Marine Biodiversity Records, page 1 of 6. © Marine Biological Association of the United Kingdom, 2011
doi:10.1017/S175526721000120X; Vol. 4; e5; 2011 Published online

Spermatangium structure and implantation sites in onychoteuthid squid (Cephalopoda: Oegopsida)

K.S.R. BOLSTAD[1] AND H.J.T. HOVING[2]

[1]Earth & Oceanic Sciences Research Institute, Auckland University of Technology, Private Bag 92006, Auckland 1142, New Zealand, [2]Ocean Ecosystems, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

Reproduction remains poorly understood in the Onychoteuthidae, with information previously published on only six of the ~25 species, from three of the seven genera. Herein new information is presented for a further five species from four genera: mated and spent females are reported from the genera Onychoteuthis, Onykia, Notonykia *and Callimachus, and the morphologies and locations of implanted spermatangia for the species* Onychoteuthis meridiopacifica *and* Onykia aequatorialis *are provided. Males of the genus* Onychoteuthis *are found to implant spermatangia within longitudinal cuts in the female's mantle surface, while males of* Onykia *implant individual spermatangia into the female's mantle at various locations, without a specific associated wound. These different implantation strategies are discussed in the context of mating and fertilization. A bulb-like structure at the aboral end of the spermatangium, possibly unique to the genus* Onychoteuthis*, is also described and examined and its function discussed. All onychoteuthids examined herein are observed to undergo extreme late-life physical degeneration.*

Keywords: Onychoteuthidae, Oegopsida, mating, spermatophores, spermatangia

Submitted 26 August 2010; accepted 11 November 2010

INTRODUCTION

Squid in the family Onychoteuthidae Gray, 1847 have been reported from every ocean but the Arctic, and are important in the diets of many apex marine predators (e.g. Clarke, 1980; Clarke & MacLeod, 1982a, b; Piatkowski *et al.*, 2001; Cherel & Duhamel, 2004). However, onychoteuthid life history remains poorly understood; several of the ~25 species remain known only from a single early- or late-life stage (Bolstad, 2008a), preventing even full morphological descriptions throughout ontogeny. Reports on biology or ecology have generally focused on either the minor commercial species *Onychoteuthis borealijaponica* Okada, 1927 (Murata & Ishii, 1977; Murata *et al.*, 1982; Okutani & Murata, 1983), *Onychoteuthis* '*banksii*' (Arkhipkin & Nigmatullin, 1997, likely comprising a number of recently disambiguated taxa—see Bolstad, 2008b), or the common notalian by-catch species *Onykia* (*Moroteuthopsis*) *ingens* Smith, 1881 (e.g. Jackson, 1993, 1995, 1997, 2001). Spent females from an indeterminate number of *Onychoteuthis* species have also been reported, under the name '*Chaunoteuthis mollis*' Appellöf, 1891 (Grimpe, 1921; Torchio, 1967; Nesis, 1970; Adam, 1972; Okutani & Ida, 1986; Bello, 1998).

Reproduction, in particular, remains largely unreported in onychoteuthids. In general, males lack a hectocotylus and transfer spermatophores directly from the terminal organ to the female, and both sexes undergo late-life degeneration of the musculature (females to a greater extent), frequently losing the tentacles (e.g. Nesis, 1995; Arkhipkin & Nigmatullin, 1997). Additional piecemeal information on physical reproductive structures has been reported for six species, mostly from the genera *Onychoteuthis* Lichtenstein, 1818, and *Onykia* Lesueur, 1821. Spent female morphology and spermatangium implantation have been reported in *Onychoteuthis borealijaponica* (Murata *et al.*, 1982), *Onykia* (*Onykia*) *robsoni* Adam, 1962 (Clarke, 1980), and *Onykia* (*M.*) *ingens* (Lipinski & Linkowski, 1986; Jackson & Jackson, 2004; Hoving & Laptikhovsky, 2007; Laptikhovsky *et al.*, 2007), and Hess (1987) reported spermatophore morphology for *Onychoteuthis compacta* Berry, 1913 (his *Onychoteuthis* '*banksi*' [*sic*]), *O. borealijaponica*, *Onykia* (*Onykia*) *robusta* Verrill, 1876, *Onykia* (*Onykia*) *robsoni* (his '*Ancistroteuthis lichtensteinii*'), and briefly *Kondakovia longimana* Filippova, 1972. Spawning and mating strategies have been reported and discussed only in *Onykia* (*M.*) *ingens* (Jackson & Mladenov, 1994; Jackson & Jackson, 2004; Jackson *et al.*, 2004; Bolstad, 2006; Laptikhovsky *et al.*, 2007).

