

The nomenclatural status, ontogeny and morphology of *Pholidoteuthis massyae* (Pfeffer, 1912) new comb (Cephalopoda: Pholidoteuthidae)

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Abstract *Pholidoteuthis* is unusual amongst genera of squid in that the mantle is beset with close-packed dermal cushions (scales). Despite frequent reference to species in this genus, considerable systematic confusion surrounds usage of the generic name, erected prematurely given that the same systematic characters apply for the earlier *Tetronychoteuthis* Pfeffer, 1900, and species attributed to it. The synonymy and ontogenetic morphology of *Pholidoteuthis massyae* (Pfeffer 1912) new comb., the senior synonym of *P. boschmai* Adam, 1950, is reported. The relationship between this species and others referred to *Tetronychoteuthis*, *Lepidoteuthis*, the Pholidoteuthidae Adam, 1950, Lepidoteuthidae Pfeffer, 1912 and Octopoteuthidae Berry, 1912, is discussed. A conjectural account of the mechanics of mating in *P. massyae* is provided based on the

nature of spermatophore insertion in the female mantle, and modification to the terminal region of the male's genital apparatus.

Keywords *Pholidoteuthis* · *Tetronychoteuthis* · Cephalopoda · Systematics · Reproduction

Introduction

Three genera of squid are characterised by dermal cushions (scales) on the mantle: *Pholidoteuthis* Adam, 1950, *Lepidoteuthis* Joubin, 1895, and *Tetronychoteuthis* Pfeffer, 1900. The status of two of these, *Tetronychoteuthis* and *Pholidoteuthis*, is a source of ongoing systematic and nomenclatural confusion, in that diagnostic characters and character states do not adequately differentiate them, and because various names and classifications could be and have been applied for any given taxon.

An untenable situation exists wherein six relatively recent classifications have been used or proposed for the three genera *Lepidoteuthis*, *Pholidoteuthis* and *Tetronychoteuthis*: (1) *Pholidoteuthis* and *Tetronychoteuthis* accommodated in the Pholidoteuthidae, and *Lepidoteuthis* in the Lepidoteuthidae (Clarke and Trueman 1988; Lu 2001); (2) species of *Tetronychoteuthis* are considered congeneric or synonymous with *Pholidoteuthis*, the latter considered distinct from

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Lepidoteuthis, and the two assigned to separate families, Pholidoteuthidae and Lepidoteuthidae (Clarke 1992; Roeleveld 1998); (3) *Lepidoteuthis* and ‘*Pholidoteuthis*’ *adami* are accommodated in the Lepidoteuthidae and *Pholidoteuthis boschmai* in Pholidoteuthidae (Okutani 1983; Roper and Lu 1989a); (4) *Lepidoteuthis* is placed in the Lepidoteuthidae, *Pholidoteuthis* in the Pholidoteuthidae and *Tetronychoteuthis* in the Onychoteuthidae (Pfeffer 1912; Clarke 1966; Voss 1967); (5) all of *Lepidoteuthis*, *Tetronychoteuthis* and *Pholidoteuthis* are accommodated in the Lepidoteuthidae (Nesis 1987; Kubodera 1990; Sweeney and Roper 1998; Dunning and Lu 1998); and (6) *Tetronychoteuthis* is considered a *nomen dubium*, the Pholidoteuthidae is treated as distinct from the Lepidoteuthidae, and only two genera are recognised, *Pholidoteuthis* and *Lepidoteuthis* (Nesis and Nikitina 1990).

It is widely accepted that the type specimen of *Onychoteuthis dussumieri* Orbigny, 1839, was an onychoteuthid (Clarke 1980; Roper and Lu 1989b; Nesis and Nikitina 1990) in that it had 30 hooks disposed in two alternating rows along the tentacle club (Orbigny 1839). Confusion ensued with the misidentification by Pfeffer (1912) of a damaged specimen attributed to Orbigny’s species that possessed both onychoteuthid and non-onychoteuthid characters, exacerbated by Pfeffer’s including magnificent illustrations that unfortunately appear to be composites of two squid species, one of Pholidoteuthidae (dermal scales), and one of Onychoteuthidae (numerous occipital folds [= ‘nuchal folds’ of Pfeffer]). Pfeffer proceeded to designate *Onychoteuthis dussumieri* Orbigny the type species of a new genus, *Tetronychoteuthis*, and followed this with a description of a second species, *T. massyae* Pfeffer, 1912.

