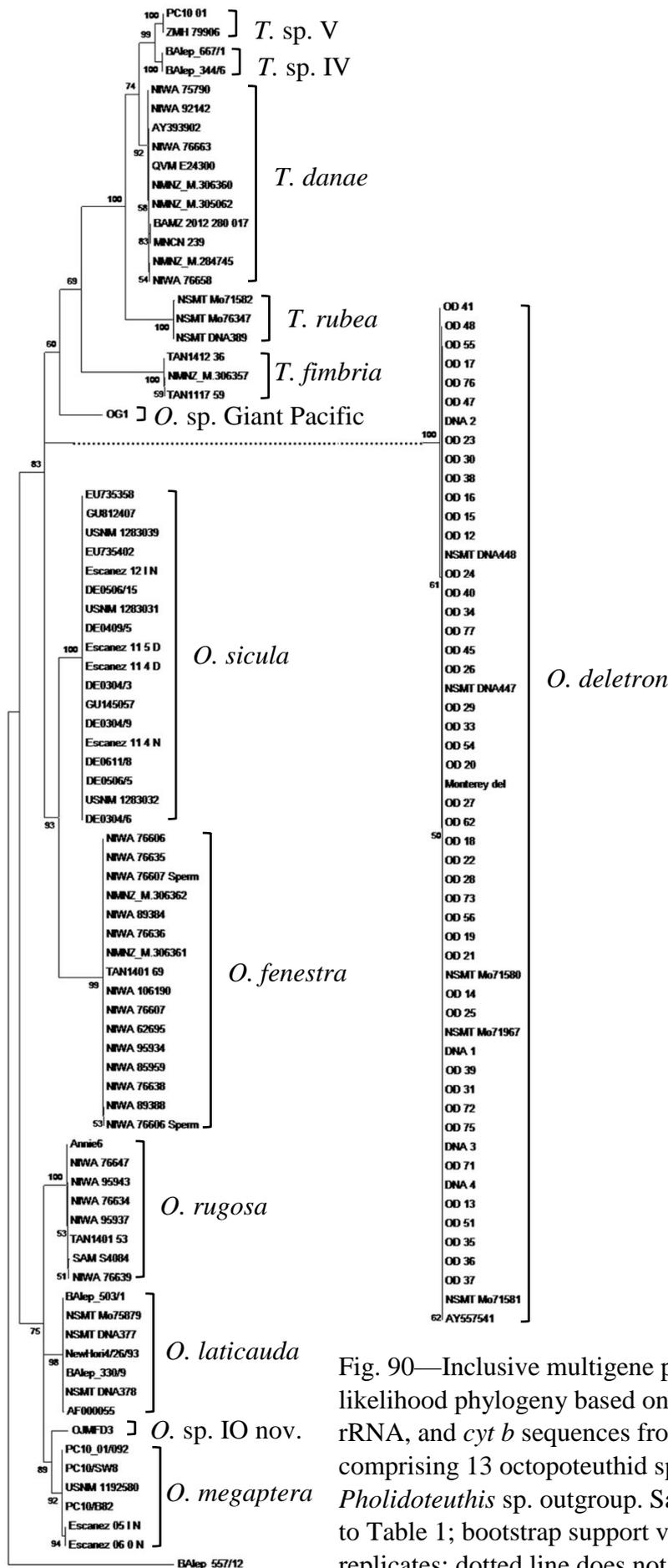


Fig. 90—Inclusive multigene phylogeny: maximum-likelihood phylogeny based on all available COI, 16S rRNA, and *cyt b* sequences from 133 individuals, comprising 13 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Samples names correspond to Table 1; bootstrap support values are based on 1000 replicates; dotted line does not indicate genetic distance.

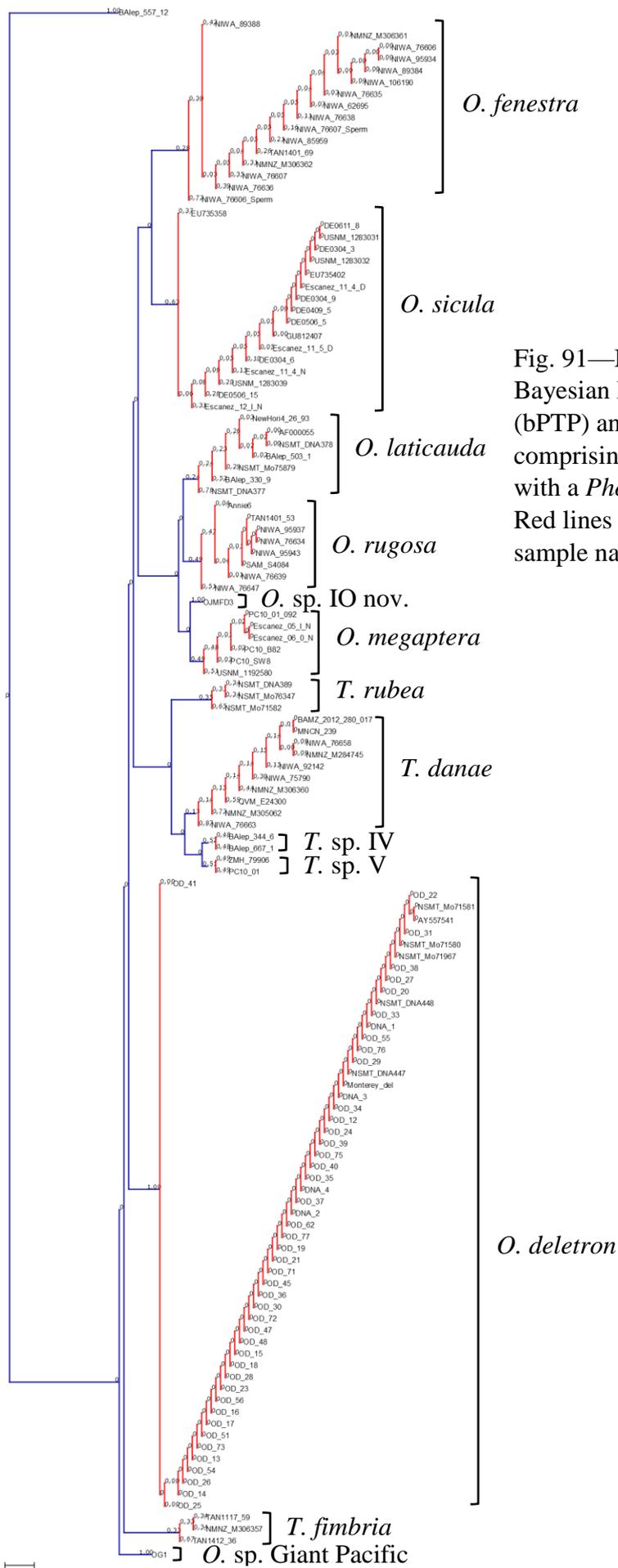


Fig. 91—Maximum likelihood Bayesian Poisson tree processes (bPTP) analysis of 133 COI sequences, comprising 13 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Red lines unite taxa, blue lines divide; sample names correspond to Table 1.

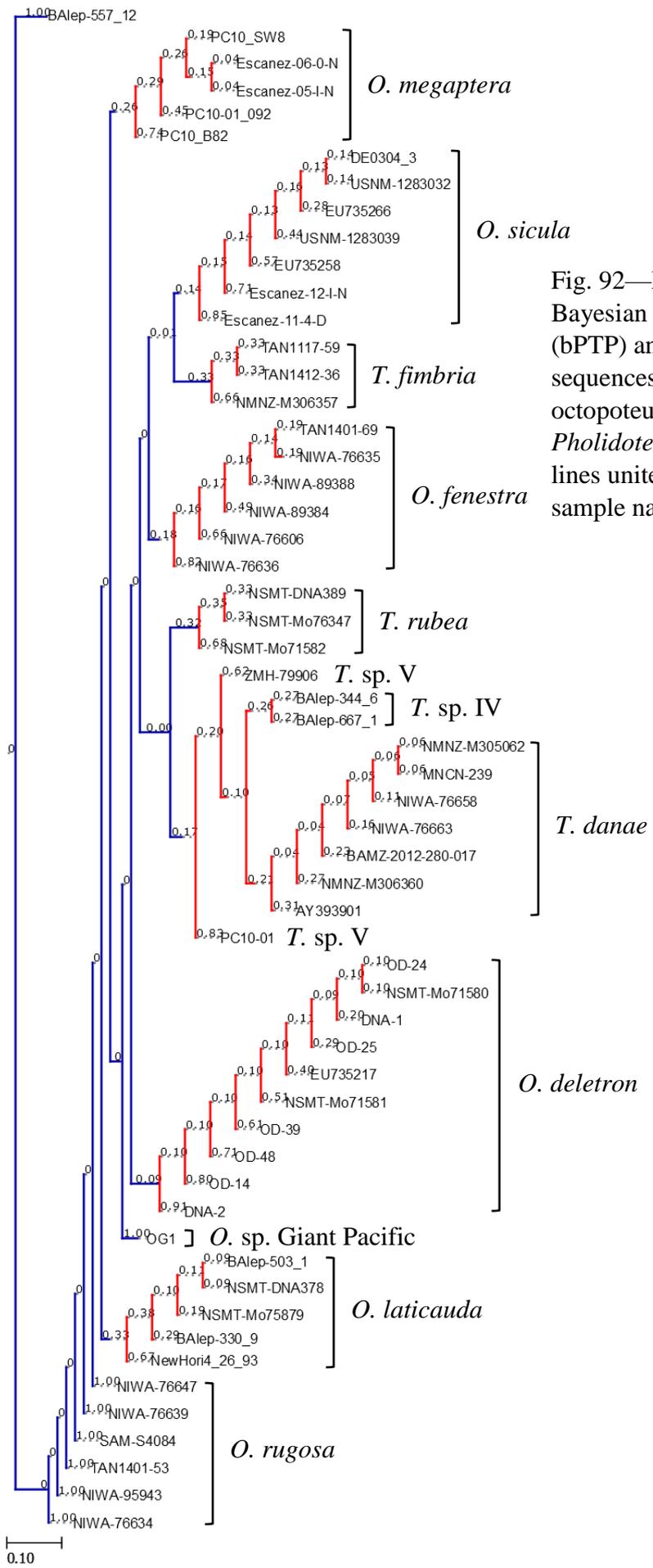


Fig. 92—Maximum likelihood Bayesian Poisson tree processes (bPTP) analysis of 51 16S rRNA sequences, comprising 12 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Red lines unite taxa, blue lines divide; sample names correspond to Table 1.

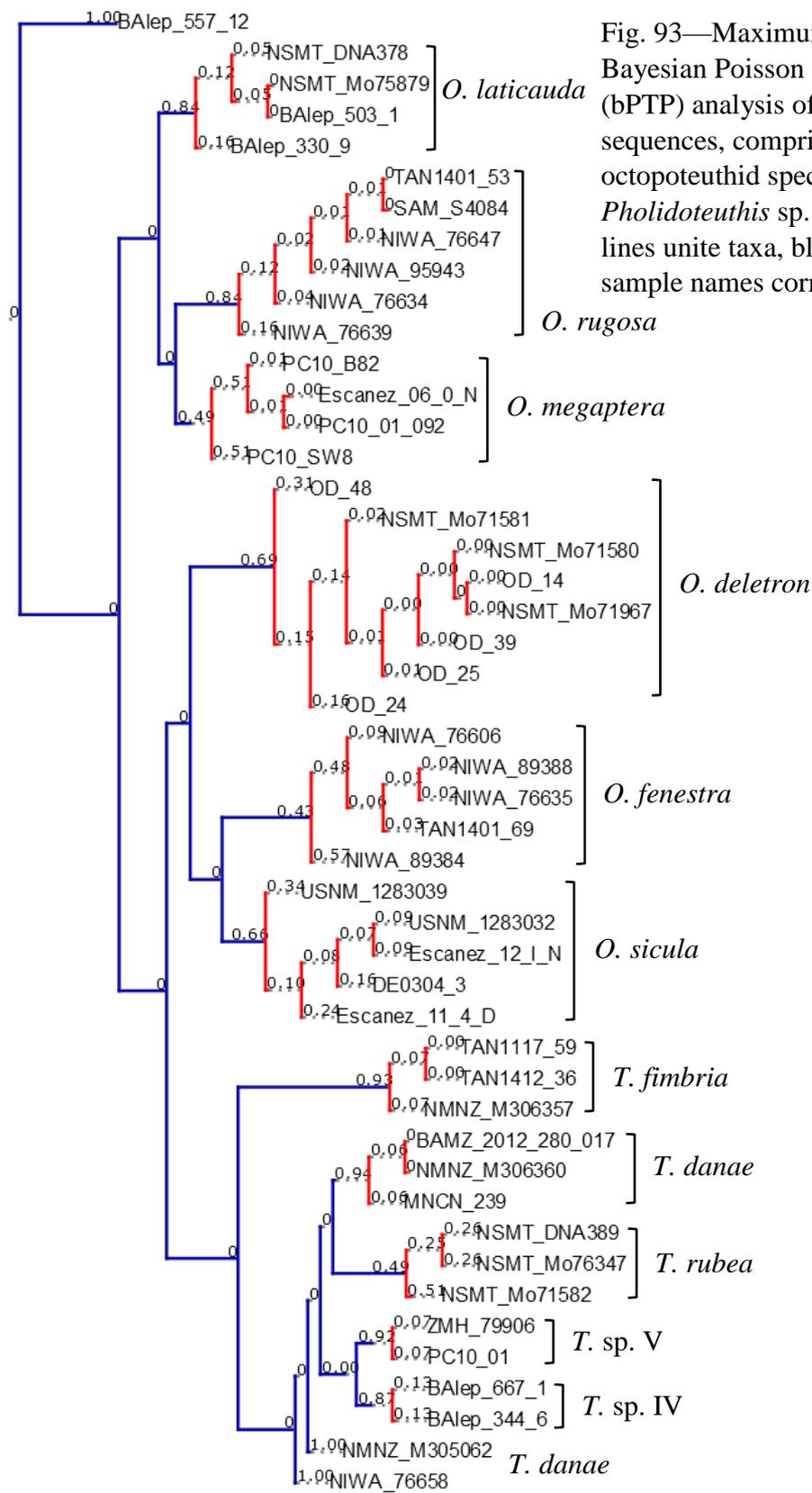


Fig. 93—Maximum likelihood Bayesian Poisson tree processes (bPTP) analysis of 42 16S rRNA sequences, comprising 11 octopoteuthid species, with a *Pholidoteuthis* sp. outgroup. Red lines unite taxa, blue lines divide; sample names correspond to Table 1.