From these reports, spermatangium implantation strategies appear to differ between onychoteuthid taxa, e.g. *Onykia* (*M.*) *ingens* and *Onychoteuthis borealijaponica* (non-localized deposition of individual spermatangia in the former, infliction of wounds with concentrations of spermatangia in the latter). In order to provide a more complete overview of spermatophore transfer strategies in the family, we provide new information on spermatangium morphologies and implantation sites for several species of *Onykia* and *Onychoteuthis*. Observations are also made on spent females of *Notonykia*

Corresponding author:
K.S. Bolstad
Email: kbolstad@aut.ac.nz

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press

Nesis, Roeleveld & Nikitina, 1998, and *Callimachus* Bolstad, 2010 for which no aspect of reproduction has been previously reported.

MATERIALS AND METHODS

Onychoteuthid specimens were loaned from, or examined at, the Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington, New Zealand; Museum Victoria, Melbourne, Australia (NMV); South African Museum, Cape Town, South Africa (SAMC); Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, USA (UMML); Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMB); and Zoological Museum, Universitetet i Bergen, Norway (ZMBN). Details of all material examined are given in Table 1, with incomplete collection data indicated 'NFD' (no further data) and collection dates given as dd/mm/yyyy. Collection acronyms include: BTT, bottom trawl; MT, motorized trawler; NORFANZ, New Zealand and Australia Norfolk Ridge-Lord Howe Rise Biodiversity Voyage; SFI, Sea Fish Institute, South Africa; RV, research vessel.

Additional morphological acronyms used in the text are: ML, dorsal mantle length; maxW, maximum width (of spermatophore or spermatangium). The term 'terminal organ' is used for the narrowed extension of Needham's sac through which individual spermatophores travel and exit during mating. This portion is often improperly referred to as the 'penis'; however, a true penis is used for internal fertilization, as in mammals.

Although Arkhipkin & Nigmatullin (1997) analysed the relationship between *Onychoteuthis* '*banksii*' Leach, 1817, and two '*Chaunoteuthis mollis*' specimens from the south-eastern Pacific, and concluded that the latter name was a junior synonym of the former, their *O.* '*banksii*' specimens appear to have included a number of recently disambiguated taxa (see Bolstad, 2008b). The *C. mollis* holotype is distinct from each of these (Bolstad, 2008a, 2010), and *Onychoteuthis mollis* (*sensu stricto*) is accordingly treated herein as a taxonomically valid species.

More complete systematic descriptions of the material reported below are given in Bolstad (2008a). Subgeneric distinctions in the genus *Onykia* follow Bolstad (2008a) and Bolstad (2010).

RESULTS

Genus *Onychoteuthis*

One spent female each of *Onychoteuthis mollis* (*sensu stricto*) and *O. meridiopacifica* was observed. The tissues of both were thin and flaccid, with the relative proportions of the mantle and fins greatly distorted, although the fin margins were whole; the tentacles were reduced to short stumps and the arms appeared shrunken, with many suckers lost. The external mantle surface of each specimen bore two longitudinal cuts (incisions part-way into the mantle musculature, with clear-cut edges), one on each side of the ventral midline. Spermatangia were implanted along the full length of each cut, with their aboral ends protruding externally and the oral portion (sperm mass) enclosed within the mantle musculature, oriented perpendicularly to the cuts in either direction (Figure 1B). Particulars of implantation for each specimen follow.

Onychoteuthis mollis (ZMBN Holotype 2428, Figure 2A): two ventral cuts, approximately parallel to ventral midline, each ~20% ML, near ventral anterior margin; one incision Y-shaped (with stem parallel to midline), with ~80 spermatangia in total; the other incision a single straight cut, with ~50 embedded spermatangia. Aboral, protruding end of each spermatangium with rounded, bulbous opening (hereafter 'bulb') (Figure 2B, C), through which spermatozoa are likely to exit spermatangium. Spermatangia not extracted (to avoid damaging holotype); approximate length of each 10 mm.

Onychoteuthis meridiopacifica (NMNZ M.172941): two cuts midway along length of mantle, with anterior end of each cut slightly closer to midline; each cut ~9 mm long (~15% ML), with 25–30 embedded spermatangia (Figure 1A, B). Spermatangium maxW 1 mm; middle membrane of oral end with invagination (Figure 1F); trailing end of spermatangium equal in length to sperm mass, terminating in a 'bulb' (Figure 1C, D) with emerging spermatozoa (Figure 1E); heads of spermatozoa (Figure 1G) 4.3–5.1 μm long and 1.2–1.7 μm

Table 1. Onychoteuthid material examined herein.

