2. SQUIDS

by Patrizia Jereb and Clyde F.E. Roper

The origin of "true" squids can be traced to the early Mesozoic (Permian/Triassic) with steady proliferation from the Jurassic through the Recent. The two main groups[1/], Myopsid squids, "covered-eyed", near-shore (neritic) squids, and Oegopsid squids, "open-eyed" oceanic (pelagic) squids, occur in the oceans and seas of the world and together form the basis of the major cephalopod fisheries production. Some species are demersal or epibenthic at some period of their life cycle, but most occur in the water column.

Diagnostic Features: Ten circumoral appendages, the fourth pair, the tentacles, contractile, **but not retractile** into pockets (occasionally tentacles secondarily lost); sucker ornamentation with chitinous rings and/or hooks. Radula teeth commonly with primary (large) projection and a secondary (smaller) cusp(s), especially on the median (rachidian) and the first lateral teeth; buccal membrane present. Olfactory organ consists of 2 projecting papillae; eyes without lids either (1) covered with a transparent membrane, with a minute pore (Myopsid squids) or (2) not covered with a membrane, but completely open to the sea (Oegopsid squids). Gills with branchial canal between afferent and efferent branchial blood vessels. Digestive gland (liver) consists of a single structure. Shell (pen or gladius) internal, simple, rod- or feather-like, chitinous.

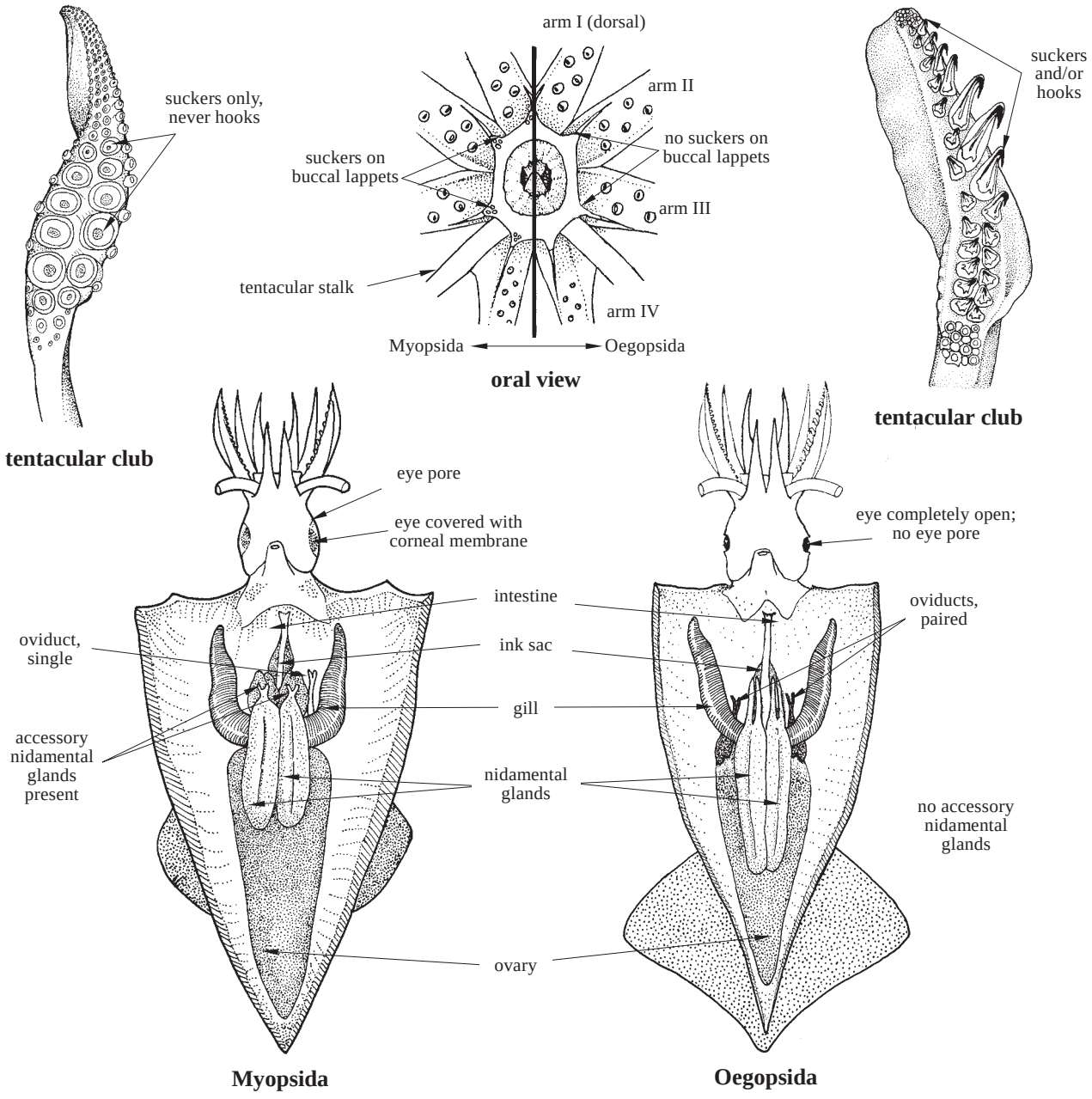


Fig. 66

1/ As referred to in this Catalogue because of the unsettled nomenclatureal situation at the time of publication.

Myopsid Squids

Diagnostic Features: Corneal membrane covers the eye, with a minute pore, anteriorly, in most species. Eyes without secondary (= ventral) eyelid. Head **with tentacle pocket**. Suckers usually present on the buccal lappets. Funnel without lateral adductor muscles. Arms and clubs with suckers, **never with hooks**. Club **without carpal-locking apparatus**. Shell a gladius, that extends the full length of the mantle. **Right** oviduct **absent**. **Accessory** nidamental glands **present**.

Size: From very small, dwarf-sized species (maximum recorded ML 20 to 22 mm) to rather large squids (over 900 mm ML).

Geographical Distribution: Myopsid squids are widely distributed near shore in all oceans and seas of the world.

Habitat and Biology: All myopsid squids are demersal, predominantly near-shore or shelf species, that frequently feed near or on the bottom. Squids of the Australiteuthidae have not been observed alive. The Loliginidae contains species which can reach a rather large size (at least 900 mm ML in ***Loligo forbesii***), along with dwarf species, like those of ***Pickfordiateuthis***, where males may mature at less than 14 mm mantle length. Some species tolerate reduced salinities and estuarine situations, like, for example, ***Lolliguncula brevis*** in the western North Atlantic. Many species show characteristic onshore-offshore migrations in spring and late autumn respectively, overwintering in deeper waters. The spawning season often is extended with peaks in early summer and autumn. Mating and spawning normally occur near the bottom, where the egg masses are attached to shells and other substrates.

Normally, many small eggs are encapsulated in gelatinous strings (strands of fingers) attached to the substrate, where they develop and hatch without parental care.

Interest to Fisheries: While the small-sized Austaliteuthidae squids are of no commercial interest, many squids of the family Loliginidae represent an important resource for many industrial and small-scale fisheries world-wide. FAO's fishery yearbook (FAO, 2009) reports about 365 000 tonnes of Loliginid squids caught in 2007, i.e. about 11.3% of the total squid catch for that year. Of this, about 98% is reported to belong to the genus ***Loligo***, a designation that includes species at present placed in other genera/subgenera, following the consensus determined by international experts of the Cephalopod International Advisory Council in Phuket, Thailand, in 2003 (Vecchione *et al*., 2005).

Remarks: Myopsid squids comprise only 2 families: the monotypic Australiteuthidae (described from the inshore waters of Northern Australia), with 1 genus and 1 very small-sized species, and the very speciose Loliginidae that currently is recognized to include 10 genera, with 9 described subgenera and 47 species.

Literature: Naef (1916, 1923), Roper *et al*. (1984), Nesis (1982, 1987), Sweeney and Vecchione (1998), Okutani (2005), Vecchione *et al*. (2005), Vecchione and Young (2008c).

2.1 Family AUSTRALITEUTHIDAE Lu, 2005

by Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione

Australiteuthidae Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66: 72 -82, figs 1-9. [72].

Type Genus: *Australiteuthis* Lu, 2005: 72.

FAO Names: En – Australasian inshore squid; **Fr** – Petite calmars Australiennes; **Sp** – Calamaretos Australianos.

Diagnostic Features: Myopsid squid with subcircular funnel-locking cartilage, bisected by a boomerang-shaped groove that extends anteroposteriorly. **A dumb-bell-shaped photophore** of sepiolid type occurs **on ventral surface of ink sac. Fins separated**, not united at posterior ends.