Pholidoteuthis Adam, 1950 was subsequently proposed as a new genus for the new species *P. boschmai* Adam, 1950, that shared all character and character states with *T. massyae* Pfeffer. With type specimens of *Onychoteuthis dussumieri* Orbigny, *T. massyae* Pfeffer, and the specimen referred to *T. dussumieri* (Pfeffer, not Orbigny) no longer extant (Lu et al. 1995; Sweeney and Roper 1998), there is little value in discussing the

confused and often contradictory literature for each, so no such critique is offered here. Nesis and Nikitina (1990) proposed all to be *nomen dubia*, but this course of action proves unnecessary, as does that of referring the case to the International Commission on Zoological Nomenclature (ICZN) (Roper and Lu 1989b). An ontogenetic series of specimens from the South Pacific herein described provides an opportunity to critically appraise the systematic status of *Pholidoteuthis boschmai* and *Tetronychoteuthis massyae*, the former considered to be a junior synonym of the latter, negating the need to recognise any species as *nomen dubium* or to refer the case to the IZCN. With *Tetronychoteuthis* a junior synonym of *Onychoteuthis*, the first available generic name for Pfeffer’s ‘*Tetronychoteuthis*’ *massyae* is *Pholidoteuthis*; and the species is herein, hereafter referred to as *P. massyae* (Pfeffer, 1912), new combination.

Materials and methods

The collections of cephalopods of the Museum of New Zealand *Te Papa Tongarewa*, and the National Institute of Water and Atmospheric Research Ltd, NIWA (international collection acronyms NMNZ and NZOI respectively), both in Wellington, New Zealand were screened for juvenile *Pholidoteuthis* specimens and other appropriate comparative material. Additional fresh fisheries-bycatch comprising mature and mated specimens of *Pholidoteuthis* trawled off Tasmania (University of Tasmania reference acronym TASPAP), Australia, were examined enabling the account of reproductive strategies in this species to be provided; beaks of this species also were sorted from the stomach contents of a bull sperm whale stranded on West Coast Auckland, New Zealand (Gomez-Villota 2006) accessioned in the collections of the Auckland University of Technology (collection acronym AUT). All illustrations have been prepared using either one of a camera lucida for drawings, or SEM or photcamera for photographs, all using conventional preparatory techniques.

Systematics

Pholidoteuthidae Adam, 1950

Pholidoteuthis massyae (Pfeffer, 1912) new comb.

Tetronychoteuthis massyae Pfeffer, 1912.

Tetronychoteuthis dussumieri (Pfeffer, 1912, not Orbigny, 1839).

Pholidoteuthis boschmai Adam, 1950.

Material examined

NMNZ M.172985: F, ML 163 mm, 32°25.94'S, 161°47.62'E, Lord Howe Rise, SE of Lord Howe Island, 1132–1197 m, 24/05/2003, RV *Tangaroa* NORFANZ Stn 73; NMNZ M.183106, 1, sex indet., ML 49 mm, c. 38°40'S, 179°E, 100–0 m, –/02/1998; NMNZ M.183107, 1, sex indet., ML 51 mm, c. 41°10'S, 179°05'E, 100–0 m, –/02/1998; NMNZ M.172805, 1, M, ML c. 76 mm, 42°54.87'S, 176°14.16'W, 829–836 m, 28/02/1992, F.R.V. *Tangaroa* Stn TAN9202/122; NMNZ M.172804, 3, sex indet., ML 45, 38, 35 mm, off and between Cascade and Jackson Bays, FMMWT, 30 m, 1988, R.V. *James Cook* Stn J4/88; TASPBP2, M, ML 412 mm (1603.2 g), taken off Bicheno, Tasmania East Coast, F.V. *Adriatic Pearl*, 21/08/2002; TASPBP5, F, ML 533 mm, (3667.4 g), taken off Bicheno, Tasmania East Coast, F.V. *Adriatic Pearl*, 21/08/2002.