Species	Registration	ML (mm)	Sex	Collection data
Onychoteuthis mollis	ZMBN Holotype 2428	153	F	Mediterranean Sea, coll. Capt. Lampe, NFD
Onychoteuthis meridiopacifica	NMNZ M.172941	90	F	26°31.42′S 166°34.42′E, NNW of Norfolk Island, 2000 m, 18/05/2003, RV 'Tangaroa', NORFANZ Station 5
Onykia (Onykia) aequatorialis	ZMB Holotype Moll.-110000	380	F	0°16′N 18°00′W, 21/09/1903, floating dead at surface, Deutsche Südpolar Expedition
Onykia (Onykia) aequatorialis	UMML 31.3148	545	F	24°34′N 77°31′W, 1742–1707 m, 19/08/1975, coll. CI-354
Onykia (Onykia) robsoni	SAMC S3444	520	F	No data
Onykia (Onykia) robsoni	SAMC S673	345	F	30°44′S 32°04′E, 26/06/1973, ex stomach of 15.5 m sperm whale, SFI Station U73/301, coll. P. Best
Onykia (Onykia) robsoni	SAMC S4111, neotype	595	M	30°03′S 14°23′E, 986 m, 11/07/1998, MT 'Iris' trawl no. 12, BTT, coll. B. Rose & R. Leslie
Notonykia africanae	NMNZ M.109066	200	F	44°17.53′S 178°55.46′E, 1176–1120 m, 06/11/1991, RV 'Tangaroa' Station TAN9104/134
Genus Callimachus	NMV F51101	150	F	Victoria, Australia, NFD

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press

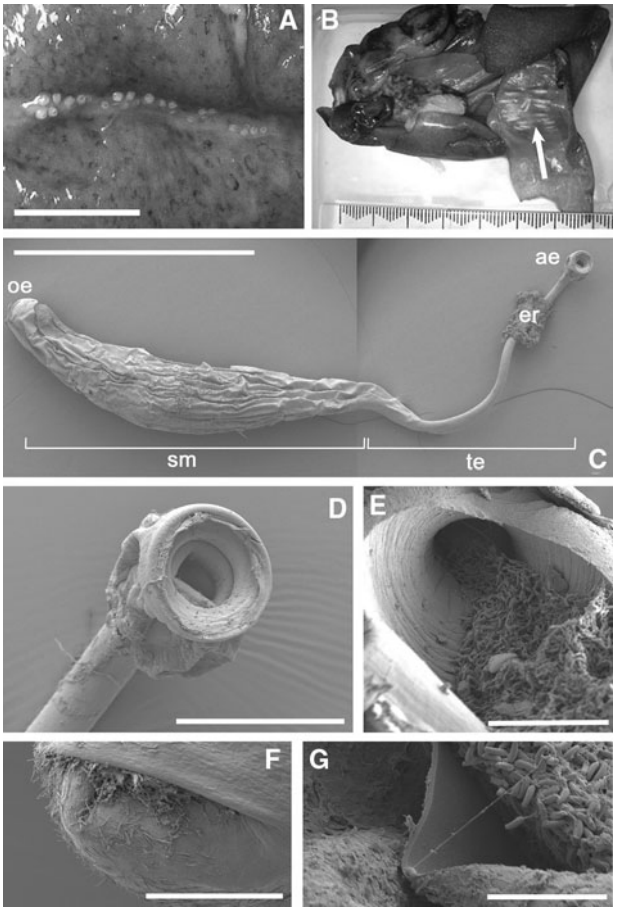


Fig. 1. *Onychoteuthis meridiopacifica* (NMNZ M.172941, ♀, ML 90 mm). (A) External view of left-hand cut with protruding spermatangium bulbs; (B) internal view of implanted spermatangia embedded in mantle wall on either side of cut (arrow); (C–G) scanning electron micrographs of spermatangia extracted from mantle wall: (C) entire spermatangium (ae, aboral end, with 'bulb'; er, epidermal remnant; oe, oral end; sm, sperm mass; te, trailing end); (D) aboral bulb; (E) spermatozoa emerging from bulb; (F) oral invagination in middle membrane; (G) breach in spermatangium wall, showing sperm mass within. Scale bars: A, 5 mm; B (major increments), 10 mm; C, 2 mm; D, 250 μm; E, 50 μm; F, 100 μm; G, 25 μm.