Size: Very small-sized squid; maximum mantle length to about 30 mm.

Geographical Distribution: North and Western Australia, Papua New Guinea, Indo-West Pacific.

Remarks: The family Australiteuthidae has some sepiolid characters, such as the deep "tentacular" pockets into which tentacles are retracted, the presence of a sepiolid-type photophore on the ink sac and the lack of acquiferous pores in the cornea. However, it also has some primarily teuthid-type characters, such as tricuspid rachidian teeth, buccal membrane connectives attached to the arm and the absence of eyelids. Within the suborder Myopsida, only one other family is known, the Loliginidae. Australiteuthidae joins the Myopsida because of the shared character of a corneal membrane. It differs from Loliginidae, however, by the shape of the funnel-mantle locking-apparatus and the absence of an aquiferous pore in the cornea. The family is monotypic.

Literature: Lu (2005), Vecchione and Young (2008b).

Australiteuthis Lu, 2005

Australiteuthis, Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66:72 -82, figs 1-9[72].

Type Species: *Australiteuthis aldrichi* Lu, 2005: 72.

Diagnostic Features: As given for the family.

Geographical Distribution: As given for the family.

Remarks: The genus ***Pickfordiateuthis***, formerly placed in its monotypic family, was incorporated into the Family Loliginidae by Brackoniecki (1996). ***Australiteuthis*** shares similarities with ***Pickfordiateuthis*** in the "sepiolid-like" separated fins, though not so distinct; the radular teeth and the gladius also are similar. However, the two genera differ significantly in the funnel-locking apparatus configuration, and ***Pickfordiateuthis*** lacks the photophore on the ventral surface of the ink sac that is very prominent in ***Australiteuthis***. The genus is monotypic.

Literature: As given for the family.

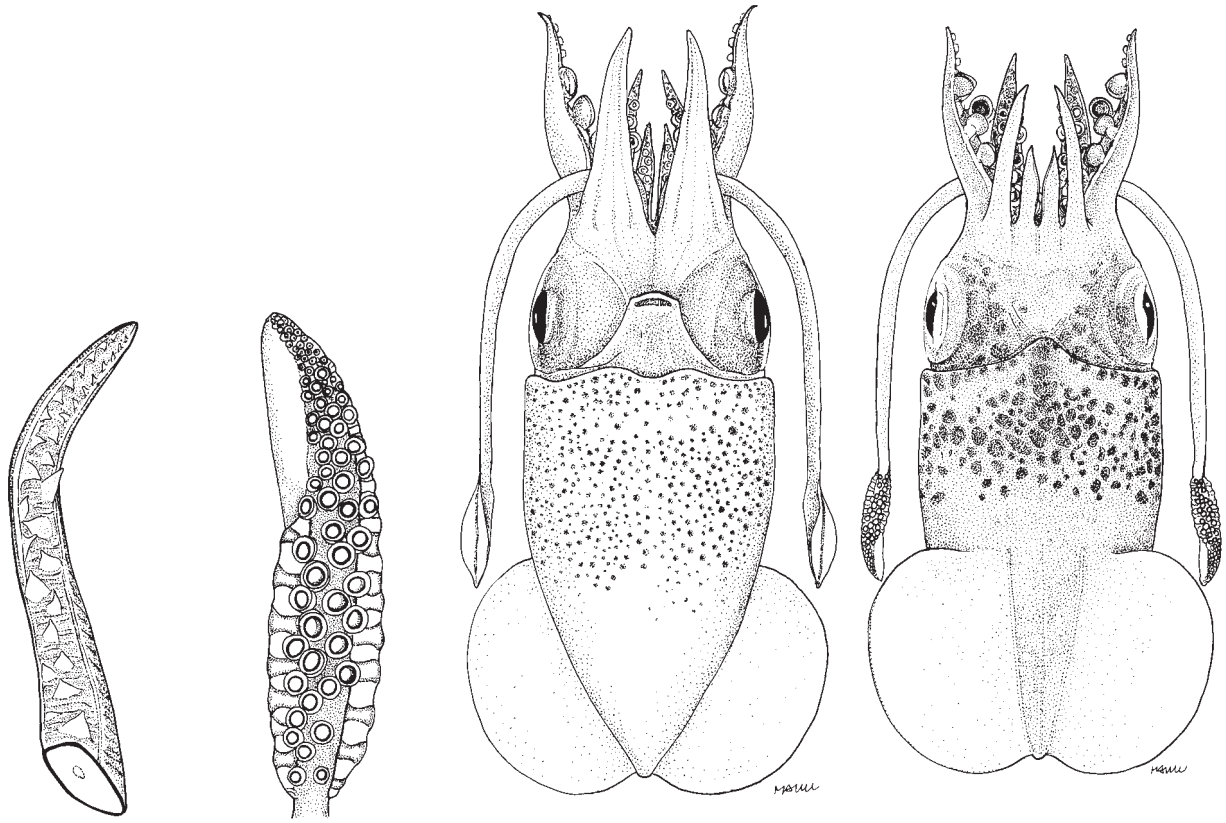
Australiteuthis aldrichi Lu, 2005 **Fig. 67**

Australiteuthis, Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66:72–82, figs 1-9. [72]. [Type locality: 14°07.30'S 28°02.00' E, Joseph Bonaparte Gulf, Western Australia].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Aldrich's Australasian inshore squid; **Fr** – Petite calmar Australien de Aldrich; **Sp** – Calamareto Australiano de Aldrich.



hectocotylus **tentacular club** **ventral view** **dorsal view**

Fig. 67 ***Australiteuthis aldrichi***

Diagnostic Features: Eyes covered with transparent cornea, but without aquiferous pores. Funnel-locking cartilage large, subcircular, bisected by a boomerang-shaped groove that runs anteroposteriorly; anterior wing of groove with wide anterior end; groove deepens and becomes slightly narrower posteriorly to form a deep, broad pit, that in turn becomes a narrow, shallow groove posteriorly and curves medially to form posterior wing or "boomerang". Left ventral arm hectocotylized by the reduction in size of suckers of the whole arm to a tiny swelling on top of enlarged conical-shaped sucker stalks. **A sepiolid-like, dumb-bell- shaped photophore is present on the ventral surface of the ink sac**. **Fins separated at posterior ends**.

Size: Very small species; 15 mm to 28 mm mantle length.

Geographical Distribution: Currently known from the Joseph Bonaparte Gulf of Western Australia, the inshore waters of the Northern Territory, Australia, and the Gulf of Papua, Papua New Guinea (PNG). Probably broadly distributed along coastal regions of northern Australia and southern PNG (Fig. 68).

Habitat and Biology: The species was known from about 3 dozen specimens at the time of the original description. They were captured in near-shore waters from 9 to 61 m deep with beam trawls (when gear type was listed). This species probably is a benthic to epibenthic form on soft substrates. Males are reported to mature around 17 mm mantle length and females at a larger size, over 22 mm mantle length.

Interest to Fisheries: None.

Local Names: None reported.

Remarks: The very small size and the apparently sparce abundance of this species make it an unlikely candidate for a fishery.

Literature: Lu (2005), Lu and Young (2005).

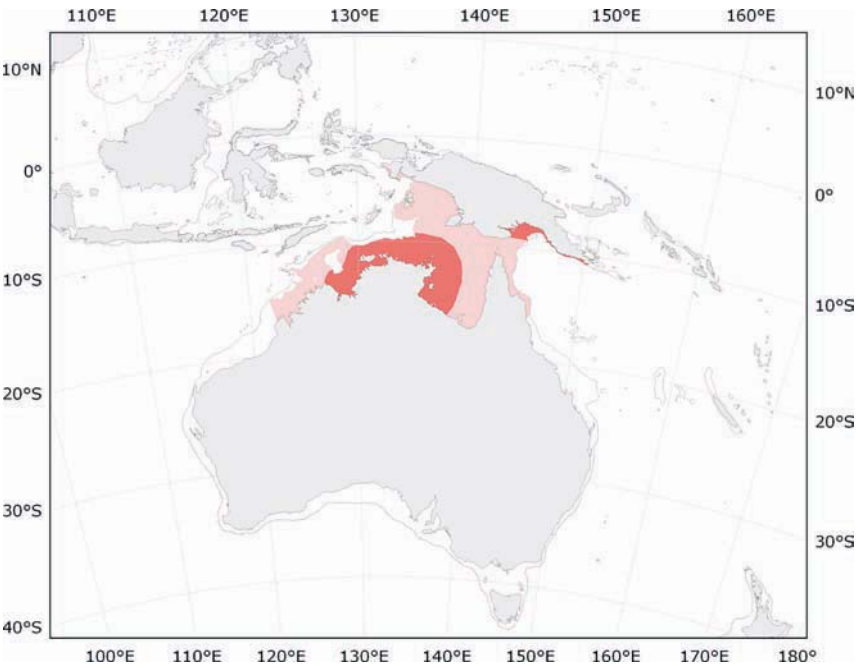


Fig. 68 ***Australiteuthis aldrichi***

2.2 **Family LOLIGINIDAE** Lesueur, 1821

by Patrizia Jereb, Michael Vecchione and Clyde Roper

Loligoidea Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, 7 pls [89].

