2.23 Family ONYCHOTEUTHIDAE Gray, 1849

by Clyde F.E. Roper and Patrizia Jereb

Onychoteuthidae Gray, 1849, Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia, 164 pp. [206].

Type Genus: Onychoteuthis Lichtenstein, 1818.

FAO Names: En – Clubhook squids; Fr – Cornets crochu; Sp – Lurias granchudas.

Diagnostic Features: Mantle densely muscular, or less muscular with softer, semigelatinous consistency, occasionally ammoniacal; tail moderately to prominently pointed (except *Onykia*). Fins with sharp lateral angles, rhomboidal, heart-shaped or transversely oval (in *Onykia*); buccal connectives (7) attach to ventral borders of ventral arms (IV); funnel-locking apparatus simple, groove and ridge straight; tentacular clubs with 2 medial series of strong hooks, those of ventromedial series the largest; 2 marginal series of small suckers on manus usually absent in subadults, or (rarely) marginal suckers rudimentary; small suckers on terminal pad; well-defined (by ridge or elevation) discoidal to oval locking apparatus on carpus with both suckers plus associated knobs; 8 muscular arms and 2 contractile tentacles around mouth; arms with 2 series of suckers with smooth, non-dentate rings, except in mature males of *Walvisteuthis*. Neck region with nuchal (occipital) folds in *Onychoteuthis*, *Ancistroteuthis* and *Notonykia*. Lower jaw (beak) with a "step" proximal to jaw angle. Photophores on ventral surface of eyes only in *Ancistroteuthis* and *Onychoteuthis*, which in addition has 2 discrete photophores on the ink sac/intestine. Hectocotylus absent in males of *Onykia* and *Onychoteuthis*, but the spermatophoric sac ("penis") elongate; unusual sexual dimorphism in *Walvisteuthis*; mature males in other genera unknown. Gladius with primary conus and with a rostrum, usually prominent. Colour: maroon to brick red, darker dorsally. *Onykia* dark blue to deep purple, especially on dorsal surface, with reflective sheen.

Size: Varies among species from 15 to 230 cm mantle length.

Interest to Fisheries: Several species from the 6 genera in this family currently are commercially exploited and have significant potential for fisheries.

Remarks: Six genera currently are recognized: *Ancistroteuthis*, *Kondakovia*, *Notonykia*, *Onychoteuthis*, *Onykia* and *Walvisteuthis*. The generic boundaries, however, are not well defined nor understood, and the family is in need of revision, in spite of several systematic studies over the past 2 decades (e.g. Kubodera *et al.* 1998, Vecchione *et al.* 2007c). *Onychoteuthis*, the most widely distributed genus, is cosmopolitan and occurs in open-ocean in all but the polar and subpolar seas; it is the only genus of the onychoteuthids to possess visceral photophores, but eye photophores are a shared character with *Ancistroteuthis*. The genus *Onykia* contains numerous described species, including a number of poorly defined species in tropical and subtropical seas, several of which are new species in need of description. Current thought confirms that the formerly recognized genus *Moroteuthis* (which includes the giants of the family, with mantle lengths up to 2.3 m) is synonymous with *Onykia* (e.g. Wakabayashi *et al.*, 2007, Vecchione *et al.*, 2007c). This concept was first expressed by Tsuchiya and Okutani (1992 [1991]), but had not been universally accepted earlier (e.g. Nesis, 2000, 2002). Thus, confusion in the nomenclature persisted for some years.

In this catalogue, the generic name *Onykia* is used to refer to all those species formerly known as *Moroteuthis* species. However, we recognize that systematics within the family is unstable and we strongly encourage that further studies and research be carried out to advance and stabilize our knowledge. We also note that while this catalogue was in press, a major revision on the family had just been completed and a summary of that work was presented in Vigo (Spain), at the 2009 CIAC meeting (Bolstad, in press). We suggest the reader refer to that very important work, that significantly improves our knowledge on this family, for additional information.

Chaunoteuthis, long recognized as a distinct genus from all other onychoteuthid genera by its gelatinous consistency and autotomized tentacles in the adult stage, clearly and unequivocally is synonymous with *Onychoteuthis banksii* (Arkhipkin and Nigmatullin, 1997); this body form represents the post-maturation, post-spawning, senescent stage of females and the existence of a "*Chaunoteuthis*" stage for other *Onychoteuthis* species is probable.

Kondakovia is an Antarctic (circum-Antarctic) form that can attain a mantle length of 108 cm, but relatively little is known about its biology. *Notonykia* was newly described in 1998 from the southern Atlantic waters off southwestern and southeastern South Africa, and subsequent reports indicate that it is circumpolar in the sub-Antarctic belt.

Phylogenetic studies on the family (Bonnaud et al. 1998; Nesis, 2000) confirm its monophyletic status to the extent that specimens were available to these authors

Onychoteuthids are very abundant oceanic forms that frequently aggregate in schools. Some species, e.g. *Onychoteuthis borealijaponica*, undergo seasonal migrations for feeding, then spawning.

Literature: Roper et al. (1984), Nesis (1982, 1987), Tsuchiya and Okutani (1992 [1991]), Arkhipkin and Nigmatullin (1997), Bonnaud et al. (1998), Kubodera et al. (1998), Nesis (2000), Sweeney and Young, 2003v), Vecchione et al. (2007c), Wakabayashi et al. (2007).

Key to the genera of Onychoteuthidae

Presence of warts or wrinkles on the ${\rm skin}^{1/}$
Mantle muscle soft, fleshy, ammoniacal
Tentacular club with 2 marginal series of small suckers
Nuchal folds numerous
Two small, round photophores (light organs) present on intestine

Table 14
Character states within genera of the Onychoteuthidae (from Vecchione et al., 2007c)

Genus	Many occipital folds	Visceral photophores	Gladius rostrum	Warts or wrinkles in skin	Club: marginal suckers	Fin shape
Ancistroteuthis	Yes	No	Thin, pointed	No	No	Sagittate
Kodakovia	No	No	Thick, pointed	No	Yes	Rhomboidal
Notonykia	Yes	No	Thin, pointed	No	No	Rhomboidal
Onychoteuthis	Yes	Yes	Thin, pointed ^{1/}	No	No/few	Rhomboidal/ sagittate
Onykia	No	No	Thick, pointed	Yes ^{2/}	No	Rhomboidal/ sagittate
Walvisteuthis	No	No	Thin, rounded	No	Few	Oval

^{1/} Somewhat rounded in *O. meridiopacifica*.

Onychoteuthis Lichtenstein, 1818

Plate IX, 60

Onychoteuthis Lichtenstein, 1818: Isis, oder Encyclopädische Zeitung, (9): 1591-1592 [1591].

Type Species: Onychoteuthis banksii (Leach, 1817).

Frequent Synonyms: Onychoteuthis Lichtenstein, 1818; Teleoteuthis Verrill, 1882a; Chaunoteuthis Appellof, 1891; Teleonychoteuthis Pfeffer, 1900.

Diagnostic Features: Mantle densely muscular, cylindrical, tapered posteriorly to pointed tail; non-ammoniacal. Skin smooth, without warts, wrinkles. Gladius visible through integument along dorsal midline; conus well developed, deep; rostrum thin, pointed, diagonally-directed dorsally, extends posterior to end of mantle musculature as characteristic spike. Fins rhomboidal, to slightly heart-shaped, sagittate, posteriorly attenuate. Nuchal folds prominent, 8 to 10. Tentacular club with 2 medial series of large, strong hooks on manus (19 to 27); no marginal series of suckers in adult (occasionally a few present). Chitinous rings of suckers on arms smooth, without dentition. Photophores present in mantle cavity: 1 small, anteriorly on ink sac, near anus; 1 large, posteriorly on intestine; a bilobed photophore present on the ventral surface of each eye.

Size: Small- to medium-sized squids, maximum mantle length 350 mm.

Geographical Distribution: Mostly in tropical and subtropical waters throughout the world's oceans, although they are also common in high latitudes of the North Pacific.

Habitat and Biology: Species are epipelagic to mesopelagic, mostly strongly eurythermal.

Literature: Vechione et al. (2007b); for additional references see the family.

^{2/} Except in "Onykia" knipovitchi.

^{1/} Except in "Onykia" knipovitchi, the atypical member of the genus Onykia.

Onychoteuthis banksii (Leach, 1817)

Fig. 327

Loligo banksii Leach, 1817, Zoological Miscellany; being Descriptions of New or Interesting Animals, 3(30): 137–141 [141]. [Type locality: not designated].

Frequent Synonyms: Loligo banksii Leach, 1817; Onychoteuthis bergii Lichtenstein, 1818; O. molinae Lichtenstein, 1818; Onykia angulatus Lesueur, 1821; Loligo bartlingi Lesueur, 1821; L. felina Blainville, 1823; L. uncinata Quoy and Gaimard, 1825 in 1824-1826; Onychoteuthis lessoni Ferussac, 1830, in Lesson 1830–1831; O. fleuryi Reynaud, 1831; O. lesueuri d'Orbigny, 1835 in Ferussac and d'Orbigny 1834–1848; O. krohni Verany, 1847; ?Loligo bianconi Verany, 1847; Onychoteuthis rutilus Gould, 1852; O. fusiformis Gabb 1862; O. aequimanus Gabb, 1868; O. lobipinnis Dall, 1871; O. raptor Owen, 1881; Chaunoteuthis mollis Appellof, 1891; Teleoteuthis caroli Joubin, 1900.

FAO Names: En – Common clubhook squid; Fr – Cornet crochu; Sp – Luria ganchuda.

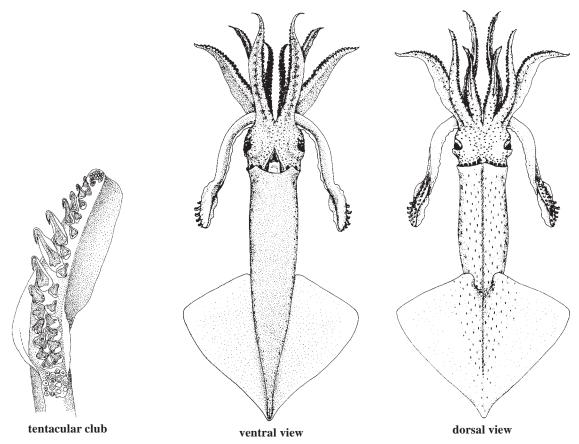


Fig. 327 Onychoteuthis banksii

Diagnostic Features: Mantle very robust, muscular; numerous (9 or 10 pairs) elongate, flap-like nuchal folds around the dorsolateral surface of the neck; a large, elongate, patch-like photophore (light organ) on ventral surface of each eye. Fins muscular, rhomboidial, with sharp lateral angles (70° to 90°), tail pointed; length of fins about 55 to 65% of mantle length. Tentacular clubs slightly expanded with 20 to 22 large, claw-like hooks in 2 medial series; no marginal series of suckers (occasionally a very few suckers); 13 to 15 small suckers in 4 series on dactylus; carpal-locking apparatus with 8 to 10 suckers plus accompanying 7 to 9 knobs; club length 35 to 45% mantle length. Gladius visible as a dark line through the skin along dorsal midline of mantle. Two large, round, bulbous light organs along ventral midline on intestinal tract/ink sac (anterior one-half diameter of posterior one).

Size: Medium-sized squid; mantle length up to 300 mm (370 mm only in the northern Pacific Ocean, Nesis 1982, 1987).

Geographical Distribution: This species occurs worldwide in tropical and temperate oceanic waters to 44°S, including the Mediterranean Sea; it is absent only from Arctic, northern boreal Atlantic, sub-Antarctic and Antarctic Oceans (Fig. 328).

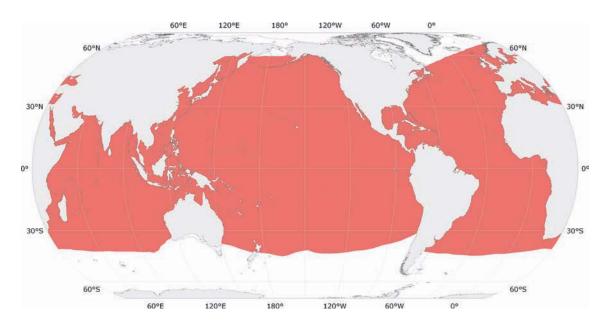


Fig. 328 Onychoteuthis banksii

Known distribution

Habitat and Biology: Onychoteuthis banksii is an oceanic, eurythermal, meso- and epipelagic species that occurs from the surface to 150 m depth, but it may be found as deep as 4 000 m. This schooling species frequently is observed "flying" above the surface to escape predators in pursuit. Its biology is poorly known, but very dense muscular structure and high respiration rates confirm it is a fast-swimming, slow-growing species. Males mature earlier than females; eggs are small (0.2 to 0.5 mm), and oocyte development is synchronous with high fecundity (over 200 000 eggs). Paralarvae are abundant in the eastern Atlantic Ocean, particularly from January to March. Spent females have severely degenerated muscular tissue of head, mantle, fins, as well as missing tentacles, so that they appear almost gelatinous; this advanced senescent form was recognized as a distinct genus and species, *Chaunoteuthis mollis* Appellof, 1891, for many years, but it has been synonymized once the mystery was unraveled. Prey consists of fishes and squids. Predators include giant red shrimp, fishes, e.g. albacore, yellowfin tuna, lancetfish, swordfish, tiger shark, smooth hammerhead shark, spinner, Frasier's striped and Risso's dolphins, toothed whales and fur seals.

Interest to Fisheries: While this is a very firm-fleshed, meaty squid, surprisingly, it has few directed fisheries at this time. A fishery exists in the Kurile Islands-Hokkaido region off Japan, where the species can reach 370 mm mantle length. It frequently is lured by a bright light and dip-netted at night. Also it is found on decks of small underway vessels in the morning. The quality of the flesh as human food is judged to be good; occasionally it is dried and sold for human consumption. It is heavily preyed upon by pelagic fishes (tunas, swordfishes, etc.), blue sharks, fur seals, odontocete (toothed) whales; e.g. southern bottlenose whales, Risso's and spotted dolphins, etc.

Local Names: ITALY: Totano dalle unghie.

Remarks: It is believed that this taxon actually represents a complex of distinct species, perhaps 4 or 5 in the world's oceans (Young, 1972a, Young and Harman, 1987, Vecchione *et al.*, 2007b); in the type locality, for example, 2 species seem to coexist (Young, pers com. in Bolstad, 2007). This, however, has not yet been confirmed because of a lack of the entire growth series of specimens for each suspected "species". The bite of this squid appears to be toxic to humans and resembles a wasp sting in its effect. There has been some confusion on the spelling of the species name, "banksi" or "banksi". Following the International Code of Zoological Nomenclature, the original "ii" ending is considered correct (Kubodera *et al.*, 1998).

Literature: Sanchez and Moli (1985), Young (1995), Arkhipkin and Nigmatullin (1997), Kubodera et al. (1998), Nesis (2000, 2002), Bolstad (2007).

Onychoteuthis borealijaponica Okada, 1927

Fig. 329

Onychoteuthis borealijaponicus Okada, 1927b, Bulletin de l'Institut Océanographique, Monaco, 494: 1–7 [7]. [Type locality: Japan].

Frequent Synonyms: Onychoteuthis banksi, Okada, 1927a.

FAO Names: En – Boreal clubhook squid; Fr – Cornet boreal; Sp – Luria boreal.

Diagnostic Features: Mantle long, slender, muscular, but rather thin (less robust than *Onychoteuthis banksii*). Fins broad (65 to 75% of mantle length), strong, muscular, their length 55 to 60% of mantle length; rhomboidal, fin angle 80° to 90°. Eight or 9 pairs of nuchal folds. Arm lengths 35 to 45% of mantle length. **Tentacular club large, length 20 to 30% of mantle length**. Numerous large, **claw-like hooks on tentacular clubs (25 to 27)** in 2 series; 13 to 15 small

suckers on dactylus; well-defined carpal apparatus with 8 to 10 suckers plus their accompanying 7 to 9 knobs. Oval photophore patch on ventral periphery of each eye; 2 ovoid light organs on ventral viscera connected by a silver iridescent band: anterior organ is small on ink duct posterior to anal papilla; posterior organ is much larger, on ink sac.

Size: Medium-sized species; maximum mantle length 370 mm in females, 300 mm in males; maximum weight 1.1 kg.

Geographical Distribution: The species is distributed in the far North Pacific Ocean from the Japan seas to off northwestern United States and Canada (Fig. 330).