0.10

7. DISCUSSION

Systematic value of characters

Octopoteuthids are an interesting group among oegopsids, being readily identifiable to family, and often genus, but difficult to attribute to species. The results achieved by the present revision were facilitated by the ability to access material on a global scale and on the recognition of novel characters and states.

Photophore pattern is arguably of greatest taxonomic significance in the family. The number and form of arm-tip photophores readily separates *Octopoteuthis* and *Taningia*, and ventral photophore pattern (and associated chromatophore patterning around PVMPs) reliably distinguishes the four *Octopoteuthis* species groups (Table 4). Photophores constitute a polarised, presence/absence character, and in most regions of the world, accurate characterisation of photophores is sufficient to identify specimens to species.

Arm-hook morphology was also found to be significant, differentiating genera, species groups, and species. Presence of an aboral hood distinguishes *Taningia* and Giant *Octopoteuthis* species from small-bodied *Octopoteuthis*. Morphology (*e.g.*, absence of accessory claws distally in *T. danae*) and number (*e.g.*, <12 pairs on Arms II in *T. rubea*) comprise important diagnostic characters for the best-known species of *Taningia*, and orientation (*e.g.*, basal hook pattern) is solely diagnostic between the two Giant *Octopoteuthis* species. Among small-bodied *Octopoteuthis*, presentation of accessory claws is useful in differentiating *O. nielseni* and *O. leviuncus* sp. nov. from others in their species groups. However, variability in the “characteristic” broad back arm hook morphology of *O. laticauda* sp. nov. and *O. sp. IO nov.* cannot currently be satisfactorily explained. Among presently available material, specimens displaying the unique morphology cannot be polarised to a particular sex, life stage, or geographic region.

Detailed characterisation of buccal connectives was also found to be valuable, differentiating all three major groups (small-bodied *Octopoteuthis*, giant *Octopoteuthis*, *Taningia*) from each other. Within the latter two groups they were of little systematic value, but among small *Octopoteuthis* paired connectives on Arms II differentiate the

deletron species group (*O. deletron*, *O. leviuncus* sp. nov.) and *O. rugosa* from all co-occurring species. This can be of particular use in identifying *O. rugosa*, which is widely distributed and overlaps with other members of its species group. The greatly developed buccal connectives in males of some small-bodied *Octopoteuthis* species can also be taxonomically relevant within their distributions.

Exclusive use of morphometric indices as diagnostic characters for octopoteuthids was not supported, with at least some overlap in ranges found among all species. Within lower-level groups, certain indices could be considered diagnostic, but sole use of them for identification is not advised as considerable variation was found in most indices herein. Examples of such characters include placement of the anterior fin margin (a novel character) for *O. laticauda* sp. nov. and *O. deletron* and tail length for *O. sp. IO* nov. within their species groups, and fin width for *T. danae* relative to congeners. For other proportions (*e.g.*, head proportions, fin width, arm length), slight but consistent shifts in the index range indicated minor differences between species. For example, while fin width ranges within the *megaptera* species group overlap, the minimum, mean, and maximum values for *O. laticauda* sp. nov. are all lower than in the other three species, indicating the tendency of *O. laticauda* toward narrower fins. When combined with available intact characters (*i.e.*, photophores), collection locality and life history traits, certain body indices can prove supportive in identification to species.

While generally very similar in appearance, subtle differences in beak morphology were useful in certain group- and, among *Taningia*, species-level differentiations. Beaks of *Taningia* can be separated from those of *Octopoteuthis* by their squat form, with the height posterior to the jaw angle greater than or equal to the height anterior to the jaw angle; and rounded, posteriorly expanding lateral wall ridges. Giant *Octopoteuthis* beaks can be differentiated from those of small-bodied *Octopoteuthis* by the fully pigmented, continuous lateral wall between the crest and ridge; and by their longer (relative to baseline) lateral walls. In addition, the wings of giant *Octopoteuthis* beaks remain unpigmented or incompletely pigmented at sizes greater than fully pigmented beaks of small-bodied *Octopoteuthis*. Lower beaks of *Taningia* species differ from congeners in the spread of free corners when viewed ventrally, the form of the posterior margin of lateral wall, and jaw angle. For the upper beak, length and steepness of the rostrum differentiate beaks of *Taningia* (short, steep) from those of giant *Octopoteuthis* (long, oblique) and small-bodied *Octopoteuthis* (very long, more gently sloped). Additionally,

the progression of pigmentation along the lateral walls of the upper beak occur in opposite directions between *Taningia* (anterior-to-posterior along oblique angle) and *Octopoteuthis* (posterior-to-anterior along oblique angle).

Some traditional characters were found to be of little value among octopoteuthids, due to a lack of differentiation among taxa (*e.g.*, gladius, palatine palp, funnel organ), intraspecific variation (*e.g.*, radula), or tendency for damage (*e.g.*, gladius, whole-arm characters). Morphology of the funnel and mantle components of the locking apparatus, as well as nuchal cartilage, among small-bodied *Octopoteuthis*, was also of little taxonomic value, although their morphology did differ from that of Giant species group and *Taningia*; locking apparatus morphology was important within *Taningia*. The propensity among small-bodied *Octopoteuthis* species to have truncated arms meant traditional characters dependent on complete arms (*e.g.*, arm length, arm hook counts, arm sucker counts, arm sucker morphology) remain incompletely investigated. However, for the same reason these are unlikely to be of great utility in identification.

Ontogenetic patterns in gross morphology

As paralarvae (ML < 9 mm), *Octopoteuthis* typically have very short, posteriorly set fins which increase in relative length, via anterior progression of the anterior fin margin, ontogenetically during this stage. Eyes are borne on low stalks, and antero-laterally directed. Arms and tentacles develop, the latter being longer and more prominent than the former; in late paralarval stages the tentacles start to regress in a manner consistent with resorption: general morphology is maintained (tentacles with clubs bearing suckers) but length and width decrease and tissues weaken, becoming translucent.

In the earliest post-larval stages some individuals were still developing arm suckers into hooks. Progression noted for *O. deletron* (see post-larvae description) is consistent with that reported by Stephen (1985b), with conversion beginning in the mid-portion of the arm and progressing in both directions. In post-larvae and juveniles (ML ~10–55 mm), fin length is largely constant (continuing into adulthood), while tail length and the anterior margin of fin change inversely, demonstrating the anterior shift in the position of the fins. Fin width decreases ontogenetically, as do head length and width and, in some species, the diameter of the eyes. In post-larvae (ML ~10–25 mm), tentacles are significantly reduced with only gelatinous vestigial nubs remaining basally between

Arms III and IV; rarely in juveniles, and only in the smallest specimens, the low thin membrane between Arms III and IV, which previously overlaid the tentacles, can remain.

From available material, no species of *Taningia* was represented by as complete an ontogenetic series as was available for some species of *Octopoteuthis*. However, current results suggests similar ontogenetic morphometric patterns as in *Octopoteuthis*. The most significant difference between the two occurs in the presentation of the tentacles. While vestigial tentacular nubs characterise *Octopoteuthis* post-larvae, *Taningia* post-larvae continue to bear regressing tentacles that maintain the general morphology, including intact suckers. These are maintained to considerably larger sizes in *Taningia* (ML ~27–59 mm), sizes comparable to juvenile *Octopoteuthis*; this difference in presentation was also found in the sole post-larva from sp. Giant species group (NHMUK 20150459, ♂, ML 47 mm). As a result, *Taningia* species descriptions lack a juvenile section, instead comprising at most three stages: paralarvae, post-larvae, subadults and adults (combined).

Unresolved taxa

‘*Cuciotheuthis unguiculata*’ (Molina, 1782) and ‘*Enoploteuthis hartingii*’ Verrill, 1880

Although formal synonymy is not possible at the present time, it appears highly probable that ‘*C. unguiculata*’ and ‘*E. hartingii*’ belong within *Taningia*. Combining the accounts of Banks (1896) and Molina (1782) yields the following picture: a very large squid without a distinct tail and with arms bearing two series of hooks that retract into sheaths. A very similar extrapolation was made by Harting from the debris available to him. Both Harting (1861) and Owen (1881) gave multiple, detailed illustrations of the arm hooks, revealing a consistent morphology among the two specimens: low main cusps, broad hollow bases into which a mass of musculature inserts, thick fleshy sheaths, and an absence of accessory claws. Among the currently known oegopsid taxa, it is difficult to find a more appropriate attribution for the undisputed arm of ‘*C. unguiculata*’ and the debris of ‘*E. hartingii*’ than within *Taningia*. The gross morphology of the arm hooks is undoubtedly octopoteuthid, and the low main cusps and absence of accessory claws eliminate the giant *Octopoteuthis* species (as well as *T. fimbria* sp. nov., although the original ‘*C. unguiculata*’ specimen was encountered

within 7° latitude [*fide* Clarke 1967] of the northern-most specimen of *T. fimbria* reported herein). No more specific locality was given for ‘*E. hartingii*’ than the Indian Ocean.

Previous reviews of *Taningia* have struggled to definitively clarify the status of ‘*Cuciotheuthis*’, largely due to doubt regarding Owen’s attribution of the extant buccal bulb to the original specimen (*e.g.*, Clarke 1967; Roper & Vecchione 1993). However, neither work included Owen (1830), Hunter (1861), or Leach (1818) which, together with Harting (1861), bridge the temporal gap between Molina (1782) and Owen (1881). Additionally, the online catalogue of the Royal College of Surgeons states that John Hunter prepared the buccal bulb mount himself in 1771 (the same year Cook’s voyage returned to England) and that it was presented to the Trustees of the Hunterian Collection in 1799 (the year Hunterian Museum opened). The original specimen is infamous for having made a surprisingly well-regarded soup (Banks 1896), and included in the online description of the mount is an aptly logical supposition: “The inedible beak was brought back to London, and was given to John Hunter.” The catalogue further includes an image of the mount which, contrary to the assertions of Clarke (1967), appears sufficiently *Taningia*-like to warrant consideration. Unfortunately, its examination was not possible during the course of study and, due to museum closure, it was also not possible to verify the records from which the online account was drawn.

Both Clarke (1967) and Roper & Vecchione (1993) also referred to ‘*E. hartingii*’; however, no reference could be found to any re-examination of this material since 1861, nor any account of its loss. Efforts herein to locate the debris identified its most likely current repository as the Naturalis Biodiversity Center, Leiden, Netherlands. A collection manager there believed the material should be housed within their collections, although a brief initial survey failed to locate it. More thorough efforts are planned in the future, and until the holotype can be established as lost, designating ‘*E. hartingii*’ a *nomen dubium* is premature.

Given their resemblance to *Taningia*, and in light of the new evidence supporting Owen’s attribution of the buccal bulb to the original ‘*Cuciotheuthis*’ specimen, ‘*C. unguiculata*’ and ‘*E. hartingii*’ are maintained as *species inquirenda*, pending examination of the extant material. Future lines of investigation also include attempts to

verify the provenance of the information detailed in the Royal College of Surgeons' online catalogue.

Octopoteuthis longiptera Akimushkin, 1963

The most distinctive identifying feature of *O. longiptera* is the long but narrow oval fins (FWI ~68%, FLI 92%), the combination of which was not observed in any other octopoteuthid specimen examined. Comparably narrow fins were observed in a single, atypical specimen of *O. sp. Giant Pacific nov.* (NIWA Z10746, see species' Remarks; FWI 70%, FLI 65%). However, based on its description and the single illustration (of its lower beak), Akimushkin's specimen was undoubtedly a non-giant *Octopoteuthis* species (e.g., lacking tentacles, double series of arm hooks terminating in suckers, most arms truncated, Arms II without large distal photophore). Given its type locality, *O. longiptera* could be a junior synonym of *O. sicula*, *megaptera* or *rugosa*, or a senior synonym to *O. leviuncus sp. nov.*; the presence of distal arm suckers exclude *O. sp. Giant Atlantic nov.* The protective membranes, while damaged, were considered to have likely been "well developed on the base of the arms," suggestive of the expanded basal protective membranes of *O. megaptera*. Akimushkin's type material was never deposited in a collection (Sweeney & Roper 1998 *vide* Nesis, pers. comm., 1988), and with the type lost and no morphologically comparable specimens encountered from the region the species is considered *nomen dubium*, in agreement with Young (1972) and Stephen (1985a).

Octopoteuthis indica Naef, 1923

Based on its type locality, *O. indica* most likely represents a senior synonym of *O. rugosa* or, less likely, *O. sp. IO nov.* However, *O. indica* is known from only three illustrations of a single paralarval specimen, which contain no salient taxonomic characters, and which could not be located during the course of study. A single specimen of Chun's (1910) five larval *Octopoteuthis* was located at MfN, Berlin; however, it was from station 190, the opposite side of the Indian Ocean and 34° latitude north of *O. indica*'s type locality; this specimen was not examined. Both *O. indica* and *T. persica* were named by Naef (1923) based on Chun's illustrations, and for which no further record could be found in the literature. Sweeney and Roper (1998) suggested these two types may have been located at MfN; however, a subsequent review of the

type collection there yielded not only neither specimen, but also no indication that they had ever been deposited (Glaubrecht & Salcedo-Vargas 2000). In addition to personally examining the collections at ZMH, the following German collections were contacted to locate the missing *O. indica* and *T. persica* types, without success: the Senckenberg collections in Frankfurt and Dresden; Naturkundemuseum, Leipzig.

Phylogeny

Octopoteuthids are an interesting group of oegopsids, being both remarkably conservative in morphology while still having considerable genetic variation among species. Historically, octopoteuthids were associated with other hook-bearing families, initially onychoteuthids (*e.g.*, Gray 1849, Hoyle 1886a) and then enoploteuthids (Pfeffer 1900, 1912; Massy 1907). After the elevation to their own family, interest in their placement among oegopsids receded somewhat until the advent of genetics. These works found a strong and consistent association among the Octopoteuthidae, Lepidoteuthidae, and Pholidoteuthidae, collectively comprising the monophyletic lepidoteuthid families (Carlini and Graves 1999; Lindgren *et al.* 2004; Lindgren 2010). Morphology has previously afforded support to certain pairs among these families (*e.g.*, dermal sculpture in Lepidoteuthidae and Pholidoteuthidae [Roper and Lu 1990], early life tentacle loss in Octopoteuthidae and Lepidoteuthidae [Clarke 1988]), but no shared morphologic character united them all.