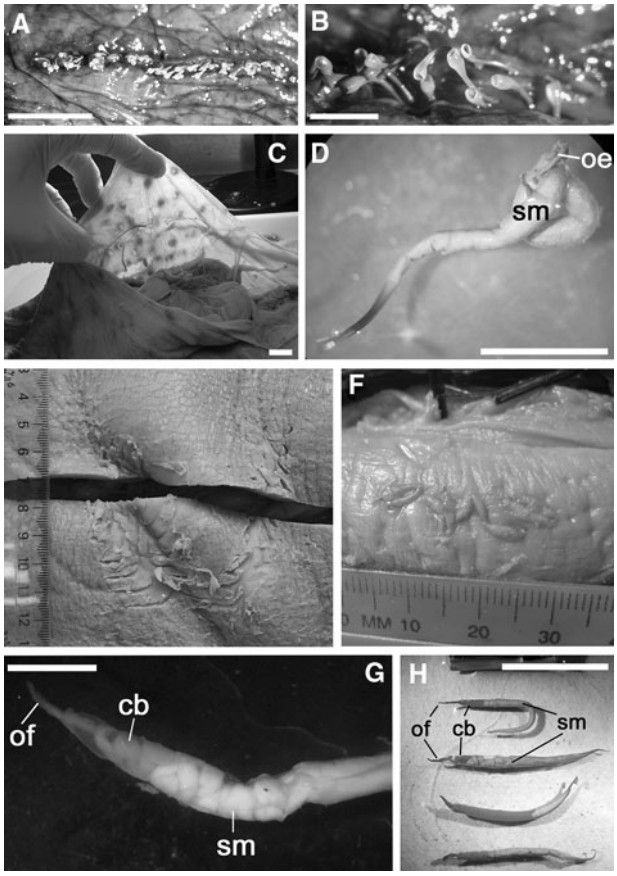


Fig. 2. (A–B) *Onychoteuthis mollis* (ZMBN Holotype 2428, ♀, ML 153 mm), cut with implanted spermatangia, with trailing ends protruding externally (B, courtesy of R. Young). (C–D) *Onykia* (*Onykia*) *aequatorialis*: (C) ZMB Holotype Moll.-110000, ♀, ML 380 mm preserved, backlit mantle wall, showing silhouettes of individually implanted spermatangia; (D) UMML 31.3148, ♀, ML 545 mm, extracted spermatangium from mantle wall (oe, oral end with filament; sm, sperm mass); (E–H) *Onykia* (*Onykia*) *robsoni* (E,G,H) SAMC S3957, ♂, ML 595 mm: (E) scratches on ventral surface of mantle (incision along ventral midline); (G, H) extracted spermatangia from terminal organ (cb, convoluted cement body; of, oral filament; sm, convoluted sperm mass); (F) SAMC S3444, ♀, ML 520 mm, implanted spermatangia visible on exterior mantle surface of specimen. Scale bars: A, C, E, F (major increments), 10 mm; B, D, G, 5 mm; H, 20 mm.

wide (N = 10). Length of entire spermatangium ~8 mm (preserved).

Genus *Onykia*

Two spent females each of *Onykia* (*Onykia*) *aequatorialis* and *O.* (*O.*) *robsoni*, and one mature male of *O.* (*O.*) *robsoni* were examined. The tissues of both *O.* (*O.*) *aequatorialis* specimens were so thin as to be translucent, with silhouettes of implanted spermatangia clearly visible when backlit (Figure 2C), while those of the *O.* (*O.*) *robsoni* remained more robust, in spite of one specimen having been collected from a sperm whale stomach. In most cases spermatangia were implanted individually into the exterior mantle surface at various positions. Particulars of implantation for each species follow.

Onykia (*Onykia*) *aequatorialis*: mantle of holotype (ZMB Holotype Moll.-110000) studded with ~80 individually implanted spermatangia in middle third of left side, dorsally and ventrally; implantation sites characterized by transverse puncture in epidermis (length 1–5 mm), dark red-purple and puckered epidermal tissue, and hard subcutaneous knot of implanted spermatangium (Figure 2C). Second specimen (UMML 31.3148) with individually implanted spermatangia over dorsal mantle surface, occasionally clustered in small groups but each separately implanted; spermatangium length ~12 mm, maxW 1.5 mm, with slender oral filamentous extension, forming a loop (Figure 2D); free trailing end of spermatangium may protrude from implantation site.

Onykia (*Onykia*) *robsoni*: females (SAMC S3444, SAMC S673) with spermatangia implanted on ventral mantle surface between fins (300–330 mm from ventral anterior mantle margin in larger specimen (ML 520 mm)), mostly individually, although groups of up to ten were observed (Figure 2E); small punctures (maximum diameter ~7 mm) overlying implanted spermatangia apparent over most external mantle surfaces; free trailing end of spermatangium may protrude from implantation site. Male (SAMC S4111, neotype) with implanted spermatangium observed in terminal organ; intact spermatophores, partly and completely everted spermatangia also removed from terminal organ (Figure 2G, H); spermatangia elongate, length 30–40 mm,

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press

maxW 1.5–2 mm, with narrow oral extension/filament; cement body visible in oral part of spermatangium, followed by sperm mass; spermatangium convoluted (Figure 2G). Large scratches observed on ventral mantle surface, 90–145 mm from anterior mantle margin (Figure 2E), and on dorso-lateral right side, 90–170 mm from anterior mantle margin.