Type Genus: *Loligo* Lamarck, 1798: 130.

FAO Names: En – Inshore squids; **Fr** – Calmars; **Sp** – Calamares.

Diagnostic Features: Transparent skin (corneal membrane) covers eye lens; with aquiferous pore. Funnel-locking apparatus a simple, straight groove and ridge. Fins attach to lateral regions of mantle. Arms with suckers in 2 series. Tentacular club with suckers usually in 4 series (2 series in at least manal region of ***Pickfordiateuthis*** clubs). **Hooks never present**. Buccal connectives attach to ventral margins of ventral arms (arms IV). **Seven buccal lappets possess small suckers in many species**. Usually the left arm of the ventral pair is hectocotylized in males; structure of the modified portion of the hectocotylus is useful as a species diagnostic character. **Females with a single oviduct and with accessory nidamental glands**. Eggs spawned in finger-like egg masses attached to substrate. Paralarvae are not radically different in appearance from adults. **Colour**: usually reddish brown, darker dorsally, but quite variable depending on behaviour.

Size: Small- to medium- and large-sized squid; maximum mantle length 937 mm (i.e. ***Loligo forbesii*** male from the Azores).

Geographical Distribution: Worldwide, in tropical, temperate and subpolar coastal waters.

Habitat and Biology: Loliginids are demersal, near-shore or shelf species. Various species occur from very shallow water in bays and estuaries, over grass flats and coral reefs, to water over 700 m depth (e.g. during seasonal offshore migrations). Loliginids are important prey for numerous groups of fishes, sharks, marine mammals, seabirds and squids.

Interest to Fisheries: Loliginids are mostly small to medium-sized squids that occur along coastal margins and continental shelves, primarily in warm to temperate waters world-wide. They form one of the major groups of commercially utilized cephalopods. Some species support extensive fisheries in several parts of the world, as the flesh is of excellent quality. As finfish populations have become overfished and exhausted, cephalopod landings have increased dramatically in some regions. For example, in the Gulf of Thailand, the finfish landings in the 1970s and 1980s declined, while landings of loliginids increased annually, to become consistently the most abundant landings.

Remarks: Other squid families that include commercial-sized species of present potential interest to fisheries (e.g. Ommastrephidae, Thysanoteuthidae, Onychoteuthidae) all lack suckers on the buccal lappets and have eye lenses open to the sea, not covered by a transparent corneal membrane. Variation in loliginids can be prominent and is a natural phenomenon. Nesis (1998) addressed the situation of several partly or wholly sympatric intraspecific groupings of squids that differ “only” in size at maturity (early- or late-maturing populations) and/or spawning season. Some groupings seem to maintain these spatial-temporal units that may represent a separate stock of a population or supra-population rank. However, such a stability and consistency in differences is not the case with the groupings of ***Doryteuthis (Amerigo) gahi*** from the same region (Carvalho and Nigmatullin 1998). Also, it is not the case with the Japanese species groups of warm-season spawning and cold-season spawning ***Uroteuthis (Photololigo) edulis*** (Natsukari and Tashiro 1991). This phenomenon is an example of incipient speciation, and such species complexes are well recognized in other loliginids, e.g. ***Loligo vulgaris*** and ***Loligo forbesii***, each of which is represented by distinct entities.

The systematics of this family has long been problematic (Vecchione *et al*., 1998b). A workshop on loliginid systematics was convened during the 2003 meeting of the Cephalopod International Advisory Council held in Phuket, Thailand (Vecchione *et al*., 2005). One goal of the workshop was to resolve conflicting generic-level classifications of the family in light of recent observations and cladistic analyses on morphological (e.g. Alexeyev, 1989; 1992 [1991]; Anderson, 1996; 2000b) and molecular (e.g. Anderson, 2000a; 2000b) characters. Among other conclusions, the workshop participants decided that the genus ***Loligo*** sensu Vecchione *et al*. (1998b) is paraphyletic and must be reorganized into geographic groups in order to be consistent with molecular inferences; currently, no morphological characters are known to distinguish these genera consistently. The assembled taxonomic experts reached consensus on the following classification:

Table 1

Taxonomic classification

Genus	Subgenus	species included
Loligo		*forbesii, reynaudii, vulgaris*
Afrololigo		*mercatoris*
Alloteuthis		*africana, media, subulata*
Doryteuthis	*Doryteuthis*	*plei, roperi*
	Amerigo	*gahi, ocula, opalescens, pealeii, surinamensis*
	subgenus undescribed	*sanpaulensis*
Heterololigo		*bleekeri*
Loliolus	*Loliolus*	*affinis, hardwickei*
	Nipponololigo	*beka, japonica, sumatrensis, uyii*
Lolliguncula	*Lolliguncula*	*argus, brevis, panamensis*
	Loliolopsis	*diomedeae*
Pickfordiateuthis		*bayeri, pulchella, vossi*
Sepioteuthis		*australis, lessoniana, sepioidea*
Uroteuthis	*Uroteuthis*	*bartschi*
	Aestuariolus	*noctiluca*
	Photololigo	*abulati, arabica, bengalensis, chinensis, duvaucelii, edulis, machelae, robsoni, sibogae, singhalensis, vossi*
	subgenus undetermined	*pickfordi, reesi*

Literature: Naef (1912a, b), Adam (1954), Roper *et al*. (1984), Alexeyev (1989, 1991, 1992), Brakoniecki (1986), Okutani *et al*. (1987), Nesis (1998), Vecchione *et al*. (1998b), Dunning (1998d), Sweeney and Young (2003o),Vecchione *et al*. (2005), Jereb and Roper (2006), Hastie *et al*. (2009).

Key to the genera of Lologinidae

1a. Suckers in 2 series on proximal tentacular clubs; fins with rounded posterior lobes, not joined posteriorly . . . . . ***Pickfordiateuthis***

1b. Suckers in 4 series on proximal tentacular clubs; fins extend to posterior end of mantle, without rounded posterior lobes . . . . . → ***2***

2a. Fins in adults occupy >85% of mantle length, combined shape broadly elliptical . . . . . ***Sepioteuthis***

2b. Fins in adults occupy <70% of mantle length, round or rhomboidal . . . . . → ***3***

3a. Fins in adults wider than long, round or auriform, not rhomboidal; mantle short, stout, broadly rounded posteriorly . . . . . → ***4***

3b. Fins in adults rhomboidal, longer than broad, not round; mantle elongate, pointed posteriorly . . . . . → ***6***

4a. Hectocotylus with ventral crest formed by fusion of the protective membrane with the ventral row of papillae . . . . . ***Loliolus***

4b. Hectocotylus without ventral crest . . . . . → ***5***

5a. American distribution; suckers on midsections of lateral arms of males not greatly enlarged . . . . . ***Lolliguncula***

5b. West African distribution; suckers on midsections of lateral arms of males greatly enlarged . . . . . ***Afrololigo***

6a. A pair of photophores on ventral surface of ink sac . . . . . ***Uroteuthis***

6b. No photophores on ventral surface of ink sac . . . . . → ***7***

7a. Northwestern Pacific distribution; dorsal series of papillae and trabeculae at distal tip of modified hectocotylus form bicuspid lamelliform flaps separated from ventral series of suckers by serrated membrane . . . . . ***Heterololigo***

7b. Not northwestern Pacific; hectocotylus tip not as above . . . . . → ***8***

8a. American distribution . . . . . ***Doryteuthis***

8b. Eastern Atlantic distribution . . . . . → ***9***

9a. Gladius with a small rostrum, posterior mantle elongated as a tail-like structure . . . . . ***Alloteuthis***

9b. No rostrum on gladius, elongation of posterior mantle not extreme and tail-like . . . . . ***Loligo***

Loligo Lamarck, 1798 — **Plate III, 12 & 13**

Loligo Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique*, 2(5):129–131 [130].

Type Species: *Loligo vulgaris* Lamarck, 1798: 130.