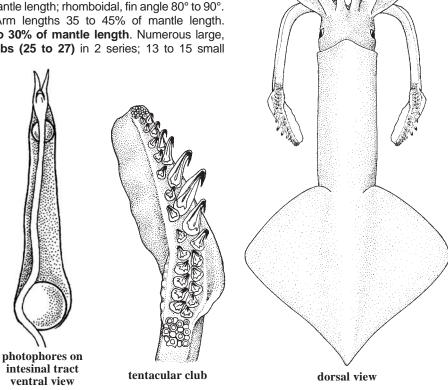


Fig. 329 Onychoteuthis borealijaponicus

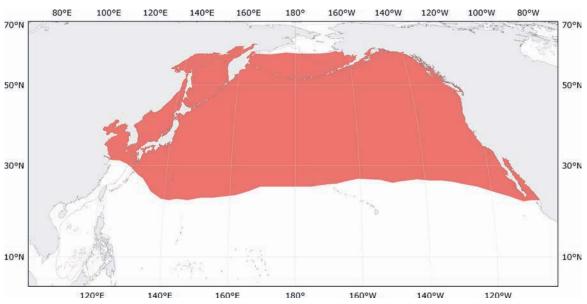


Fig. 330 Onychoteuthis borealijaponicus

Habitat and Biology: Onychoteuthis borealijaponica is an oceanic, epipelagic to mesopelagic species that occurs from the surface down to undetermined upper mesopelagic depths. It is most abundant in the northwestern North Pacific Ocean in surface waters of 9° to 13°C. It replaces Onychoteuthis banksii in colder, northern Pacific waters and it migrates to sub-Arctic waters in summer to feed, then returns to subtropical oceanic waters in autumn and winter to mate and spawn. East of Hokkaido, Japan, adults concentrate along the 10°C isotherm. The population around the Japanese Islands appears to undergo seasonal north-south migrations. Juveniles are encountered exclusively in the warm-water area off southwestern Japan in the Kuroshio Current and the countercurrent area, while adults occur in the cold water zones off Hokkaido, further north. In June, subadults from the south arrive on these fishing grounds and remain there feeding until autumn. Then they migrate southwards to mate and spawn at medium depths from late autumn through the winter southwest of Japan. The life span of both sexes is approximately 1 year, but males mature at smaller sizes (i.e. about 250 mm), and younger ages than females, where mantle length at maturity varies between 300 and 350 mm. The species preys on small fishes, and cannibalism is common. Predators of this species include: epipelagic fishes, e.g. Pacific pomfret, swordfish, salmon shark; marine mammals, e.g. dolphins, sperm whales, Guadalupe fur seals and, most significantly in the central North Pacific Ocean, northern fur seals. Ommastrephes bartramii is a major predator in the transitional waters of the central North Pacific Ocean.

Interest to Fisheries: Following the decline in the yields of *Todarodes pacificus*, *O. borealijaponica* increasingly is being fished commercially off northwestern Honshu, eastern Hokkaido, and in the northeastern Pacific off Washington State and British Columbia. It is taken primarily with jigs and drift gillnets. Jigging is particularly successful at night. The photophores make it appear as a dark shadow irradiating pale blue light near the surface. Sometimes it soars aboard moving vessels at night. It has been suggested that the species might support commercial fishing operations in the northwestern Pacific north of the sub-Arctic boundary, particularly during late summer and autumn.

Local Names: JAPAN: Tsumeika.

Remarks: Onychoteuthis borealijaponica is distinguished from *O. banksii* by its smaller clubs with a larger number of hooks, 2 oval visceral photophores connected by a silvery strand, of which the anterior is much smaller than the posterior; its size at maturity and maximum size are much larger than in *O. banksii*; its distribution is restricted to the far northern Pacific where it prefers much cooler water than does *O. banksii*.

Literature: Yamamoto and Okutani (1975), Kubodera et al. (1998), Nesis (2002), Watanabe et al. (2006b).

Ancistroteuthis Gray, 1849

Ancistroteuthis Gray, 1849, Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia, 1–164 [55].

Type Species: Ancistroteuthis lichtensteini (Férussac, 1835).

Diagnostic Features: Mantle densely muscular, cylindrical, slender, tapered posteriorly, **non-ammoniacal**; **tail acutely pointed**, supported by long spine of gladius. **Fin heart-shaped, sagittate, attenuate into elongate tail**. Gladius not visible through dorsal mantle. **Nuchal folds prominent, 6 to 10**. Tentacular club with 2 medial series of large, strong hooks on manus, no marginal series of suckers. **Photophores absent on ink sac/intestine**; an oval, opaque zone with small posterior patch of photophoric tissue on ventral surface of eyes. Skin smooth on mantle, head.

Remarks: The genus currently is monotypic. However, 3 geographic forms occur in the Atlantic Ocean (type locality of *Ancistroteuthis lichtensteini* sensu stricto is in Mediterranean Sea) and 1 in the Pacific Ocean, so the species as currently designated actually represents a complex of closely related species, as yet not fully understood nor named. These currently are termed *A. lichtensteini* senso stricto, Mediterranean Sea, *A. lichtensteini*, central Atlantic Ocean form, *A. lichtensteini*, South Atlantic Ocean form, and *A. lichtensteini*, Pacific Ocean form (see Kubodera *et al.*, 1998). According to Vecchione *et al.* (2008b), however, the South Atlantic and South Pacific forms, probably belong to *Notonykia africanae* (Nesis *et al.*, 1998b). Additional systematic study is needed to clarify the status of this species complex.

Ancistroteuthis lichtensteini (Férussac, 1835)

Fig. 331

Onychoteuthis lichtensteini Férussac, 1835, in Férussac and d'Orbigny, 1834-1838, Histoire Naturelle Générale et Particulière des Cèphalopodes Acètabulifères Vivants et Fossiles, Atlas, Onychoteuthis, [pl.8]. [Type locality: Mediterranean Sea, near Nice, France).

Frequent Synonyms: Onychoteuthis lichtensteini d'Orbigny, 1839; Onychoteuthis hamatus Risso, 1854.

FAO Names: En – Angel squid; Fr – Cornet archangel; Sp – Luria paloma.

Diagnostic Features: Mantle slender, very muscular, posterior end acutely pointed and supported by long, thin, pointed spine of gladius. Occipital folds numerous. Skin smooth. Fins strong, lanceolate, sagittate posteriorly; posterior margins concave. Fin length 60% of mantle length, width 57% of mantle length. Tentacular clubs in adults slightly expanded, length 30% of mantle length, with 2 median series of hooks (20 to 21); lateral series of suckers absent; 16 or 17 small suckers on dactylus; carpal-fixing apparatus of club elliptical with 9 or 10 suckers plus 9 or 10 knobs; 8 or 9 pairs of flap-like nuchal folds in neck area. Arm formula IV>III=II>I, lengths 40 to 53% of mantle length. Rachis of gladius not visible along dorsal midline of mantle in subadults, visible anteriorly in adults; conus a minute spoon and long, thin, pointed rostrum. Light organs absent on intestinal tract; a small posterior patch of bioluminescent tissue occurs on the ventral surface of each eye.

tentacular club ventral view dorsal view

Fig. 331 Ancistroteuthis lichtensteini

Size: Maximum mantle length is 300 mm.

Geographical Distribution: Eastern Atlantic Ocean from northwestern Spain and the Straits of Gilbraltar to Angola, and throughout the Mediterranean Sea; the Gulf of Mexico, the central eastern Atlantic Ocean, and the South Atlantic Ocean; Melanesia and the southwestern Pacific (Fig. 332).

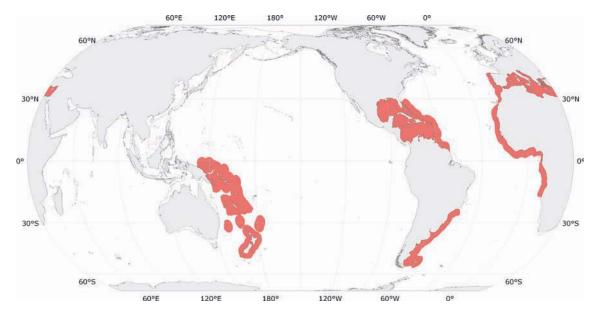


Fig. 332 Ancistroteuthis lichtensteini

Habitat and Biology: Ancistroteuthis lichtensteini is an epipelagic, mesopelagic to benthi-bathyal species that occurs in open warm-temperate waters from the surface to about 250 m depth; open net records to 1 270 m bottom depth. In the western Mediterranean it is associated with gravel bottoms during spring and summer. Males mature at around 200 mm mantle length; spawning occurs in the summer. It feeds on epipelagic and upper mesopelagic finfishes and crustaceans, and in turn is preyed upon by cetaceans, e.g. Risso's dolphin and striped dolphins, sperm whales, and pelagic fishes, e.g. swordfish, and by giant red shrimp in the Mediterranean.

Interest to Fisheries: Currently no directed fishery exists for this species; it is taken only as bycatch in pelagic and deep, open benthic trawls. However, the size and firm consistency of the flesh make it a potential target for a fishery.

Local Names: ITALY: Totano angelo; USA: Lichtenstein's angel squid.

Remarks: The geographical distribution of this species complex is incompletely known. The distribution appears very disjunct because so few specimens have been reported in the scientific literature.

Literature: Kubodera et al. (1998), Lefkaditou et al. (2003), Okutani (2005), Vecchione et al. (2008b).

Notonykia Nesis, Roeleveld and Nikitina, 1998

Notonykia Nesis, Roeleveld and Nikitina, 1998b, Ruthenica, 8(2): 153–168 [154].

Type Species: Notonykia africanae Nesis, Roeleveld and Nikitina, 1998.

Frequent Synonyms: None.

Diagnostic Features: Photophores absent. Dorsal **nuchal folds numerous, at least 4 or 5**. Conus of gladius short, chitinous; rostrum thin, pointed. Skin smooth, without wrinkles or warts. Marginal club suckers absent. Fins rhomboidal. See species characters for details.

Literature: Nesis et al. (1998b), Bolstad et al. (2007).

Notonykia africanae Nesis, Roeleveld and Nikitina, 1998

Notonykia africanae Nesis, Roeleveld and Nikitina, 1998b, Ruthenica, 8(2): 153–168 [154], 6 figs. [Type locality: 33°42'S, 17°21'E, off South-Western Cape, South Africa].

Frequent Synonyms: None.

FAO Names: En – African notalian clubhook squid; Fr – Cornet crochu africane; Sp – Luria ganchuda africana.

Diagnostic Features: Mantle densely muscular (non-ammoniacal), broad, cylindrical anteriorly, tapers to moderately pointed, conical tail. Fins large, muscular, rhomboidal; length 58 to 66% of mantle length (average 59%), width 66 to 84% of mantle length (average 72%). Anterior margins of fins slightly convex, posterior margins nearly straight, very slightly drawn out into a short tail. Skin smooth, not rugose or tubercular. Nuchal folds present, 4 or 5 per side. Photophores absent. Tentacular club narrow, with 2 medial series of 14 to 20, usually 17 or 18, hooks; fifth to sixth hooks in ventral row by far the largest; hooks on dorsal row small. No marginal series of suckers. Dactylus with 20 to 38 minute suckers; carpus well-defined, with 6 to 12 suckers plus their accompanying knobs. Buccal connectives attach dorsally to arms I and II, ventrally to III and IV (type DDVV). Hectocotylus absent. Gladius with strong longitudinal ridge, with short, terminal conus and short, thick, chitinous, cartilaginous rostrum.

Size: Small-sized species; maximum known mantle length 180 mm.

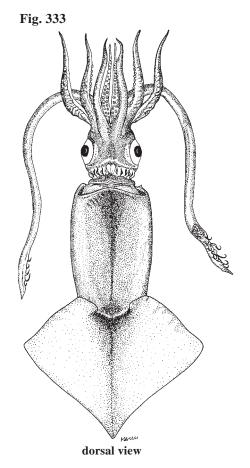


Fig. 333 Notonykia africanae

Geographical Distribution: This species is circumpolar in a sub-Antarctic belt between 30°S (off Western Cape, South Africa) and 53°S (south of New Zealand): it occurs off South Africa, off southern Chile, off southern Australia, off eastern North Island, New Zealand to about 145°W (Fig. 334).

Habitat and Biology: Notonykia africanae has a distribution range intermediate between a Southern Subtropical Convergence distributional pattern and the true notalian type of distribution. The species has a very broad vertical distributional range, also, as it occurs in epi-, meso- and bathypelagic layers, between 0 and 1 200 m, mostly 30 to 200 m, and ascends to the surface at night. Subadults and the earliest stages of maturity are broadly eurybathic, from approximately 0 to 1 000 m, but they are primarily mesopelagic with records from approximately 500 120°W to 900 m. Maturation in males begins at 90 to 100 mm mantle length and in females at 100 to 130 mm mantle length. The size at full maturity for males seems to be greater than 130 mm and for females greater than 150 mm.

Interest to Fisheries: No interest in a fishery exists at the present time. But, because it is a member of the muscular, non-ammoniacal group of onychoteuthids, it seems possible that a fishery could develop in the future if large concentrations of this small squid are

Literature: Nesis et al. (1998b), Nesis (2000), Bolstad (2007).

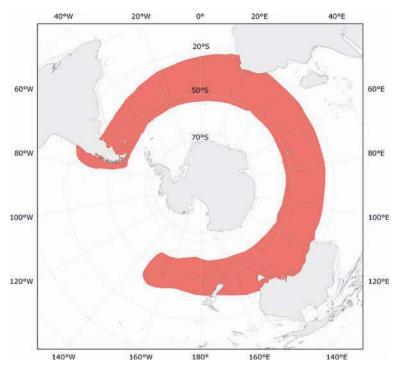


Fig. 334 *Notonykia africanae*Known distribution

Notonykia nesisi Bolstad, 2007

discovered.

Notonykia nesisi Bolstad, 2007, Reviews in Fish Biology and Fisheries, 17(2–3): 305–335 [327]. [Type locality: 46°06′80″S, 171°52′00″E, New Zealand waters, over 1 333 m].

Frequent Synonyms: Ancistroteuthis lichtensteini, southern Pacific form (Kubodera et al. 1998: 282; non Ferussac 1835: 334, Pls. 8, 14); Nesis et al., 1998: 164.

FAO Names: En – Nesis notalian clubhook squid; Fr – Cornet crochu de Nesis; Sp – Luria granchuda de Nesis.

Diagnostic Features: Neck (shaft) of largest ventral tentacular hooks straight; profile of hook forms an overall 'J'-shape; carpus with 7 to 9 suckers; dorsal tentacular hooks 1 and 2 noticeably larger than ventral tentacular hooks 1 and 2.

Size: Small-sized species, up to 105 mm mantle length.

Geographical Distribution: Currently known only from the sub-Antarctic ocean, principally above and south of Chatham Rise, east of New Zealand, South Pacific Ocean.

Habitat and Biology: Occurs at depths of 0 to 950 m, mostly the upper 300 m.

Literature: Bolstad (2007), Bolstad et al. (2007).

Onykia Lesueur, 1821

Plate X, 61

Onykia Lesueur, 1821, Journal of the Academy of Natural Sciences of Philadelphia, 2(1): 86–101 [98].

Type Species: Onykia carriboea Lesueur, 1821.

Frequent Synonyms: Onychia Latreille, 1825; Steenstrupiola Pfeffer, 1884.

Diagnostic Features: Mantle muscular to moderately soft; dermis of mantle with warty structures or soft wrinkles in adults (*Onykia knipovitchi* with smooth skin only). Gladius not visible through skin along dorsal mantle midline. Three occipital folds present on lateral side of posterior head; dorsalmost fold with occipital membrane curves dorsally and extends to or nearly to nuchal cartilage. Tentacular club in subadults and adults with 2 medial series of hooks on manus, no suckers; suckers occur only on carpal cluster (with alternating knobs), and minute suckers occur on the distal terminal pad. Photophores are absent. Funnel groove with inverted y-shaped ridge in animals longer than 100 mm mantle length (possibly absent in *O. ingens* and *O. knipovitchi*); anterior margin of funnel groove rounded. Gladius with long, thick cartilaginous rostrum; long, lanceolate vanes extend to the conus field without a narrow posterior 'neck', as occurs in *Onychoteuthis*, *Ancistroteuthis* and *Notonykia*.

Size: Medium-sized (275 mm mantle length) to very large (1.6 to 2.3 m mantle length) squids.

Remarks: For many years a number of species now recognized as members of *Onykia* were placed in the genus *Moroteuthis*. Tsuchiya and Okutani (1992 [1991]), demonstrated that specimens historically attributed to *Onykia* Lesueur, 1821, were the young stages of known species of *Moroteuthis* Verrill, 1881c, thus making the generic name *Moroteuthis* a junior synonym of *Onykia*. Tsuchiya and Okutani (1992 [1991]) also demonstrated that "*Moroteuthis*" *japonica* Taki, 1964, and "*Moroteuthis*" *pacifica* Okutani, 1983a, were growth stages of *Onykia robusta*. Kubodera *et al.* (1998) state that *Onykia indica* Okutani, 1981 probably is the young form of some known species of *Onykia. Onykia rancureli* Okutani, 1981, has been widely recognized as being very different from other members of this genus and several authors have suggested that a new generic name is needed (e.g. Toll, 1982; Tsuchiya and Okutani, 1992 [1991]). Recent evidence suggests that this generic designation should be *Walvisteuthis*, and consequently, the species is considered to be identical to *Walvisteuthis virilis* (see Remarks section under *W. virilis*) by an authoritative fraction of the scientific community (Young *et al.*, 2003). Molecular results of the genetic studies by Bonnaud *et al.* (1998) and Wakabayashi *et al.* (2007) indicate that the genus *Onykia* may not be monophyletic, since "*O. knipovitchi*" represents an atypical member of the genus. We strongly encourage that further research be carried out on this genus, in particular.