Genus *Notonykia*

One spent female *Notonykia africanae* was observed (NMNZ M.109066). Numerous white sucker-ring imprints over all external surfaces of mantle, fin, head and arms. Single remaining fin greatly enlarged relative to mantle and brachial crown; tentacles absent, ~1 cm long stumps remaining; some arm tips and arm suckers missing; tissues loose and flaccid in general; some residual mature eggs present in ovary, but nidamental glands and other viscera shrunken. No implanted spermatangia apparent.

Genus *Callimacus*

One spent female of *Callimacus rancureli* was observed (NMV F51101). Fins greatly enlarged relative to mantle and brachial crown; tentacles absent, ~1 cm long stumps remaining; some arm tips and arm suckers missing; some residual mature eggs present in ovary, but nidamental glands and other viscera shrunken. No implanted spermatangia apparent.

DISCUSSION

What little is known of mating in oceanic and deep-sea squid has been extrapolated almost exclusively from dead specimens. To date, only one potential mating event has been observed between live deep-sea squid (*Brachioteuthis beanii*, see Roper & Vecchione, 1996). However, our body of knowledge is slowly increasing; descriptions of many mated female deep-sea squid are available, and Nesis (1995) published an overview of then-known sperm transferral and storage strategies, recently augmented by Hoving (2008). Several trends in squid reproductive morphology are apparent, including the presence of seminal receptacles or seminal tissues (a specialized organ or modified tissue for the reception of sperm) in some taxa. In species lacking seminal receptacles (including all presently known Onychoteuthidae), spermatangia are implanted directly and deeply into the female's tissues (for overviews, see Nesis, 1995 and Hoving, 2008). More specific strategies for sperm transfer and storage vary between, but also within squid families, as observed in the present study.

Onychoteuthids employ at least two different strategies for spermatangium implantation and storage. At present, these strategies appear generally consistent within, yet specific to, the two most speciose onychoteuthid genera: males of *Onychoteuthis* species make longitudinal cuts in the female's exterior mantle surface, and implant rows of spermatangia along the length of the cuts, while males of *Onykia* species implant spermatangia individually on various parts of the female's mantle externally or internally; wounds may be inflicted in the process but do not appear required for/associated with spermatangium implantation in *Onykia*. (One apparent exception was a female of *Onykia* (*Onykia*) *robsoni* reported by Clarke (1980, p. 118) with 'large longitudinal cuts in the anterior mantle with spermatophores embedded in them;' he also reported one female with embedded spermatophores that were apparently not associated with cuts.) Ventral longitudinal cuts with embedded spermatangia have been reported for *Onychoteuthis borealijaponica* (Murata *et al.*, 1982) and '*Chaunoteuthis mollis*' (=*Onychoteuthis* spp.: Grimpe, 1921; Torchio, 1967; Nesis, 1970; Adam, 1972; Okutani & Ida, 1986; Bello, 1998; not Appellöf, 1891). Jackson & Jackson (2004) reported scattered, individual spermatangia implanted externally and internally in the mantles of female *Onykia* (*M.*) *ingens*. Thus, the patterns observed on specimens herein are consistent with those previously reported in congeners, although some variability in the use of cuts is possible, given those observed by Clarke (1980) in *O.* (*O.*) *robsoni*.

The specific function of (or advantage conferred by) cuts into the mantle remains unknown. The external mantle surface certainly differs between genera, being smooth in *Onychoteuthis* and rugose or longitudinally ridged in all species of *Onykia* where adults are known. The chemistry of the mantle musculature is also believed to vary by genus, with *Onykia* tissues containing higher levels of ammonia than those of *Onychoteuthis* (Nesis, 2000). It is possible that the cuts therefore overcome some not-yet-understood physical or chemical barrier to implantation, but in the absence of evidence it is unwise to speculate further.