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Hectocotylus with proximal suckers unmodified; ventral crest absent; suckers in modified portion of reduced size; sucker stalks elongated to form papillae in either dorsal or both dorsal and ventral series. **Fins posterior**. **Eggs small to moderate sized – less than 4 mm**. Spermatophore cement body short. Photophores absent.

Size: Small- to medium- and large-sized squids; maximum recorded mantle length 937 mm.

Geographical Distribution: Eastern Atlantic Ocean and Mediterranean Sea.

Habitat and Biology: As given for the family.

Literature: As given for the family.

Loligo vulgaris Lamarck, 1798 — **Fig. 69**

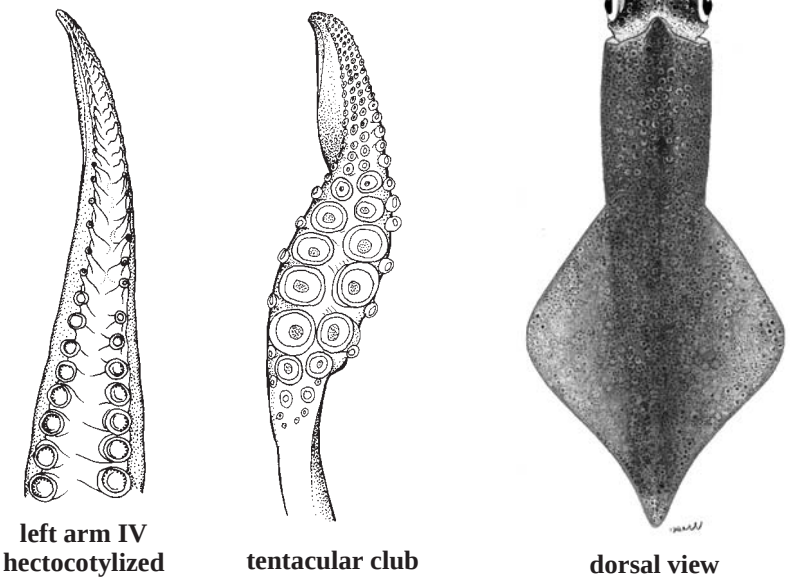
Loligo vulgaris Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique*, 2(5):129–131 [130]. [Type locality: Not designated].

Frequent Synonyms: *Loligo pulchra* Blainville, 1823, *Loligo rangii* Ferussac, 1835, *Loligo berthelotii* Verany, 1839a, *Loligo neglecta* Gray, 1849, *Loligo breviceps* Steenstrup, 1862, *Loligo mediterranea* Targioni-Tozzetti, 1869, *Loligo affinis* Lafont, 1871, *Loligo microcephala* Lafont, 1871.

Misidentifications: *Loligo forbesii* (formerly, multiple authors).

FAO Names: En – European squid; **Fr** – Encornet européenne; **Sp** – Calamar europeo.

Diagnostic Features: Mantle long, moderately slender, muscular, cylindrical. Fins rhomboidal, their length **up to two-thirds of mantle length** (exceeds 50% mantle length), posterior border slightly concave. Manus of tentacular **clubs with 4 longitudinal series of suckers; 2 median series with 6 to 8 enlarged suckers each**; sucker rings of median series on manus with approximately 30 irregularly-sized and distributed teeth; **clubs with about 36 transverse rows of suckers**. Arm suckers biserial; sucker rings with about 20 teeth, the distal ones large and pointed, the proximal ones small or absent. **Left ventral arm hectocotylized in males along its distal one-third to one-quarter** by modification of **suckers into papillae that decrease in size distally**.



left arm IV hectocotylized **tentacular club** **dorsal view**

Fig. 69 ***Loligo vulgaris***

Size: Maximum mantle length 640 mm in males, 485 mm in females (West African coast); maximum body weight, 2.3 kg for the same males, 1.32 kg for a slightly smaller female from the English Channel.

Geographical Distribution: Eastern Atlantic Ocean: from approximately 55°N, around the British Isles, the North Sea (including the Skagerrak, the Kattegat and the western Baltic Sea), to 20°S, off the southwestern coast of Africa, including Madeiran waters. Mediterranean Sea: from the western to the eastern basins, including the Adriatic Sea (Fig. 70).

Habitat and Biology: A neritic species that inhabits the circumlittoral region in temperate waters, the European squid ranges in depth from the surface down to the upper slope (200 to 500 m), mainly near coasts with abruptly sloping bottoms, but it is more abundant in waters shallower than 100 m in most of its range. It occurs mainly over coarse sand bottoms, but it also is reported over silt and other different mixtures of sediments and terrain, including sea grass beds. It lives in water temperatures that range from 12.5° to 20°C, with salinity ranges of between 30 psu (North Atlantic) and 38 psu (western Mediterranean), but it can tolerate lower salinity waters, e.g. Sea of Marmara. ***Loligo vulgaris*** generally has a pelagic habitus, but it becomes more dependent on the bottom during spawning seasons. Animals, especially young individuals, perform daily vertical migrations mainly related to feeding; they remain close to the bottom during the day, then disperse into the water column at night. Vertical as well as horizontal migrations in response to changes in environmental conditions also are known. The northeastern Atlantic population overwinters in deeper waters off the French coasts then migrates farther north from May through June-July, into the North Sea to spawn. A similar migration from the Bay of Biscay and more southern waters to the English Channel probably also occurs. Southward migrations take place in the autumn. Offshore and onshore migrations related to reproduction also occur. In the western Mediterranean, European squid migrate into deeper water in late autumn; the largest individuals begin their onshore migration as early as January and February, followed in summer by the smaller ones. Sex ratios slightly different from the usual 1:1 value may occur along the distributional range of the species. In

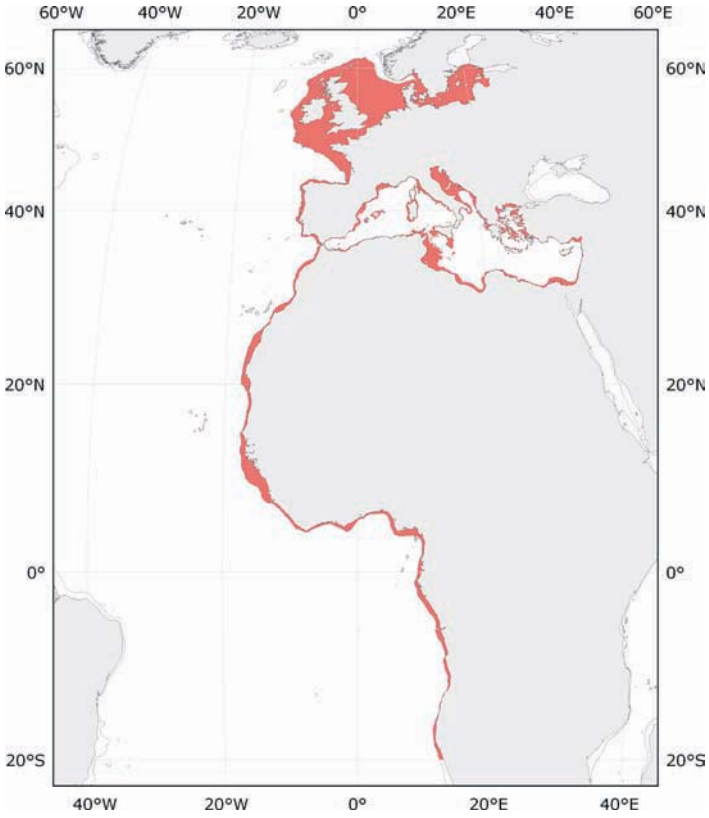


Fig. 70 ***Loligo vulgaris***

Atlantic waters, females were found to slightly outnumber males during some parts of the year, while the opposite occurs in some Mediterranean areas. No segregation between sexes has been reported for the Atlantic populations, whereas observations from landings in the western Mediterranean suggest that males and females may congregate in different schools.

No dramatic changes in the general morphology occur with sexual maturity; males attain larger sizes and weights than females, but females generally exhibit higher weights than males at a given length. A north–south (in the Atlantic) and west–east (from the Atlantic towards the eastern Mediterranean) decreasing gradient occurs in the weight to length growth ratio. Size at maturity is variable, depending on the geographic location, but generally males mature at a smaller size than females. The minimum reported size at maturity is 80 mm mantle length for males and 119 mm mantle length for females, with size at 50% mature (ML50) 168 mm and 188 mm mantle length for males and females, respectively, based on samples collected from different areas from the Atlantic Ocean and the Mediterranean Sea. The smaller-maturing males are reported from the Greek seas, the smaller females from the waters off France, while the larger animals for both sexes come from the Saharan Bank region, eastern Atlantic Ocean. Two modes in size at maturity are reported for males from most areas in the Atlantic.