Between group-level relationships

The morphologic findings herein support *Taningia* as basal within the Octopoteuthidae. The epidermal tubercles of *T. fimbria* align it, and its congeners, with the closely related Lepidoteuthidae and Pholidoteuthidae. Furthermore, considering the loss of tentacles a derived character among squid, it could be argued that the retention of them to greater sizes in *Taningia* than *Octopoteuthis* suggests the former demonstrates a less derived presentation of the synapomorphy relative to the latter.

Similarly, within *Octopoteuthis* the Giant species group is considered basal, based on morphology, in part, due to the retention of tentacles to larger body sizes (Table 4). However, it also shares a number of additional characters with *Taningia*, including the absence of embedded ventral body photophores, large adult size, arm hooks with an

Table 31. Species and subspecies historically attributed to the Octopoteuthidae, listed chronologically.

Species	Current systematic status	Type specimen(s)	Condition	Remarks
<i>Sepia unguiculata</i> Molina, 1782	<i>Cuciotheuthis unguiculata</i> , species inquirenda	Arm fragment, RCSHC	Not extant	
<i>Octopoteuthis sicula</i> Rüppell, 1844	<i>Octopoteuthis sicula</i>	Holotype, NHMUK 1845.9.8.13	Fair (pers. obs.)	Redescribed above
<i>Enoploteuthis molinae</i> d'Orbigny, 1845	<i>Cuciotheuthis unguiculata</i> , species inquirenda	None designated		Junior synonym of <i>C. unguiculata</i>
<i>Enoploteuthis hartingii</i> Verrill, 1880	<i>Taningia</i> sp.	?Naturalis Biodiversity Center	Unknown	Possibly extant
<i>Enoploteuthis cookii</i> Owen, 1881	<i>Cuciotheuthis unguiculata</i> , species inquirenda	RCSHC/308, half of buccal mass	Good (images)	Only images so far examined; dissected, prepared mount
<i>Ancistrocheirus megaptera</i> Verrill, 1885	<i>Octopoteuthis megaptera</i>	USNM 40128	Not extant	Neotype proposed
<i>Octopodoteuthis sicula atlantica</i> Grimpe, 1922	<i>Octopoteuthis sicula</i>	None designated		
<i>Octopodoteuthis sicula mediterranea</i> Grimpe, 1922	<i>Octopoteuthis sicula</i>	None designated		
<i>Octopodoteuthis indica</i> Naef, 1923	Unresolved	Repository unresolved, ?MFN	Unknown	Holotype illustrated in Chun (1910)
<i>Octopodoteuthis persica</i> Naef, 1923	<i>Taningia danae</i>	Repository unresolved, ?MFN	Unknown	Holotype illustrated in Chun (1910)
<i>Octopodoteuthis danae</i> Joubin, 1931	<i>Octopoteuthis sicula</i>	Holotype, ZMUC CEP-89	Good (pers. obs.)	Redescribed above
<i>Taningia danae</i> Joubin, 1931	<i>Taningia danae</i>	Holotype, ZMUC CEP-90	Good (pers. obs.)	

Table 31. (cont.)

Species	Current systematic status	Type specimen(s)	Condition	Remarks
<i>Octopoteuthis nielseni</i> Robson, 1948	<i>Octopoteuthis nielseni</i>	Syntypes NHMUK 1947.7.7.10, 20180142	Poor (pers. obs.)	Dehydrated, reconstituted; redescribed above
<i>Octopoteuthis longiptera</i> Akimushkin, 1963	<i>Nomen dubium</i>	Not deposited	Not extant	Nesis pers. comm., in Stephen (1985a)
<i>Octopoteuthis deletron</i> Young, 1972	<i>Octopoteuthis deletron</i>	Holotype, SBMNH 34966; paratypes, SBMNH 34967, 34968, 360102	Excellent (pers. obs.)	
<i>Octopoteuthis rugosa</i> Clarke, 1980	<i>Octopoteuthis rugosa</i>	Holotype, NHMUK1973100; paratype, NHMUK1973101	Fair (pers. obs.)	Two additional paratypes designated (Table 29, Clarke 1980) but not found (nor in Stephen 1985a)
<i>Octopoteuthis fenestra</i> sp. nov.	<i>Octopoteuthis fenestra</i> sp. nov.	Holotype, NIWA 62695; paratypes, NIWA 71844, 71835, NMNZ M.287224, 287225, 277829	Good	
<i>Octopoteuthis laticauda</i> sp. nov.	<i>Octopoteuthis</i> <i>laticauda</i> sp. nov.	Holotype, USNM 814611; paratype 729746, 1283023	Excellent	
<i>Octopoteuthis</i> sp. IO nov.	<i>Octopoteuthis</i> sp. IO nov.	None designated		Formal name, type designation under review
<i>Octopoteuthis leviuncus</i> sp. nov.	<i>Octopoteuthis</i> <i>leviuncus</i> sp. nov.	Holotype, NHMUK 20130457; paratypes ZMH 11198, USNM 885294, 885295	Excellent (pers. obs.)	

Table 31. (cont.)

Species	Current systematic status	Type specimen(s)	Condition	Remarks
<i>Octopoteuthis</i> sp. Giant Pacific nov.	<i>Octopoteuthis</i> sp. Giant Pacific nov.	Holotype, AUT OGI	Good (pers. obs.)	To be accessioned at NMNZ
<i>Octopoteuthis</i> sp. Giant Atlantic nov.	<i>Octopoteuthis</i> sp. Giant Atlantic nov.	Holotype, USNM 1283027	Excellent (pers. obs.)	
<i>Taningia fimbria</i> sp. nov.	<i>Taningia fimbria</i> sp. nov.	Holotype, NIWA 95882; paratypes USNM 817618, NIWA 71438, 71439, TAN1117/59	Good	
<i>Taningia rubea</i> sp. nov.	<i>Taningia rubea</i> sp. nov.	Holotype, NSMT DYMO 1195; paratypes NSMT Mo75355, DYMO 1196, DYMO 1114	Good	
<i>Taningia</i> sp. IV	<i>Taningia</i> sp. IV	None designated		Additional material required
<i>Taningia</i> sp. V	<i>Taningia</i> sp. V	None designated		Genetics only, specimens not examined

aboral hood, lack of distal arm suckers, form of the *recti abdominis* muscles, and having a fully pigmented lateral wall between the crest and ridge of the lower beak, among others. Indeed, morphologically Giant *Octopoteuthis* species appear intermediate between the two genera, not as a blend of their forms but in having distinct character states that could align them with each genus. With *Octopoteuthis*, Giant species share the diagnostic genus character of all eight arms terminating in photophores, as well as arms equivalent in length relative to the mantle, an outer gelatinous tissue layer, and rugose furrows along the anterior mantle in females.

Both basal groups (*T. fimbria* sp. nov. and giant *Octopoteuthis* species) are considerably different from congeners, morphologically and genetically. The remaining species of both genera are generally more similar to each other morphologically than to their basal representative. The considerable genetic differences between basal taxa and congeners caused issues with constructing cohesive phylogenies, with *T. fimbria* and *O.* sp. Giant Pacific nov. placed some distance from congeners in some analyses (Figs 86, 87).

Among the small-bodied *Octopoteuthis* species groups, no single distinct pattern is clear as various character states are shared by different pairs of species groups (Table 4): paired PVMP in *megaptera* and *sicula* groups, MEPs in *megaptera* and *deletron* groups (as well as paired Arm II buccal connectives in *O. rugosa* only but both *O. deletron* and *O. leviuncus* sp. nov.), the single chromatophore patch and absence of EPs in *sicula* and *deletron* groups. A basic, manually preformed character matrix using the first 7 columns of characters from Table 4 yielded the most parsimonious species group order (that with the fewest number of changes, multiple evolutions, and subsequent losses) as sp. Giant group, *sicula*, *deletron*, *megaptera* groups. This best accommodated a single evolution of MEPs and paired buccal connectives on Arms II. However, it counterintuitively splits the two paired PVMP groups. A theoretical evolutionary history based on morphology that would support such relationships is as follows. From a Giant-*Octopoteuthis*-like ancestor, *sicula*-group-like species evolved with LHP, *recti* photophores, two PVMP under a single chromatophore patch, but still without MEPs, EPs, and a single buccal connective on Arms II. From among this group (which survived to the present with this morphology), a separate lineage diverged which first evolved MEPs and paired connectives on Arms II. It then split into two different lineages. In the first lineage, the paired PVMP organs migrated medially and fused, the single chromatophore patch contracting accordingly, becoming the *deletron* species group of today. The second

lineage maintained paired PVMPs, but these migrated laterally along with their overlying chromatophore patch until it split into two. This second lineage also evolved EPs, and in the more derived three extant species, the paired buccal connectives were subsequently reduced to a single dorsal connective. This lineage became the present *megaptera* species group. Such an evolutionary history follows a theme of diversifying radiation, with the derived groups arising through divergence from an ancestral “midpoint.”

Alternatively, a more intuitive evolutionary history would place the two paired PVMP species groups together, with the *deletron* group either basal (*deletron*, *sicula*, *megaptera*) or derived relative to them (*megaptera*, *sicula*, *deletron*). Such evolutionary histories suggest a linear trend in regards to PVMPs, either from 0 (Giant group), to 1 (*deletron* group) to 2 (*sicula*, *megaptera* groups) or 0 to 2 to 1. The issue with both hypotheses involves how to sort the characters shared by different pairs of species groups. Additional characters may need to be considered to improve resolution, and biogeography may also be of potential importance for consideration. For example, *T. fimbria* sp. nov., as a basal octopoteuthid, has a circumglobal southerly distribution and is the most southerly distributed species in the family. Both paired PVMP species groups have members whose distribution is similarly confined to the southern hemisphere: *O. fenestra* sp. nov. and *O. rugosa*, which are also the two most southerly distributed species of *Octopoteuthis*, respectively, and co-occur with *T. fimbria* and *O.* sp. Giant Pacific nov. (one of the basal Giant *Octopoteuthis* species) in New Zealand waters. Additionally, some specimens of *O. fenestra* sp. nov. were noted to have faint whitish patches in the region of the MEPs, suggesting a possibly primitive form of the latter state. Both species of the *deletron* group have a more latitudinally varied distribution, and their southern-most record is an *O. leviuncus* sp. nov. from 35°12'S in the Atlantic Ocean.

Unfortunately, current genetic analyses did not provide consistent or logical insights into between group relationships within the Octopoteuthidae. The COI and 16S rRNA single-gene phylogenies were largely unorganised bushes (Figs 86, 87), with *cyt b* having the only cogent topography (Fig. 88). As a result, the relationships suggested among the multigene phylogenies are mostly reflective of those of *cyt b* (Figs 89, 90). Missing taxa are considered a significant factor in this ambiguity. During the course of study, preliminary phylogenies were sequentially constructed (employing a simplified

methodology) as new samples and species were sequenced. It was qualitatively observed that as the phylogeny became more complete, it corresponded increasingly to a hypothetical phylogeny based on morphology. Although this study is by far the most complete on the Octopoteuthidae, three species remained unavailable for sequencing (*O. nielseni*, *O. leviuncus* sp. nov., *O. sp. Giant Atlantic* nov.) and two others were only represented by single COI sequences (*O. sp. IO* nov., *O. sp. Giant Pacific* nov.).

Within group-level relationships

Within *Taningia*, *T. fimbria* is considered basal due to its dermal sculpture and modified basal armature in males only, a second character similar to *Lepidoteuthis* (Jackson and O'Shea 2003). Genetic analyses supported this position, returning *T. fimbria* as basal in the *Taningia* clade (Figs 88–90) as well as being the most genetically distant from congeners. Interestingly, *T. fimbria* is also the most *Octopoteuthis*-like of *Taningia* species: it has longer, thinner arms than congeners, a longer tail, and its rectum-*recti* morphology is the most like *Octopoteuthis* of the *Taningia* species. Genetic analyses reliably returned *T. rubea* as intermediate between *T. fimbria* and *T. danae* (Figs 88–90), which was supported morphologically with *T. rubea* sharing characters with both of these latter taxa (see *T. rubea* Remarks). *Taningia* sp. IV and V were sister species, forming the crown group within *Taningia*, in all phylogenies except the 16S rRNA. For further treatment of these species see below.

Within the *Octopoteuthis* species groups, only the *megaptera* group was represented in genetic analyses by more than two species. COI sequences were obtained for all four species, and the single-gene tree showed a sister relationship between *O. megaptera* and *O. sp. IO* nov., with *O. megaptera* (the sole exclusively Atlantic species) as the crown species in the group. No ordered relationship was found between *O. rugosa*, *O. laticauda* sp. nov., and the crown branch, nor was any apparent in 16S rRNA phylogeny. Only three species were represented in the *cyt b* phylogeny, but a more distinct order was found with *O. laticauda* sp. nov. as basal and *O. rugosa* the crown species. Conflicting patterns and incomplete sampling between genes leaves too much uncertainty within the species group to make any further conclusions.

Octopoteuthis species groups as potential genera

While the requirements for delineating cephalopod genera have not been standardised, an intuitive definition of a descriptively useful genus is one that is monophyletic (*i.e.*, represents the most closely related species), reasonably compact, and distinct in some relevant criteria (e.g., morphologically, biogeographically, ecologically; Gill *et al.* 2005). Within the now-recognised diversity of the genus *Octopoteuthis*, four morphologic species groups of 2–4 species were identified via the abundance and form of photophores along the ventral body surface. Analysis of genetic sequences to date was indicative of monophyly in at least two of these groups, suggesting they may in fact represent genus-level divisions. Additionally, considerable genetic variation was found within *Octopoteuthis* species groups, indicating that they constitute genetically distinct but internally variable units within the wider family. However, each octopoteuthid species was more closely related to its most genetically distant member of the family than to the outgroup from a closely related family (the Pholidoteuthidae), verifying the unity of the Octopoteuthidae. Recent work on another family of deep-sea squid, the Mastigoteuthidae, resulted in the division of a single, diverse genus, with previously established species groups, into five genera (Braid *et al.* 2014; Young *et al.* 2014). Minimum intergeneric percent differences observed for COI ranged from 12.25–16.35–19.64% ($N = 14$) (Braid 2013; Braid pers. comm. 2016), comparable to the minimum between-species-group differences found in *Octopoteuthis* (Table 29). Similar work on the Onychoteuthidae yielded slightly lower intergeneric differences (4.7–13.4–18.8%; $N = 21$), despite more striking morphologic differences between onychoteuthid genera than between those of mastigoteuthids or *Octopoteuthis* species groups (Bolstad *et al.* 2018).