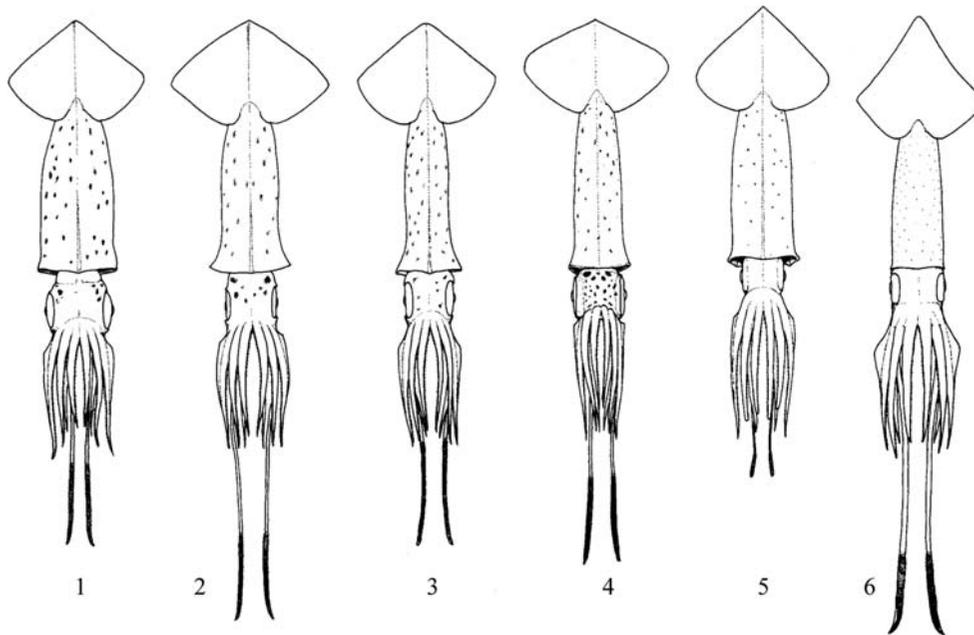
Description

Mantle slender, width ~30% ML in smallest individual, narrowing to 17–23% ML in larger individuals 38–163 mm ML; cylindrical, wider than head, slightly flaring at anterior margin in smaller individuals between 35 and 76 mm ML; length 57–60% standard length (Figs. 1–6). Dorsal anterior margin with weak nuchal peak; ventral anterior margin with broad, shallow emargination between distinct ventro-lateral prominences demarcating mantle-locking cartilages. Gladius apparent dorsally through anterior 25–50% of mantle in specimens of 35–76 mm ML,

but not apparent in larger individual (ML 163 mm). Fins large, heart-shaped in smaller to sagittate in larger individuals, broader in juveniles, length and width ~40–50%, 48–60% ML respectively; posterior fin margin slightly convex in small individuals to weakly concave in larger individuals; anterior margin moderately to broadly convex; fin with pronounced anterior lobe. Mantle dorsal and ventral surfaces, with the exception of a smooth region ventral to the fins, studded with dense-set star-shaped papillae on all specimens examined (ML 35 mm and larger), each on a short pedestal (Figs. 7–9); papillae on larger specimens more stellate, with central depression, but otherwise differing in no remarkable character. All surfaces of fins, head and arms smooth; sub-adult to adult blood-red over all of mantle, head and arms; preserved juvenile material faded.

Head narrower than mantle, as broad as or broader than deep or long (width ~18–27% ML, height ~13–17% ML, length ~17–21% ML), with convex dorsal and dorso-lateral surfaces; ventral surface concave, with depression formed by two large, laterally directed orbits of diameter ~100% head depth. Occipital region with three pronounced folds, decreasing in development from dorsal- to ventral-most fold: dorsal fold posterior to dorsal margin of eye, lateral fold posterior to the mid-point of eye, and ventro-lateral fold, slightly below that of lateral fold; small lappet-like prominence present where nuchal crest adjoins posterior border of funnel groove; funnel groove deep, broadly U-shaped. Funnel with well-developed bridles, between which can be discerned a small diverticulum of the anterior vena cava.

Arms short, attenuating rapidly to tips, 41–53% ML, with arm II usually longest, arms I, III and IV of sub-equal length, although arm I tends to be shortest, formula 2.3 = 4.1; suckers in two rows; total arm sucker count 100–112 per arm, each raised on distinct short stalk, bordered by narrow protective membrane with short trabecula. Keels present on arms II–IV; that on arm II being narrow, positioned on dorso-lateral face of arm, extending to approximately mid-arm length; that of arm III being broad, more aboral in orientation than either dorso- or ventro-lateral, rapidly increasing in width from arm base to proximal



Figs. 1–6 Ontogenetic series, dorsal view: 1–3, NMNZ M.172804, ML 35, 38, 45 mm respectively; 4, NMNZ M.183106, ML 49 mm; 5, NMNZ M.172805, ML c. 76 mm; 6, NMNZ M.172895, ML 163 mm