Hoving & Laptikhovsky (2007) demonstrated that spermatophores of *Onykia* (*M.*) *ingens* implant autonomously into squid tissue, once the spermatophoric reaction is initiated by the tip of the terminal organ (as each spermatophore leaves the terminal organ, the oral end is pressed, triggering eversion). Given that all reported mature male onychoteuthids have a long terminal organ for spermatophore storage and transfer (in *O.* (*M.*) *ingens*, terminal organ length may exceed mantle length—see Bolstad, 2006; Arkhipkin & Laptikhovsky, 2010), and that the sperm mass portions of all implanted spermatangia observed herein were fully embedded within, and difficult to extract from, the female mantle musculature, the mechanism reported by Hoving & Laptikhovsky (2007) is likely consistent throughout the family (although it is not necessary in all squid—see Drew, 1919). Autonomous spermatangium implantation would permit rapid deployment of many spermatophores, whether in individual locations or within purpose-inflicted cuts.

Several insights into the more specific mechanics of spermatangium implantation and subsequent deployment in *Onychoteuthis* and *Onykia* are suggested by the morphology of structures reported herein for *Onychoteuthis meridiopacifica* (Figure 1C–G), and *Onykia* (*Onykia*) *aequatorialis* and *robsoni* (Figure 2E–H). In *Onychoteuthis meridiopacifica*, the oral part of the spermatangium is smooth, as in *Rossia moelleri* (a sepiolid). The cement body is orally secreted during implantation in the latter (Hoving *et al.*, 2009), and probably also in *O. meridiopacifica*, through the oral invagination of the middle membrane on the spermatangium (Figure 1F), facilitating implantation into the female's tissues. In contrast, the oral part of the spermatangium is typified by a filamentous extension in *Onykia*. Oral extensions of the spermatangia probably also facilitate implantation and originate from the cement body in the intact spermatophore; although morphologically different, oral extensions of the spermatangium have also been described for *Todarodes*

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press

pacificus (a spike-like extension (Takahama *et al.*, 1991)) and *Octopoteuthis sicula* (a tubular extension with an oral broadening, which extends forward during implantation but adheres closely along the spermatangium in the final implanted spermatangium (Hoving *et al.*, 2008)).

In other morphological aspects, similarities were observed between the spermatangia of *Onychoteuthis* and *Onykia*. The mid-section of the implanted spermatangium (encasing the sperm mass) is firmly attached and difficult to extract intact in both genera. The trailing end of the spermatophore protrudes through a small window in the tissue, through which the spermatangium would have entered during implantation (Figure 1C). This trailing end quite evidently forms the exit route for spermatozoa, at least in *Onychoteuthis*, since hundreds of spermatozoa were observed within each in *O. meridiopacifica* (Figure 1E). In other (non-onychoteuthid) taxa, spermatozoa presumably also exit the spermatangium through the trailing end during fertilization (*Architeuthis* sp., Hoving *et al.*, 2004; *Octopoteuthis sicula*, Hoving *et al.*, 2008; *Rossia moelleri*, Hoving *et al.*, 2009). The 'bulb' observed in *Onychoteuthis* spermatangia has not been described for any other squid; it may serve to prevent the trailing end of the spermatangium from becoming completely implanted into the tissue, where the spermatozoa would be unable to exit. However, the bulb does not sit flush with the female's external tissues, and the same risk of over-implantation would affect other taxa, so the bulb may serve some additional function that is not apparent at present.

Spermatangium implantation was not observed in *Notonykia* or *Callimachus*. Given the degenerate state of the reproductive systems in these specimens, it is possible that spermatangia had been implanted and used in spawning, leaving no evidence. The general state of these specimens was consistent with spent females of other onychoteuthid genera, notably the thinned, loosened mantle musculature, lost tentacles, and distorted mantle and fin proportions. Arkhipkin & Nigmatullin (1997) suggested that evolution of this late-life '*Chaunoteuthis*' stage in onychoteuthids permitted mature females to 'escape from the ecologically active epipelagic zone [. . .] into a deep water refuge characterized by low predator densities and low temperatures,' and to utilize earlier accumulated energy to fuel the final stages of maturation. Of the five spent females examined herein with known collection depths, four were taken in relatively deep water (986–2000 m), so conclusion of the life cycle at these depths may be a strategy common to most onychoteuthid genera.

ACKNOWLEDGEMENTS

Thanks to the following persons and institutions for facilitating collection visits and specimen loans: the Museum of New Zealand Te Papa Tongarewa; Museum Victoria; South African Museum; Rosenstiel School of Marine and Atmospheric Science; Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin; and Zoological Museum, Universitetet i Bergen; B. Marshall (NMNZ), M. Norman and C. Rowley (NMV); L. Hoenson and M. Cochrane (SAMC), N. Voss (UMML); F. Köhler and M. Glaubrecht (ZMB); E. Willassen and J. Kongsrud (ZMBN). S. O'Shea (AUT), S. Donati (University of Groningen), V. Laptikhovsky (Falkland Islands Government Fisheries Department), A. Turner and B. James (University of Auckland) provided additional assistance in the preparation of this manuscript. This research was supported by the following institutions (K.S.R.B.): Auckland University of Technology, the American Museum of Natural History (Lerner–Gray Fund for Marine Research); the Malacological Society of London (Research Grant), and the Harvard Museum of Comparative Zoology (Ernst Mayr Travel Grant in Animal Systematics).