In the present study, species groups are maintained (rather than elevating these groups to generic status) due to the incomplete species coverage in genetic analyses for most species groups. The taxonomic status of *Octopoteuthis* species groups will be revisited once sequences for *O. nielsenii* and *O. leviuncus* sp. nov. are obtained, which would complete the currently recognised diversity of three of the four species groups. The capture of fresh specimens of *O.* sp Giant Atlantic nov., while valuable both phylogenetically and to verify the species, cannot be depended on as only five specimens are known to have been caught since 1966. Should formalisation of these species groups be considered prudent in the future, two potential classifications are

logical: 1) raising species groups to genus status and erecting subfamilies to maintain the division presently represented between *Octopoteuthis* and *Taningia*, as in the Cranchiidae or 2) maintaining the current genus-level divisions and raising the species groups to subgenera, as in the Enoploteuthidae. Given the considerable genetic divergence and distinct morphologic separation between species groups, the former classification is considered most appropriate, raising the species groups to full genus status. Under such a classification, *Octopoteuthis* would be retained for the *sicula* species group and *Octopodoteuthopsis* Pfeffer, 1912 resurrected for the *megaptera* species group; the *deletron* and Giant species groups would require novel designations. Subfamilial designations are considered prudent to maintain a term for all *Octopoteuthis* species, as they remain more similar morphologically to each other than to *Taningia*, and would be designated Octopoteuthinae and Taningiinae. An additional taxon, possibly the tribe Octopoteuthini, may further prove useful when delineating the three small-bodied *Octopoteuthis* species groups from the Giant species group.

Taningia species vs subspecies

Two genetically distinct taxa recognised herein, *Taningia* spp. IV and V, had the smallest interspecific differences at all three loci examined of any octopoteuthid taxa (Table 28). Despite this, both are presently maintained at the species level, and not considered subspecies of a single taxon, due to their consistent genetic separation at multiple loci and their recovery as separate species from bPTP analysis of both coding gene regions (Figs 91, 92). Furthermore, their interspecific difference at COI (3.04%), while small relative to other octopoteuthids (5.90–25.47%), also supports their species-level ranking. DNA-based thresholds for delimiting species (*i.e.*, a percent difference cut-off at COI) have been proposed in multiple studies (*e.g.*, 2.7% in Hebert *et al.* [2004]; 1.6% in Kerr *et al.* [2009]), and were initially based around a concept that ten times the mean intraspecific difference would capture the vast majority of species (Hebert *et al.* 2004). Recent work on the mastigoteuthids and onychoteuthids estimated mean intraspecific differences for COI at 0.12% and 0.24%, respectively, producing a theoretical species threshold of 1.2% and 2.4% (Braid 2013; Bolstad *et al.* 2018). For mastigoteuthids, the minimum interspecific difference was estimated at 6.9%, approximately six times both the theoretical threshold and the greatest pairwise intraspecific difference (1.12%); for onychoteuthids the minimum interspecific difference was 3.8%, 150% the theoretical threshold. In the present study, the mean

intraspecific difference at COI was 0.15%, resulting in a similar potential species-delimiting threshold of 1.5%. The observed difference between *Taningia* spp. IV and V was double this threshold and three times the maximum pairwise difference in *T. danae* sequences (1.08%; Table 27), the next-most-closely related species, supporting their distinction as separate species. Furthermore, available specimens of *Taningia* spp. IV and V were considerably isolated from each other geographically, with the whole of the Americas interrupting the most direct route between their localities, although only two collection localities are known for each species. Morphologically, among available and comparable specimens, *Taningia* sp. IV had relatively longer arms than *T. danae*, especially the ventral pairs which were also longer than the dorsal pairs (whereas in *T. danae* arms were more equal in length); genetically identified specimens of *Taningia* sp. V were not available for examination. While additional material is required to solidify these two species morphologically, as well as clarify their geographic distributions and how those relate to that of *T. danae*, they were treated as distinct species in the present study.

Interfamilial relationships

Within the previously established monophyletic lepidoteuthid families clade, the Lepidoteuthidae has been placed basally (giving the group its name) with a closer relationship inferred, somewhat awkwardly, between the Octopoteuthidae and Pholidoteuthidae (Roper & Lu 1989; Roper & Lu 1990; Lindgren 2010). Herein, octopoteuthids are considered most closely related to lepidoteuthids. In addition to the specific characters allying the two noted in *T. fimbria*, as well as those noted by previous workers (*e.g.*, Clarke 1988; Roper and Lu 1990), the following shared characters are added based on opportunistic examinations of *Lepidoteuthis* specimens: lower beaks with a lateral wall ridge shelf as described herein; upper beaks with near-rectangular lateral walls; and domed arm sucker morphology with typically few, long apical sucker ring teeth. Conversely, pholidoteuthids lacked a lower beak shelf (as did a brief survey of beaks from the Ancistrocheiridae, Onychoteuthidae, Mastigoteuthidae, Chiroteuthidae); had upper beaks with triangular lateral walls; and bore weakly domed suckers with short triangular teeth. Additionally, preliminary results from an ongoing clade-wide phylogenetic revision support a closer relationship between Lepidoteuthidae and Octopoteuthidae, and placed Pholidoteuthidae as basal in the clade (Kelly and Braid 2015). In a broader sense, previous works found a consistent relationship between the

lepidoteuthid families clade and the chiroteuthid families (Lindgren 2010). Concurrent phylogenetic revisions ongoing at AUT on these two broad groups thus far continues to support such a relationship (J. Kelly pers. obs.).

Taking into consideration their closest relatives, basal taxa, and conserved morphologies, the following form is proposed as a potential basal octopoteuthid: a large squid with large, rhombic fins and distinct tail formed by the posterior projection of the mantle; some form of epidermal sculpture along the mantle; a trapezoidal head, with arms bearing biserial hooks with accessory claws and some number of them terminating in photophores; reduced tentacles, possibly already lost in subadult or juvenile stages; and rudimentary photogenic structures associated with the ventral surfaces of the ink sac and eyes.

Appraisal of gene regions

Minimum pairwise interspecific differences were at least three times greater than maximum intraspecific differences, indicating that all three gene regions can be used to distinguish species of the Octopoteuthidae. COI and *cyt b* yielded similar interspecific percent differences, which were typically 2–3 times greater than 16S rRNA. 16S rRNA produced the least resolved tree, likely due to the presence of indels which impacted the alignment of sequences. Although *cyt b* is not a gene region typically used in cephalopod phylogenetics (*e.g.*, Lindgren 2010), it yielded the most resolved tree and was the only single-gene tree to recover *Taningia* with all five species (bootstrap support 99%). This strong support was likely the reason for a unified *Taningia* in both multigene phylogenies, with the difference in bootstrap support due to the dilution of *cyt b* in the inclusive tree. Other results were similar between *cyt b* and COI: both recovered the *sicula* and *megaptera* species groups with 61–66% bootstrap support (except in COI, where *megaptera* species group had 91% support); bPTP analysis returned all available species for COI and all but one in *cyt b*, while only 8 of 12 were supported in the 16S rRNA tree. While some differences in performance do appear consistent between gene regions, the number of species and sequences per species varied somewhat among them, the impact of which remains unquantified.

While in some ways *cyt b* could be considered a replicate of COI in single-gene phylogenies, present results suggest it may be a valuable addition to the standard gene

regions used in cephalopod phylogenetics. Both *cyt b* and COI are coding regions of mitochondrial DNA, and both yielded similar results for the present data set. However, in addition to producing cleaner raw sequence reads that required less editing than the other regions, *cyt b* sequences yielded a more resolved single-gene phylogeny, one which transferred valuable topology to the multigene phylogenies. Despite this, the primer sequences used herein require adjusting and are not recommended for broader application; while sequences were successfully obtained from all samples attempted from the Octopoteuthidae and Pholidoteuthidae, and elsewhere sequences have been recovered from the Gonatidae, Architeuthidae, Loliginidae, Ommastrephidae, Sepiolidae, Sepiidae, and Octopodidae (Santaclara *et al.* 2007; Espiñeira *et al.* 2010), all samples from the Lepidoteuthidae trialed herein failed to amplify. In the present study, *cyt b* was included to evaluate its performance in cephalopod phylogenetics, and primer sequences for *cyt b* were chosen that would yield sequences of comparable length to those of COI for an unbiased assessment. The current results demonstrate several advantages of *cyt b* over the more broadly used COI and 16S rRNA, and, despite publications and published sequences of the latter two vastly outnumbering those of *cyt b*, it remains a worthy gene region for further investigation.

Reproductive biology in O. sicula, octopoteuthids

With the documented group-synchronous ovulation and assuming hypothesised growth during the reproductive phase, *O. sicula* would be classified as employing either a multiple spawning strategy or a polycyclic strategy (formerly iteroparous; Rocha *et al.* 2001). The point differentiating these two is whether egg batches are spawned during a single spawning season (monocyclic, without ovary regeneration in between) or during different spawning seasons (polycyclic, with ovary regeneration). The ovaries of resting females reported here retained hundreds to thousands of uniformly undeveloped oocytes. Nidamental and oviducal glands demonstrated the ability to regress, which could suggest the capability to regenerate as well. The evolution of a resting state implies a prolonged reproductive phase within which spawning events are sufficiently temporally segregated to afford a selective advantage to resorbing developed reproductive tissues over maintaining them. It also suggests that spawning events are cued in some way, possibly externally (*e.g.*, seasonal), so that reproductive capacity can be redeveloped in advance). The temporal distribution of presently staged female *O. sicula* could be consistent with a single annual spawning period, taking place sometime

between late May and September, with maturation (or regeneration) preceding it during January–April; following spawning, and until the next maturation cycle, a resting state is initiated and maintained. The combination of the above evidence and supposition are highly suggestive of polycyclic spawning in *O. sicula*.

Unfortunately, differentiation could not be made between individuals maturing for the first time and those potentially redeveloping for subsequent spawning events. Furthermore, age estimates do not yet exist for *O. sicula*. Hoving and Robison (2017), studying *O. deletron* off California, calculated a slow growth rate for that species, with the oldest specimen (aged 1050 days) only ML 133 mm; two others aged >750 days were ML ~150 mm. Specimens examined herein of *O. deletron* reached sizes of ML 227 mm, comparable to the largest *O. sicula* at ML 206* mm, suggesting these species may live well beyond the reported 3-year lifespan. However, unpublished data on *O. sp.* IO nov. suggests a much faster pace of life, with individuals reaching sizes of ML 79 and 116 mm in 174 and 154 days, respectively (K. Sajikumar pers. comm.). Maturity observations reported herein support the existence of developmental plasticity within *Octopoteuthis* at least in regard to size-at-maturity (see *O. megaptera*, *O. sp.* IO nov.), thus, species-specific growth rates and lifespans may also be discovered, in time. The only other available octopoteuthid age estimates are for two specimens of *Taningia* from the coast of Spain, aged 647 and 1052 days (ML 1050 and 1320 mm, respectively; González *et al.* 2003).

Females with sheathed nidamental gland morphology were also observed in *O. megaptera*, *O. deletron*, *T. danae*, *T. fimbria* and *T. rubea*, although not as rigorously demonstrated as in *O. sicula*. Finding similar reproductive morphology across both species groups and genera suggests that the proposed polycyclic spawning of *O. sicula* may be a strategy more widely employed within the Octopoteuthidae. Alternatively, the resting stage, as described herein, could represent spent morphology in octopoteuthids: reproductive tissues were altered in appearance relative to both maturing and mature stages. However, resting individuals were otherwise indistinguishable from other specimens in terms of gross morphology, and did not appear to undergo the extreme decline into a spent state reported in other oegopsid families (e.g., gonatids, onychoteuthids; Katugin *et al.* 2004; Bolstad & Hoving 2016). Such extremes, however, may be more a result of brooding behaviour in those groups than of spawning itself. A multiple-spawning strategy could be employed instead, with prolonged maturation (as

shown for *O. deletron*) followed by a hypothetically extended but single reproductive phase comprising multiple batch spawning with maintained growth throughout. Taken together, this could equate to a lifespan of 3–5 years.

Sexual dimorphism

As has been documented previously (e.g., Hoving *et al.* 2008), octopoteuthids appear to share a trend in sexual dimorphism by size: among examined material, the largest specimen of each species was female for eleven of fourteen species (*T.* sp. IV and V were excluded due to limits of material). Similarly, the smallest mature specimen of each species was male for all thirteen octopoteuthid species where mature individuals were available (excludes *O.* sp. Giant Atlantic, *T.* sp. IV and V). Both of these patterns were also reflected in beak morphology, best demonstrated in *O. deletron*: females had larger beaks than males of equivalent body size, and pigmentation occurred at smaller sizes in males than females. However, despite maturing at smaller sizes, males of at least some species do go on to achieve similarly large sizes as females. This is most notable in *O. fenestra* sp. nov., where the largest male examined was ML 234 mm and two others were also ML >200 mm.

Sexual dimorphism was also expressed in several morphologic characters, the best-established of which is the rugose tissue furrows found along the anterior mantle margin in female *Octopoteuthis*. While both males and females have an outer gelatinous layer, only in females is it ever furrowed. Potential functions of the furrows related to reproduction could include: as a modified tissue for spermatangium reception (*i.e.*, mating site) and storage, potentially even long-term (some resting females without immediate ability to spawn based on glandular morphology still retained implanted spermatangia); as a tactile sexual recognition character; or as a protective barrier to the grasping hooks of a male (Fig. 14G). Morphologically, the rugose furrows of female *Octopoteuthis* could be considered an additional form of dermal sculpture. They comprise a three-dimensional formation in the outer-most layer of the mantle, and have a consistent, ordered appearance and location. However, its presumed function in reproduction differs from those proposed for lepidoteuthids and pholidoteuthids by Roper and Lu (1990), which mainly considered their buoyancy and hydrodynamic properties. However, roles in species or sexual recognition were not considered and could be relevant given that these species inhabit the dark vastness of the open ocean.

Somewhat relatedly, while reporting on the significantly enlarged, sabre-like hooks of male *Lepidoteuthis*, Jackson and O'Shea (2003) suggested these could be used to lock into the grid-like dermal cushions of females for purchase during mating. Further study of the rugose furrows requires histology and electron microscopy analyses, which have not yet been reported.