Literature: Tsuchiya and Okutani (1992 [1991]), Kubodera et al. (1998), Bonnaud et al. (1998), Nesis (2000), Vecchione et al. (2007c), Wakabayashi et al. (2007).

Onykia carriboea Lesueur, 1821

Fig. 335

Onykia carriboea Lesueur, 1821, Journal of the Academy of Natural Sciences of Philadelphia, 2(1): 86–107 [98]. [Type locality: Gulf of Mexico and Gulf Stream].

Frequent Synonyms: Loligo cardioptera Lesueur and Petit, 1807; L. laticeps Owen, 1836; L. plagioptera Souleyet, 1852 in 1841–1852; Onychia binotata Pfeffer, 1884; Steenstrupiola atlantica Pfeffer 1884; Teleoteuthis carriboea Verrill, 1885; Teleoteuthis (Onychia) agilis Verrill, 1885; Teleoteuthis jattai Joubin, 1900.

FAO Names: En – Caribbean clubhook squid; Fr – Cornet crochu de Caraïbes; **Sp** – Luria ganchuda del Caribe.

Diagnostic Features: Mantle muscular, cross-section nearly ellipsoidal in young, to cylindrical with growth. Fins much wider than long; length nearly 50% of mantle length; width 70 to 75% of mantle length; fins subrhombic, convex anterior and posterior margins, bluntly rounded lateral angles. Tentacle club with 2 medial series of about 10 to 12 hooks each (total 20 to 24 hooks), 2 marginal series of small suckers; well-developed carpus with 8 or 9 suckers, plus their accompanying knobs; dactylus with a few very small to minute suckers. Gladius with short, dorsally curved rostrum. Skin surface smooth with dense, purplish chromatophores and reflective, silvery sheen, even ventrally. Chromatophores of a vivid, deep purple colour, particularly densely packed on dorsal mantle and dorsal head.

Size: The maximum known mantle length is 100 mm.

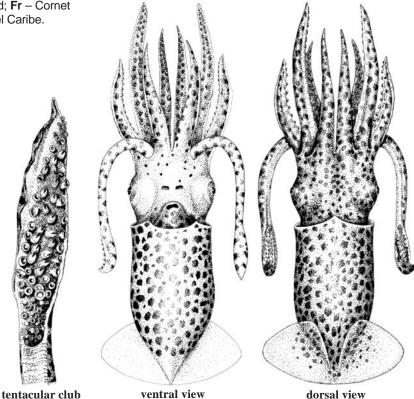


Fig. 335 Onykia carriboea

Geographical Distribution: This species is believed to have a cosmopolitan circumglobal distribution, throughout tropical and subtropical/warm temperate oceans. However, no definitive statement can be made before its specific status is clarified (see Remarks) (Fig. 336).

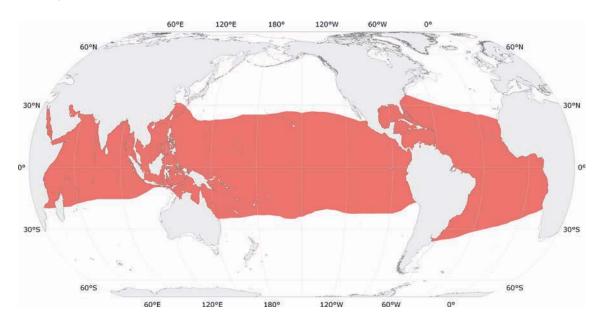


Fig. 336 Onykia carriboea

Known distribution

Habitat and Biology: Paralarvae and juveniles of *Onykia carriboea* live near and at the surface, often in association with *Sargassum* weed. Biology, growth and maturity are very poorly known. This species is preyed upon by squid, *Sthenoteuthis oualaniensis*, and by yellowfin and bigeye tunas, and undoubtedly by many other epipelagic fishes and pelagic birds.

Interest to Fisheries: Currently no interest exists for a fishery.

Remarks: *Onykia carriboea* is known, with certainty, only from small juveniles: no adult, mature specimen has been found/described. This suggests that the name could represent the immature growth stage of other onychoteuthid species (Kubodera *et al.*, 1998, Bolstad, 2007). For example, as reported above, the type locality of the species is the Gulf of Mexico and the Gulf Stream; several subadult/adult specimens from the NMNH (Smithsonian Institution) from the Gulf of Mexico, originally labelled "*Ancistroteuthis*" were subsequently classified as *Onykia robsoni* (Kubodera *et al.*, 1998). Therefore, *O. carriboea* from that geographic area could be *O. robsoni*, in which case *O. robsoni* could ultimately prove to be a junior synonym of *O. carriboea* (see also Vecchione *et al.*, 2003b). However, detailed comparisons of specimens from their respective type localities are needed before this problem can be resolved. This problem is further complicated by the fact that the holotype of *O. carriboea* no longer exits (Sweeney and Roper, 1998).

Local Names: None available.

Literature: Nesis (1982, 1987), Kubodera et al. (1998), Sweeney and Roper (1998), Vecchione et al. (2003b).

Onykia ingens (Smith, 1881)

Fig. 337

Onychoteuthis ingens Smith, 1881, Proceedings of the Zoological Society of London, 1881(1): 22-44 [25]. [Type locality: Port Riofrio, west coast of Patagonia, southeastern South Pacific Ocean].

Frequent Synonyms: Onychoteuthis ingens Smith, 1881; Moroteuthis ingens (Smith, 1881).

FAO Names: En – Greater clubhook squid; Fr – Cornet commun;

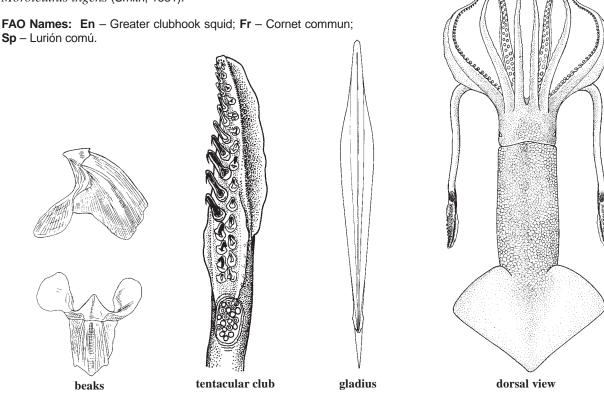


Fig. 337 Onykia ingens

Diagnostic Features: Mantle robust, broad, thick, heavily muscled, not drawn out into a sharp tail; skin covered with fleshy warts, as flat, elongate or curved tubercles, in a paving-stone pattern. Fins large, broad, with broad fin angles of 50° to 55° each; fin length about 50% (or slightly larger) of mantle length; rhomboidal, not attenuate into a tail. Rostrum of gladius triangular in cross-section, 10 to 12% of mantle length; endcone very short, shortest of all congeners. Tentacular clubs unexpanded, with 28 to 32 hooks in 2 medial series; hooks on ventral series much larger than on dorsal series, largest hooks positioned at sixth to eighth pair; carpus with 10 to 13 suckers plus their associated knobs; dactylus with 16 or 17 minute suckers. Longest arms (II and III) about 70% of mantle length.

Size: Large sized species; maximum mantle length 520 mm.

Geographical Distribution: Onykia ingens is a notalian circumpolar species in sub-Antarctic waters north of the Antarctic convergence, south of the Subtropical Convergence. It occurs on the Patagonian shelf, in southern Chile and the Prince Edward, Crozet, Kerguelen Islands and southern New Zealand islands (Antipodes, Campbell, etc.) as well as southern Australian and southern South Africa waters (Fig. 338).

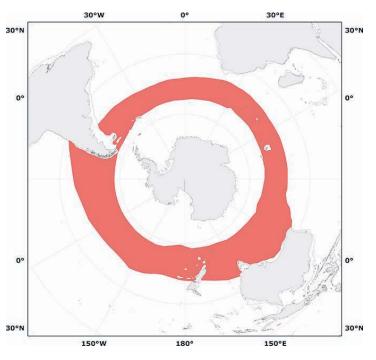


Fig. 338 Onykia ingens Known distribution

Habitat and Biology: Adults of *Onykia ingens* apparently are primarily benthic/epibenthic in lower sublittoral and bathyal zones, having been caught in demersal trawls from 300 to 1 450 m in continental slope and bathyl waters. Juveniles and subadults are epi- to mesopelagic. This species is the prey of lancetfishes, slender and yellowfin tunas, southern opah, king penguin, wandering albatross. It also is a major food item of sperm whales, bottlenose whales and southern elephant seals. For example, the stomach of one stranded sperm whale in New Zealand, *O. ingens* represented the second most abundant species, 11.06%, and third most in weight by wet mass, 15.26%, following 2 specimens of *Architeuthis*. Similar results for *O. ingens* were exhibited by sperm whales from the Tasman Sea. *Onykia ingens* preys on krill, deep water fishes, e.g. myctophids, viperfish, dragonfish, and on other species of squids. It exhibits strong sexual dimorphism: mature females weigh 5 times as much as mature males. This is an annual species and peak spawning and hatching occur in autumn and winter (June to August) near the bottom. Female reproduction is characterized by synchronous oocyte growth and ovulation; female fecundity approaches 400 000 oocytes and egg size is 1.8 to 2.7 mm. Females apparently undergo strong ontogenetic descent, but males do not exhibit such a behaviour. Mature and spent males and especially laying and spent females exhibit massive mantle tissue degradation, eventually into a complete, gelatinous consistency.

Interest to Fisheries: This extremely abundant species in sub-Antarctic waters is believed to have some fishery potential, but as a neutrally buoyant, ammoniacal species, this seems problematic currently. However, like so many other similarly endowed species, *Onykia ingens* could provide huge tonnage if the ammoniacal problem can be solved. In any case, it is an extremely important prey species for a number of commercially important fishes.

Local Names: None available.

Literature: Kubodera et al. (1998), Nesis (2002), Arkhipkin (2003b), Vecchione et al. (2003c), Bolstad (2007).

Onykia knipovitchi (Filippova, 1972)

Fig. 339

Moroteuthis knipovitchi Filippova, 1972, Malacologia, 11(2): 391–406 [392]. [Type locality: sub- Antarctic waters near South Georgia Island, South Atlantic Ocean].

Frequent Synonyms: Moroteuthis knipovitchi Filippova, 1972.

FAO Names: En – Smooth clubhook squid; Fr – Cornet lisse; Sp – Lurión liso.

Diagnostic Features: Mantle moderately broad, stout, not drawn out into prominent tail; ammoniacal; thin, smooth-textured skin surface. Fins large, broad, rhomboidal, not attenuate; fin angles 45° to 50° each; fin length 50 to 60% of mantle length. Gladius with cartilaginous conus, triangular in cross-section, 10 to 13% of mantle length. Tentacular club manus long, slender, with 20 to 30 long, narrow hooks in 2 medial series, those of ventral series larger than hooks on dorsal series; the second to fourth hooks on the dorsal series and sixth to eighth hooks on ventral series are the largest in respective series; 12 to 13 small suckers plus their accompanying knobs on carpus; 14 to 16 minute suckers on dactylus. Longest arms (II) 50 to 90% of mantle length.

Size: Large-sized species: maximum mantle length 450 mm.

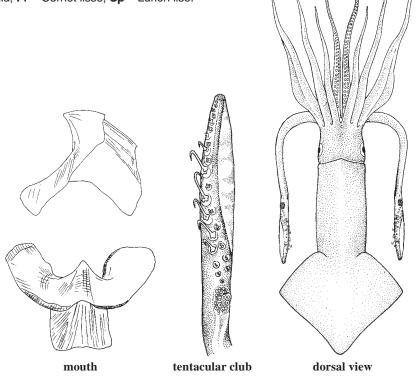


Fig. 339 Onykia knipovitchi

Geographical Distribution: This species is circum-Antarctic in distribution, south of the Antarctic Convergence. It occurs in the Scotia Sea, Argentine Basin, Drake Passage and around South Georgia, Kerguelen, Crozet, and Prince Edward Islands (Fig. 340).

Habitat and Biology: Onykia knipovitchi is an oceanic, mesopelagic, bathyal, ammoniacal species. The potential fecundity of females is 100 000 oocytes. Juveniles, young and adults occur near the surface in the austral winter where they are heavily preyed upon by king penguin, wandering, black-browned albatrosses and other pelagic birds. Larger and mature animals occur in deeper waters (at least to 550 m), where they are captured by fur seals, southern elephant seals (up to 31% of prey biomass), Ross seals and southern sea lions. Cetaceans also are major predators: southern bottlenose whales, sharp-toothed whales, other smaller odontocetes, and sperm whales, which take the large and mature animals as a major component of their diet. Circumglobal in the Southern Ocean.

Interest to Fisheries: Its abundance, size and consistency before spawning make this species a potential target for a significant fishery. However, as it is an ammoniacal species, *Onykia knipovitchi* is unsuitable for human consumption until a neutralizing process becomes available.

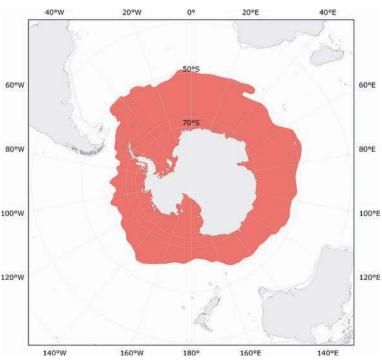


Fig. 340 Onykia knipovitchi

Known distribution

Remarks: According to the molecular studies by Bonnaud *et al.* (1998) and Wakabayashi *et al.* (2007), this is the only species of the formerly recognized *Moroteuthis* genus that does not fit into the *Onykia* group, being more closely related to the genus *Onychoteuthis* than to the genus *Onykia*. Therefore Wakabayashi *et al.* (2007) did not use the generic name *Onykia* for this species, referring to it as to "*Moroteuthis*" *knipovitchi*. Additional research is needed to solve this problem; however, several morphological features (e.g. smooth skin, long, asymmetrical ventral club hooks), support the fact that "*Onykia knipovitchi*" is, indeed, an atypical member of the genus (see also Vecchione *et al.*, 2007c).

Local Names: None available.

Literature: Okutani (1980), Rodhouse (1989), Bonnaud et al. (1998), Kubodera et al. (1998), Vecchione et al. (2007c), Wakabayashi et al. (2007).

Onykia lönnbergi (Ishikawa and Wakiya, 1914)

Fig. 341

Moroteuthis lönnbergi Ishikawa and Wakiya, 1914, Journal of the College of Agriculture, Imperial University of Tokyo, 4(7): 445–460 [445]. [Type locality: Sagami Bay, Japan, northwestern North Pacific Ocean].

Frequent Synonyms: Moroteuthis lönnbergi Ishikawa and Wakiya, 1914.

FAO Names: En – Japanese clubhook squid; Fr – Cornet japonais; Sp – Lurión japonés.

Diagnostic Features: Mantle robust, muscular; skin rugose, with short, narrow, curved, fleshy ridges or pads that fuse with each other; **posterior tip drawn out into a moderately long, pointed tail.** Fins large, rhomboidal; fin length 50 to 60% of mantle length; fin width, broad, up to 50 to 55% of mantle length, roughly equal to fin length; fin angles about 35° to 40° each. Rostrum of gladius narrowly triangular in cross-section.

Tentacular club long, unexpanded, with about 25 (maximum 30) hooks in 2 median series on manus; fourth to sixth hooks largest on dorsal series, sixth or seventh hook largest on ventral series; 7 or 8 small suckers plus associated knobs on carpus; 10 to 13 minute suckers on extreme tip of dactylus. Longest arms (IV) 60% of mantle length.

Size: Medium-large sized squid; maximum mantle length 350 mm.

Geographical Distribution: This species is distributed in the western North Pacific Ocean off eastern Honshu, Japan in the north, southward to Tsugaru Strait, the Kuroshiro Current, into the Indian Ocean (Saya-de-Malha Bank), and southward to the North West Shelf, Australia (Fig. 342).

Habitat and Biology: *Onykia lönnbergi* is an oceanic, ammoniacal, neutrally buoyant species (epipelagic, mesopelagic, bathyal) from temperate and subtropical waters. Its exact depth distribution is unknown, but it has been caught in open nets in depths between 730 and 920 m. However, it also occurs in depths of less than 200 m, because it is preyed upon by northern fur seals, as well as deeper-ranging sperm whales.

Interest to Fisheries: Undetermined, but currently unsuitable at full maturity because of its ammoniacal composition. It attains a size suitable for utilization.

ength; fin width, les about 35° to

Fig. 341 Onykia lönnbergi

dorsal view

tentacular club

Local names: None available.

Literature: Okutani *et al.* (1987), Nesis (1982, 1987), Kubodera *et al.* (1998), Nesis (2002), Vecchione *et al.* (2007c), Wakabayashi *et al.* (2007).