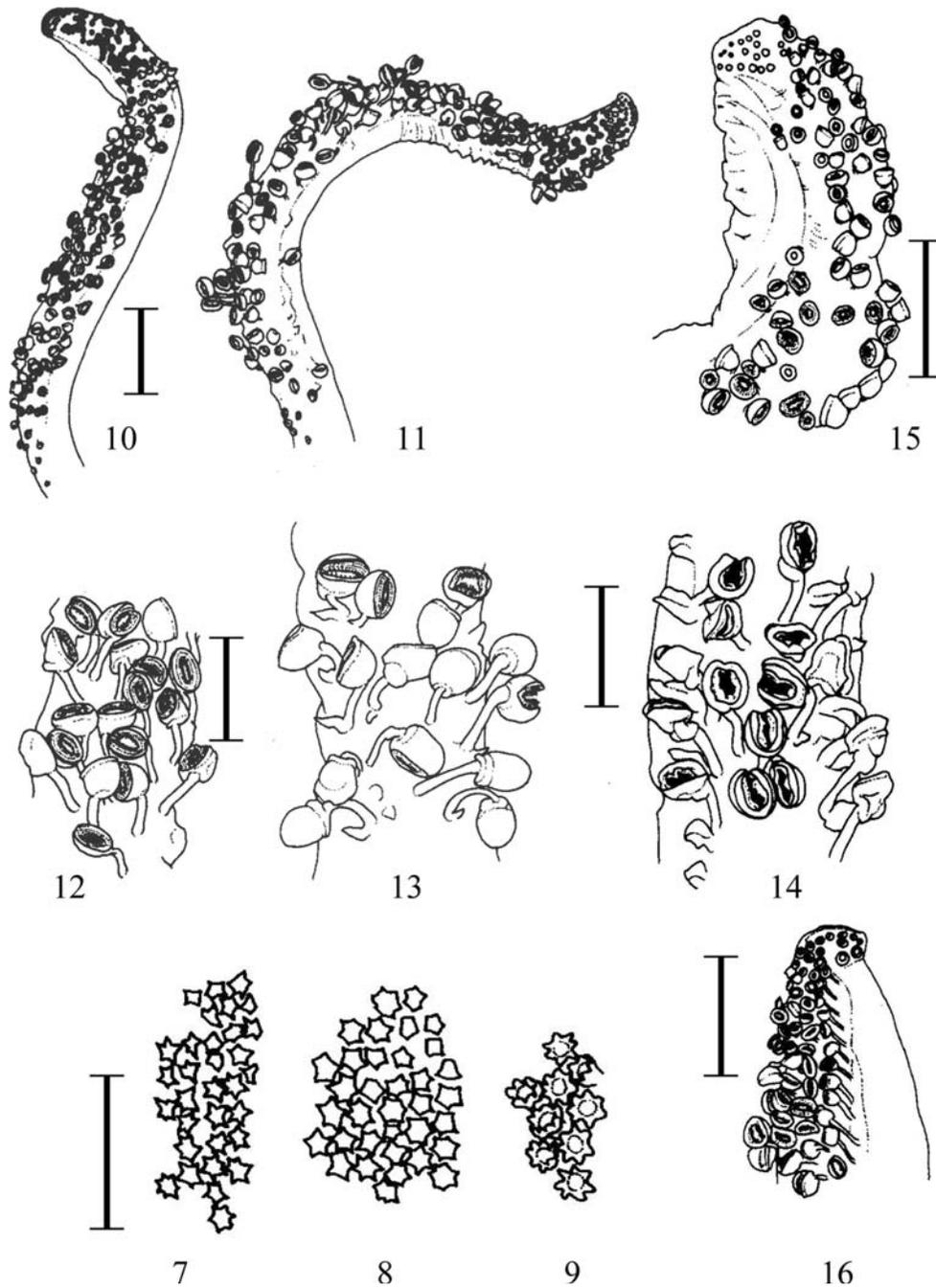
quarter arm length, then rapidly decreasing to the mid-portion of the arm, thereafter scarcely discernible through to the distal quarter and absent thereafter; that on arm IV being broader than that on arm II, but narrower than that of arm III, dorso-lateral in orientation, gradually decreasing in width and extending almost to arm tip. Buccal membrane with formula DDVV.

Tentacles (Figs. 1–6, 10, 11, 17) almost invariably lost, presumably autotomised, from large trawl-caught specimens; length variable, ~65–120% ML; rectangular in cross section, oral and aboral surface narrower than lateral surface, with greatest dimension slightly less than that of adjacent arms at bases excluding arm keels; oral surface with few scattered suckers distributed from carpus to within arm crown, but not extending to tentacle base. Club only slightly expanded, variable in length relative to both tentacle and mantle length, ~13–40% and 10–42% respectively (club length ~30–35% ML in 4 of 6 individuals). Carpus poorly defined, with 5–8 suckers (Figs. 10, 11, 17). Manus with 46–48 transverse rows of similarly sized suckers disposed in four longitudinal rows (Figs. 10–14, 17); dactylus with dactylic pouch and ~18 small suckers set in six oblique

rows of three (Figs. 15, 16, 19). Club margins not bordered by obvious membranes, but with small flaps and trabeculae near bases of marginal suckers in individuals of ML exceeding ~50 mm (Figs. 13, 14, 18).

Sucker rings on manus of tentacle (Figs. 18, 20, 21) laterally compressed; ring with 2 proximal, 3 lateral and 5 distal concentric rows of flat-topped pegs; innermost ring on lateral surface with demonstrably longer and larger pegs; entire circumference of sucker ringed with flattened plates, broadest proximally and most dense and narrow distally. Sucker rings on dactylus (Fig. 22) with ~11 low-profile rounded teeth around the circumference, surrounded by 3 or 4 concentric rows of rounded pegs. Arm sucker rings (Figs. 23–28) variable in morphology on all arms, with 17–24 variably developed teeth, largest in distal-most to disto-lateral quarter, thereafter gradually decreasing in size to proximo-lateral margin, at which point teeth fail to differentiate, forming a weakly crenulate proximal margin.