REFERENCES

Adam W. (1972) Notes sur les Céphalopodes: 25. Contribution à la connaissance de *Chaunoteuthis mollis* Appellöf, 1891. *Mededelingen van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 48, 1–7.

Appellöf A. (1891) Teuthologische Beiträge II: *Chaunoteuthis* n. g. Oegopsidarium. *Bergens Museums Årsberetning* 1891, 1–29.

Arkhipkin A.I. and Laptikhovsky V.V. (2010) Observation of penis elongation in *Onykia ingens*: implications for spermatophore transfer in deep-water squid. *Journal of Molluscan Studies*, first published online 30 June 2010. doi: 10.1093/mollus/eyq019

Arkhipkin A.I. and Nigmatullin C.M. (1997) Ecology of the oceanic squid *Onychoteuthis banksii* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the United Kingdom* 78, 839–869.

Bello G. (1998) *Chaunoteuthis mollis*: re-examination of a Mediterranean specimen and its identity with *Onychoteuthis banksii* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the United Kingdom* 78, 1027–1030.

Bolstad K.S. (2006) Sexual dimorphism in the beaks of *Moroteuthis ingens* Smith, 1881 (Cephalopoda: Oegopsida: Onychoteuthidae). *New Zealand Journal of Zoology* 33, 317–327.

Bolstad K.S. (2008a) *Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida)*. PhD thesis. Auckland University of Technology, Auckland, New Zealand.

Bolstad K.S. (2008b) Two new species and a review of the squid genus *Onychoteuthis* Lichtenstein, 1818 (Oegopsida: Onychoteuthidae) from the Pacific Ocean. *Bulletin of Marine Science* 83, 481–529.

Bolstad K.S.R. (2010) Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Zootaxa* 2696, 1–186.

Cherel Y. and Duhamel G. (2004) Antarctic jaws: cephalopod prey of sharks in the Kerguelen waters. *Deep-Sea Research I* 51, 17–31.

Clarke M.R. (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37, 1–324.

Clarke M.R. and MacLeod N. (1982a) Cephalopod remains in the stomachs of eight Weddell seals. *British Antarctic Survey Bulletin* 57, 33–40.

Clarke M.R. and MacLeod N. (1982b) Cephalopods in the diet of southern elephant seals *Mirounga leonina* at Signy Island, South Orkney Islands, South Atlantic Ocean. *British Antarctic Survey Bulletin* 57, 27–32.

Drew G.A. (1919) Sexual activities of the squid *Loligo pealii* (Les.). II. The spermatophore; its structure, ejaculation and formation. *Journal of Morphology* 32, 379–435.

Grimpe G. (1921) Das Leipziger Stück von *Chaunoteuthis mollis* Appellöf. *Zoologischer Anzeiger* 52, 289–296.

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press

Hess S.C. (1987) *Comparative morphology, variability, and systematic applications of cephalopod spermatophores (Teuthoidea and Vampyromorpha)*. PhD thesis. University of Miami, Florida, USA.

Hoving H.J.T. (2008) *Reproductive biology of oceanic decapodiform cephalopods*. PhD thesis. University of Groningen, Groningen, The Netherlands.

Hoving H.J.T. and Laptikhovsky V. (2007) Getting under the skin: autonomous implantation of squid spermatophores. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 212, 177–179.

Hoving H.J.T., Lipinksi M.R. and Videler J.J. (2008) Reproductive system and the spermatophoric reaction of the mesopelagic squid *Octopoteuthis sicula* (Rüppell, 1844) (Cephalopoda: Octopoteuthidae) from southern African waters. *African Journal of Marine Science* 30, 603–612.

Hoving H.J.T., Nauwelerts S., Van Genne B., Stamhuis E.J. and Zumholz K. (2009) Spermatophore implantation in *Rossia moelleri* Steenstrup, 1856 (Sepiolidae, Cephalopoda). *Journal of Experimental Marine Biology and Ecology* 372, 75–81.

Hoving H.J.T., Roeleveld M.A.C., Lipinski M.R. and Melo Y. (2004) Reproductive system of the giant squid *Architeuthis* in South African waters. *Journal of Zoology* 264, 153–169.