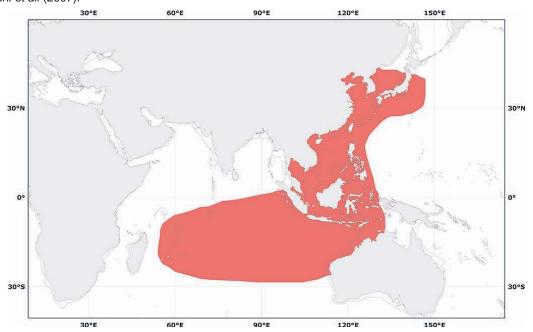


Fig. 342 *Onykia lönnbergi*Known distribution

Onykia robsoni (Adam, 1962)

Fig. 343

Moroteuthis robsoni Adam, 1962, Memórias da Junta de Investigações do Ultramar, series 2, 33: 9–64. [24]. [Type locality: 16°35.6'S, 11°19.5'E, Angola, southeastern South Atlantic Ocean].

Frequent Synonyms: Moroteuthis robsoni Adam, 1962.

FAO Names: En – Rugose clubhook squid; Fr – Cornet rugueux; Sp – Lurión rugoso.

Diagnostic Features: Mantle long, slender; skin rugose, covered with flat, fleshy, irregular tubercles, deep reddish coloration; posterior tip drawn out into a very long, sharp tail. Fins heart-shaped, very long, attenuate (not rhomboidal); length 60 to 67% of mantle length; together they form a very sharply pointed, lanceolate tail; relatively narrow, 45 to 50% of mantle length; fin angle 30° to 40° each. Rostrum of gladius triangular in cross-section, with ventral length of 23 to 36% of mantle length. Tentacular club very narrow, unexpanded; carpus with 10 to 12 small suckers plus their associated knobs; manus with 26 to 32 hooks in 2 median series; dactylus with 12 to 17 minute suckers. Arms attenuate, longest (IV) about 57 to 86% of mantle length.

Size: Large-sized species: maximum mantle length 750 mm.

Geographical Distribution: The distribution of *Onykia robsoni* is circumglobal in southern subtropical and notalian regions. The species occurs in the southern Atlantic to South Georgia,

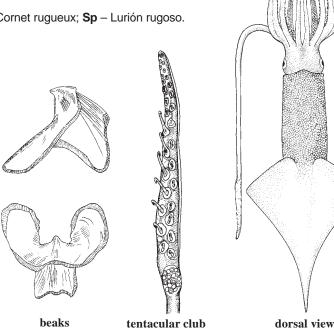


Fig. 343 Onykia robsoni

off southern and southwestern South Africa, as well as off southwestern Australia and southern New Zealand (Fig. 344).

Habitat and Biology: Onykia robsoni appears to be very similar to O. robusta. It is an oceanic species, both pelagic and benthic. It is taken with open midwater trawls fished between 250 and 550 m depths (exact depth distribution unknown). Commonly it is bottom-trawled from deeper than 500 m. Analysis of sperm whale stomach contents indicates that O. robsoni spawns in the austral autumn off South Africa on the lower continental slope possibly to 2 500 m. Females are in maturing condition at 560 mm mantle length; life span approximately 2 years until single spawning occurs, followed by severe muscular degeneration and death. This species is heavily preyed upon by sperm whales and smaller odontocetes, including sharp-toothed and southern bottlenose whales. One New Zealand sperm whale stomach contained 1.25% by number and

5.35% by wet mass of this species. Fish predators include sharks, e.g. blue sharks and tiger sharks. *Onykia robsoni* preys on krill (*Euphausia superba*), fishes and other squids.

Interest to Fisheries: This species is caught by deep-set bottom trawls; it is believed to have some fishery potential on stages prior to full maturity. As it is an ammoniacal species, however, this is currently problematic, because maturation and spawning lead to severe muscular degeneration.

Remarks: Onykia aequatorialis (Thiele, 1920) was described from the eastern equatorial South Atlantic at 18°07'W. Kubodera, et al., 1998, examined a spent female of O. robsoni from Bermuda that was very similar to O. aequatorialis which caused them to question the validity of the latter. Since the holotype of O. aequatorialis has been lost and there are no distinguishing features in the type description, they designated O. aequatorialis a nomen dubium (Vecchione et al. 2003d).

Local Names: None available.

Literature: Nesis (1982, 1987), Kubodera *et al.* (1998), Nesis (2002), Bolstad (2007), Vecchione *et al.* (2003d, 2007c).

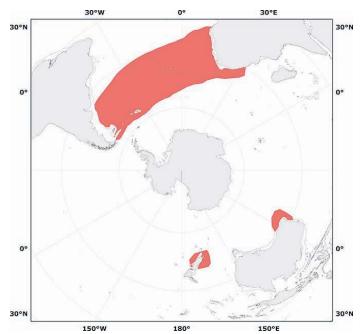


Fig. 344 *Onykia robsoni*Known distribution

Onykia robusta (Verrill, 1876)

Fig. 345

Ommastrephes robusta Verrill, 1876, American Journal of Science and Arts, 12: 236–237 [237]. [Type locality: Aleutian Islands, North Pacific Ocean].

Frequent Synonyms: *Moroteuthis robusta* (Verrill, 1876); *Ancistroteuthis robusta* Steenstrup, 1882; *Onykia japonica* Taki, 1964; *Moroteuthis pacifica* Okutani, 1983a.

FAO Names: En – Robust clubhook squid; Fr – Cornet mange-piquants; Sp – Lurión maximo.

Diagnostic Features: Mantle robust, relatively broad; skin surface covered with raised, fleshy, soft, relatively wide, longitudinal ridges; posterior tip drawn out to a moderately long pointed tail. Fins large, saggitate, longer than broad; fin length 50 to 60% of mantle length; fin width narrower than mantle length, about 45% of mantle length or less. Rostrum of gladius large, round or oval in cross-section, length about 25 to 40% of mantle length (considered homolog of rostrum in extinct Belemnitida). Tentacular club narrow, slender; manus with 32 to 36 hooks on 2 medial series, third or fourth hook on ventral series the largest; 10 to 12 small suckers plus their associated knobs on carpus; 8 to 10 minute suckers on dactylus. Longest arms (IV) 90 to 100% of mantle length.

Size: Very large species; maximum mantle length reportedly up to 2.3 m, but this old record might be in error. The species commonly grows to 1.6 m mantle length and to 50 kg in weight.

Geographical Distribution: *Onykia robusta* is a panboreal species that spans the eastern and western far North Pacific Ocean in offshore waters from northeastern Japan throughout the Bering Sea, along the Aleutian Islands and into the Gulf of Alaska, and southward into deep southern California waters (Fig. 346).

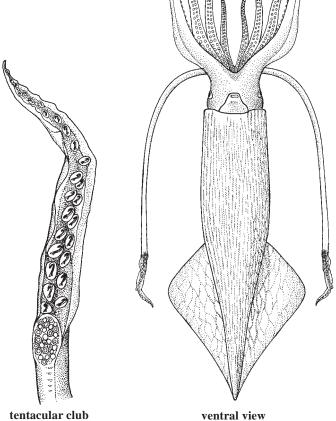


Fig. 345 Onykia robusta

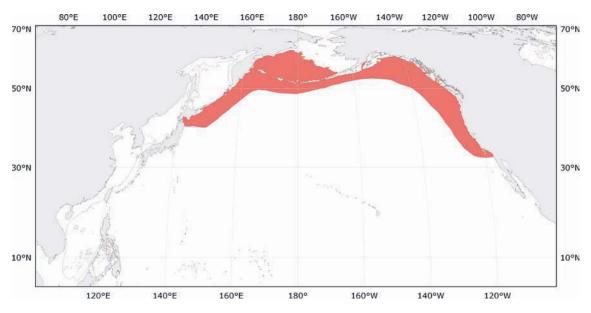


Fig. 346 Onykia robusta

Habitat and Biology: An oceanic, boreal species, *O. robusta* occurs at or near the bottom, especially as adults, in lower sublittoral to upper bathyal waters, to at least 900 m. Juveniles and adolescent animals inhabit the midwater up to the surface, and the species has been identified as a component of the sound-scattering layer. This very abundant species attains a huge size, often leading to its being erroneously referred to as a "giant squid", but it bears no relationship to the true giant squid, *Architeuthis* spp. It is an ammoniacal species, so it is neutrally buoyant or nearly so. Adults feed on benthic fishes, e.g. blackcod, and have been reported to feed on benthic heart urchins such as *Brisaster townsendi*, as well as on epipelagic "jelly-fish" species such as *Velella velella*. *Onykia robusta* in turn is heavily preyed upon by sperm whales (e.g. to 72% numerically) and other marine mammals, e.g. northern elephant seals, pelagic fur seals.

Interest to Fisheries: This species is believed to have some fishery potential, even though attempts to prepare it for food in California have failed. The flesh is ammoniacal and fully mature adults become soft and semi-gelatinous as the mantle muscle degenerates during final maturation and spawning. Consequently, any fishery would have to target sub-mature animals, if the ammoniacal characteristic can be treated. Animals are taken as bycatch in the benthic blackcod long-line fishery; larger animals have been observed to attack and feed on hooked blackcod, often "riding" them to the surface. It is taken in large numbers in midwater/pelagic longline fisheries, as well.

Local Names: None available.

Literature: Okutani (1980), Nesis (1982, 1987), Kubodera et al. (1998), Vecchione et al. (2003e), Wakabayashi et al. (2007).

Kondakovia Filippova, 1972

Kondakovia Filippova, 1972, Malacologia, 11(2): 391-406 [395].

Type Species: Kondakovia longimana Filippova, 1972.

Frequent Synonyms: None.

Diagnostic Features: Currently the genus is monotypic, so the characters are included in the species description below.

Remarks: This is a large squid, perhaps second in size to the largest known onychoteuthid, Onykia robusta.

Kondakovia longimana Filippova, 1972, Malacologia, 11(2): 391–406 [395]. [Type locality: north of the South Orkney Islands, South Atlantic sector, Antartctic Ocean]. Frequent Synonyms: None. FAO Names: En – Antarctic clubhook squid; Fr – Cornet crochu antarctique; Sp – Luria ganchuda antarctica.

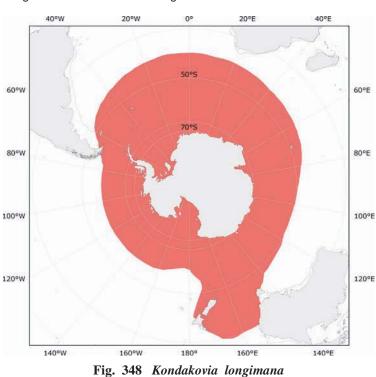
Fig. 347 Kondakovia longimana

Diagnostic Features: Mantle soft, fleshy, ammoniacal, broadly cylindrical, slightly tapered posteriorly; numerous soft longitudinal ridges in outer integument external to thick, soft muscle layer, especially in young stages. Skin thick, rugose, tuberculate in young. Fins rhomboidal, but weak, short, broadly heart-shaped, length about 42% of mantle length, width about 60% of mantle length. Gladius thin, fragile, with narrow, longitudinal thickenings; ventral length of thick, pointed cartilaginous rostrum 5 to 12% of mantle length. Tentacular club elongate, with 2 medial series of a total of 27 to 38 hooks, and always 2 marginal series of small suckers on manus throughout development to adulthood; carpus well-developed with 9 to 13 small suckers plus their associated knobs; dactylus with 17 to 40 minute, closely-set suckers. Nuchal folds absent. Photophores absent. Head and arms more massive than in Onykia ("Moroteuthis") Moroteuthis, and together they are longer than the mantle; arms become very attenuate at the tips.

Size: Large-sized species; maximum reported mantle length of 108 cm and a total length of 225 cm.

Geographical Distribution: This species is circumglobal in the Antarctic Ocean. It occurs in the Tasman Sea, and around South Georgia, Falkland, South Orkney (Scotia Sea), Prince Edward, Marion, Gough, Auckland, Antipodes, and Macquarie islands, as well as off Chile (Fig. 348).

Habitat and Biology: Kondakovia longimana is a large, very broadly distributed, abundant epipelagic to mesopelagic and benthic-bathyal species. It occurs from the surface to considerable depths, judging from their presence in predators' stomachs: Patagonian toothfish, sleeper sharks, wandering grey-headed and black-browed albatrosses, king penguins, southern elephant seals, southern bottle-nosed whales, sperm whales, hake; southern giant petrels, cape petrels, and brown skuas that were observed to scavenge on floating specimens. A principal prey item is the krill, *Euphausia superba*. Because it is an ammoniacal species, it is considered to be neutrally buoyant and to exhibit a rather passive life mode, feeding on massive, almost stationary, shoals of krill. It appears to mate and spawn in the austral winter around Crozet Island, and presumably around the other sub-Antarctic Islands listed above. Apparently this species is most abundant near the Antarctic Polar Front.



Known distribution

Interest to Fisheries: Because this large species is

a soft-bodied, ammoniacal squid, its potential as a fishery target for human consumption currently seems questionable. However, its value as a major food source for a broad cross-section of predators is massive.

Literature: Filippova (1972), Bonnaud et al. (1998), Kubodera et al. (1998), Nesis (2002).

Walvisteuthis Nesis and Nikitina, 1986

Walvisteuthis Nesis and Nikitina, 1986a, Zoologicheskij Zhurnal, 65(1): 47-54 [47].

Type Species: Walvisteuthis virilis Nesis and Nikitina, 1986.

Frequent Synonyms: None.

Diagnostic Features: The tissues of mantle, fins, head, appendages are watery, semigelatinous. No warts, ridges, wrinkles on surface of mantle. Mantle broadly conical, bluntly rounded posteriorly, not drawn out into a tail. Fins very short (about one-third of mantle length), broad, transversely oval, width about 90% of mantle length; posterior lobes meet in midline, not separate. Head short, broad, narrower than mantle width. Eyes large, sinus present; olfactory papilla tongue-shaped. Nuchal folds absent. Funnel wide and long, reaches level of mideye; funnel-locking cartilage a simple, straight groove, slightly broader distally; mantle component a long, narrow, straight ridge. Buccal membrane with 7 lappets; connectives DDVV, i.e. arm IV connectives attach to ventral edge. Arms short, about half the mantle length; formula 4.3=2.1; arms I without keels, arms II with low keel the entire length, arms III with large, broad keel in distal portion; arms IV with well-developed keel, unusually broad along proximal portion. Arm suckers biserial, large, short-stalked, flattened, no hooks; especially significant are the 3 or 4 pairs of greatly enlarged suckers on the midportion of arms III, globe-shaped and twice as large as the normal suckers. Tentacles very thin, weak, non-muscular, short; length only approximates arm length; club occupies more than half the tentacle length; carpus with

well-developed, dispersed, locking apparatus, 8 or 9 suckers, less than half the diameter of the normal arm suckers; 5 or 6 pairs

of minute, widely spaced, medial suckers in 2 series on long stalks on manus; a few marginal suckers may occur. No visceral photophores. Needham's sac and penis extremely well-developed, at least half the mantle length, reach mantle opening; hectocotylus absent. Gladius with short, thin, blunt rounded rostrum oriented perpendicular to the gladius.

Geographical Distribution: The genus appears to be a southern subtropical to notalian bathypelagic form; it has been found in the topical Indian Ocean, in the temperate and tropical South Atlantic and in the tropical North and South Pacific.

Remarks: The genus currently is monotypic, comprised of the sole species *Walvisteuthis virilis*. However, the very broad distribution of this species, unusual for an onychoteuthid, suggests that "*Walvisteuthis virilis*" probably represents a species complex. However, squid in present collections are insufficient to define possible species differences (Young *et al.*, 2003).

Walvisteuthis virilis Nesis and Nikitina, 1986

Fig. 349

Walvisteuthis virilis Nesis and Nikitina, 1986a, Zoologicheskij Zhurnal, 65(1): 47–54. [47]. [Type locality: 33° 06'S, 02°7'E, Walvis Ridge, eastern South Atlantic Ocean, bottom trawl at 960 to 1080 m].

Frequent Synonyms: None.

FAO Names: En – Whale squid; Fr – Encornet baleine; Sp – Luria ballena.

Diagnostic Features: See generic section.

Size: Small-sized species; maximum mantle length to 103 mm.

Geographical Distribution: Worldwide in tropical to temperate seas (Fig. 350).

Habitat and Biology: Walwisteuthis virilis is an epipelagic to upper mesopelagic species. Paralarvae are known as small as 1.9 mm mantle length. The smallest paralarvae are extremely slender with a mantle width about 25% of the mantle length. Between this size and about 4 to 5 mm mantle length they are easily recognized by their slender appearance and a distinctive elongate patch of large chromatophores along the dorsal midline. The eyes are dorsoventrally elongate and strongly bulge from the head. Club suckers are in 2 series, large (about the same size as the arm suckers) and prominent. At roughly 4 to 5 mm mantle length the paralarvae undergo a strong morphological change. They become relatively broad, the eyes become hemispherical and the fins become much more prominent. At 7 mm mantle length the squid is very broad for its length. Chromatophores are small and scattered but larger on the dorsal surfaces than on the ventral surfaces. On the

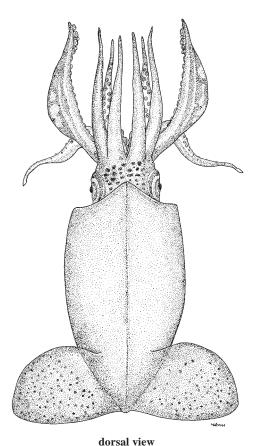


Fig. 349 Walvisteuthis virilis

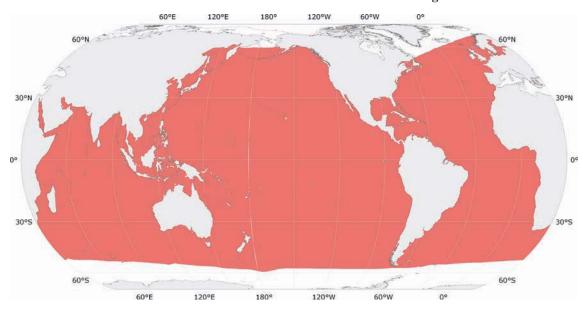


Fig. 350 Walvisteuthis virilis

Known distribution

ventral surface of the head the chromatophores lie deep within the tissue and are not readily visible in preserved specimens. By 12 mm mantle length the V-shaped funnel groove and the distinctive rostrum are present and hooks begin to form in the medial-ventral series on the club.