Sexual dimorphism was also apparent in various arm structures among octopoteuthids. Minor variations in buccal connective pattern were observed between the sexes of some species of *Octopoteuthis* (see *O. fenestra* sp. nov., *O. megaptera*), but more prominent were the greatly developed proximal protective membranes and buccal connectives of male *O. deletron*, *O. megaptera*, and, possibly, *O. laticauda* sp. nov. The sexual dimorphic nature suggests some male-specific role, but outside of a possibly chemosensory role the recessed location makes proposing functionality difficult. Alternatively, if males are generally smaller, the expanded 'webbing' may aid in capture or retention of smaller prey items. In *Taningia*, males also had modification to the arms, most notably to their armature. Large mature male *T. danae* bore an expanded distal section of Arms II with proportionally larger hooks, while the basal-most hooks of Arms I in male *T. fimbria* were greatly enlarged and morphologically modified. The use of the latter modification in observed traumatic insemination of female *T. fimbria* (Hoving *et al.* 2010, as "*T. danae*") is considered well supported at present, and constitutes another character relating it to *Lepidoteuthis*: singular, basal armature modification in males only. These modifications suggest that the changes in male *T. danae* may also have a role in securing purchase during mating. While not sex specific, the funnel projections observed in *T. fimbria* most intuitively would serve a role in the manipulation of female reproductive products, or ink, or as an exceptionally unique species recognition character. Unfortunately, no egg mass has ever been attributed to the Octopoteuthidae and no further correlates are possible at present.

A final difference between sexes was observed in the sex ratio of *Taningia* specimens collected from New Zealand waters, although sample sizes for both species remains very low. Female *T. danae* were considerably more common in collections than males (12♀:5♂) and comprised mostly large adults, with five specimens ML >800 mm and four moderate to large heads (along with two post-larvae and one subadult, ML 495* mm); the few male specimens were roughly evenly spread across the size range. The opposite was found in *T. fimbria*, with more males present in collections than females

(10♂:6♀) and all being between ML 177 and 435 mm; females showed a similar skew in body size as *T. danae*, with three specimens ML >700 mm, one ML 555* mm, and a single subadult (ML 240* mm). Although sample sizes are small, New Zealand collections house the largest preserved individuals (a specimen reported by Roper and Vecchione [1993] of ML 1600 mm is likely a fresh measurement) and the greatest number of them encountered during this study (followed by NSMT). However, this could be partially an artefact of human interest in giant-sized squids, for which New Zealand is famous; some of these large specimens were retained from fishing vessels either by observers or crew. While their representation in collections may be embellished, their presence in New Zealand waters is not. For both species, present material demonstrates that large reproductive females and mature males (which develop at smaller sizes) mix in the waters around New Zealand, strongly suggestive of suitable mating or spawning conditions, or both, in the area.

Octopoteuthid biology, ecology

Octopoteuthis deletron has previously been shown to have multiple fracture planes along the length of its arms (Bush 2012). These are thought to serve as decoys, allowing the animal to escape a distracted predator. Given the prevalence of truncated arms encountered during specimen examinations, this defensive strategy is presumed to extend to all small-bodied *Octopoteuthis* species. Conversely, complete arms were frequently found on both Giant species (see *O. sp. Giant Pacific* nov. Remarks), and, when incomplete, arms were worn as would be caused by net abrasion and not abruptly severed. It is thus proposed that giant *Octopoteuthis* species, as well as those of *Taningia*, lack such fracture planes, and that multiple fracture planes provide an additional character unifying the small-bodied *Octopoteuthis* species groups. Alternatively, the observed difference could be an effect of size and stronger construction of the arms in giant *Octopoteuthis* and *Taningia*.

Species-specific regressions were calculated herein for one species of each *Octopoteuthis* species group (data were pooled for the two giant species), as well as two species of *Taningia*. These regressions differed to varying degrees from the previous “genus-wide” equations of Clarke (1980) and Lu & Ickeringill (2002). (In reality, these regressions should only ever be considered reflective of at most three *Octopoteuthis* species as both studies only used regionally available specimens.) Among small-bodied

Octopoteuthis species, relationships from all studies generally corresponded better for ML than for body mass, which tended to diverge at greater rostral lengths; for the pooled giant *Octopoteuthis* species, previously published “genus-wide” regressions underestimated both ML and body mass. Differences in how the present, more refined regressions compared to the published ones suggest there is sufficiently meaningful variation in such relationships, at least at the species-group level, to warrant the use of more specific equations. This is best illustrated in *O. deletron*, which had both the largest dataset and best-fitting relationships overall. For *Taningia*, only one previous regression has been calculated for LRL against ML and BM, which tended to underestimate size for *T. fimbria* and was generally mismatched for the LRL against ML data of *T. danae* herein (Clarke 1980).

Unfortunately, while body mass is a more biologically meaningful measure, as it more accurately reflects nutritional contribution to predators, it is also more variable due to damage inflicted during capture (*e.g.*, organ rupture). Furthermore, given the readiness of arm autonomy in small-bodied *Octopoteuthis*, calculated regressions against body mass should always be assumed to underestimate the true value. This is an important consideration for predator–prey relationship studies as the few ex-gut content specimens examined herein were typified by having at least some intact, non-regenerating arms; the four intact arms of NMNZ M.277829, from a fish stomach, comprised 50% of those encountered across all 46 specimens of *O. fenestra* sp. nov. (Fig. 5H top). Thus, *Octopoteuthis* prey items likely constitute a greater mass in the diets of predators than a regression based on damaged, trawl-caught specimens will estimate. The importance of giant *Octopoteuthis* species is also likely to have also been underestimated in previous studies. Until species-specific regressions are available for all octopoteuthid species, or the need for them has been better assessed, future works should employ the regression of the most closely related species (*i.e.*, from the same species-group) as calculated herein.

The importance of accurate beak regressions is underlined by the number and nature of octopoteuthid predators. A brief literature review yielded 20 cetacean, 15 fish, 11 sea bird, and 4 pinniped species, to which an additional 4 species of fish can be added following specimen exams herein (Tables 32, 33). This fauna comprises top predators from surface waters down to deep ocean habitats, and includes several members of the poorly known *Mesoplodon* beaked whales, wide-ranging and vulnerable species of

petrels and albatrosses, commercially important fishes, and critically endangered and endemic pinnipeds and sea birds. Although octopoteuthids were not main prey items for many of these, they were considered a major component in the diet of the hammerhead sharks *Sphyrna lewini* and *S. mokarran* (Smale & Cliff 1998); swordfish *Xiphias gladius* and Portuguese dogfish *Centroscymnus coelolepis* (Smale 1996); Cuvier's beaked whale *Ziphius cavirostris* (Santos *et al.* 2007) and Risso's dolphin *Grampus griseus* (Sekiguchi *et al.* 1992); comprised >5% of prey mass for three species of seabird (Croxall & Prince 1996); and are generally considered one of the most important cephalopod families by mass in the diet of sperm whales (Clarke 1996; Gómez-Villota 2007). Several trends are evident within and among predator groups, including abilities for high activity and speed, deep-diving capabilities or deep-water habitation, as well as open ocean occupants and wanderers. Parallels can also be found in the biology and ecology of their octopoteuthid prey: an active lifestyle and ability for rapid escape (Kubodera *et al.* 2007), occurrence in deep water (Gomes-Pereira & Tojeira 2014), diel migration (Roper & Young 1975; Young 1978), and relatively diffuse but ubiquitous distribution.

Conversely, almost nothing is known about the diet of octopoteuthids; the stomach contents of only two *Taningia*, from off Spain, have been published, and were found to contain remnants of blue whiting (*Micromesistius poutassou*), crustacean integument, hooks and a beak from a *Gonatus* sp. (González *et al.* 2003). Similarly, other aspects of octopoteuthid biology are poorly studied, with literature on non-systematic aspects focused primarily on *O. deletron* (*e.g.*, Bush & Robison 2007; Bush *et al.* 2009; Hoving *et al.* 2011; Bush 2012; Hoving & Robison 2017) and new distribution records of "*T. danae*" (Zeidler 1981; Santos *et al.* 2001a; Quetglas *et al.* 2006; Gomes-Pereira & Tojeira 2014; Escáñez & Perales-Raya 2017). Several studies have recently been carried out on octopoteuthid reproductive biology (Gonzalez *et al.* 2003; Hoving *et al.* 2008; Hoving *et al.* 2010), and some information has been accumulated regarding bioluminescence in the family, including its potential role in countershading (Young & Roper 1977; Young 1978), communication (Roper & Vecchione 1993; Kubodera *et al.* 2007), and a detailed investigation of photophore ultrastructure (Herring *et al.* 1992).

Table 32. Octopoteuthid predators from the literature, with prey identity simplified into small-bodied *Octopoteuthis* (*O.*), giant *Octopoteuthis*, and *Taningia* (*Tan.*) species. Blank prey attribution denotes identification to family only.

Predator	Small <i>O.</i>	Giant <i>O.</i>	<i>Tan.</i>	Reference
Fish				
Tiger shark <i>Galeocerdo cuvier</i>	X		X	Smale & Cliff 1998
Scalloped hammerhead <i>Sphyrna lewini</i>	X		X	Smale & Cliff 1998; Galván-Magaña <i>et al.</i> 2013
Smooth hammerhead <i>S. zygaena</i>	X			Smale & Cliff 1998; Galván-Magaña <i>et al.</i> 2013
Great hammerhead <i>S. mokarran</i>	X			Smale & Cliff 1998
Shortfin mako <i>Isurus oxyrinchus</i>	X			Rosas-Luis <i>et al.</i> , 2016
Blue shark <i>Prionace glauca</i>	X			Rosas-Luis <i>et al.</i> , 2016
Thresher shark <i>Alopias</i> spp.	X			Rosas-Luis <i>et al.</i> , 2016
Sleeper shark <i>Somniosus</i> cf. <i>microcephalus</i>			X	Cherel & Duhamel 2004
Portuguese dogfish <i>Centroscymnus coelolepis</i>	X		X	Clarke & Merrett 1972; Ebert <i>et al.</i> 1992
Abyssal grenadier <i>Coryphaenoides armatus</i>	X			Pearcy & Ambler 1974
Filamented rattail <i>C. filifer</i>	X			Pearcy & Ambler 1974
Long snouted lancetfish <i>Alepisaurus ferox</i>			X	Okutani & Tsukada 1988; Potier <i>et al.</i> 2007
Swordfish <i>Xiphias gladius</i>			X	Moreira 1990
Atlantic bluefin tuna <i>Thunnus thynnus</i>	X			Battaglia <i>et al.</i> 2013
Albacore tuna <i>Th. alalunga</i>	X			Bouxin & Legendre 1936
Bigeye tuna <i>Th. obesus</i>	X			Kornilova 1980
Cetaceans				
Sperm whale <i>Physeter macrocephalus</i>	X	X	X	Clarke 1962a; Akimushkin 1963; Clarke & Young 1998; Fernández <i>et al.</i> 2009
Pygmy sperm whale <i>Kogia breviceps</i>	X		X	Sekiguchi <i>et al.</i> 1992; dos Santos & Haimovici 2001; Beatson 2007; Fernández <i>et al.</i> 2009
Dwarf sperm whale <i>K. sima</i>	X			Ross 1984; dos Santos & Haimovici 2001

Table 32. (cont.)

Predator	Small <i>O.</i>	Giant <i>O.</i>	<i>Tan.</i>	Reference
Cuvier's beaked whale <i>Ziphius cavirostris</i>	X		X	Sekiguchi <i>et al.</i> 1992; Santos <i>et al.</i> 2001b; Santos <i>et al.</i> 2007
Strap-toothed whale <i>Mesoplodon layardii</i>	X			Sekiguchi <i>et al.</i> 1992
Blainville's beaked whale <i>M. densirostris</i>	X			Santos <i>et al.</i> 2007
Gervais' beaked whale <i>M. europaeus</i>	X			Debrot & Barros 1992
Hector's beaked whale <i>M. hectori</i>	X			Mead 1981
Hubbs' beaked whale <i>M. carlhubbsi</i>	X			Mead <i>et al.</i> 1982
Northern bottlenose whale <i>Hyperoodon ampullatus</i>	X			Santos <i>et al.</i> 2001c
Southern bottlenose whale <i>H. planifrons</i>			X	Sekiguchi <i>et al.</i> 1992
Short-beaked common dolphin <i>Delphinus delphis</i>	X			Pusineri <i>et al.</i> 2007
Risso's dolphin <i>Grampus griseus</i>	X		X	Sekiguchi <i>et al.</i> 1992; Clarke & Young 1998
Bottlenose dolphin <i>Tursiops truncatus</i>	X			Rancurel 1964
Striped dolphin <i>Stenella coeruleoalba</i>	X			Fernández <i>et al.</i> 2009
Pantropical spotted dolphin <i>S. attenuata</i>	X			Perrin <i>et al.</i> 1973
Fraser's dolphin <i>Lagenorhynchus hosei</i>			X	Sekiguchi <i>et al.</i> 1992
Long-finned pilot whale <i>Globicephala melas</i>	X			dos Santos & Haimovici 2001
Short-finned pilot whale <i>G. macrorhynchus</i>	X		X	Kubodera & Miyazaki 1993
Orca <i>Orcinus orca</i>	X			dos Santos & Haimovici 2001
Pinnipeds				
Juan Fernandez Fur Seal <i>Arctocephalus philippii</i>	X			Torres 1987
Sub-Antarctic Fur Seal <i>A. tropicalis</i>				Bester & Laycock 1985
Northern elephant seal <i>Mirounga angustirostris</i>	X		X	Condit & Le Boeuf 1984
Hawaiian monk seal <i>Monachus schauinslandi</i>	X			Goodman-Lowe 1998

Table 32. (cont.)