Male and female upper and lower beaks as per Figs. 29–32; both lower beaks characterised by deep indentation in midline of hood, curved rostral edge, usually longer than rostral base,

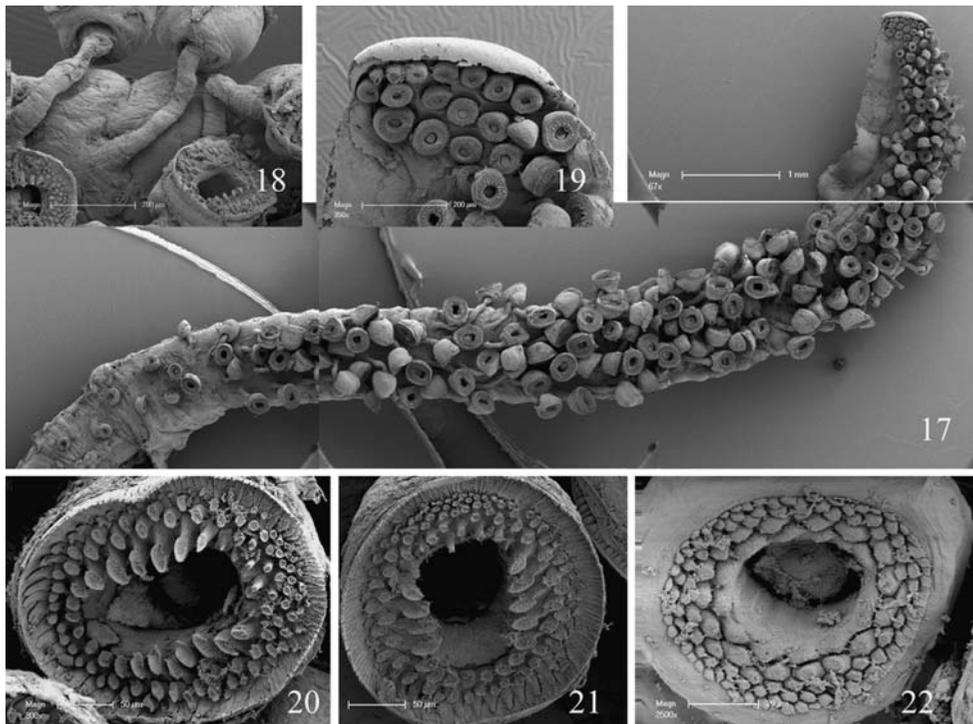


Figs. 7–16 Dermal papillae: 7, 8, NMNZ M.172804, ML 35, 45 mm respectively; 9, NMNZ M.183107, ML 51 mm. Scale bar 1 mm. Tentacle club: 10, 11, tentacle club; 12–14, mid-portion of manus; 15, 16, distal portion of manus and

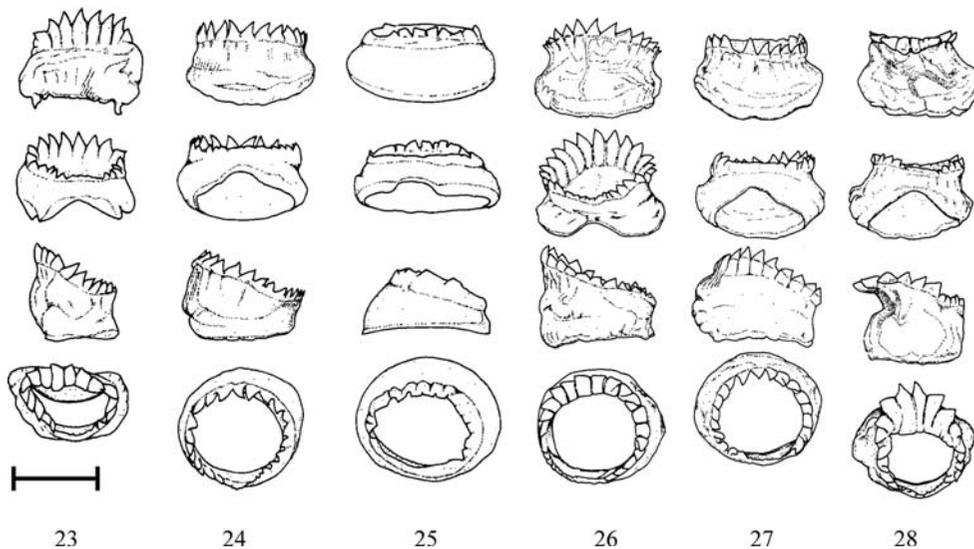
dactylus. Figs. 10, 12, 15, NMNZ M.172804, ML 35 mm; Figs. 11, 13, NMNZ M. 183104, ML 51 mm; Figs. 14, 16, NMNZ M.172985, ML 163 mm. All scale bars 1 mm

about half wing length; low wing fold; thickened shoulder, with short ridge or tooth; recessed jaw angle, with short step below the angle; crest and

lateral wall fold not discernibly thickened; and a lateral wall fold that extends to a point about halfway between crest and free corner of the



Figs. 17–22 SEM tentacle club and suckers, NMNZ M.172804, ML 38 mm: 17, tentacle club; 18, marginal suckers, devoid of trabeculae; 19, dactylus; 20, 21, laterally compressed manus suckers; 22, dactylic sucker