Interest to Fisheries: None.

Remarks: Nesis and Nikitina (1986) described the new family of squids, Walvisteuthidae, based on a mature male which they named *W. virilis*. The squid was somewhat similar to onychoteuthids but it had a number of very peculiar features that caused the authors to erect the new family. The status of this family recently has been reviewed by Tsuchiya (in preparation) who concluded that *W. virilis* is a synonym of the onychoteuthid *Onykia rancureli*. The peculiar features noted by Nesis and Nikitina (1986) appear to be modifications that arise at sexual maturity. In fact, *Onykia rancureli* had been widely recognized as being very different from other members of the genus and several authors have suggested that a new generic name is needed (e.g. Toll, 1982; Tsuchiya and Okutani, 1992 [1991]). This generic name is considered to be *Walvisteuthis* and the new combination *Walvisteuthis rancureli* currently is used by an authoritative fraction of the scientific community (e.g. Young *et al.*, 2003).

Literature: Rancurel (1970), Okutani (1981, 1995), Nesis and Nikitina (1986a), Young et al. (2003).

SPECIES OF NO CURRENT INTEREST TO FISHERIES,OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST

Onychoteuthis compacta (Berry, 1913)

Teleoteuthis compacta Berry, 1913b, Proceedings of the United States National Museum, 45(1996): 563–566 [565]. [Type locality: Hawaii, Central North Pacific Ocean].

Size: A small-sized species; maximum observed length 127 mm (mature male).

Geographical Distribution: Eastern Central Pacific Ocean, approximately 150°W to 180°W, 15°N to 30°N; Hawaiian waters.

Habitat and Biology: The species descends between 50 and 150 m depth during the day, and goes back to surface waters (i.e. 0–25 m) at night.

Literature: Bower et al. (1999c), Vecchione et al. (2003a), Okutani (2005).

Onychoteuthis meridiopacifica Rancurel and Okutani, 1990

Onychoteuthis meridiopacifica Rancurel and Okutani, 1990, Venus, 49(1): 25–30 [25]. [Type locality: 21°15'S, 155°11.5'E, Western South Pacific Ocean].

Size: Small-sized species; maximum recorded mantle length 90 mm.

Geographical Distribution: Southwestern Pacific Ocean, between 16°37'S to 23°56'S and 162°00'E to 133°15'W.

Habitat and Biology: The species is abundant in the central water mass of the South Pacific Ocean. Epipelagic (possibly to mesopelagic), it is preyed upon by lancetfish, *Alepisauris ferox*, and tunas.

Remarks: This may be the smallest species in the genus. The short, broad fins and the presence of a few marginal suckers on the tentacular clubs of adults are diagnostic of this species.

Literature: Rancurel and Okutani (1990), Okuntani (2005), Vecchione et al. (2008d).

DOUBTFUL SPECIES, CONSIDERED TO BELONG TO THE GENUS WALVISTEUTHIS BY AN AUTHORITATIVE FRACTION OF THE SCIENTIFIC COMMUNITY

Onykia rancureli Okutani, 1981

Onykia rancureli Okutani, 1981, Bulletin of the National Science Museum, Tokyo, series A (Zoology), 7(4): 155-163 [155]. [Type locality: from the stomach of a lancetfish, *Alepisauris ferox*, 07°51'S, 88°02.5'E, tropical central Indian Ocean].

DOUBTFUL AND QUESTIONABLE SPECIES FOR WHICH ADDITIONAL MATERIAL, NEW DATA AND FURTHER RESEARCH ARE NECESSARY BEFORE THEY CAN BE ACCEPTED AS VALID

Onykia appellöfi (Pfeffer, 1900)

Teleoteuthis appellöfi Pfeffer, 1900, Mitteilungen aus dem Naturhistorischen Museum Hamburg, 17(2): 147–198 [158]. [Type locality: Atlantic Ocean].

Onykia intermedia (Pfeffer, 1912)

Teleoteuthis intermedia Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [68]. [Type locality: 38°S, 54°W, southwestern South Atlantic Ocean].

Onykia platyptera (d'Orbigny, 1834 [1834-1847])

Onychoteuthis platyptera d'Orbigny, 1834 (1834-1847), Voyage dans l'Amérique Méridiaonale, 5(3):1–758 [41]. [Type locality: 40°S and 85°W of Paris, off the coast of Chile, Southeastern South Pacific Ocean].

Onykia verrilli (Pfeffer, 1900)

Teleoteuthis verrilli Pfeffer, 1900, Mitteilungen aus dem Naturhistorischen Museum Hamburg, 17(2): 147–198 [157]. [Type locality: 46°S, 147°E, southwestern South Pacific Ocean].

2.24 Family PHOLIDOTEUTHIDAE Voss, 1956

by Clyde F.E. Roper and Patrizia Jereb

Pholidoteuthidae Voss, 1956, Bulletin of Marine Science of the Gulf and Caribbean, 6(2): 85–178. [132].

Type Genus: Pholidoteuthis Adam, 1950.

FAO Names: En – Scaled squids; Fr – Loutène commune; Sp – Luria escamuda.

Diagnostic Features: Mantle cylindrical, elongate, thick, spongy, moderately to almost completely weakly-muscled, tapers posteriorly to a moderately to sharply pointed tail. Mantle of young and adults covered with numerous, tightly-packed, rounded to polygonal, dermal cushions or papillose tubercles; dermal cushions terminate abruptly on ventral mantle at about midpoint of fins. Fins with distinct anterior lobes, posterior borders extend to tip of tail, rhomboidal to heart-shaped, elongate; fins devoid of dermal cushions or tubercles; fin length variable between species, 35 to 75%. Tentacles long, slender; tentacular clubs very long, only slightly expanded; manus length about 2 times longer than dactylus; carpal locking mechanism absent. Club suckers tetraserial, laterally compressed in late juveniles and adults (> 20 to 25 mm mantle length), with slit-like apertures and accute, peg-like teeth on inner ring; small flaps with short membranes occur along lateral edges of club adjacent to stalks of lateral rows of suckers, not attached to protective membranes. Arms robust, subequal in length, maximum length 30 to 60% of mantle length in adults; suckers biserial, toothed (about 18 teeth); hooks absent. Buccal membrane with 7 lappets; connectives to arms IV attach to ventral margins. Funnel-locking cartilage a straight, simple groove. Gladius long, slender with narrow vane, constricted in posterior one-third, with a short to long conus. Photophores absent. Hectocotylus absent. Colour a dull mauve or purple, or lighter pinkish tone.

Size: Large-sized squids; maximum mantle length up to 800 mm.

Geographical Distribution: Oceanic, cosmopolitan in tropical and temperate seas.

Habitat and Biology: Formerly *Pholidoteuthis* species were considered relatively rare squids. However, considerable research on predator species, as well as trawl surveys in appropriate regions and depths, indicate that the 2 recognized species are geographically widespread and numerous. Among their predators are sperm whales, pilot whales, dolphins, tunas, deep-sea sharks, lancet fish, scabbard fish, swordfish and deep-sea rays. The vertical distribution is difficult to assess, but net captures indicate that paralarvae and juveniles occur in the upper 500 m, while adults occur in daytime bottom trawls to at least 1 500 m. Adults probably leave the bottom at night and disperse into the bathy-mesopelagic zone. *Pholidoteuthis adami* has been observed from a submersible in the slope waters at 592 m in the Bahama Islands; the squid was well off the bottom and was hovering in the "J-posture" (hanging vertically with head down, arms curved dorsally over the head and mantle), swimming with slowly flapping fins. Other specimens were observed off Cape Hatteras, North Carolina, aggregated in slope water off the bottom (Vecchione and Roper, pers. obs). *Pholidoteuthis* species are considered to be nerito-oceanic species that migrate to or over slopes as they mature, then spawn on or near the bottom. The paralarvae and juveniles are very widely dispersed by currents, even circumglobally in the case of *P. massyae* in the Southern Hemisphere.

Interest to Fisheries: Although the 2 species are large and at least regionally abundant, the weakly-muscled, spongy consistency of the mantle precludes an interest in a directed fishery.

Remarks: Two genera have been placed in this family: *Tetronychoteuthis* and *Pholidoteuthis*. Current thought, however, recognizes the sole genus *Pholidoteuthis* as valid (see details in the genus **Remarks** section). The family, therefore is monotypic.

Literature: Roper and Young (1975), Clarke (1980), Nesis and Nikitina (1990), Roper and Lu (1990), Vecchione and Roper (1991 [1992]), Nesis (1999b), Sweeney and Young (2003w), O'Shea et al. (2007), Vecchione and Young (2007f).

Pholidoteuthis Adam, 1950

Pholidoteuthis Adam, 1950b, Koninklijke Nederlandse Academie van Wetenschappen, 53(10): 1592–1598 [1592].

Type Species: *Pholidoteuthis massyae* (Pfeffer, 1912).

Frequent Synonyms: None.

Diagnostic Features: Only 1 genus currently is included in the Pholidoteuthidae, so the characters of the genus are the same as those given for the family.

Remarks: Pfeffer erected the genus *Tetronychoteuthis* in 1900 based on a damaged specimen he incorrectly thought to be *Onychoteuthis dussumieri* d'Orbigny, 1839, but was actually a specimen of *Tetronychoteuthis massyae*, a species he described in 1912 (Vecchione and Young, 2007d). Pfeffer designated *Onychoteuthis dussumieri* d'Orbigny, 1839 the type species of his new genus. The specimen's illustrations show both onychoteuthid and non-onychoteuthid characters, such as

numerous occipital folds and dermal scales; a confusing combination (see O'Shea et al. 2007, for further details). Additional confusion arises because *Onychoteuthis dussumieri* d'Orbigny, 1839, is considered a species dubium by some authors (i.e. Nesis and Nikitina, 1990). Adam (1950) erected *Pholidoteuthis* for his new species, *P. boschmai*, without realizing that it shared all character states with *T. massyae* Pfeffer 1912. The type specimens of *O. dussumieri* d'Orbigny, *T. massyae* and the specimen referred to *T. dussumieri* by Pfeffer are no longer extant (Lu et al., 1995, Sweeney and Roper, 1998). Consequently, resolution of the nomenclatural problem based solely on the confused and often contradictory literature is not possible. Recently O'Shea et al. (2007), based on additional specimens from the South Pacific, designated P. boschmai as the junior synonym of T. massyae. Consequently, Tetronychoteuthis becomes a junior synonym of Onychoteuthis. Since the first available generic name for Pfeffer's "Tetronychoteuthis" massyae is Pholidoteuthis, the authors referred to Pfeffer's species, i.e. the type species of the genus, as *Pholidoteuthis massyae*, new combination (O'Shea et al., 2007). Leta (1987b) described P. uruguayensis from off Uruguay, but Nesis and Nikitina (1990) synonymized this species with P. adami. The 2 recognized species, P. massyae (Pfeffer, 1912) and P. adami Voss, 1956, are considered to be closely related, as indicated by the nearly identical, unique, tentacular clubs. But, in general aspect, they look quite distinct. In particular, P. massyae has dermal structures that are solid papillose tubercles, while those of *P. adami* are vacuolate dermal cushions. The fins of *P. massyae* are short (35 to 45% of the mantle length), diamond-shaped or rhomboidal, not drawn out into a tail, while the fins of *P. adami* are much longer (65 to 75% of the mantle length), heart-shaped with rounded, less angular borders that extend posteriorly into a relatively elongate tail.

Key to the species of Pholidoteuthis

Pholidoteuthis massyae (Pfeffer, 1912)

Fig. 351

Tetronychoteuthis massyae (Pfeffer, 1912) Ergebnisse der Plankton-Expedition der Humboldt-stiftung, 2:1–815, 48 pls. [102, pl. 14, figs 15–19]. [Type locality: 48°N, 15°W, eastern North Atlantic Ocean].

Frequent Synonyms: *Onychoteuthis dussumieri* d'Orbigny, 1839–1842 (*in* Ferussac and d'Orbigny, 1834–1848); *Tetronychoteuthis dussumieri* (d'Orbigny, 1839–1842 [*in* Ferussac and d'Orbigny, 1834–1848]); *Tetronychoteuthis massyae* Pfeffer, 1912.

FAO Names: En – Coffee bean scaled squid; Fr – Loutène battoir; **Sp** – Luria escamuda cafetal.

Diagnostic Features: Mantle elongate, thick-walled, spongy in consistency, tapers to moderate point posteriorly. Beginning at about 20 to 25 mm mantle length, the mantle is covered with dermal structures (papillose tubercules) that consist of solid, densely packed material, histologically reminiscent of elastic cartilage, evenly distributed throughout the dense connective tissue matrix; these tubercules are roughly mushroom-shaped in cross section, with a slightly concave central disc and a thick base; the periphery of the tubercle contains 7 to 10 conical papillae, each with 2 to 4 prongs. Fins short with distinct, small anterior lobes, rhomboidal in outline, do not form elongate tail, fin length 35 to 45% of mantle length, fin width 50 to 70% of mantle length. The arms are relatively short, 30 to 60% of mantle length, robust, subequal in length; suckers biserial, no hooks. The gladius has a narrow lateral vane constricted in the posterior third, and a short needle-like rostrum on the tip of the conus. Tentacles long, clubs virtually unexpanded, long; club suckers tetraserial (no hooks), compressed in late juveniles and adults into ovoid, elongate structures with slit-like opening; the long sides of inner rings lined with acute teeth.

Size: Maximum recorded mantle length 720 mm.

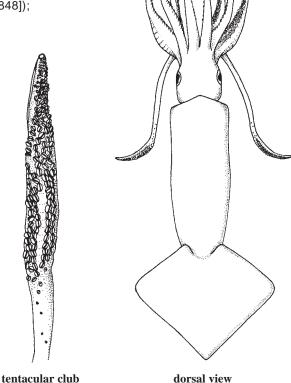


Fig. 351 Pholiditeuthis massyae

Geographical Distribution: A widely distributed, cosmopolitan species in southern subtropical, southern temperate and sub-Antarctic waters of the Atlantic, Pacific and Indian oceans (Fig. 352).

Habitat and Biology: The vertical distribution of adults encompasses mesopelagic to bathypelagic, bathybenthic zones. Paralarvae can occur in upper 200 m, while adults are mesopelagic to bathypelagic, concentrated in the 600 to 800 m zone; descent to bathyal bottom depths coincides with maturation. Spawning apparently occurs on or near the bottom, to at least 1 500 m. The species is heavily preyed upon by sperm whales, pilot whales, dolphins, tuna, swordfish, lancet fish, scabbard fish, deep-sea sharks and rays.

Interest to Fisheries: Currently this species is of no interest to fisheries because of its inaccessability in deep water and its spongy consistency and ammoniacal tissue. When a processing technique is developed, this species should be considered a potential resource because of its size, abundance and broad distribution.

Local Names: None available.

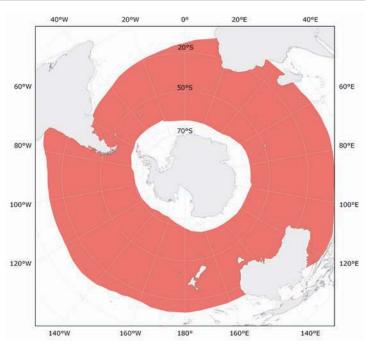


Fig. 352 Pholiditeuthis massyae

Known distribution

Remarks: The papillose tubercules on *P. massyae* are believed to function to reduce hydrodynamic drag over the surface of the mantle, thus increasing the swimming efficiency. For details concerning the tubercles see Roper and Lu, 1990.

Literature: Nesis (1982, 1987), Nesis and Nikitina (1990), Roper and Lu (1990), Vecchione and Roper (1992 [1991]), O'Shea et al. (2007), Vecchione and Young (2008d).

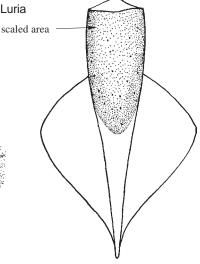
Pholidoteuthis adami Voss, 1956

Fig. 353

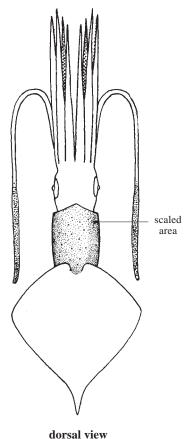
Pholidoteuthis adami Voss, 1956, Bulletin of Marine Science of the Gulf and Caribbean, 6(2): 85–178. [132]. [Type locality: 29°11.5'N, 88°07.5'W, Gulf of Mexico, western Central Atlantic].