Predator	Small <i>O.</i>	Giant <i>O.</i>	<i>Tan.</i>	Reference
Seabirds				
Bulwer's Petrel <i>Bulweria bulwerii</i>	X		X	Waap <i>et al.</i> 2017
Grey-Faced Petrel <i>Pterodroma gouldi</i>	X			Imber 1973
Galapagos petrel <i>Pt. phaeopygia</i>	X			Imber <i>et al.</i> 1992
Black petrel <i>Procellaria parkinsoni</i>	X			Imber 1976
Westland petrel <i>Pr. westlandica</i>	X			Imber 1976
Buller's albatross <i>Thalassarche bulleri</i>	X			James & Stahl 2000
Black-browed albatross <i>Tl. melanophrys</i>			X	Cherel <i>et al.</i> 2000
Black-footed albatross <i>Phoebastria nigripes</i>				Harrison <i>et al.</i> 1983
Waved albatross <i>Ph. irrorata</i>	X			Harris 1973
Laysan albatross <i>Ph. immutabilis</i>			X	Nishizawa <i>et al.</i> 2018
Wandering albatross <i>Diomedea exulans</i>	X		X	Imber & Russ 1975

Distribution

Following the detailed morphologic and genetic review, it appears that octopoteuthid species are confined to a single ocean basin or water mass with few exceptions (arguably only *T. danae*). Newly recognised species of *Taningia* were generally represented by few specimens, making any assertion of opaque species boundaries premature. Currently available material suggests: separate northwest and northeast Pacific species (*T. rubea* sp. nov. and *T. sp. IV*, respectively); a circum-southern hemisphere species (*T. fimbria* sp. nov.); and a widespread but genetically connected (at least between Australasian and north Atlantic waters) species (*T. danae*) that overlaps with *T. fimbria* in the south and *T. sp. V* in the temperate north Atlantic.

Within the more speciose and better represented *Octopoteuthis*, species of the same species group tend to inhabit different ocean basins, and generally each basin is occupied by a single member of each species group (a pattern also found recently for mastigoteuthids; Braid pers. comm. 2017). However, comparisons between the

distributions of co-occurring *Octopoteuthis* species of different species groups suggests some degree of geographic segregation even within ocean basins. In the Atlantic, available *O. sicula* were proportionally more abundant (*i.e.*, comprised the majority of *Octopoteuthis* caught) in northern current-driven waters, with a strong adherence to the Gulf Stream, North Atlantic Drift and Canary Current, and only a few specimens from the south Atlantic. *Octopoteuthis megaptera* tended to predominate more southern current-driven waters, having greater proportional representation in western equatorial currents, the Brazil Current, Caribbean Current, through the Gulf of Mexico and in the southern Gulf Stream. Distribution of the third small-bodied Atlantic *Octopoteuthis* species (*O. leviuncus* sp. nov.) appears to centre around the more slack waters of the

Table 33. Predators and their octopoteuthid prey species, verified in this study during specimen examinations (Spec) or through synonymy (Ref; see species descriptions for references).

Predator	Prey species	Verification
Fishes		
Blue shark		
<i>Prionace glauca</i>	<i>O. deletron</i>	Spec
Long-snouted lancetfish		
<i>Alepisaurus ferox</i>	<i>O. rugosa</i>	Spec
	<i>O. nielsenii</i>	Spec
	<i>O. laticauda</i> sp. nov.	Spec
	<i>T. rubea</i> sp. nov.	Spec
	<i>T. sp. IV</i>	Spec
Crocodile shark		
<i>Pseudocarcharias kamoharai</i>	<i>T. danae</i>	Spec
Orange roughy		
<i>Hoplostethus atlanticus</i>	<i>O. rugosa</i>	Spec
Antarctic butterfish		
<i>Hyperglyphe antarctica</i>	<i>T. fimbria</i> sp. nov.	Spec
Bigeye tuna		
<i>Thunnus obesus</i>	<i>T. danae</i> / <i>T. sp. IV</i>	Spec
Cetaceans		
Sperm whale		
<i>Physeter macrocephalus</i>	<i>O. deletron</i>	Spec
	<i>O. rugosa</i>	Spec, Ref
	<i>O. laticauda</i> sp. nov.	Spec
	<i>O. sp. Giant South</i>	Spec, Ref
	<i>O. sp. Giant Atlantic</i>	Spec, Ref
	<i>T. danae</i>	Spec, Ref
	<i>T. fimbria</i> sp. nov.	Spec, Ref
	<i>T. rubea</i> sp. nov.	Spec, Ref
Pygmy sperm whale		
<i>Kogia breviceps</i>	<i>O. rugosa</i> / <i>O. fenestra</i> sp. nov.	Spec
Southern bottlenose whale		
<i>Hyperoodon planifrons</i>	<i>T. fimbria</i> sp. nov.	Spec

North and South Atlantic Gyres, areas largely uninhabited by both *O. sicula* and *O. megaptera*.

Species distributions in the Pacific appear to be more exclusive than in the Atlantic, but this is likely due to poorer sampling coverage and representation of Pacific specimens in collections. *Octopoteuthis nielseni* was the only species collected from the southeastern Humboldt Current and the eddying waters off west coast of Central America. Contrary to its close relative *O. leviuncus* sp. nov., *O. deletron* appears to favour current-driven waters, being predominate in the Japan Current, North Pacific Drift, and California Current. Also known from Japan, along with Hawaii and the north-east Australian coast, *O. laticauda* sp. nov. appears to occupy the complex western equatorial current system, with the Japan and East Australian Currents constituting its latitudinal limits. An exception to the sparsity of Pacific coverage is the waters around New Zealand, from which both *O. fenestra* sp. nov. and *O. rugosa* are well-represented in local collections. *Octopoteuthis fenestra* sp. nov. predominates the cooler waters of the Subtropical Front through Australasia, while *O. rugosa* prevails in the immediately adjacent warmer waters north of the front (a pattern that continues for *O. rugosa* throughout the southern hemisphere). This example demonstrates the fine-scale resolution that can be achieved in regions with good sampling coverage and rigorous taxonomy. In general, the distribution of a species appears to be formed of a system of interacting currents (with the possible exception of *O. leviuncus*), whether within a single ocean basin or between different ones.

In no geographic realm were members of the species Giant group proportionally abundant. In fact, their extreme scarcity in collections, compared to other octopoteuthids, suggest these species are relatively rare in the world's oceans. Support for this can be found in stomach content reports of sperm whales, generally acknowledged to be better samplers of large cephalopods than vessels (Clarke 1980). Three studies, two from Australasia and one from the Azores, reported considerably fewer *Octopoteuthis* beaks of Giant morphology ($n = 49, 115, 22$) relative to beaks attributed to small-bodied species ($n = 715, 371, 340$) and to *Taningia* ($n = 348, 1198, 113$; Clarke and MacLeod 1982; Clarke *et al.* 1993; Gómez-Villota 2007, respectively). However, small-bodied *Octopoteuthis* beaks are largely indistinguishable and, in these studies, likely encompass two species. Similarly, *Taningia* beaks, at least from the southern hemisphere, likely also comprise two species (*T. danae* and *T. fimbria* sp.

nov.). Alternatively, members of the Giant species group may benefit from some currently unknown biological or ecological quirk which renders them less vulnerable to both nets and predators.

Although new records for *O. deletron* from Alaskan waters and for *O. sp. Giant Atlantic nov.* from Iceland push the northern-most records of the Octopoteuthidae poleward, the family remains specifically antipolar.

Geologic events in the evolutionary history of the Octopoteuthidae

The presence of very closely related species (*T. sp. IV and V*) separated by the American landmasses presents an intriguing case in oceanic cephalopod evolution. For a variety of groups, the ranges of species pairs have been observed to be split by Central America (*e.g.*, gastropods, bivalves, echinoderms, crustaceans, fishes; Lessios 2008). This has been attributed to the rising of the Isthmus of Panama around 3 million years ago (mya; O’Dea *et al.* 2016), which divided the marine fauna of the Central American Seaway and significantly altered the oceanographic conditions of both the eastern Pacific and western Atlantic Oceans (Lessios 2008). Nesis (2003) reported nine cephalopod species pairs that fit this distribution pattern, two loliginids and seven octopods (Voight 1988), all shallow-water species. He concluded that too much time had passed (3–5 my) since the trans-Panamanian deep-water fauna was split for any relatedness to still be detectable, suggesting that it had been erased by their high dispersal capacity. However, for all three loci sequenced here, the interspecific distances between *Taningia sp. IV and V* are well within the ranges of other trans-isthmian taxa, and, surprisingly, align best with those whose divergence is likely attributable to the final closure of the isthmus (Lessios 2008). Agreement is closest with the values reported for fishes which, while predominantly reef fish, were the most nektonic of summarised groups. While an intriguing avenue of investigation among oegopsids, any conclusion about *T. sp. IV and V* remains premature due to their incomplete distributions, as well as the small number of available sequences.

Despite such limitations, similar geologic events could be significant contributors to the divergence of other octopoteuthid species. The other species pair identified, *O. megaptera* and *O. sp. IO nov.*, are slightly more divergent from each other than *T. sp. IV and V* (COI: 5.90% and 3.04%, respectively), suggesting a more distant event

involving the Atlantic and Indian Oceans. The final closure of the Tethys Seaway, around 14 mya, could have halted mid-latitude dispersal between their ancestral species with a hypothetically continuous range from the Indian to the Atlantic via the proto-Mediterranean Basin (Hamon *et al.* 2013). Alternatively, a founding population could have earlier made its way around the southern tip of Africa into the nascent south Atlantic (where *O. megaptera* still predominates, see below) as the climate of the early Miocene was warmer and more even (Knorr *et al.* 2011). In the subsequent cooling period following the closure of the Tethys, dispersal south of Africa would have been cut off and the two populations diverged under differing selective pressures. A final, older split between two discretely distributed species, *T. fimbria* and *T. rubea*, seems intuitively related to the commencement of the Antarctic Circumpolar Current, around 34–40 mya (Barker and Thomas 2004). This circumglobal current, or at least the opening of the Drake Passage and Tasmanian Seaway which allowed for the Current, characterise the distribution of *T. fimbria* sp. nov. today. Previously, a single *fimbria-rubea* ancestor may have occurred throughout the Pacific Ocean; however, the changes in oceanographic conditions brought on by the circumglobal current, in addition to its strong influence on dispersal, may have been sufficient to cause a southern population to diverge from those in the north. Interestingly, the western and eastern Pacific *Taningia* species, *T. rubea* sp. nov. and *T. sp. IV*, are only slightly less divergent from each other (COI: 11.30%) than they are from *T. fimbria* sp. nov. (14.83 and 15.28 %, respectively), suggesting a second divergence within *Taningia* shortly after. All hypothesised divergence events above are basally bounded by the proposed divergence of several oegopsid families around 80–90 mya (Tanner *et al.* 2017).

8. CONCLUSION

This study is the first global revision of the Octopoteuthidae to date, as well as the largest genetic analysis of the family. Sixteen proposed octopoteuthid species are described, doubling the number previously attributed to the family (Nesis 1987). In addition, refined intrafamilial relationships were established in the form of species groups in *Octopoteuthis*. All extant type material was examined, and taxa historically attributed to the family have been critically reviewed. External and selected internal morphologies are described herein in a detailed, consistent format, augmented by novel characters and complemented with genetic, biogeographic, and life history traits.

The considerable increase in familial diversity demonstrates the overdue nature of such a critical review. Indeed, the first specimens of all newly designated species were collected between 1958 and 1979, and have been awaiting taxonomic attention for 40–60 years. Furthermore, two strikingly different octopoteuthid species were repeatedly referred to informally in the literature for decades: *Octopoteuthis* sp. A Young, 1972 (= *O. leviuncus* sp. nov.) and the giant *Octopoteuthis* of Clarke (= *O.* sp. Giant Atlantic nov.; first mentioned in Clarke and MacLeod 1976). Taken together, these observations stress the difficult but important nature of global-scale taxonomic revisions, and the need to build support structures that enable such works.

The robustness of this study is considered reliant on the treatment of the family at a global scale, and incorporating several independent lines of evidence (*i.e.*, employing an integrative taxonomic approach) to establish and test species concepts. These two factors are especially crucial when working with any highly morphologically conservative group (*e.g.*, skates; McEachran & Dunn 1998) or cryptic taxa (*e.g.*, giraffe; Brown *et al.* 2007). This study also demonstrates that morphology-based studies, accessing already established collections, can contribute to fields beyond systematics, including reproductive biology, trophic interactions, biogeography and distribution patterns. In addition, such works can provide support for phylogenetic inferences as well as a second line of evidence to fill in gaps when species are unavailable for sequencing, a common occurrence when working with difficult to collect taxa. Similarly, concurrent genetic analyses, even when incomplete, can also contribute interesting, albeit opportunistic, insights into other aspects of biology and biogeography.

With a substantial amount of the fundamental taxonomic work now resolved within the Octopoteuthidae, it is hoped that studies into their biology and ecology can begin in earnest. Indeed, morphologic examinations herein have already suggest interesting patterns in their biology and ecology. In particular, given the present state of marine resource overexploitation, more refined studies of predator-prey relationships are advocated for to better understand marine food web dynamics and biodiversity resilience.

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11. APPENDIX A

‘Book 4. Worms, Insects, Reptiles, Fishes, Birds, and Quadrupeds of Chile’
G. I. Molina, 1782, pp. 199

Translated from Italian, Latin

‘In addition to *Seppia Officinale*[sic] there are located in the Sea of Chile three other species of very singular cuttlefish. The first is *Seppia unguiculata* (*), which it is of a great mass, and has in place of suckers armed arms of a double row of claws, or sharp nails similar to those of a cat, and that they withdraw, like them, in a sort of sheath. This species has a delicate flavor, but not very common in those seas.

...

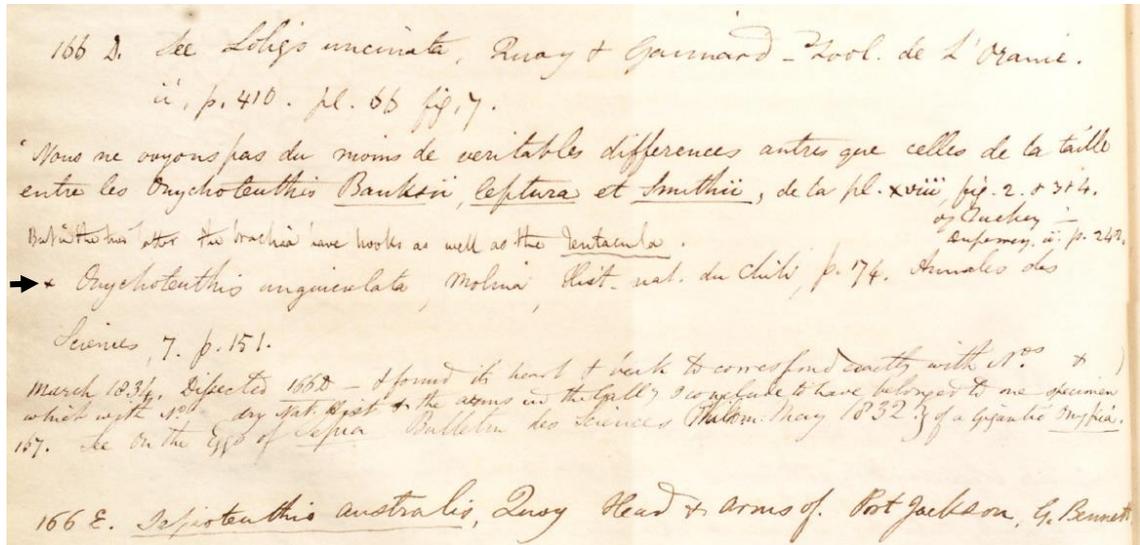
‘(*) Cuttlefish body tailless, arms clawed.’