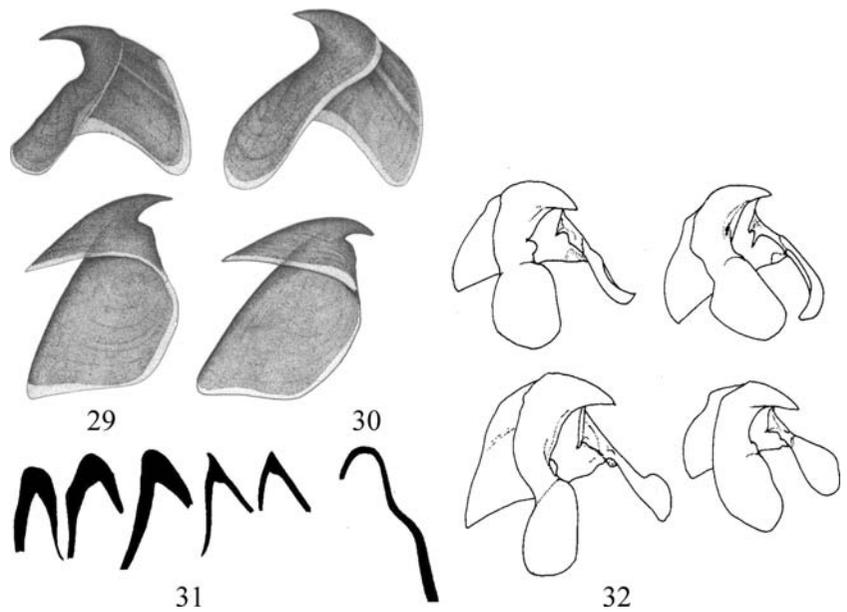


Figs. 23–28 Mid-arm sucker rings, posterior, anterior, lateral and oral perspectives, NMNZ M.172985, ML 163 mm: 23–25, arm IV; 26, arm III; 27, 28, arm II. Scale bar 1 mm

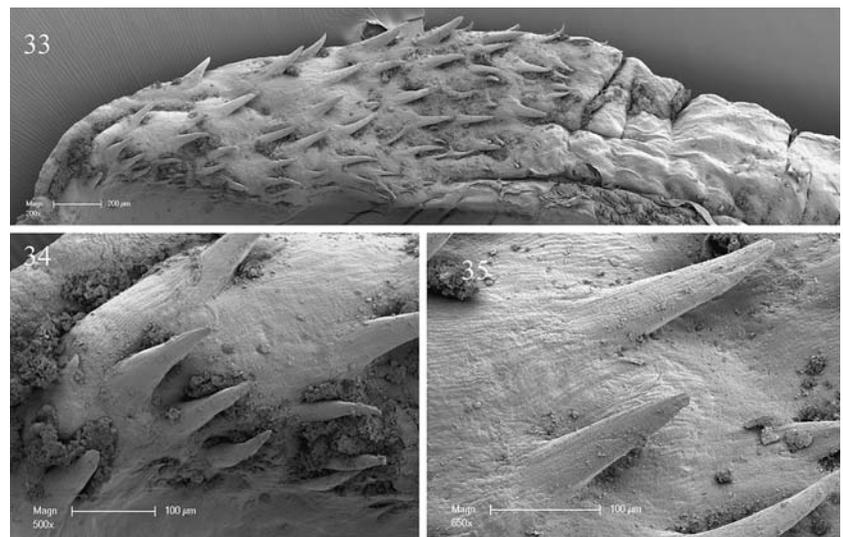
lateral wall. A wedge of cartilage, present on the inner face of the lateral wall near the wing fold, becomes less apparent in larger beaks. Male beak further characterised by short rostrum, female by

long rostrum. Wing fold more apparent in specimens recovered from stomach contents of sperm whales. Upper beaks included for completeness of illustration, but not described.

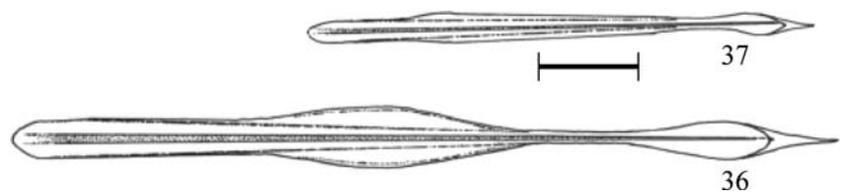
Figs. 29–32 Upper and lower beaks: 29, female (TASPBAP5); 30 male (TASPBAP2); 31, sections through jaw to wing (left to right), and crest (extreme right), lower beaks (AUT); 32, 4 beaks ex stomach contents of sperm whales (AUT), showing jaw detail, lower beaks



Figs. 33–35 Palatine palp and teeth: 33, entire palp; 34, 35, teeth in anterior-most and central region of the tooth-bearing portion of palp