Frequent Synonyms: Pholidoteuthis uruguayensis Leta, 1987b.

FAO Names: En – Western Atlantic scaled squid; Fr – Loutène commune; **Sp** – Luria escamuda.







cartilaginous scales

Fig. 353 Pholidoteuthis adami

Diagnostic Features: Mantle thick, moderately muscled, yet spongy; it tapers significantly from about the midpoint of the fins into a very long, thin, pointed tail; mantle length to 800 mm. Beginning with juvenile stage, the mantle surface is covered with a layer of very closely set, small, soft dermal structures, called dermal cushions, that are irregularly rounded to crudely pentagonal in outline; these dermal cushions do not overlap and are about 0.5 mm in diameter and 0.3 mm in height (300 mm mantle length specimen); internally the cushions are almost entirely vacuolate, with thin-walled, irregularly shaped chambers (see Remarks); the ventral mantle is devoid of dermal cushions posteriorly from about the anterior third of the fins. Fins very long in adults, length 70 to 75% of mantle length, width 60 to 70% of mantle length, extend to tip of long tail, ventral margins concave, heart shaped; in juveniles the fins are 65 to 70% of mantle length, strongly heart-shaped, drawn out along the spike-like tail; anterior lobes strongly developed. Arms relatively long (65 to 75% of mantle length), slender, drawn out into long, sharply pointed tips; arms II and III the longest; suckers biserial, hooks absent. Basal suckers on arms with pointed teeth on distal half of inner ring; midarm suckers with teeth around entire margin, larger distally. The gladius is long, narrow, with a slightly widened vane and a secondary conus. Tentacles long; clubs very long, only slightly expanded, protective membranes low; suckers tetraserial, hooks absent, carpal knobs absent; club suckers compressed (folded) laterally, apertures elongate, slit-like.

Size: Maximum recorded mantle length attains 780 mm.

Geographical Distribution: The species is distributed in the western North Atlantic Ocean from off New England southward, where it is very abundant in the Gulf of Mexico; also, it is common throughout the Caribbean Sea to off Uruguay (Fig. 354).

Habitat and Biology: This species inhabits temperate to tropical zones in deep water. Adults are bathyl, captured in deep-set bottom trawls at least to 1 500 m (records to 2 000 m). One specimen has been observed from a submersible just above the bottom (about 850 m) on the continental slope off Cape Hatteras, North Carolina, eastern USA. A number of daytime captures occurred in the Gulf of Mexico at 360 to 925 m (predominately 625 to 750 m). No nighttime captures are recorded from deep benthic trawls, so this species probably disperses up off the bottom waters and into the water column to feed at night. In fact, huge "schools" of *Pholidoteuthis adami* have been observed at night at the surface in the Gulf of Mexico.

Interest to Fisheries: To date no interest exists for this species as a fishery product, even though extremely large concentrations have been reported in the Gulf of Mexico. The relatively soft ammoniacal mantle tissue currently precludes *P. adami* from interest for human consumption. When a processing technique is developed, this species should be considered a potential resource because of its size and broad distribution.

Remarks: The dermal cusions of $\emph{P. adami}$ are hypothesized to contain ammonium chloride solution

100°W 80°W 60°W 40°W 20°W 50°N 50°N 30°N 30°N 10°N 10°N 10°S 10°S 30°S 30°S 60°W 100°W 20°W

Fig. 354 Pholidoteuthis adami

Known distribution

that provides a buoyancy mechanism for these squids. The morphology and histology of the cushions are detailed in Roper and Lu, 1990.

Literature: Roper et al. (1969b), Nesis (1982, 1987), Roper and Lu (1990), Nesis (1993a); Vecchione and Young (2007f), O'Shea et al. (2007).

2.25 Family PROMACHOTEUTHIDAE Naef, 1912

by Clyde F. E. Roper and Patrizia Jereb

Promachoteuthidae Naef, 1912a, Zoologischer Anzeiger, 39(7): 241-244 [244].

Type Genus: Promachoteuthis Hoyle, 1885

FAO Names: En – Warrior squids; Fr – Encornets guerrier; Sp – Lurias guerreas.

Diagnostic Features: Squids of very small to medium-size. Mantle short, broad, weakly muscled; largest recorded (but not described) is 184 mm mantle length; all other described specimens are less than 50 mm mantle length. Fins large to very large, round, usually with posterior lobes that extend beyond pointed tip of mantle. Eyes small to very small, embedded in gelatinous tissue, reduced eye openings; eyes connected to eye openings via narrow channel; a semi-translucent section of eyelid may partially cover eye ("pseudocornea"). Head often fused to mantle in dorsal nuchal region. Funnel-locking component a simple, ovoid depression. Arms with 2 to 6 series of suckers (variable among species). Tentacles thick, much larger in diameter than arm width (except in 1 species); clubs not expanded; club suckers minute, numerous, in irregular transverse series across the oral surface. Photophores absent. Ink sac absent. Anal flaps absent. Gladius reduced in size, considerably shorter than the mantle, highly variable in shape among species.

Size: Squids of very small- to medium-size; largest recorded (but not described) is 184 mm mantle length; all other described specimens are less than 50 mm mantle length.

Geographical Distribution: As a family, species have been recorded from discrete localities in the northwestern North Pacific Ocean, northeastern North Atlantic Ocean, South Pacific Ocean, South Atlantic Ocean and southeastern South Atlantic Ocean.

Habitat and Biology: All species are truly bathypelagic to abyssopelagic, and the species appear to be geographically isolated, an unusual circumstance for such deep sea forms. Some depths of capture (open nets) are: 1 550 m, 1 830 m, 1 900 m, 2 440 m, 2 650 m, 2 972 m and 3 431 m.p

Interest to Fisheries: The extreme rarity, extreme depth range and very small size preclude any fishery potential.

Remarks: The Promachoteuthidae is monogeneric. This is an uniquely unusual family. Since the first specimen was described by Hoyle from the Challenger Expedition as *Promachoteuthis megaptera* Hoyle, 1885, only 12 additional specimens have been recorded, until recently. Remarkably, these specimens have been recognized as belonging to 5 different species; two of these have not been named yet (i.e. *Promachoteuthis* sp. B and D, Young *et al.*, 2007), but are being formerly described currently by Young and Vecchione (pers. comm.).

Table 15Species characters^{1/}

Species	Mantle fused to head	Tentacle wider than arm III	No. sucker series on arms	Unique tentacle character	Fin length	Habitat
Promachoteuthis megaptera	No	Yes	2	Pigment band	75% of ML	NW Pacific
Promachoteuthis sloanii	No	Yes	2–6	Papillae	70% of ML	NE Atlantic
Promachoteuthis sulcus	Yes	Yes	2–3 (mostly 3)	Sunken club base; Aboral groove	35% of ML	South Atlantic
Promachoteuthis sp. B	Yes	Yes	2	Reduced club diam.	40% of ML	South Pacific, NE Atlantic
Promachoteuthis sp. D	Yes	No	2–3 (mostly 2)	?	45% of GL	SE Atlantic

^{1/} from Young and Vecchione (2003b). The undescribed species are being formerly described by R. Young and M. Vecchione.

Literature: Hoyle (1885a), Sweeney and Young (2003y), Young and Vecchione (2003a,b,c,d), Young et al. (2006a, 2007).

Promachoteuthis Hoyle, 1885

Promachoteuthis Hoyle, 1885a, Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–76, Narrative, 1(1): 269–274 [273].

Type Species: *Promachoteuthis megaptera* Hoyle, 1885.

Diagnostic Features: Characteristics are the same as given for the monogeneric family, but the following diagnosis should be adequate to delineate the genus. Eyes small to very small with reduced opening to exterior. Funnel-locking apparatus with oval depression. Arms with 2 or 3 or more sucker series. Tentacular stalks generally thick; stalk width greater than width of arm III in most species. Tentacular club not expanded; club without keel, locking apparatus or terminal pad; club with suckers in numerous irregular series. Anal flaps absent. Ink sac absent. Photophores absent. Gladius reduced and variable in shape among species.

Promachoteuthis megaptera Hoyle, 1885

Promachoteuthis megaptera Hoyle, 1885a, Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–76, Narrative, 1(1): 269–274 [273]. [Type locality: 31°00'N, 147°00'E, 2 750 m depth, eastern North Pacific Ocean].

FAO Names: En – Bigfin warrior squid; **Fr** – Encornet guerrier ailé; **Sp** – Luria guerrera alada.

Size: The mantle length reaches 52 mm.

Geographical Distribution: Off Japan in the western North Pacific Ocean: 34°37'N, 140°32'E, 0 to 3 690 m (Fig. 356).

Remarks: Only two specimens are known, both from off Japan.

Literature: Roper and Young (1968), Young and Vecchione (2003b) [See family literature listing].

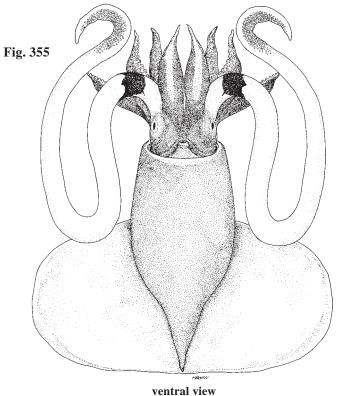


Fig. 355 Promachoteuthis megaptera

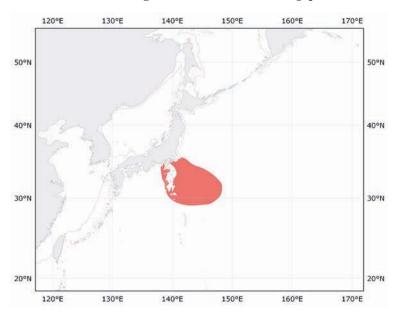


Fig. 356 Promachoteuthis megaptera

Known distribution

Promachoteuthis sloani Young, Vecchione and Piatkowski 2006

Promachoteuthis sloani Young, Vecchione and Piatkowski 2006a. Proceedings of the Biological Society of Washington, 119(2): 287–292 [289 figs 1–3]. [Type locality: 53°05'N, 36°46'W, 0 to 2 792 m, North Atlantic Ocean].

Size: The mantle length of the holotype is 58 mm and of the paratype 104 mm.

Geographical Distribution: Only 2 specimens of this species are known from the North Atlantic Ocean. The holotype was captured at 53°05'N, 36°46'W, 0 to 2 792 m, and the paratype was taken at 46°00'N, 15°49'W, 0 to 2 650 m.

Remarks: Only 2 specimens of this species are known.

Literature: Young and Vecchione (2006c), Young et al. (2006a).

Promachoteuthis sulcus Young, Vecchione and Roper, 2007

Promachoteuthis sulcus Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [359, figs 15–22]. [Type locality: 36°49'S, 12°17'W at 1 750 to 2 000 m depth, off Tristan da Cunha, South Atlantic Ocean].

Size: The mantle length of the lone specimen is 25 mm.

Geographical Distribution: The single specimen was captured in the South Atlantic Ocean off Tristan da Cunha, at 36°49'S, 12°17'W at a depth of 1 750 to 2 000 m in an open net.

Remarks: Only one specimen was caught, in an open net.

Literature: Young et al. (2007).

Promachoteuthis sp. B Young, Vecchione and Roper, 2007

Promachoteuthis sp. B Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [362]. [Type locality: 33°18'S, 72°27'W (0–1800 m) and 56°06'S, 79°04'W (0–1400 m), eastern South Pacific Ocean].

Size: The known mantle length reaches 50 mm.

Geographical Distribution: Three specimens are known from the eastern South Pacific Ocean (10.5 to 17 mm mantle length) and one from the western South Pacific Ocean. One specimen of unconfirmed identification was captured in the western North Atlantic Ocean. Depths of capture are recorded from 1 400 to 2 972 m in open nets.

Literature: Young and Vecchione (2003c), Young et al. (2007).

Promachoteuthis sp. D Young, Vecchione and Roper, 2007

Promachoteuthis sp. D Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [362]. [Type locality: 16°35'E, 34°15'S in the south Atlantic Ocean. Captured from the WALTHER HERWIG R/V, at 1550 m depth].

Size: Mantle length as currently known is 16 mm. Original mantle length at capture was 42 mm.

Geographical Distribution: This species is known from only a single specimen that was taken at 34°15'S, 16°35'E in the South Atlantic Ocean, at 1 550 m, in an open net.

Literature: Young and Vecchione (2003d), Young et al. (2007).

2.26 Family PSYCHROTEUTHIDAE Thiele, 1920

by Clyde F.E. Roper and Patrizia Jereb

Psychroteuthidae Thiele, 1920, Deutsche Südpolar Expediton, 1901 to 1903, Zoologie, 16(8):433–465 [440]. [note: published in 1920, not 1921].

Type Genus: Psychroteuthis Thiele, 1920.

FAO Names: En – Glacial squids; Fr – Encornets glaciaire; Sp – Lurias glaciales.

Diagnostic Features: Mantle elongate, muscular, tapers to pointed tail. Fins sagittate, rhomboidal, muscular, length 55 to 60% of mantle length; anterior fin lobes distinct; posterior margins join mantle to form pointed tail. Eyes proportionally very large. Buccal connectives attach to dorsal borders of arms IV (formula DDVD). Funnel-locking cartilage a very slightly curved, narrow, simple groove. Arms muscular, subequal in length; arm suckers biserial; sucker rings smooth except on distalmost suckers. Tentacles long, muscular; tentacular clubs expanded; carpal locking region extends proximally along ventral edge of tentacular stalk with a row of alternating knobs and suckers (some may be biserial) and dorsally along distal portion; manus with suckers quadriserial proximally, the ventromedian series with greatly enlarged suckers, those of the dorsomedian series somewhat enlarged; distal manus and dactylus with 4 to 7 series of suckers. Gladius long, slender, with short rachis and very long vane that is widest anteriorly, then tapers evenly to the narrow, cup-like terminus. A large, composite photophore occurs on the tips of arms III in mature females (males?), consisting of transverse light-producing plates arranged in a zig-zag pattern and covered with black-pigmented shields. Photophores on mantle and head absent. Mantle length to 440 mm. Lower beak with an obtuse jaw angle not obscured from the side by a low wing fold; a long, curved jaw edge almost as long as the wing; wings broad; rostrum moderately narrow; hood stands high above unthickened crest and has a shallow notch; a thick fin or ridge runs to the middle of the posterior edge of the lateral wall.

Size: Medium-sides squid; maximum mantle length up to 440 mm.

Geographical Distribution: Southern Ocean.

Remarks: This monotypic family is based on *Psychroteuthis glacialis*, originally described from incomplete specimens from the stomachs of penguins and seals. Two other species have been suggested (Roper *et al.*, 1969b, Nesis, 1982), but they never have been described nor named. Specimens of *P. glacialis* now are very abundant in research collections as a result of several decades of intensive research and collections in Antarctic waters, as well as on Antarctic marine and terrestrial predators. The sole species, *Psychroteuthis glacialis*, has been shown to be the most abundant species of muscular squid in the Weddell Sea, as well as the only pelagic cephalopod that occurs in considerable abundance in the Antarctic Sea Ice Zone (Piatkowski, 1999). It is the predominant squid in the Southern Ocean in waters close to the Antarctic continent.

Literature: Roper et al. (1969b), Nesis (1982, 1987), Roper et al. (1985), Sweeney and Young (2003x), Piatkowski (2008).

Psychroteuthis Thiele, 1920

Psychroteuthis Thiele, 1920, Deutsche Südpolar-Expediton, 1901 to 1903, Zoologie, 16(8): 433–465 [440].

Type Species: Psychroteuthis glacialis Thiele, 1920.

Diagnostic Features: The distinguishing features are the same as those of the monotypic family.

Psychroteuthis glacialis Thiele, 1920

Psychroteuthis glacialis Thiele, 1920, Deutsche Südpolar-Expediton, 1901 to 1903, Zoologie, 16(8): 433–465 [440]. [Type locality: 66°S, 89°E, southern Ocean].

Frequent Synonyms: None.

FAO Names: En - Glacial squid; Fr - Encornet glacial; Sp - Luria glacial.

Diagnostic Features: Since the family and genus are monotypic the characters listed under the family currently are applicable.

Geographical Distribution: This species is circumglobal in Antarctic waters, principally south of the Antarctic Convergence (Fig. 358).