...

12. APPENDIX B

'Catalogue of the contents of the Museum of the Royal College of Surgeons in London. Fasciculus I., comprehending the First Division of the Preparations of Natural History in Spirit (Vegetabilia and Animalia evertebrata)'

R. Owen, 1830, accompanying hand-written notes



Transcription, beginning at arrow

* *Onychoteuthis unguiculata*, Molina, Hist. nat. du Chili, p. 74. Annales des Sciences, 7. p. 151.

March 1834, Dissected 166D - I found its heart & beak to correspond exactly with Nos. &) which with No. dry Nat. Hist. & the arms in the Gallery I conclude to have belonged to one specimen'

Owen left the catalogue numbers blank, but they likely correspond to 903, 308, and 1436, respectively, according to Owen (1881).

13. APPENDIX C

‘Description of some fragments of two gigantic cephalopods’
P. Harting, 1861, pp. 199

Translated from French, current taxa and terminology given in square brackets at first usage

‘When I was put in charge, two years ago, of the direction of the Museum of Natural History of the University of Utrecht, I found a jar containing the detached pharynx or buccal mass and a number of suckers, whose dimensions indicated that they belonged to a gigantic cephalopod. All I could learn concerning the origin of this piece was merely that it, and several other objects now part of the Museum, came from a collection of natural history objects assembled by the care of a Mr. Juliaans, once an apothecary in this town, and that these objects were purchased for the museum by the end of the last century or the beginning of this one.

‘I gave a short description of these fragments in the meeting of the Academy of June 26, 1858.

‘During this communication, Mr. W. Vrolik indicated the existence of other fragments of a very large individual, belonging to the same class and preserved in the collection of the Zoological Garden of Amsterdam. I turned therefore to Mr. Westerman, director of that institution, who, with his well-known benevolence, kindly placed at my disposal the fragments in question. They were found in the stomach of a shark, caught in the Indian Ocean by the crew of a commerce/commercial vessel returning from the East Indies to Amsterdam.

‘In the description that follows, I will refer primarily to the two individuals, of which these pieces have been part, simply as No. 1 and 2.

‘No. 1. The pharynx or buccal mass, as preserved in the museum, is represented in natural size, in various ways, in figures 1, 2 and 3, Pl. 1. All the external adherent parts, such as the lips, the esophagus, the salivary glands etc., have been detached, so that one can no longer see any trace of them. The piece has undergone a preparation, consisting of an incision on the ventral side by a longitudinal section and the lingual unit or “*glottidium*”, which in the natural state lies within the buccal cavity, has been removed and inverted outside, the lips of the wound being extended by means of a pen rod.

‘The dimensions of the pharyngeal bulb are the following: the height is 8 cm, the transverse diameter is 10.5 cm; the greatest diameter in a slightly oblique direction is 12 cm; finally, the circumference measures 35 cm.

‘As for the structure of the various parts, we do not notice anything which is not already well known in cuttlefish and squid. A detailed description is therefore superfluous, and inspection of the figures is enough to show the details. I only point out the enormous development of the two lateral lobes of the lingual unit (Fig. 1 and 2), together forming a sort of mobile palate, its inner surface equipped of small conical papillae and leading to the gutter-shaped channel in the posterior part of the tongue and from there to the esophagus, whose opening is at the lower surface in *o* (Fig. 1).

‘The horny part of the tongue [=radula] is surmounted, as is customary in sepiids and loliginids, of seven rows of teeth or hooks. The middle row (see Fig. 4, representing the upper part of the tongue at a low magnification) is composed of triple-pointed hooks, the hooks of the adjacent rows are double, those of the outer rows single; all in all, these rows remain distinct and separated from each of the others, for the entire length of the horny plate.

‘The suckers, which were found in the jar that also contains the buccal mass, and can therefore be considered as having belonged to the same animal, have dimensions ranging from 13 to 25 mm. Their form (see figs 5, 6, 7, 8) generally responds to that of the arm suckers of the *Loligo*'s, *Ommastrephes* and related genera. They are more or less hemispherical, mounted on a small foot eccentrically placed, and having a horny circle (Fig. 8'), oblique, slightly convex and armed with a very large number of small teeth of equal size. On their concave surface one sees a depression in the center and two other annular depressions around it.

‘No. 2. The fragments of the second individual in question are more numerous. They are: 1. the buccal mass with a large part of the esophagus, 2. one of the arms, 3. a portion of one of the tentacles, and 4. one eye.

‘All these pieces, having spent some time in the stomach of a shark, have suffered the commencement of decomposition. However they are still in good enough shape to allow some detailed anatomical examination of their structure.

‘1. The muscular bulb of the pharynx (Fig. 9 and 10, Pl 2), having a height of 11 cm, a width in the two transverse diameters of 7 and 8 cm, and a circumference of 23 cm, is still wrapped in its membranous sac, surmounted of the two lips, one of which (the outer, *a*) is only the folded terminal edge of this sac, the other (the inner, *b*) distinguishes itself, as in the cephalopods in general, by its papillose structure. On the exterior of the membranous sac one will still see a few fragments (*cc*), remnants of tissue, by which the bag was attached to the surrounding parts.

‘The upper portion of the membranous sac up to the curved line of Fig. 9 is in immediate union with the muscular bulb, included therein, but, by splitting the sac by a longitudinal section at its ventral surface, one finds (see Fig. 11) that its lower portion is free and covers not only the lower surface of the pharyngeal bulb, but also two small salivary glands *cc*, placed next to the sub-pharyngeal ganglion *d* (Fig. 11 and 12), through which passes the common excretory duct *e* of the two major salivary glands. On the outer and bottom surface of the ganglion, we noticed a gutter-shaped indentation *f*, in which the upper part of salivary duct is received. The latter then passes through the substance of the ganglion, and, after reaching its opposite surface, it bifurcates and the two branches (*gg* Fig. 12), forming an angle of more than 90°, go under the base of the tongue in the cavity of the pharynx.

‘In the lowest part of the membranous sac is an opening, serving as a passage to the esophagus (Fig. 9 and 11 *i*) and to the salivary duct.

‘Figure 11 shows the lingual unit or “*glottidium*”, contained between the two branches of the upper mandible, and therefore seen from its lower and posterior surface. In Fig. 13 the tongue, detached from the buccal cavity, is viewed from the side. The two lateral lobes *aa*, with small conical papillae on their surface, are much smaller than in the previous case. The retractor muscle of the tongue (Fig. 11 *l*, Fig 13 *e*) is very long and

very slender, so that at first it looks like a nerve. I made sure, however, that it only contains fibrous cells and connective tissue (cellular). The horny plate (Fig. 14) shows on its upper part seven rows of hooks, of which the two outers come together, so that towards the middle of the plate, there are only five rows. Towards the base, the two outer pairs of these five rows become so close, that they appear to form a single one, though in fact they are separated by a very small interval.

‘The anterior and fleshy part (*c*) of the tongue possesses on its concave surface, which turns toward the radula, a cavity *d*, which appears to serve the purpose of receiving the radula temporarily, in order to cover it as a hood, so that the small hooks are protected from contact with hard objects ingested in the mouth. Besides this observation also applies to analogous organs in No. 1, and probably in all other sepiids, loliginids, etc.

‘The portion of the esophagus still attached to the pharynx has a length of 52 cm. In Fig. 11 and 13 only a portion has been represented. Its diameter, unchanging throughout its length, is about one cm. On its surface two nerves can still be seen (Fig. 9 *k* and *l*).

‘2. The terminal part of one of the arms (Fig. 16, Pl 3), 13 cm long, having at its base a diameter of about 6 cm and a circumference of 13 cm. Its shape is roughly that of a triangular pyramid, with one side wider than the other two. It is equipped with a pronounced swimming ridge *b* [=arm keel]. Its muscular portion is tapered conically. In *a* is seen its central channel. Its entire surface is smooth and covered with a purple-coloured epidermis. The suckers, occupying two rows, all bear hooks. They are very large towards the base, much smaller towards the tips.

‘3. A portion of the terminal part of one of the tentacles (Fig. 17), 17 cm long. Its greatest transverse diameter, from the side equipped with hooks to the opposite surface, is 7 cm; the one that runs vertically through is only 5 cm, so the section, with a circumference of 18 cm, has an elliptical figure.

‘The epidermis is destroyed in several locations. Where it is found, it is smooth. Its colour is a blackish-purple, more or less dark in various places. The fleshy mass of the arm is entirely composed of fibrous cells of a length, so great, that one rarely succeeds in seeing both ends. Among the muscular fibers the microscope allows us to meet here and there some fragments of capillary vessels (Fig. 21), whose structure does not essentially differ from those of the capillary vessels of vertebrate animals. The larger branches possess two tunics, the external one of longitudinal fibers, the other composed of annular or reticulated fibers. These tunics are lacking in true capillary vessels, which have only a simple wall, and without further recognisable elements. The diameter of these vessels is 7 mm [=7 μ m], that is to say it is approximately equal to those of most capillary vessels in humans and other mammals. This fact demonstrates that cephalopods possess a capillary system of distribution just as fine as that of vertebrate animals.

‘In *a* the axillary channel can be seen, in *b* the nerve contained therein. Figure 18 represents a part of this channel, opened by a longitudinal section, to better see the tentacular nerve and its branches. The primitive tubes have walls with double contours; their diameter varies from 5 to 9.6 mm and averages 7.2 mm.

‘The inner surface of this portion of the tentacle is topped with fifteen hooks, alternating in two rows, close to one another. There is no protective membrane, but the base of each cup is received in a slight depression of the arm, to which it is held by a small eccentric foot. The structure of these suckers is absolutely the same as those of the arm. Only they are all bigger. Their figure is pyriform. Not far from the top of each sucker is a lateral triangular opening (Fig. 22), from where the tip of the hook emerges, 7 to 9 mm in length and which is only an external extension of the horny circle (Fig. 24), which is found included between the outer skin of the sucker and the circular cavity, resulting from the contiguity of these two parts, one nesting into the other and both covered by their epidermis, which is consequently in immediate contact with the two surfaces of the horny circle. This manner, in which the circle is implanted in the sucker, is shown in Figure 23, representing a vertical section, low magnification. In this figure *ee* is the epidermis of the skin of the sucker, reflecting inward and meeting in *dd*, that is to say at the place where the bottom edge of the horny circle is, at the epidermis *bbbb* of the muscular skin *a*, in order to receive this circle between the two epidermal surface. Apart from the figure of the circle, there is therefore a complete analogy with the mode of implantation and formation of the nails of vertebrates. Thus the horny circle is found to have the same composition as the horny tissues in general. Only the elements here are of an extreme fineness. Employing a high magnification we see that the substance, either the hook or the circle itself, is composed of undulating parallel plates, whose thickness is only 0.5 to 0.8 mm (Fig. 25). After a stay of twenty-four hours in a concentrated solution of caustic potassium, the majority of the tissue (Fig. 26) is transformed into an assembly of utricles or polyhedral areolas, whose diameter varies from 20 to 30 μ m. Inside and against the walls of these utricles one can see small drops of a fluid, whose refractive power slightly exceeds that of the solution of potassium/potash. At sites of tissue where the action of the reagent was not prolonged long enough to produce the full effect, we see fusiform cavities between the still distinctly visible horny plates, and in these cavities a number of septa. It is therefore by this that begins the transformation, whose final result indicates the origin of the horny plates of superimposed epidermal cells, as we have known for a long time for nails in general.

‘The muscular tissue of the ball is an extension of that of the arms itself, through the little foot that connects them. Only the fibrous cells (Fig. 19, 20) are very much shorter than those that are part of the fleshy substance of the arm. Furthermore they are united in a large number of small bundles, among which is found the connective tissue, already distinguishable with the naked eye, by its colour, whiter than the rest of the tissue.

‘4. An eye, front view in Fig. 27, and consists only of the ocular capsule, the eyeball itself having completely disappeared. Its height is 7.5 cm, its width 8.5 cm, its diameter front to back is 5 cm. These dimensions exceed those of the eye of the right whale.

‘The anterior surface of the eye, as in the oegopsids in general, is provided with an irregular oval opening, 3.7 cm long, and a very pronounced lachrymal sinus. At its posterior surface is found the cartilaginous plate riddled with pores, through which enter the many threads of the optic nerve, as is represented in part in Figure 28. The number of pores ranges from 8 to 12 in a square centimetre. Their face is round or elliptical, and they have diameters ranging from 0.25 to 1.5 mm.

 ‘After having briefly described the various pieces, I will now endeavour to bring them together with facts already known, to determine the natural affinity of the animals, to which they have belonged.

‘It has long known that there exists in the seas cephalopods of gigantic dimensions, though no naturalist has been fortunate enough to be able to examine at leisure a complete individual.

‘The tales of the the Kraken, extending like a promontory into the seas of Norway, of which Olaus Magnus, Archbishop of Upsala, made the first mention of in 1555 - of the colossal squid that Denys de Montfort represented as entwining in its enormous arms a three-masted frigate, are only exaggerations of a truth beyond dispute.

‘The largest cephalopod, of which a complete and detailed description and a figure has been published, is *Ommastrephes giganteus* D'Orb. [= *Dosidicus gigas*], whose total length is 1.11 m, that of the body being only 0.44 m.

‘The animal, to which Mr. Gray has given the name of *Sepioteuthis major* [= *Thysanoteuthis rhombus*], was not complete, seeing as only the bases of the arms were preserved, but the body had a length of 0.75 m.

‘However, several facts more or less well proven indicate, that some species can achieve considerably greater dimensions.

‘Aristotle assigned to the great squid of the Mediterranean a length of five cubits, or about 1.8 m, a measurement that Pliny repeats.

‘The same author reports that Trebius Niger had seen a Polypus, arrived on the shore, and that they only managed to take with dogs. This Polypus had a body as big as a barrel, having a capacity evaluated equal to fifteen amphorae, which is equivalent to five hectoliters. The arms had a length of thirty feet and were so thick a man could hardly embrace them with both arms. The remains of the animal weighed seven hundred pounds.