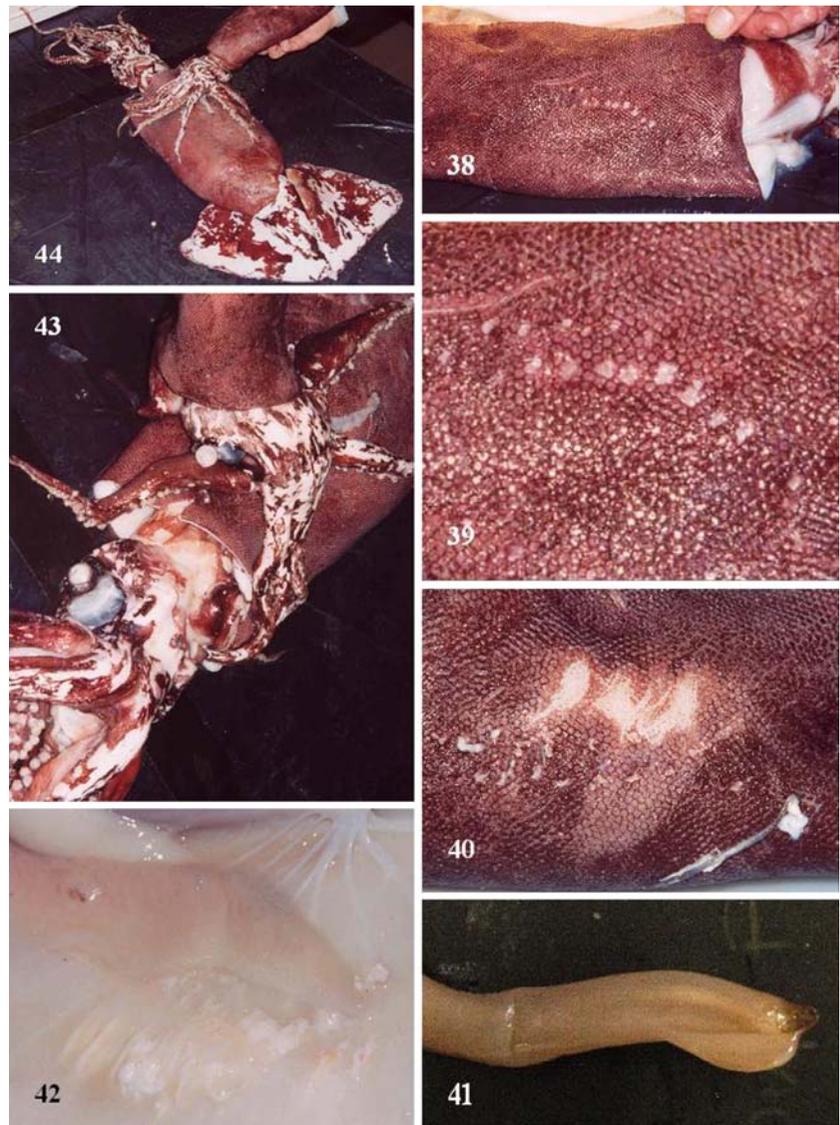
Figs. 36, 37 Gladius: 36, NMNZ M.172805, ML c. 76 mm; 37, NMNZ M.183106, ML 49 mm. Scale bar 10 mm



Palatine teeth (Figs. 33–35) with ~72 variably sized, non-articulated teeth irregularly embedded in membrane over inner face of palatine palp; largest teeth on outer margin and toward base of

palp, smallest on inner margin and toward tip of palp, proximal to free-edge of radula. Teeth long, narrow-based, flattened, gradually tapering from base to tall cusp; limited to distal half of palp.

Figs. 38–44 Reproductive biology: 38–40, female, ML 533 mm, lateral mantle wall showing nature of spermatophore insertion, Figs. 38 and 39 without and 40 with extensive dermal papilla abrasion; 41, terminal portion of genital apparatus, showing hardened terminal point, subterminal genital aperture and lobe-like lateral guide; 42, sub-epithelial spermatophores proximal to base of gill and stellate ganglion; 43, 44, reconstructed reproductive embrace (female larger)



Debris on palp is the remains of disintegrated globigerinid foraminifera.

Gladius (Figs. 36, 37) with vanes expanding anteriorly and posteriorly, terminating in a secondary conus; broader in larger individual than smaller. Distance from anterior tip of free rachis to anterior-most limit of vane insertions (FRL) in two specimens examined (ML *c.* 76, 51 mm) ~16 and 23% gladius length; gladius width ~8 and 6% gladius length anteriorly; gladius width posteriorly (conus-field width) ~4.5% for both individuals; conus length ~12 and 8.1% gladius length.

Mated females (to ML 533 mm) with spermatophores implanted proximal to dorso-lateral anterior mantle margin in one or more rows of up to 9 (Figs. 38–40), sometimes penetrating the inner mantle epithelium, but with contents not discharged into mantle lumen (Fig. 42). Mantle variably abraded, with deep dermal abrasion and removal of dermal papillae consistent with male beak rasping; and less-severe dermal papilla rubbing, consistent with male arm sucker-ring abrasion (Fig. 40), or without apparent damage (Fig. 38). Mature male to ML 412 mm; terminal portion of genital apparatus with hardened prom-

inence; genital aperture subterminal, opening on a lobe-like, thickened lateral guide (Fig. 41). The most plausible simulated mating posture is depicted in Figs. 43 and 44.