Habitat and Biology: Psychroteuthis glacialis is an oceanic species reported from less than 200 to 920 m, taken with benthic and bentho-pelagic trawls. Paralarvae and juveniles occur at or near the surface because they frequently are preyed upon by many species of seabirds, penguins and marine mammals. Likewise, adults as they undergo ontogenetic descent into the depths are a major prey species for deeper-diving forms. Among its predators are the following: seabirds, such as the sooty albatross, grey-headed albatross, white-chinned petrel; penguins, like the Emperor penguin, Adelie penguin, gentoo penguin; pinnipeds, as the

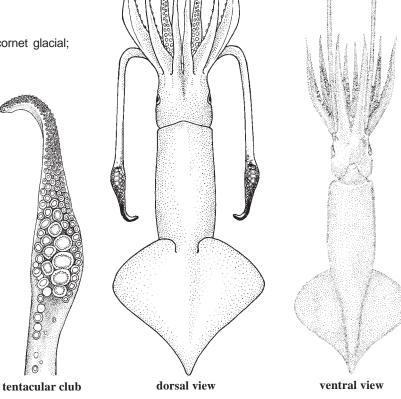


Fig. 357 Psychroteuthis glacialis

southern elephant seal, Weddell seal, Ross seal, Antarctic fur seal; odontocete cetaceans, such as the southern bottlenose whale and sperm whale; fishes, like the albacore tuna and other large species. In turn, *P. glacialis* preys on krill, *Euphausia superba*. Size-frequency data indicate that the species has a 2-year life cycle; males mature earlier and at a smaller size than females. Paralarvae, especially, show a strong similarity to paralarvae of Histioteuthidae, especially with regard to the shape of

Fig. 357

the fins, tentacular club with suckers much smaller than those on the arms and the anteriormost position in the mantle cavity of the digestive gland.

Size: The maximum mantle length reported is 440 mm.

Interest to Fisheries: Currently no specific direct interest as a fishery resource exists, but the species is of major importance as prey for both exploited and unexploited predatory species. Furthermore, since the musculature is firm, non-ammoniacal, and since the species is large (up to 440 mm mantle length) and apparently very abundant, it should be considered a potentially valuable resource. This seems more likely now that deep trawling activities continue to probe mesopelagic and upper bathypelagic depths.

Local Names: None available.

Literature: Filippova (1972, 1992 [1991]), Roper *et al.* (1969b), Nesis (1982, 1987), Piatkowski (1989, 2008).

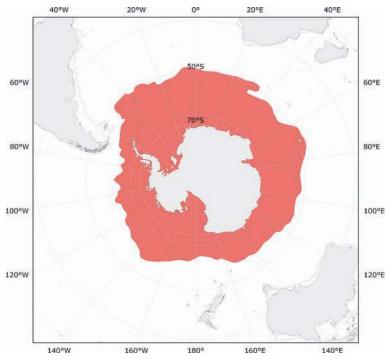


Fig. 358 Psychroteuthis glacialis

2.27 Family PYROTEUTHIDAE Pfeffer, 1912

by Clyde F.E. Roper and Patrizia Jereb

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Pyroteuthidae Pfeffer, 1912, Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, 2F(a): 815pp, 48 plates [189].

Type Genus: Pyroteuthis Hoyle, 1904.

FAO Names: En – Fire squids; Fr – Encornet feu; Sp – Fuegolurias.

Diagnostic Features: Buccal crown with 7 or 8 supports. Buccal connectives attach to dorsal margins of arms IV. Secondary buccal connectives attach to ventral margins of arms I and II. Gladius with small, strongly pointed conus and elongate cone field; rostrum absent. Straight mantle-funnel locking apparatus; biserial armature on arms. Hooks present on arms I to III (at least); hook presence on tentacular club varies with genus; armature on manus always in 4 series. Photophores present on viscera, eyeballs, and tentacles. Photophores absent from fins, mantle, funnel, head, and arms. Nidamental glands present; oviducal glands normal on one side, may be reduced or absent on other side. Oviduct single, unpaired. Right or left arm IV hectocotylized. Fins subterminal; posterior lobes distinct. Tail not fleshy but acute, supported by needle-like terminal conus of gladius; vesicles absent. Nuchal folds absent. Tentacles with permanent constriction and angular bend near base; stalk "ligament" and vein leave tentacle distal to base and not in membrane. Ink sac embedded in digestive gland.

Size: Small-sized squid; maximum mantle length 50 mm.

Geographical Distribution: The species of this family are broadly distributed worldwide throughout the major oceans and the Mediterranean Sea in tropical and temperate waters. They are epipelagic as paralarvae and juveniles, then as adults they descend to upper mesopelagic habitats, from which they undergo diel vertical migrations into the epipelagic zone at night.

Habitat and Biology: Pyroteuthids are among the more common squids found in the midwaters of the open ocean. They are epipelagic as paralarvae and juveniles, then as adults they descend to upper mesopelagic habitats, from which they undergo diel vertical migrations into the epipelagic zone at night.

Remarks: The Pyroteuthidae was raised to full familial level together with its sister taxa, formerly subfamilies, Enoploteuthinae and Ancistroteuthinae by Clarke (1988b). Young et al. (1998b) present the history of these familial changes, diagnostic features of their genera, a list of currently accepted species and their distributions. A phylogenetic study confirmed the validity of dividing the group into 3 families (Young and Harman, 1998). The 2 genera currently recognized in the family Pyroteuthidae are *Pyroteuthis* and *Pterygioteuthis*, species of which are very broadly cosmopolitan in tropical to temperate waters, principally as members of the upper mesopelagic realm. All species undergo diel vertical migrations into the epipelagic waters at night.

Key to the genera of Pyroteuthidae

- 1a. Hooks present on tentacular clubs and on arms IV; hooks on club arranged in 1 series, on arms in 2 series over entire length; relatively numerous; 12 photophores on ventral side of eyeball (none lidded), 9 large (of different sizes) and 3 small; 10 photophores in mantle cavity include 3 in a row transverse to the longitudinal axis of body at the level of gills; 6 or 7, sometimes 8, photophores on tentacular stalk of young and adults; right ventral arm hectocotylized; without a tooth plate; only left oviduct developed; right oviduct may be present but significantly reduced Genus Pyroteuthis Hoyle, 1904

Literature: Roper et al. (1969b), Young et al. (1998b), Sweeney and Young (2003z), Lindgren et al. (2008).

Pyroteuthis Hoyle, 1904

Pyroteuthis Hoyle, 1904, Bulletin of the Museum of Comparative Zoology, Harvard, 43(1): 1-71 [42].

Type Species: Pyroteuthis margaritifera (Rüppel, 1844).

Frequent Synonyms: Charibditeuthis Vivanti, 1912; Ioteuthion Pfeffer, 1912 (pars); Pterygonepion Pfeffer, 1912.

Diagnostic Features: More than 13 hooks per arm, in 2 transverse series; hooks present on arms IV. Tentacular club with 1 series of hooks and 3 series of suckers on manus. Twelve photophores on ventral surface of eyeballs. Eyeball photophore number 6 (= lidded photophore) absent. Six or 7 separated photophores embedded along tentacular stalk. Oviducts are paired; left oviduct reduced in size. Right arm IV hectocotylized; toothed plate absent.

Remarks: Three species of *Pyroteuthis* currently are recognized (*P. margaritifera*, *P. addolux*, *P. serrata*). However, because entities are so widely distributed and exhibit marked variation, most notably in *P. margaritifera*, for example, it seems probable that a considerable species complex is involved.

Pyroteuthis margaritifera (Rüppel, 1844)

Fig. 359

Enoploteuthis margaritifera Rüppel, 1844, Giornale del Gabinetto Letteràrio di Messina, 5(27–28): 129–135 [130, fig.1]. [Type locality: Messina, Sicily, southern central Mediterranean Sea].

Frequent Synonyms: Pyroteuthis (Pterygonepion) mediterranea Pfeffer, 1912; Charibditeuthis maculata Vivanti, 1912; Pyroteuthis margaritifera aurantica Joubin, 1924.

FAO Names: En – Jewel enope squid; Fr – Encornet-bijouter; Sp – Enoploluria joyera.

Diagnostic Features: Longitudinal membrane of hectocotylus on right arm IV long, about 33% of arm length (measured from first proximal hook); membrane begins distal to seventh to ninth pair of hooks. Normally no additional small photophores on tentacular stalk between first (proximal) and second photophores (but present in southern and western Australian specimens). Arms long, very strong; all, including arms IV, bear hooks in 2 series, almost to tips. Tentacular clubs with 1 central series of 3 or 5 hooks and 2 series of suckers.

Size: The maximum mantle length reaches to 50 mm.

Geographical Distribution: This species is cosmopolitan in tropical, subtropical to temperate waters of all oceans and the Mediterranean Sea (where it is the sole representative of the genus) (Fig. 360).

Habitat and Biology: The upper mesopelagic zone is the daytime adult habitat; adults then undergo diel vertical migration into epipelagic waters at night. For example, off Bermuda, closing-net studies showed that *P. margaritifera* occurs principally at 375 to 500 m during the day and ascends to 75 to 175 m at night. Open net studies off the Canary Islands placed animals at 400 to 800 m during the day and at 50 to 100 m to 200 m at night. In the South Pacific Ocean the species is common in the mixed waters of the subtropical frontal zone and the sub-Antarctic waters. The species occurs in the eastern Mediterranean Sea/northern Aegean Sea in the mesobathyal basins.



Fig. 359 Pyroteuthis margaritifera

Interest to Fisheries: The species is of no interest to fisheries at the present time.

Local Names: ITALY: Totanello perlifero.

Literature: Young (1972a), Roper and Young (1975), Alexeyev (1994a), Lindgren et al. (2008).

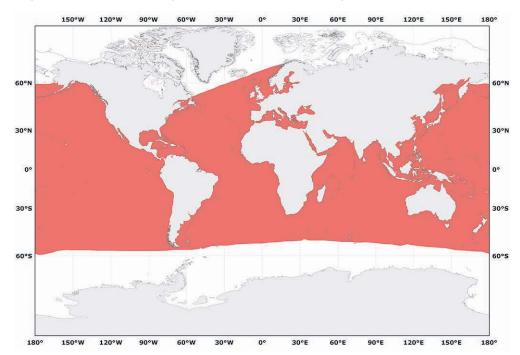


Fig. 360 Pyroteuthis margaritifera

Known distribution

Pyroteuthis addolux Young, 1972

Plate X, 62

Pyroteuthis addolux Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [22, pls. 3 B, 4 I-Q, S]. [Type locality: 31°39'N, 133°16'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 50 mm.

Geographical Distribution: This species occurs in the eastern sector of the central North Pacific Ocean from Hawaii to California as well as in the California Current.

Habitat and Biology: Adults are mesopelagic inhabitants that probably undergo ascent into the epipelagic zone at night.

Interest to Fisheries: No interest in a commercial fishery exists at present.

Literature: Young (1972a), Young (1978), Lindgren et al. (2008).

Pyroteuthis serrata Riddell, 1985

Pyroteuthis serrata Riddell, 1985, *Fisheries Research Bulletin, New Zealand*, 27: 1–52 [10, figs 3, 4a, b, d, f]. [Type locality: Kermadec Islands, northeast of New Zealand's North Island, western South Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 40 mm.

Geographical Distribution: This species occurs off New Zealand north of the tropical convergence, around 30°S.

Habitat and Biology: The species inhabits mesopelagic to epipelagic zones and presumably is a diel vertical migrator.

Interest to Fisheries: None.

Literature: Riddell (1985).

Pterygioteuthis Fischer, 1896

Plate X, 63

Pterygioteuthis Fischer, 1896, Journal de Conchyliologie, Paris, 43(4): 205-211, pl. IX [210].

Type Species: *Pterygioteuthis giardi* Fischer, 1896.

Frequent Synonyms: Ioteuthion Pfeffer, 1912 (pars).

Diagnostic Features: Very few arm hooks exist, located only in middle portions of arms I to III, in 1 or 2 transverse series; a maximum of 2 hooks on arms IV, sometimes none. Tentacular clubs without hooks. Fourteen or 15 photophores on ventral surface of eyeballs, 10 large, 4 or 5 small; eyeball photophore number 6 is lidded. Four photophores embedded on tentacular stalk. Only right oviduct developed. Left arm IV hectocotylized; toothed plate present.

Remarks: Three species currently are recognized: *Pterygioteuthis giardi*, *P. gemmata* and *P. microlampas*. Each species is very broadly distributed in its own particular pattern, throughout the tropical, subtropical (occasionally temperate) Atlantic, Pacific and Indian Oceans and the Mediterranean Sea. Given such broad distributions, considerable geographic variation exists, some of which has been recognized as subspecific in nature; with continued exploration additional taxa could be described.

Pterygioteuthis giardi Fischer, 1896

Fig. 361

Pterygioteuthis giardi Fischer, 1896, *Journal de Conchyliologie, Paris*, 43(4): 205–211 [211, pl. IX: figs 1–7]. [Type locality: off Cape San Francisco, Galapagos Islands, south of Guaylas, eastern Equatorial Pacific].

Frequent Synonyms: Pyroteuthis (Pterygonepion) planctonica Pfeffer, 1912.

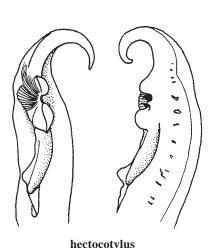
FAO Names: En – Roundear enope squid; Fr – Encornet boubou; Sp – Enoploluria orejuda.

Diagnostic Features: Mantle small, acutely tapered to a short, sharp tail. Fins rounded with large anterior and posterior lobes; fins do not meet posteriorly. Ventral surface of each eye studded with 15 iridescent photophores; photophore number 6 is lidded. Tentacles long, thin. Tentacular clubs compact, without hooks, 4 series of suckers on manus. Arms short, strong; arms I to III with 2 series of hooks, fewer than 8 per arm, only in middle section; hooks absent from arms IV, except on adult males with a few hooks (usually no more than 2), but no suckers; arms IV in females devoid of suckers; left arm IV hectocotylized; toothed plate present; 1 or 2 hooks on right arm IV in males. Eight visceral photophores; 15 photophores on ventral and posterior surface of eyeballs. Oviduct developed on right side only; left oviduct absent.

Size: The maximum mantle length attained is 40 mm.

Geographical Distribution: This species/subspecies complex is distributed worldwide as a cosmopolitan tropical- subtropical form in oceanic waters. It is mesopelagic and ascends into the epipelagic zone at night. This is the sole species of the genus reported so far for the Mediterranean Sea (Fig. 362).

Habitat and Biology: This is a predominantly oceanic species with a depth distribution that ranges from just below the surface to about 500 m. It is known to undertake diel vertical migrations: off Bermuda it is found in 250 to 500 m by day and in 50 to 250 m at night. Off Hawaii it is a facultative inhabitant of the mesopelagic boundary zone. The species is preyed upon by large dolphins (e.g. *Tursiops truncatus*) and pelagic fishes.



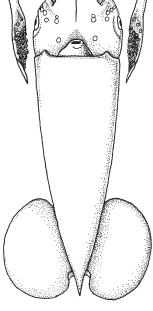


Fig. 361 Pterygioteuthis giardi

261 Dtomociotouthia ciandi ventral view

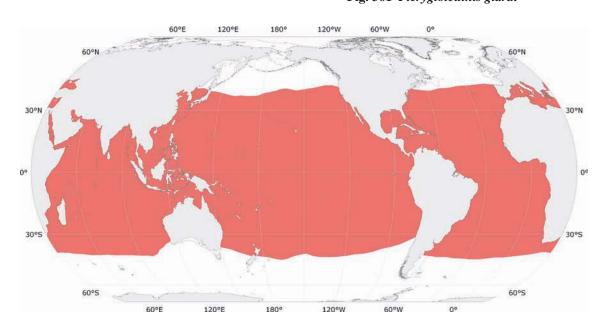


Fig. 362 Pterygioteuthis giardi

Interest to Fisheries: No interest to fisheries exists at present.

Remarks: Nesis (1982, 1987) distinguishes 2 subspecies: *Pterygioteuthis giardi giardi (Atlantic)* and *P. giardi hoylei* (Indo-Pacific) based on differences in the size of the hooks on the right arm IV of males. These forms were first given this taxonomic status by Pfeffer (1912) based on descriptions by Hoyle (1904) of the latter form from the eastern Equatorial Pacific. A careful study, however, of speciation in this taxa has never been made (Young and Mangold, 1996b)

Local Names: ITALY: Totanello orecchiuto.

Literature: Young (1972a,b), Clarke and Lu (1975), Young and Mangold (1996b), Lindgren et al. (2008).

Pterygioteuthis gemmata Chun, 1908

Pterygioteuthis gemmata Chun, 1908, Zoologischer Anzeiger, 33(2): 86–89 [87]. [Type locality: 5°51'N, 21°40'W, North Atlantic Ocean].

Frequent Synonyms: ?*Pyroteuthis (Ioteuthion) schnehageni* Pfeffer, 1912.

Size: The maximum mantle length reaches 40 mm.

Geographical Distribution: *Pterygioteuthis gemmata* is principally an anti-equatorial species in the Atlantic, Pacific and Indian Oceans. It is not recorded from the Mediterranean Sea to date.

Habitat and Biology: Adults are mesopelagic at 300 to 600 m during the day off southern California, then they ascend into the upper 200 m of the epipelagic zone during nightly vertical migrations. In the Canary Basin the species occurs at 50 to 100 m to 200 m at night and descends to 400 to 800 m during the day.

Interest to Fisheries: No interest exists at present.

Literature: Young (1972a,b), Cairns (1976), Nesis (1993d), Arkhipkin (1997b).

Pterygioteuthis microlampas Berry, 1913

Pterygioteuthis microlampas Berry, 1913b, Proceedings of the United States National Museum, 45(1966): 563–566 [566]. [Type locality: Kaiwi Channel, Hawaiian Islands, central North Pacific].