Spawning extends throughout the year in most of the distributional range of the species, usually with 2 seasonal peaks that occur earlier in the south than in the north in Atlantic waters and earlier in the Atlantic than in the Mediterranean. A more restricted spawning period is reported for the North Sea and for the Greek Seas. A potential fecundity of more than 70 000 eggs is estimated for this species; fecundity usually varies with the size of females, as do spermatophore number and size in males, but sometimes small mature females may have a larger number of oocytes than larger-sized mature females. The maximum number of spermatophores reported is slightly over 1 000, and spermatophore length varies between 7.5 and 18 mm. Males reproducing for the second time usually carry more spermatophores than those reproducing for the first time. Eggs are small (diameter about 2 mm), although variability exists in egg size in relation to geographical area; they are deposited in gelatinous capsules (“fingers”) 60 to 160 mm long. Each capsule contains tens of eggs. Capsules are attached in clusters to rocks, debris and other hard objects on sandy to muddy bottoms. Females tend to lay eggs close to or on top other egg masses, so that large clusters of up to 40 000 eggs occur in nature. The individual contribution by a single female is limited to a thousand, up to 6 000, eggs. Apparently certain strains of *Roseobacter* bacteria associated with the accessory nidamental glands function to aid in the production of carotenoids and in the protection of eggs by production of antibiotics and toxins.

Embryonic development lasts from a few weeks to a few months, depending mainly on the ambient water temperature, e.g. 25 to 27 days at 22°C; 30 days at 17°C and 40 to 45 days at 12ºC to 14°C. A longer incubation time increases mortality risks for egg masses attached to the sea bottom; however, slow development at a lower temperature can improve yolk conversion and produce larger hatchlings, likely with increased hatching competence. Consequently, a compromise between longer-versus-shorter incubation time and related characteristics seems to exist. Paralarvae have a planktonic life style that lasts about 2 months. Although specific identification of ***L. vulgaris*** paralarvae is known in samples from the Galician and Portuguese waters, in general, little knowledge exists on this phase of the life cycle of the European squid in the wild, due mainly to the close resemblance with the juveniles of the co-occurring species, ***L. forbesii*** and ***Alloteuthis*** spp. Paralarvae in captivity feed on crustacean and fish larvae and small mysids; occasionally they attack conspecifics, but cannibalism seems not to occur in the wild. Hatchling growth rates are highly variable and strongly dependent on the water temperature. Experimental rearing under very different temperature regimes, i.e. summer-like and winter-like, resulted in sizes twice as large in the summer-like regime. As a consequence, sizes of juveniles and adults are strongly related to the environmental conditions close to hatching times, and growth rates are dependent on the hatching season. Early paralarval growth in ***L. vulgaris*** is exponential. Several mathematical models have been used to describe growth in juveniles and adults, namely, power, exponential, double exponential and logistic models. Differences in the growth rates between sexes also occur; males show higher growth rates than females. In both sexes, however, growth is not isometric and weight increases more slowly than length.

Life span duration based on statolith analysis is estimated to range between 9 and 10 months (southern Portuguese and West Saharan shelf waters) and 1.5 years (north Portuguese waters), considerably shorter than the 2 to 4 years previously estimated on the basis of length frequency analyses. Spawning represents the terminal phase of the life cycle. It progresses with active feeding in between periods of egg releases, as has been noted for other loliginid species. This behaviour is defined as “intermittent terminal spawning”, a strategy that combines with continuous oocyte maturation in the ovary to better utilize the high potential fecundity during the long periods of intermittent spawning.

The European squid feeds mainly on fishes and crustaceans. Cannibalism seldom occurs and no differences in the feeding habits exist between sexes. Young squids feed mainly on planktonic crustaceans and fish larvae, while fish dominate in the diet of adult animals. Diet and food intake vary with season, probably in relation to seasonal changes in the foraging grounds. ***Loligo vulgaris*** is preyed upon by a variety of whales and fishes, including comnmon dolphin, pilot whale, bottlenose dolphin, swordfish, greater amberjack and many other fishes and marine mammals. ***Loligo vulgaris*** is an important intermediate host for the parasitic nematode *Anisakis simplex*, to top-level predators such as marine mammals.

Interest to Fisheries: ***Loligo vulgaris*** is taken throughout its distributional range all the year round, mainly as a by catch of the multi-species bottom and pelagic trawl fisheries. Major fishing grounds are located off Portugal, on the West African Banks and in the western Mediterranean, where the species is caught in the international fisheries with otter trawls and purse seines in daytime and occasionally at night with light attraction. Usually it is landed mixed with ***L. forbesii***, and specific catch statistics are not recorded. In the western Mediterranean, however, it is one of the most important commercial species of cephalopod, and it has the highest market value. Also, it is a secondary target species in the Saharan Bank cephalopod trawl fishery. Throughout its distributional range, the European squid is the object of local artisanal fisheries that deploy a variety of gears, particularly jigs. Some directed small-scale hand-jig artisanal fisheries exist in Spain, Portugal and southern Italy. The species is marketed fresh and frozen. Catches by commercial beach seines in the Thracian Sea (eastern Mediterranean) are affected to a varying degree

by meteorological conditions, e.g. temperature, rainfall and local wind conditions, all negatively correlated. Also, in other areas, occurrence and abundance are related to oceanographic conditions, especially to sea temperature and salinity, and seasonal and annual abundance can be markedly variable (e.g. as recently is the case for the Catalan coast, northwestern Mediterranean).

Remarks: Male specimens occasionally may display stripes similar to those typical of ***Loligo forbesii***, on the ventral sides of the mantle; however, these stripes are much smaller, less numerous and less intensely coloured than in ***L. forbesii***. ***Loligo reynaudii*** was proposed to be subspecies of ***L. vulgaris*** (Augustyn and Grant, 1988). However, Vecchione *et al*. (2005) reinstated ***Loligo vulgaris*** and ***Loligo reynaudii*** as distinct species, a decision with which we concur.

Local Names: ALGERIA, BULGARIA, TURKEY, RUSSIA: Kalmar; CYPRUS, GREECE: Kalamari; FRANCE: Encornet; ITALY: Calamaro, Calamaro comune; EGYPT: Sobbeit Totanu; LIBYA: Habbar; MALTA: Kalamar; MOROCCO, SPAIN: Calamar; TUNISIA: Mettik; YUGOSLAVIA: Lignja.

Literature: Naef (1923), Mangold Wirz (1963), Worms (1983a, b), Roper *et al*. (1984), Nesis (1982, 1987), Augustyn and Grant (1988), Guerra (1992), Guerra and Rocha (1994), Boyle and Pierce (1994), Belcari (1999e), Moreno *et al*. (2002), Vecchione (2008e), Hastie *et al*. (2009).

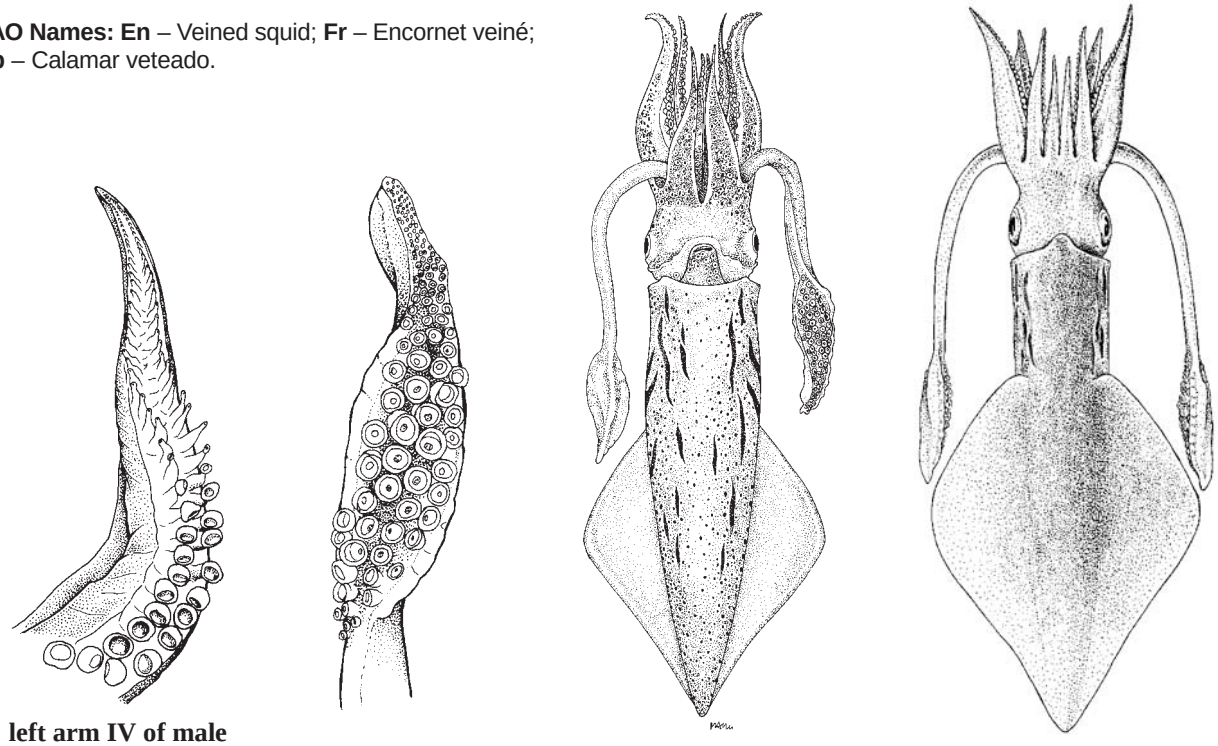
Loligo forbesii Steenstrup, 1856 **Fig. 71; Plate III, 14**