‘The same story with some slight variations is repeated by Aldrovandi, after the story of Fulgosus. He adds other similar facts, reported by Aelianus, but which are too extravagant to take into serious consideration.

‘As for the Polypus of Trebius Niger, I admit that the simplicity of the narrative and numerical data, contained therein, seems to me to militate quite well in favor of the veracity of the author, not to be regarded as one of those beings wholly fabulous, of which science has little to hold into account. Indeed we will see that the dimensions of the animal, that he says he saw, although certainly enormous, do not outweigh those of other cephalopods so much, whose existence these days seems to be proved, to need to conclude that this story deserves no credit, as many authors assume.

‘Mr. Sander-Rang, speaking of the octopods, said he encountered, in the middle of the Ocean, a species very distinct from others, of a very dark red colour, with short arms, but the body size of a barrel.

‘Péron reported the following: "That same day (January 9) near the island of Van Diemen [= Tasmania], we sighted in the waves, a short distance from the ship, a huge specie of *Sepia*, likely of the genus *Calmar*, the size of a barrel; it rolled noisily on the waves, and its long arms extended to the surface of the agitated water like as many huge

reptiles. Each of these arms was not less than six to seven feet long and a diameter of seven to eight inches.”

‘Quoy and Gaimard collected in the Atlantic Ocean, near the equator, in calm weather, the remains of a huge squid; that which the birds and dogfish had left could weigh a hundred pounds, and it was only a longitudinal half, completely deprived of its tentacles; so they assessed the entire mass of the animal to at least two hundred pounds. These remains, brought back from the voyage of the *Urania*, are still preserved in the Museum of Garden Plants. They are, undoubtedly, the same as those Mr. J. van der Hoeven saw when he visited the establishment in 1824. Only, the inscription bears: Various parts of the intestines of a huge squid, found dead in the sea near the equator, weight about 400 pounds, by Mr. de Freycinet. The probable weight of the animal is therefore doubled. Indeed, adding the weight of the arms and the half of the body already lost to that which still remained, one would think that assessment somewhat exaggerated.

‘Ms. Graham, quoted by Mr. Johnston, saw a species of Cephalopod, whose arms were 18 feet long, and Schwediaver reports that a whaler harpooned a sperm whale with an arm of a cuttlefish about 23 feet long in its mouth, without it even being whole.

‘At the Hunterian Museum in London the fins, sections of the arms, the heart and the beak of an *Onychoteuthis* (subgenus *Enoploteuthis*) are preserved, whose total length must have been at least six feet. These debris derive from a dead individual that Banks and Solander, the companions of the Captain Cook on his first trip, found floating in the sea between Cape Horn and Australia, latitude 30° 44' S, longitude 110° 33' W.

‘Here is certainly enough to see that the fears of fishermen of coral and pearls of being taken away by such an animal, which captures them and wraps them in their arms, armed with suckers or hooks, real claws, are not absolutely unfounded.

‘In recent times it is mostly Mr. Steenstrup who has done research of a high interest in the existence of gigantic cephalopods. To date, however, only part of his research has been published, the total of which, together with several plates, is intended to appear in *Memoirs of the Royal Academy of Copenhagen*. I had the privilege, however, of seeing three of these plates already completed, that Mr. J. van der Hoeven received from the author, and moreover, Steenstrup was good enough to give me a letter containing a summary of the main results of his research, documented in the memoir the publication of which will not be long in coming.

‘It results from the research of Mr. Steenstrup, that in the Atlantic, in the northern seas and even the entry of the Baltic Sea, live decapod cephalopods which are not much smaller in size than the *Polypus of Trebius Niger* nor the cuttlefish to which Schwediaver referred, or the one that Ms. Graham saw one of the arms of.

‘In a brochure, remarkable in several respects, published two years ago in Copenhagen, Mr. Steenstrup showed with rare sagacity, that the singular animal, which was caught by fishermen in 1546 in the Sound [=the Øresund], in the vicinity of Malmö, and that several naturalist authors of the sixteenth century, such as Rondelet, Belon and Gesner, described and figured under the name *Marine monk* that superstition had given it, was nothing else than a cephalopod, neighbour of the *Loligo's*, but of enormous dimensions, since its length, from the posterior margin of the mantle to the top of the arms was 4

Danish yards or 8 feet or 2.5 m. Adding that of the tentacles, this length would be at least doubled.

‘In December 1853 another animal, probably of the same species and about the same size as the Marine monk, was thrown on the shore of Jutland near Ålbæk. Mr. Steenstrup could only collect the horny beak, the rest having been carried away by fishermen to serve as bait for their lines. Several wheelbarrels had been filled. Mr. Steenstrup gave this species name of *Architeuthis monachus*.

‘Later he received from a captain, who had made this catch in the Atlantic Ocean, several parts (the pharynx, a fragment of an arm, the reproductive organs, and the gladius) from another gigantic cephalopod, neighbour of the first by the shape of the mandibles, but differing enough to distinguish it as a particular species under the name *Architeuthis dux*. The gladius is only 6 feet in length, and the pharynx is as big as a child's head.

‘Finally Mr. Steenstrup collected some information in Iceland that he considers to be authentic, concerning two decapod cephalopods cast on the shore of this island in 1639 and 1790, one of which equaled the Marine monk in size, and the other still far surpassed it as it was several yards long.

‘Let us now return to the pieces which I have described above.

‘Those of No. 1 undoubtedly belonged to an individual of the same species to which Mr. Steenstrup just gave the name *Architeuthis dux*. I was able to convince myself first by the perfect resemblance of the suckers of which Mr. Steenstrup has given the figure, but especially by that of the mandibles, of which I owe a sketch to the kindness of this learned naturalist. By comparing Fig. 1A, which is a copy of that of the lower mandible, to Fig. 1, one sees readily that the two figures are in all respects similar. Even the dimensions of one compares so exactly to those of the other, that they seem modeled on the same object.

‘As for No. 2, the total absence on the arms of ordinary suckers with denticulate horny circles, all being replaced by hooks, is sufficient to report this to the genus *Enoploteuthis* of d'Orbigny, which is distinguished by this character from the true *Onychoteuthis*. It can be assumed still with some probability, that the species is the same as that of the fragments which are preserved in the Hunterian Museum, but of which I know only the single figure of the inner parts of the mouth, published by Mr. Owen. This figure corresponds fairly well to the object which I described, but is not enough by itself to establish the identity.

‘De Férussac believes that this species is the same as the *Sepia unguiculata* of Molina. Also, Mr. Owen designates it by the name of *Enoploteuthis unguiculata*. However, I think that Orbigny is right in changing this specific name, which is applicable to more than one species, to that of *Enoploteuthis Molinae*.

‘However, there is still another question that one could ask, before accepting these species as distinct from others that live in the Ocean. That question is this: how certain are we that these large individuals are specifically different from other much smaller ones, which are found in large numbers and are already much better known by naturalists? One might doubt. The size of the body cannot serve as a character to distinguish the species, especially when it comes to animals that probably grow for as

long as they continue to live. Already more than once naturalists have believed to see various species among individuals which differed only by age; witness the history of the orangutan, the salmon, etc. Yet, the number of cephalopods of small size in the seas is excessively large, but they are at the same time exposed to fall prey to a multitude of enemies, such as various species of seabirds, of sharks, dolphins etc. On January 10, 1858, latitude 43° 12' S, longitude 37° 15' E, the crew of the merchant vessel Vriendentrouw, captained by De Greevelink, found, for a duration of a two hour walk from the ship, as far as the sailor on watch could see, the sea covered with dead Loligo's. Mr. W. Vrolik found in the stomach of a *Hyperoodon* about ten thousand Loligo mandibles! Therefore there will only be few that will reach a slightly considerable size, and this is probably only by taking refuge in the depths of the sea, that this small number, escaped from their voracious enemies, continues to grow and that some of them acquire a last these gigantic dimensions, which we have seen some examples of in the preceding pages. But then it is very probable that their species in a much younger state, when individuals were much more numerous, had not entirely escaped the research of naturalists. – However, we must admit that given the present state of our knowledge and in the presence of only a few isolated fragments, it is quite difficult to recognize in them, with sufficient certainty, the species of which we know smaller individuals and that one could believe consequently to be younger. Yet it is possible to hazard a guess. Thus, for example, using the suckers and mandibles as terms of comparison, the only characteristic parts which I have at my disposal, I suspect that Orbigny's *Ommastrephes todarus* [= *Todarodes sagittatus*] could well be the young of cephalopod No. 1 and consequently of *Architeuthis dux* of Mr. Steenstrup. Actually Orbigny's *Ommastrephes todarus* lives in the Mediterranean and *Architeuthis dux* was taken in the Atlantic, but several other cephalopods are common to both seas. However, I will only express this suspicion with great reservation, since Mr. Steenstrup, who is in possession of some other parts of this species, believes it to be sufficiently different to report it to a new genus. We observe, otherwise, that the *Ommastrephes todarus* differs from its congeners by its tentacles covered along their entire length by suckers. It is consequently very easy to verify the assumption that I just made regarding the identity of the two species, for the one who will be able to examine a complete individual, or only a complete tentacle of the *Architeuthis dux*.

'As for the *Enoploteuthis*, of which I described some debris, I cannot make any well founded suspicion equating it to some other known species. *Enoploteuthis Lesueurii* [= *Ancistrocheirus lesueurii*], to which it still seems to resemble the most, yet still differs by the shape of the beak, and especially by the suckers with hooks, which, judging from the figure published by M. d'Orbigny, are much flatter in the vertical direction and do not consequently possess the figure of a reversed pear, which could well be a good characteristic sign to recognize in a sequence species at an earlier age, unless this form undergoes modification during growth of the animal.

'Description of the Figures

'With the exception of figures 4, 15, 19, 20, 21, 22, 23, 25 and 26, where the magnification is indicated in the description, all of the figures represent objects in their natural size.

'First Plate

'Fig. 1. Pharynx or buccal mass of cephalopod No. 1, side view, with the lingual unit everted.

a. Upper mandible

- b. Lower mandible
- c. One of the lateral lobes of the lingual unit or “*glottidium*”
- d. Coated part of the horny plate
- e. Anterior fleshy part of the tongue
- f. Retractor muscle of the tongue
- o. Place where the oesophagus opens into the pharynx

Fig. 1 A. Outline of the lower mandible of *Architeuthis dux* Steenstrup.

Fig. 2. The pharynx viewed from its underside. The letters have the same meaning as in Fig. 1.

Fig. 3. The same object viewed from the front, in a slightly oblique direction.

Fig. 4. Upper part of the horny plate of the lingual unit, viewed at a low magnification.

Fig. 5, 6, 7. Cups or suckers.

Fig. 8. Vertical section through a sucker; *a* and *b* indicate lower limits of the horny circle.

Fig. 8'. An isolated horny circle, side view.

‘Second Plate

‘Fig. 9. Pharynx or buccal mass of cephalopod No. 2, side view.

- a. Exterior lip
- b. Interior lip
- cc. Shreds of ligaments which unite the membranous sac of the pharynx to the surrounding tissues
- d e'*. Line indicating the attachment points of the membranous sac to the surface of the fleshy bulb of the pharynx
- e. Common excretory duct of the large salivary glands
- g h*. Lower opening of the membranous sac
- i. A part of the oesophagus
- k* and *l*. Nerves on the oesophagus

Fig. 10. The same, front view.

- a* and *b*. exterior and interior lips.

Fig. 11. The same, opened at its lower surface by a longitudinal section.

- a* and *b*. lips
- c c*. Small salivary glands
- d*. Sub-pharyngeal ganglion
- e*. Common excretory duct of the large salivary glands
- f*. Median gutter-shaped depression in the substance of the ganglion, serving to receive the upper portion of the salivary duct until the point where this duct crosses it.
- g h*. Opening of the membranous sac, serving as passage to the salivary duct and to the oesophagus.
- i*. Part of the oesophagus
- k*. Lingual unit or “*glottidium*” viewed from its lower surface and occupying its natural place between the branches of the upper mandible
- l*. retractor muscle of the tongue
- m*. Cavity between the membranous sac and the fleshy bulb of the pharynx.

Fig. 12 *d*. sub-pharyngeal ganglion

- k*. Posterior part of the tongue
- n*. Space between the posterior surface of the tongue and the upper surface of the ganglion
- e*. Common excretory duct of the large salivary glands

- f.* gutter-shaped depression, in which is lodged the superior part of the excretory duct
- g g.* Branches resulting from the bifurcation of the excretory duct at its exit from the ganglion

Fig. 13. Lingual unit of the same, side view.

- a a.* Lateral lobes
- b.* Horny plate
- c.* Anterior fleshy part
- d.* Its anterior and upper cavity
- e.* retractor muscle

Fig. 14. Horny plate, front view.

Fig. 15. Teeth of the horny plate, slight magnified.

- a.* Median row
- b.* One of the lateral rows

'Third Plate

'Fig. 16. Upper part of one of the arms of the same

- a.* Axillary canal
- b.* Swimming ridge

Fig. 17. Fragment of one of the tentacles of the same.

- a.* Axillary canal
- b.* Nerve contained therein

Fig. 18. A part of the axillary canal opened by a section, to better see the tentacular nerve and its branches

Fig. 19. Fibrous muscular cells forming the mass of the fleshy substance of the arms as well as that of their extensions into the suckers, viewed at a magnification of 300X.

Fig. 20. A part of one of these fibrous cells at a magnification of 1000X.

Fig. 21. Part of a capillary vessel in the fleshy substance of the arm, at a magnification of 300X.

Fig. 22. Upper part of one of the suckers, side view of the opening from which emerges the hook, viewed at low magnification.

Fig. 23. Vertical section of a sucker slightly magnified.

- a.* Internal muscular ball
- bbbb.* Its epidermis
- c.* Small foot, uniting the sucker to the arm
- d d.* Lower edge of the horny circle.
- e e.* Epidermis of the skin of the sucker, reflecting inwards and uniting with the epidermis of the internal ball at *d d*, so as to receive the horny circle between these two epidermal surfaces.
- f.* Hook
- g.* Cavity of the horny circle

Fig. 24. Isolated horny circle.

Fig. 25. Horny substance of the hook, view at a magnification of 1000X.

Fig. 26. The same substance, after an exposure of some hours to caustic potassium/potash.

Fig. 27. An eye of the same individual.

Fig. 28. A portion of the posterior cartilaginous membrane, riddled with pores, through which enter the branches of the optic nerve.'