Frequent Synonyms: None.

Geographical Distribution: This species occurs in the central Pacific Ocean and the South Pacific Ocean, north of the tropical convergence.

Literature: Arnold and Young (1974), Bower et al. (1999c).

2.28 Family THYSANOTEUTHIDAE Keferstein, 1866

by Clyde F.E. Roper and Patrizia Jereb

Thysanoteuthidae Keferstein, 1866, *In Bronn*, H.G., *Die Klassen und Ordnungen des Thierreichs wissenschftlich dargestellt in Wort und Bild, 1862–1866, Weichtier (Malacozoa),* 3(2): 1307–1464 [1445].

Type Genus: Thysanoteuthis Troschel, 1857.

FAO Names: En - Rhomboid squids, Diamondback squids; Fr - Chipilouas; Sp - Chipirones

Diagnostic Features: Mantle is very muscular, powerful (in adults to 60 to 85% body weight) with bluntly rounded posterior end and highly developed collagenous tunic system; mantle thickness in adults up to 50 mm (6.5% mantle length); width 25% of length. The long, broad, very muscular rhomboidal fins extend entire length of mantle, not fused together along dorsal midline; greatest fin width at anterior two-thirds to three-fourths of fin length; fin width 75 to 85% of fin/mantle length in adults. Head width similar to mantle width. Funnel strongly muscular, accompanied with prominent funnel groove. Mantle-funnel and mantle nuchal locking apparatus unique, well developed, the most characteristic familial traits. Funnel-locking apparatus subtriangular with rounded angles, long, narrow longitudinal groove, short, broad transverse groove, knobs at juncture of grooves; forms a "sideways-T" shape: ¬; large and robust, its length is from 13 to 15% mantle length. Mantle component with ridges of corresponding form. Nuchal locking apparatus extremely well developed, with 2 large, swollen, hook-like knobs on mantle component that interlock with 2 conforming depressions and knobs on the nuchal component. Buccal connective formula DDVV. Arms with no sexual dimorphism in shape or external morphological traits in adults, but differences occur in length of arms III in immature squids of 120 to 450 mm mantle length (arms III length in males 75 to 110% of mantle length, in females about 50% mantle length). Arm formula III.II.IV.I (or IV = I). Arms relatively short, strongly muscled, with 2 series of suckers (no hooks) and well-developed wide protective membranes expanded on long cirri-like trabeculae; especially well developed on arms III, less so on arms II; arms I to III with distinct aboral keels. Arm sucker rings with 20 to 26 sharp conical teeth. Tentacles relatively short, strongly muscled; tentacular clubs widened, relatively long; manus with 4 series of suckers that extend together to tip of dactylus; carpal-locking apparatus extends proximally along stalk as 2 series of alternating knobs and suckers. Suckers on manus of clubs with 15 to 29 fine, strongly pointed, conical teeth. Left ventral arm (IV) hectocotylized. In mature males the hectocotylized distal region occupies from 13 to 20 sucker rows and 30 to 35% of the arm length. The modified part of the arm has tiny untoothed suckers with smooth horny rings and 2 oval glandular enlargements. The male reproductive system is characterized by a very long, narrow Needham's sac (40 to 60% mantle length) and a long muscular penis; the female system has hypertrophied oviducal glands (40 to 52% mantle length) with a very large lancet-like second section (30 to 40% mantle length) and relatively small oviducts, with distribution of the main ovarian afferent and efferent blood vessels in mesentery protruding dorsally into the ovary. One well-developed anal photophore on ink sac near anal papilla in young squid from 60 to 350 mm mantle length; photophore gradually reduced, non-functional in adults. The gladius very unusual for oegopsid squids. Pro-ostracum very wide, greatest width near anterior margin of gladius; rachis narrow with short anterior free lobes; lateral plates (the first paired elements from the rachis) narrow with hyperbolic anterior margins; wings (the second paired elements from the rachis) gradually widen anteriorly, their width about equal to the width of the rachis plus the lateral plates; anterior lobes of wings protrude beyond the lateral plates almost to the level of the anterior margin of the rachis; the conus is greatly reduced, cup-shaped; the rostrum is absent; the anterior, enlarged part of the gladius bends strongly toward the ventral side of the mantle and protrudes into the mantle cavity; consequently, the dorsal and lateral parts of the inner complex of organs are covered by the curved wings of the gladius, and the gills are situated between the gladius wings and the inner surface of the mantle. The radula has 7 transverse rows of teeth. The beak is very characteristic with small, robust rostra on both mandibles; rostrum of lower jaw pointed; jaw angle is distinct, sharp, with a shoulder tooth; the hood is short with a curve on the ventral edge; a well-pronounced transparent strip present; the shape of the beak closely resembles that of Architeuthis but differences exist: the form of the rostrum (no small hook on rostrum); the jaw edge to wing angle is more acute and beak size is smaller when the wings begin to darken.

Size: Large nektonic squid; adult size attains 100 cm or even 130 cm mantle length.

Interest to Fisheries: A strong local interest exists for the fishery in the Sea of Japan and in waters around Okinawa and Taiwan Province of China. The high commercial value makes it an important target species in Japan.

Remarks: This family now is considered to be monotypic. Formerly, 2 genera, *Thysanoteuthis* Troschel, 1857 and *Cirrobrachium* Hoyle, 1904, were included in the family. However, *Cirrobrachium* was declared to be a junior synonym of *Thysanoteuthis* (Nigmatullin and Arkhipkin, 1998: 158). Based on an analysis of gladius morphology of recent and extinct squids 3 evolutionary lines were distinguished: myopsid, oegopsid and thysanoteuthid (Bizikov, 1996). The thysanoteuthid gladius is archaic and unique among the squids: it most resembles gladii of Jurassic Loligosepiida. As a result, Bizikov (1996: 231–233) removed *Thysanoteuthis* from the suborder **Oegopsida** and created for it a new suborder, **Thysanoteuthida**, within the order **Teuthida**. The rest of the oegopsid squids remained in the suborder, **Oegopsida**. This opinion also is supported by some archaic and distinct features in the structure of the female reproductive system, spermatozoa, hectocotylus (Nigmatullin, *et al.*, 1991a; Nigmatullin and Arkhipkin, 1998) and statocyst (Young, 1989; Nixon and Young, 2003) that seem more closely related to **Myopsida** than to **Oegopsida**.

Literature: Roper *et al.* (1984), Nesis (1982, 1987, 1992a) Guerra (1992), Nigmatullin *et al.* (1995), Nigmatullin and Arkhipkin (1998), Sweeney and Young (2003aa).

Thysanoteuthis Troschel, 1857

Thysanoteuthis Troschel, 1857, Archiv für Naturgeschichte, Berlin, 23(1): 40-76 [69].

Type Species: Thysanoteuthis rhombus Troschel, 1857.

Frequent Synonyms: Cirrobrachium Hoyle, 1904.

Diagnostic Features: The family is monotypic and generic characteristics are the same as given for the family.

Remarks: See remarks given for family.

Thysanoteuthis rhombus Troschel, 1857

funnel-locking apparatus

Fig. 363

Thysanoteuthis rhombus Troschel, 1857, Archiv für Naturgeschichte, 23(1): 40–76 [70, pls. 4, 5]. [Type locality: Messina, Sicily, Mediterranean Sea].

Frequent Synonyms: Sepioteuthis major Gray, 1828;
Thysanoteuthis elegans Troschel, 1857; T. nuchalis Pfeffer, 1912;
Cirrobrachium filiferum Hoyle, 1904; C. danae Joubin, 1933.

FAO Names: En – Diamondback squid, Rhomboid squid;
Fr – Chipiloua commun; Sp – Chipiron volantin.

Fig. 363 Thysanoteuthis rhombus

tentacular club

dorsal view

Diagnostic Features: *Thysanoteuthis rhombus* is monotypic, so the characters detailed at the family level are diagnostic. The most characteristic traits are the long, broad rhomboidal fins that occupy the entire length of mantle, the \dashv -shaped mantle-funnel locking cartilages, the presence of the anterior intestinal (anal) photophore in immature squid and the unique shape and structure of the gladius.

Size: The maximum mantle length of both sexes is the same, 100 cm, possibly to 130 cm, and the maximum body weight known is 24 to 30 kg, probably more. Maximum size of a sexed and measured male is 85 cm mantle length and of a female is 82 cm mantle length.

Geographical Distribution: *Thysanoteuthis rhombus* is a cosmopolitan species, a common circumglobal inhabitant of warm tropical and subtropical open waters of the world oceans, the Mediterranean Sea and the Caribbean Sea. It also reaches higher latitudes, the temperate boreal and notalian regions, transported by warm currents, e.g. the Tsushima, Kuroshio, Agulhas, Brazil Currents and the Gulf Stream. Thus, with the Tsushima Current, it penetrates into the Sea of Japan to 41°57'N to 140°57'E, and with the Agulhas Current to the Cape of Good Hope area. It inhabits open oceanic waters and only rarely approaches the shelf zone driven there by warm currents in the peripheral range of the species. It avoids the oligotrophic central waters of the open ocean. It occupies epipelagic to upper mesopelagic depths, and it undergoes diel vertical migrations (Fig. 364).

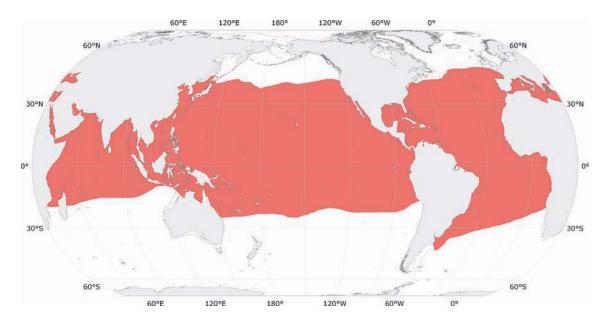


Fig. 364 *Thysanoteuthis rhombus*Known distribution

Habitat and Biology: Thysanoteuthis rhombus is an epipelagic to mesopelagic species that inhabits open oceanic waters in excess of 400 m bottom depth where surface water temperature principally is greater than 20°C. Paralarvae and juveniles live in the epipelagic zone. Subadults and adults (300 to 850 mm mantle length) make daily vertical migrations in the upper 600 to 800 m. At night most of the population migrates toward the surface (0 to 50 m), then in daytime descends to depths from 400 to 800 m, mainly 450 to 650 m. Distribution and migration depend on the surface circulation of oceanic waters. Despite its eunektonic appearance, T. rhombus is a relatively passive migrant that undertakes long seasonal migrations in the warm waters of peripheral oceanic currents. Consequently, it is characterized paradoxically as a planktonic nekteur. During most of its life cycle it does not swim actively. Rather, it propels itself slowly by gentle undulation of its long, broad, diamond-shaped fins. However, when it encounters danger, T. rhombus is capable of a powerful reactive jet of short duration. This low-energy life style enables the rhomboid squid to maintain very high growth rates, among the highest of all squids. By the age of 300 days the squid reach 800 mm mantle length and 17.5 kg body weight. Males reach maturity mainly at 400 to 550 mm mantle length (age 170 to 200 days), and females mature at 550 to 650 mm mantle length (age 230 to 250 days). The life span is 1 year. Spawning lasts throughout the year in tropical waters and during the warm season in peripheral regions. Needham's sac stores from 10 to 40 spermatophores 60 to 100 mm long. The potential fecundity of females is from 2.5 to 5 million oocytes. The development of oocytes is asynchronous. The size of ripe eggs is from 1.6 to 1.8 mm. Maximum egg numbers in oviducts is up to 140 000; spawned egg masses contain from 32 000 to 75 000 embryos. Spawning is intermittent, with multiple fillings and evacuations of the oviducts. In females 8 to 30 seminal receptacles are located on the ventral part of the buccal membrane. Mating occurs in the "head to head" position. The pelagic egg mass is a large cylinder (0.6 to 2 m long, 0.11 to 0.3 m diameter) of transparent gelatinous mucus with pink-violet embryos that are distributed in a double spiral in the outer layer. Hatching size is 1.4 to 1.6 mm mantle length. Development includes a paralarval stage. No pronounced geographical variability occurs in the main morphological features and ecological-population parameters (e.g. size and age at maturity). The same phenomenon is observed for genetic variability: mitochondrial DNA sequences differ very little between conspecific individuals from the western and eastern Pacific Ocean. The population density is low, mainly from 0.01 to 100 specimens per km². Total minimum estimated biomass within the vast geographical range of the species is only about 1.5 to 2.5 million tonnes only. The greatest abundance occurs in the productive zones of the open ocean and in coastal areas at the periphery of the range, mainly in the southwestern part of the Sea of Japan. The social organization is unique among squids. It consists of pairs formed of same-sized males and females that occur at an immature stage of less than 100 mm mantle length, and they probably remain together constantly during their lifetimes (monogamy). Small schools of pairs may be locally common. Arm length and probably the anal photophore play the key role in pair formation in immature squids. The reproductive and behavioural strategies are adaptations to low population density and inactive life style. Juveniles feed on crustaceans, small cephalopods and fishes in subsurface waters,

but subadults and adults feed mainly in daytime in deep-water layers mostly from 400 to 650 m on dense concentrations of non-active midwater fishes. Predators include different species of ommastrephid squids, dolphin fish (*Coryphaena*), lancet fish (*Alepisarus* 2 species), various species of tuna, e.g. *Thunnus albacares*, *T. obesus*, *T. alalunga*, *Katsuwanus pelamis*, swordfish, *Gempylus serpens*, sharks and mammals (e.g. dolphins, rough-toothed dolphin (*Steno bredanensis*), false killer whale, sperm whale).

Interests to Fisheries: The flesh is firm and flavorful and a significant fishery exists in the coastal waters of the Sea of Japan and around Okinawa. Its high commercial value makes it an important target species in these waters. The only commercial fishery for this species is in Japan and locally in Taiwan. This species has a very high quality, tender meat that yields a very high price (about 0.7 to 2 million yen per tonne), a highly profitable fishery. Catches are not reflected in FAO statistics. The T. rhombus fishery began in the Sea of Japan off Hyogo Prefecture in 1962 as a nighttime fishery from small boats using baited hooks. In 1967, angling gear called "taru-nagashi", comprising a buoy and a vertical line with 1 or 2 attached jigs, was introduced as a daytime fishery. Annual catches varied from 0 to 2 tonnes to 232 tonnes (1964), 619 tonnes (1967) and 516 tonnes (1972). In 1990 to 1995 total annual Japanese catches varied between 1 613 tonnes and 2 670 tonnes, then in 1998 it decreased to 200 tonnes and in 2001 peaked to almost 6 000 tonnes. Since 1998 annual catches averaged close to 4 900 tonnes. The main fishing grounds (90% of catch) are situated in the Sea of Japan, Okinawa Prefecture, and Kagoshima Prefecture. A small fishery also occurs near the Ogasawara Islands (2 to 7 tonnes in 1995 to 2000). Currently T. rhombus is caught in the Sea of Japan using "taru-nagashi" and inshore stationary trap nets. The fishing grounds occur at bottom depths of 100 to 500 m, where the jigs are set in midwater near the 100 m zone. The Sea of Japan fishery runs from July to February, with peak catches in September to December. In Hyogo Prefecture, the fishery typically starts in August and peaks in October. In Toyama, Kyoto and Hyogo, the peak catches occur in October to December when the squid are 200 to 700 mm mantle length. The fishery started in Okinawa Prefecture in 1989 with the same type of fishing gear as used in the Sea of Japan. Catches in Okinawa peaked in 2003 at 2 300 tonnes; these usually comprise about half of the national catch. Highest catches occur in March to April when adult squid of 700 to 850 mm mantle length are caught. This is primarily a daytime fishery with "hata-nagashi" gear, which consists of several jigs fished at depth on a line attached to several buoys with flags at the surface. The gear is set to about 500 m depth near the salinity minimum layer. The fishery employs boats smaller than 5 tonnes during the daytime and each boat uses 15 to 20 sets of fishing gear. This squid also has the potential for a valuable fishery resource in the different parts of its range as bycatch whenever squid and finfish pelagic trawl fisheries develop in slope and oceanic areas, especially in highly productive frontal zones.

Local Names: ARGENTINA: Calamar rombo; CANARY ISLANDS: Calamar de lo alto, Calamar obispo; FRANCE: Chipilona, Chipiloua commun; ITALY: Totano rombo; JAPAN: Common – Sode-ika and more local – Aka-ika, Beni-ika (the Oki Islands), Taru-ika (area near Wakasa Bay), Kannon-ika (Toyama Prefecture) and Sei-ika (Okinawa Prefecture); KOREA: Nal-Ge-O-Jing-Eo; MEXICO (the Gulf of California): Calamar de aleta corrida; PERU: Calamar diamante; UKRAINE: Kal'mar-romb; SPAIN: Chipirone, Chipiron volantin; SOUTH AFRICA: Diamond squid; UK: Diamondback squid; USA: Diamondback squid; TAIWAN: Líng-qí-yóu.

Literature: Roper et al. (1984), Nigmatullin et al. (1995), Nigmatullin and Arkhipkin (1998), Takeda and Tanda (1998), Bower and Miyahara (2005), Miyahara et al. (2005).