Loligo forbesii Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4:185-216, 2 pls [189]. [Type locality: Atlantic Ocean].

Frequent Synonyms: *Loligo fusus* Risso, 1854, *Loligo moulinsi* Lafont, 1871.

Misidentifications: *Loligo vulgaris* (formerly, multiple authors).

FAO Names: En – Veined squid; **Fr** – Encornet veiné; **Sp** – Calamar veteado.



left arm IV of male hectocotylized **tentacular club** **ventral view** **dorsal view**

Fig. 71 ***Loligo forbesii***

Diagnostic Features: Mantle long, moderately slender, cylindrical; fins rhomboidal, **their length three quarters that of mantle**, their posterior borders slightly concave. **Suckers on manus of tentacular club subequal in size**; sucker rings **regularly toothed** all around, with 13 to 18 larger sharp, conical teeth; largest arm sucker rings with 7 or 8 teeth; **left ventral arm hectocotylized in its distal third** by modification of **sucker stalks into long papillae which gradually decrease in size** distally; **accessory nidamental** glad present **in males**. **Colour**: prominent longitudinal **flame-like stripes** of purplish dark chromatophores on the anterior and ventrolateral surfaces of the mantle.

Size: Maximum mantle length 937 mm in males (8.3 kg weight) and 462 mm in females (2.2 kg weight), for animals from the Azores. Common at smaller sizes (200 to 300 mm mantle length) in the Mediterranean and on the eastern North Atlantic continental shelf.

Geographical Distribution: Eastern North Atlantic: 20°N to 60°N, including the North Sea; absent in the Baltic Sea. It ranges from the Faeroe Islands, along the western European coasts, west to the Azore Islands and south to the Canary Islands, along the West African coast. Its southern boundary is unknown. Occurs throughout the Mediterranean Sea, but early records of the species farther east and south, in the Red Sea and along the east coast of Africa are not confirmed (Fig. 72).

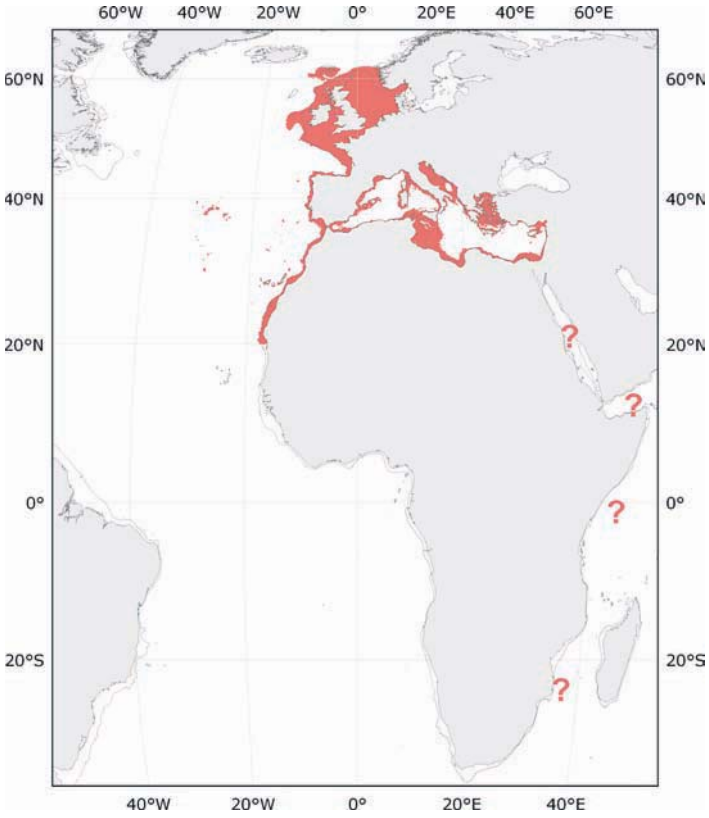


Fig. 72 ***Loligo forbesii***

Habitat and Biology: ***Loligo forbesii*** is a species of subtropical and temperate waters; it avoids temperatures below 8.5°C. It occurs over the continental shelf in the temperate part of its distributional range, but it is found in deeper waters in subtropical areas. Its entire vertical range extends from depths shallower than 50 to over 700 m, while the Azores population occurs deeper than 1 000 m. In the Mediterranean Sea, it very seldom occurs in waters less that 80 to100 m depth, and its bathymetric range overlaps only slightly with that of its congener ***Loligo vulgaris***. In Atlantic waters depth distribution varies by season, with squid remaining mostly in waters along the shelf edge (100 to 200 m), then gathering in waters of less than 50 m during the spawning peaks. In the North Sea and in the eastern North Atlantic, squid move inshore during winter, whereas they are more abundant in offshore waters during summer. Seasonal migrations also occur in the southern North Sea area, where the squid spend the summer in the eastern part of the English Channel and southern North Sea, then return to the deeper southwestern part of the Channel in winter. Sea surface temperature (SST), bottom water temperature (BWT) and the North Atlantic Oscillation (NAO) all are critical factors to ***L. forbesii*** abundance. Peak squid abundance in the English Channel coincides with bottom water temperatures of 13°C and squid abundance in the Northeast Atlantic, as well as in the Portuguese and Greek waters, is positively correlated with local SST.

No clear seasonal trend occurs in sex ratio in populations of the eastern North Atlantic waters, although in the Scottish population more young animals are males but adults are mostly females. Sexual dimorphism is striking: males attain much larger sizes and weights than females, but, as in ***L. vulgaris***, females generally exhibit higher weights than males at a given length. Size at maturity is very variable, as is the rule in many loliginids. The smallest mature male measured 80 mm mantle length, and the smallest mature female 103 mm mantle length, both recorded in Portuguese waters; considering the whole northeastern Atlantic range of the species, however, males start to mature at a minimum size around 150 mm mantle length and females around 170 mm mantle length. The Azores population exhibits the largest minimum mature sizes, 240 mm mantle length and 200 mm mantle length for males and females respectively. Two or 3 different size modes of maturity exist in both sexes, but they are more pronounced in males; this makes it less convenient to compute standard parameters like mean size at maturity (i.e. 50% maturity; ML 50).

Spawning occurs nearly throughout the year, with different seasonal peaks that depend on the geographical area, and multiple peaks may occur. For example, most of the Atlantic populations have winter breeding peaks, but secondary peaks may occur in other seasons, including summer. Little information is available on spermatophores. The maximum reported number of spermatophores is slightly over 1 000. Males show a positive relationship between spermatophore length and body length, but a weak relationship between total number of spermatophores and body size; males that mature at a larger size produce fewer but larger spermatophores than those that mature at a small size.