Jackson G.D. (1993) Growth zones within the statolith microstructure of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae): evidence for a habitat shift? *Canadian Journal of Fisheries and Aquatic Sciences* 50, 1–9.

Jackson G.D. (1995) The use of beaks as tools for biomass estimation in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology* 15, 9–14.

Jackson G.D. (1997) Age, growth and maturation of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology* 17, 268–274.

Jackson G.D. (2001) Confirmation of winter spawning of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Chatham Rise of New Zealand. *Polar Biology* 24, 97–100.

Jackson G.D. and Jackson C.H. (2004) Mating and spermatophore placement in the onychoteuthid squid *Moroteuthis ingens*. *Journal of the Marine Biological Association of the United Kingdom* 84, 783–784.

Jackson G.D. and Mladenov P.V. (1994) Terminal spawning in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae). *Journal of Zoology* 234, 189–201.

Jackson G.D., Semmens J.M., Phillips K.L. and Jackson C.H. (2004) Reproduction in the deepwater squid *Moroteuthis ingens*, what does it cost? *Marine Biology* 145, 905–916.

Laptikhovsky V.V., Arkhipkin A.I. and Hoving H.J.T. (2007) Reproductive biology in two species of deep-sea squids. *Marine Biology* 152, 981–990.

Lipinski M.R. and Linkowski T.B. (1986) Some aspects of the biology of squid *Moroteuthis ingens* (Onychoteuthidae) from New Zealand waters. *Reports of the Sea Fisheries Institute* 21, 97–105.

Murata M. and Ishii M. (1977) Some information on the oceanic squid, *Ommastrephes bartrami* (Lesueur) and *Onychoteuthis borealijaponicus* Okada, in the Pacific Ocean off northeastern Japan. *Bulletin of the Hokkaido Regional Fisheries Research Library* 42, 1–23.

Murata M., Ishii M. and Osako M. (1982) Some information on copulation of the oceanic squid *Onychoteuthis borealijaponicus* Okada. *Bulletin of the Japanese Society of Scientific Fisheries* 48, 351–354.

Nesis K.N. (1970) Occurrence of a rare squid *Chaunoteuthis mollis* Appellöf (family Onychoteuthidae) in the Indian Ocean. *Veliger* 12, 290–292.

Nesis K.N. (1995) Mating, spawning and death in oceanic cephalopods: a review. *Ruthenica* 6, 23–64.

Nesis K.N. (2000) Squids of the family Onychoteuthidae: phylogeny, biogeography, and way of life. *Zoologichesky Zhurnal* 79, 272–281.

Okutani T. and Ida H. (1986) Rare and interesting squid in Japan—MIX. A mass occurrence of *Chaunoteuthis mollis* Appellöf, 1891 (Oegopsida: Onychoteuthidae) from off Japan. *Venus* 45, 53–60. [*Japanese Journal of Malacology*.]

Okutani T. and Murata M. (1983) A review of the biology of the oceanic squid *Onychoteuthis borealijaponica*. *Memoirs of the National Museum of Victoria* 44, 189–195.

Piatkowski U., Heinemann H. and Pütz K. (2001) Cephalopod prey of king penguins (*Aptenodytes patagonicus*) breeding at Volunteer Beach, Falkland Islands, during austral winter 1996. *Fisheries Research* 52, 79–90.

Roper C.F.E. and Vecchione M. (1996) *In situ* observations on *Brachioteuthis beanii* Verrill: paired behavior, probably mating (Cephalopoda, Oegopsida). *American Malacological Bulletin* 13, 55–60.

Takahama H., Kinoshita T., Sato M. and Sasaki F. (1991) Fine structure of the spermatophores and their ejaculated forms, sperm reservoirs, of the Japanese common squid, *Todarodes pacificus*. *Journal of Morphology* 207, 241–252.

Torchio M. (1967) Eccezionale reperto di *Chaunoteuthis mollis* (Appelöff [*sic*]) nello Stretto di Messina (Cephalopoda: Dibranchiata). *Natura (Milano)* 58, 193–207.

and

Young R.E., Vecchione M. and Tsuchiya K. (2003) *Walvisteuthis* Nesis and Nikitina 1986. *Walvisteuthis rancureli* (Okutani 1981). Stubby hooksquid. Version 23 (under construction) [online]. Tree of Life Web Project, available from: http://tolweb.org/Walvisteuthis/19957 (accessed 1 September 2007).

Correspondence should be addressed to:
K. Bolstad
Earth & Oceanic Sciences Research Institute
Auckland University of Technology
Private Bag 92006, Auckland 1142, New Zealand
email: kbolstad@aut.ac.nz

https://doi.org/10.1017/S175526721000120X Published online by Cambridge University Press