Discussion

With the exception of possible narrowing of the mantle with age, slight differences in fin shape, and the reduction of gladius visibility through the dorsal surface of the mantle musculature, no major ontogenetic change is apparent in overall body proportions through the ontogenetic series herein reported; morphology and dermal sculpture of juveniles reported herein are consistent with the even-smaller paralarva of 14 mm ML reported by Clarke (1992), and the two largest specimens from Tasmanian waters.

Pholidoteuthis boschmai is considered to be a circumglobal species (Vecchione and Young 1999), and characters and character states of systematic importance for it are consistent in all ways with the same characters/states reported for *P. massyae* by Pfeffer (once the composite nature of the original figures for *P. massyae* is recognised), and for the ontogenetic series of specimens herein described; all in turn are consistent with those of considerably larger specimens typically referred to *P. boschmai*. Accordingly, we are compelled to treat these two species as synonyms, *P. boschmai* and *P. massyae*, with the most appropriate name to apply to this species being *P. massyae* (Pfeffer, new combination).

Although mature female *Pholidoteuthis massyae* (Pfeffer) attain larger size than males, and the two sexes have markedly different lower beak morphology, no other remarkable sexually dimorphic character or state is apparent. No appreciable difference exists between lower beaks reported herein and those of Clarke (1980), although Clarke's beaks are described with a lateral wall that is thinner between the summit of the fold and the crest than is reported for any beak herein. The two beak types reported for this species by Clarke (1980) and Clarke et al. (1993) are herein recognised as sexual dimorphs of *P. massyae*, rather than evidence for the existence of another species, of which two others have been already described: *P. adami* Voss, 1956 and the

obscure *P. uruguayensis* Leta, 1987 (cited in Nesis and Nikitina 1990, but for which no further information has been found).

Pholidoteuthis adami is similar to *P. massyae* (= *boschmai*), but differs from it most notably in its attenuated fin shape, produced into a distinct 'tail'; the type of *P. uruguayensis* is no longer extant, and the description is obscure. Roper and Lu (1989b) maintained *P. adami* was so different from *P. boschmai* that a congeneric relationship was untenable, and believed a closer relationship existed between *P. adami* and *Lepidoteuthis grimaldii*; *P. adami* Voss was accommodated in the Lepidoteuthidae with *L. grimaldii*, although no appropriate generic name could be assigned to it (until the status of *P. boschmai*, the type of the genus, was established). This is achieved herein, and the systematic status of both *P. adami* and the problematic *P. uruguayensis* can now be appraised relative to the type species of the genus.

With the exception of similarities in gladius morphology (Toll 1998) we see little similarity between *Lepidoteuthis* and *P. adami*, based on an examination of *Lepidoteuthis* specimens and literature accounts of *P. adami*, and in accordance with the phylogenetic analyses (Carlini and Graves 1999) do not support separation of *P. massyae* and *P. adami* into different families. Moreover, we recognise four rows of suckers on the tentacle club, both upper and lower beak morphology, overall body proportions, funnel- and mantle-locking cartilage morphology and relative length, the presence of a diverticulum of the anterior vena cava (*sensu* Lipinski 1998), and, at least in common with several onychoteuthid genera, wart-like structures on the dorsal and ventral surfaces of the mantle (in marked contrast to otherwise smooth fins), to be characters or character states common to both the Pholidoteuthidae and the Onychoteuthidae. We accordingly propose a much closer relationship between these two families than between either of the aforementioned and the Lepidoteuthidae or Octopoteuthidae. The occurrence of a single hook on each dorso-lateral arm on male *L. grimaldii* (Jackson and O'Shea 2003), similarities in beak morphology (Clarke 1986) and genetic relationships (Carlini and Graves 1999), have shown already that a closer relationship exists between *Lepidoteuthis* and *Octopoteuthis* than between

either of these and *Pholidoteuthis*. Of the six classifications proposed for species in this complex, we favour the second, that of Clarke (1992) and Roeleveld (1998), arriving at this classification by recognising *P. boschmai* Adam to be a junior synonym of *P. massyae*, and *Tetronychoteuthis* to be a junior synonym of *Onychoteuthis*.

The rather unique terminal portion of the male's genital apparatus, combined with the presence of mated females, also enables us to offer a conjectural account of the mechanics of mating for this squid—for which reproductive behaviour is otherwise unknown. Species with such long organs presumably use them to implant spermatophores hydraulically into the female, and as a rule lack modification of either ventral arm (hectocotylus) for spermatophore transfer (Jackson and O'Shea 2003). Male *P. massyae* would appear to 'stitch' spermatophores through the wall of the female's mantle in rows either side of the dorso-lateral midline. In some instances spermatophores penetrate the inner mantle epithelium, but contents do not appear to have been discharged into the lumen of the mantle. To do so the male likely approaches the female from the side, wraps his arms around her mantle (often gnashing his beaks upon it while obtaining purchase, resulting in abrasion of her dermal papilla), then with genital apparatus protruding through the funnel as a guide, stabs directly into her mantle, inserting spermatophores in rows. As for most squid the egg mass of *Pholidoteuthis* is unknown, although the lack of accessory nidamental glands suggests that it is a free-floating gelatinous structure.

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