Potential fecundity is low compared with that of ***L. vulgaris***; it varies between 1 000 and 23 000 eggs and it is slightly positively related to the size of the female, but small mature females may have a larger number of oocytes than larger-sized mature females. Permanent oocyte maturation occurs, as it does in ***L. vulgaris***. Eggs are large compared to those of ***L. vulgaris*** and ***L. reynaudii***, about 3 mm x 2 to 2.8 mm, and they are more elongate in shape; they are embedded in the gelatinous substance produced by the oviducal and nidamental glands and then deposited in finger-like strings that usually contain 50 to 130 eggs each. Strings are attached in clusters to hard objects on various kinds of substrate (rocky, sandy or muddy bottoms). The number of egg strings in each cluster is variable and clusters may be formed by strings spawned by more than one female. Because mated females may carry spermatophores of more than one male, each string may be multi-paternal (i.e. fertilized by more than one male). Most egg mass records from the eastern North Atlantic are from shallow waters in inshore areas; only three records exist of deposition in offshore waters, 2 from off the west coasts of Ireland and France at 135 and 507 m depths,

and another caught by deep trawlers in the Aegean Sea from 720 to 740 m depth. Since most of the commercial samples that contain spawning animals are obtained from offshore waters, these findings support the hypothesis that ***L. forbesii*** may spawn at those sites, as suggested for this species in the Scottish waters. The scarcity of data may be due to unreported records of trawled egg masses and/or to the squids' preference for rocky substrates inaccessible to the bottom trawl fisheries. Embryonic development duration is closely related to water temperature; it increases as temperature decreases and varies between a few weeks (36 days at 16°C) and a few months (60 to 75 days at 12°C, 140 days at 8°C). Variation of the incubation period of eggs from strings in the same mass range between 45 to 64 days at 12°C; within-string variation in development time occurs in the majority of egg strings, with about 20 days between the first and last hatchling emergence. Such a wide variability in development may assure a spread of paralarval survival and recruitment. Newly hatched animals have mantle lengths between 3.0 and 4.6 mm, and they are already strong swimmers. An optimum temperature range of around 13°C is necessary for normal hatchling development. Growth is rapid, and males grow faster and attain a much larger size than females. As is the case observed in most loliginids, growth rates are higly variable, and growth itself is usually best described by an exponential phase in juveniles, followed by a secondary, slower, logarithmic stage. Several studies on ***L. forbesii*** growth patterns and characteristics in an aquarium include length-frequency, statolith and gladius increment analyses. Much variation in growth rates by sex, maturity stage, season and reproductive strategies exists. Despite the differences in age estimations by different techniques, a life span between 1 and 2 years generally is acknowledged. Sexual differences in the length-weight relationships indicate that females are always heavier than males at a given length.

Spawning represents the terminal phase of the life cycle. As with its congenerics, ***L. forbesii*** is an intermittent terminal spawner, wherein females lay several batches of eggs before they die.

Loligo forbesii feeds on small fishes and to a minor extent on other cephalopod species, crustaceans and polychaetes; cannibalism also occurs, but it seems limited to large squids feeding on much smaller ones. Primary prey items vary among geographical areas and seasons. The main food sources are as follows: in Scottish waters whiting (*Merlangius merlangius*), poor-cod (*Trisopterus* spp.) and sandeels (Ammodytidae) comprise the most abundant fish species in the diet, whereas in Irish waters sprat (*Sprattus sprattus*) and poor-cod *Trisopterus* spp., and off the Azores blue jack mackerel (*Trachurus picturatus*) dominate. Ontogenetic shifts in feeding habits occur. Crustaceans dominate in the diet of juveniles, but no sex-related nor maturation-related differences occur. Biochemical studies indicate than the veined squid is an important part of the benthic food-web. Several marine mammals like pygmy sperm whales, orca (killer) whales, common, striped and bottle-nosed dolphins, large demersal fishes (e.g. cod and scabbardfish), seals and seabirds feed on this species.

Interest to Fisheries: ***Loligo forbesii*** is one of the loliginid species of commercial importance in the eastern North Atlantic, especially in Scottish and Irish waters and the English Channel. It is taken mainly as bycatch in deeper water trawl fisheries throughout its range, and it rarely is abundant in the Mediterranean Sea, although some exceptions are known. A long-term, directed, strongly seasonal, fishery exists in the Moray Firth (North Sea, Scotland), and this has increased dramatically in recent years. Also, a directed jigging fishery is carried out off Madeira and the Azores, where the veined squid is the only squid species of economic importance. It is fished in the English Channel and marketed along with ***L. vulgaris*** which also occurs in Portuguese waters, where local artisanal hand-jig fisheries occur. Specific statistics do not exist, but this squid is highly appreciated for human consumption and as bait. It is marketed fresh, frozen and canned (small quantities in the Azores).

Remarks: Confusion about the name of the species exists (i.e. ***forbesi*** versus ***forbesii***). According to the International Code of Zooogical Nomenclature, both forms, in principle, are admissible (see Art. 31.1 and 3.1.2; ICNZ, 1999). However, Steenstrup's original description ended in "ii". According to Art. 32 (ICZN, 1999) original spelling is correct unless it is in one of the categories listed in Art. 32.5 as "spellings that must be corrected". In our opinion, this is not the case and the change in ending is an unjustified emendation (see also Sweeney and Vecchione, 1998).

Long placed in the genus ***Loligo***, the species was discussed as one of those with "unresolved generic affinities" in Vecchione *et al*. (1998). This was due to reports on potential bioluminescence and photophores presence (i.e. Alexeyev, 1992 [1991], Lum-Kong and Hastings, 1992), which were not confirmed subsequently. General consensus was reached in the 2003 CIAC meeting in Phuket to place the species back in the genus ***Loligo*** (Vecchione *et al*., 2005).

Various studies of morphometric variability throughout the species range in the Atlantic, along with molecular observations, suggest that no significant stock separations exist among mainland coastal populations (Pierce *et al*., 1994d, Brierley *et al*., 1995, Collins *et al*., 1999, Shaw *et al*., 1999). However, evidence indicates that animals from the offshore population around the Rockall Bank are different from coastal populations and that the Azores population is highly isolated. ***Loligo forbesii*** experienced a strong population decline in the southern end of its range in Atlantic waters in the 1990s, while its abundance increased in the northern areas (Chen *et al*., 2006); these trends seemed to be related to variations in the North Atlantic Oscillation (NAO). Also, changes in some Mediterranean areas occurred in the species distribution in recent decades, with an abrupt decrease in the Sicilian Channel, while the population in the Ionian Sea increased. Studies suggest that the changes in the deep water layers of the eastern Mediterranean influence these distributional shifts (Chen *et al*., 2006). *Roseobacter* bacteria in the accessory nidamental glands may aid in carotenoid production and in production of antibiotics and toxins for egg protection (Pichon *et al*., 2005b).

Local Names: FRANCE: Calmar, Encornet de Forbes, Encornet veiné; GERMANY: Langflossenkalmar; ITALY: Calamaro venato, Occhione; NETHERLANDS: Noordse pijlinktvis; PORTUGAL and AZORES: Lula, Lula riscada; SPAIN: Calamar veteado, Calamar de Forbes; RUSSIA: Dlinnoperiy Kalmar; UNITED KINGDOM: Common squid, Forbe's squid, Veined squid.

Literature: Naef (1923), Holme (1974), Martins (1982), Roper *et al*. (1984), Mangold and Boletzky (1987), Segawa *et al*. (1988), Guerra (1992), Boyle and Pierce (1994), Guerra and Rocha (1994), Boyle *et al*. (1995b), Belcari (1999d), Chen *et al*. (2006), Vecchione (2008e), Hastie *et al*. (2009).

Loligo reynaudii Orbigny, 1839–1841

Fig. 73; Plate III, 15–16

Loligo reynaudii Orbigny, 1839-1841, *in* Ferussac and D'Orbigny, 1834–1848, *Histoire Naturelle Générale et Particuliere Céphalopodes Acétabulifères Vivants et Fossiles*. 96 pages + lvi pages + 361 pages, Atlas with 144 plates. Paris. [315, Calamar pl 24]. [fide Tillier and Boucher-Rodoni (1994:102); taxon dated from plate]. [Type locality: Cape of Good Hope, Atlantic Ocean].

Frequent Synonyms: *Loligo vulgaris reynaudii*, Augustyn and Grant, 1988.

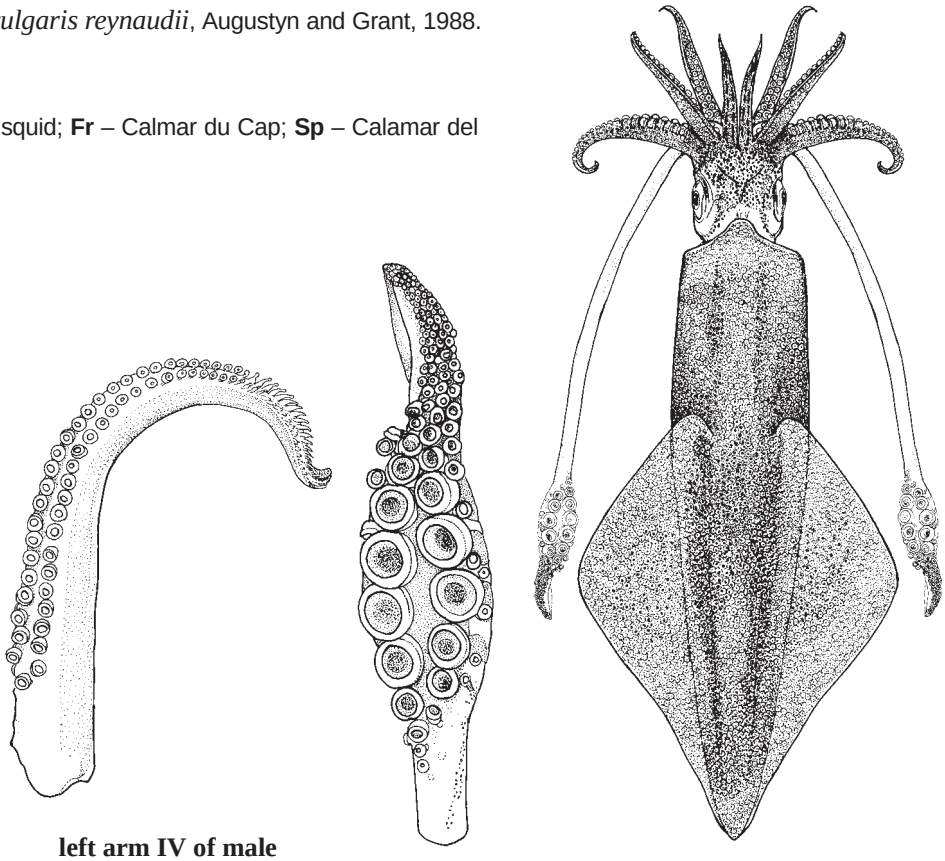
Misidentifications: None.

FAO Names: En – Cape Hope squid; **Fr** – Calmar du Cap; **Sp** – Calamar del Cabo.

Diagnostic Features: Mantle narrow, elongate. Fins long, 65% or more of mantle length. Tentacles long; **clubs expanded, with more than 36 transverse rows of suckers**; **club suckers on the manus** (medial series) **greatly enlarged**, club sucker rings smooth (medial manal sucker), or with 16 to 20 teeth.

Size: Maximum mantle length 400 mm; weight more than 1 kg.

Geographical Distribution: Southern African waters: eastern South Atlantic and southwestern Indian Ocean, from Namibia (28°S) on the west coast of Africa, to Cape Agulhas (35°S) and north on the east coast to at least 34°S, Port Alfred. Its eastern limits are unknown (Fig. 74).



left arm IV of male hectocotylized **tentacular club** **dorsal view**

Fig. 73 ***Loligo reynaudii***

Habitat and Biology: ***Loligo reynaudii*** occurs mainly along the continental shelf, down to depths of about 200 m. Offshore distribution reaches depths of 300 to 350 m. A migratory pattern exists for a large fraction of the population. Hatching occurs on the south and the east coasts of South Africa, between Plettenberg Bay, Cape St Francis and Port Alfred, where the major spawning areas are located. Paralarvae and juveniles are transported westward to the main nursery area on the Central Agulhas Bank, where feeding grounds for the adults also are located. The young squid migrate farther north along the southwestern African coast where they take advantage of the Benguela Current system to feed and grow; then they return to the eastern inshore waters to spawn. Size at maturity is highly variable, depending on geographic location and time of year. Males may be mature at 90 mm mantle length or immature at 250 mm mantle length and females at 100 mm mantle length and

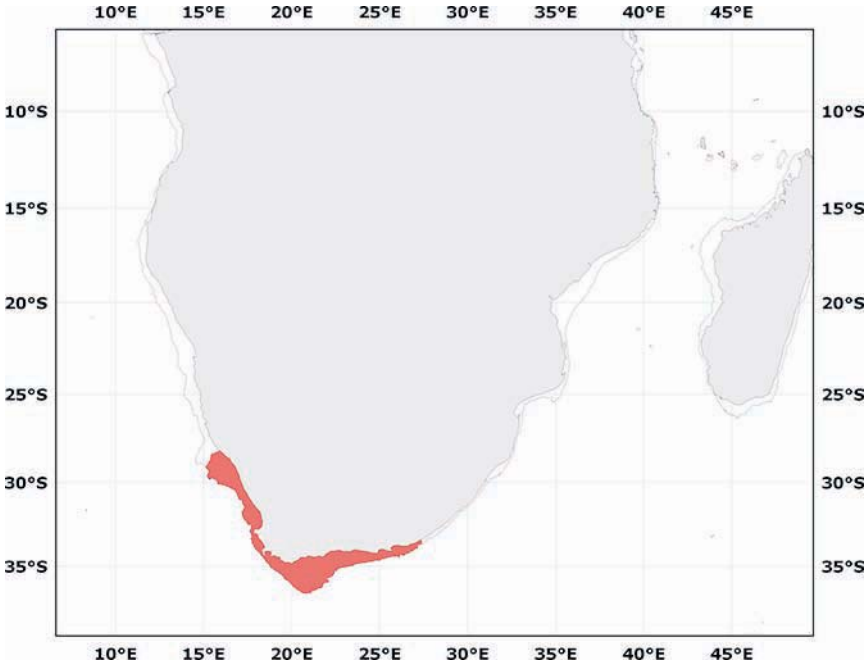


Fig. 74 ***Loligo reynaudii***

180 mm mantle length respectively. Modal length at spawning varies between 265 and 305 mm mantle length in males and between 175 and 195 mm mantle length in females. Spawning occurs mainly in shallow inshore waters (<60 m) of the bays off the Eastern Cape, with peaks in spring and summer (September to February), when the water temperature exhibits considerable variability (9° to 25°C), due mainly to wind-induced coastal upwellings. This may affect survival and development in the eggs and embryos. However, a small fraction of the spawning population occurs in deeper, cooler waters offshore to 120 m depth at 9° to 12°C, where the temperature regime remains relatively stable. Spawning concentrations are greater in association with westerly winds, zero turbidity conditions and sea surface temperature between 15° and 17°C.

Mature squid arrive on the spawning grounds in sexually segregated schools. Sandy areas or low-profile rocky reefs are favoured by spawning squid, and upwelling events, coincident with the formation of spawning aggregations, support the hypothesis that changes in temperature trigger spawning. Complex reproductive nuptial rituals occur on the spawning grounds. These rituals involve fighting, guarding, sneaking, mating and egg-laying behaviour. Mating occurs after the formation of squid "pairs", where large males mate with ripe females. Smaller, "sneaker" males frequently are excluded by the coupled pairs, but eventually are successful in mating with paired females.

Tagging studies, histological examination of the ovaries and aquarium observations confirm that the chokka squid is a serial spawner, and the term "uniseasonal iteroparity" has been proposed to define this spawning pattern, in which batch spawning occurs over an extended period of time and at different sites.

Ovulation in this species appears to be a rapid process, seen by the occurrence of both mature oocytes and post-ovulatory follicles in partially spent ovaries. Squid exhibit a diel pattern of spawning, with egg accumulation at night and active spawning during the day. During the spawning phase, ovaries go through ripe, partially spent and recovering stages by undergoing a process of maturation, ovulation and redeveloping, where a new batch of advanced oocytes is recruited. The cycle typically appears to last between 24 and 36 hours, and may depend on a number of factors such as environmental conditions and the presence of predators. Potential fecundity is about 17 000 eggs, and egg strands that contain an average of about 150 eggs are concentrated into distinct, aggregated spawning beds. Eggs are ovate, heavily yolked, about 2.8 mm long and 2.0 mm wide, and they are arranged in a spiral of about 100 eggs each in the gelatinous capsule ("finger"). Early-stage egg capsules are smooth, elongate, bright orange-coloured and transparent, with the eggs clearly visible. The capsules are attached to each other by interwined stalks that form large clusters embedded into the substrate. The eggs require about 35 days to hatch at 14°C and 16 days at 21° to 22 °C; they do not develop normally at temperatures below 10°C or above 24°C. The optimum temperature range for normal embryonic development is between 12° and 17°C, at which the development takes between 50 and 27 days, respectively.

Newly hatched chokka squid range between 2.3 and 2.5 mm mantle length; they are not strong swimmers and live a planktonic life for a short period. Abundant food for paralarvae exists in all regions of the Agulhas Bank. While paralarvae feed mainly on copepods, fishes constitute the main prey of adult squids, followed by crustaceans, polychaetes and cephalopods; maximum cannibalism occurs on the spawning grounds during the day. Chokka squid are preyed upon by several fishes, sharks and marine mammals when they congregate on their spawning beds. They also constitute the main prey for the groundfish community in the southern Benguela system. The duration of the life cycle is less than 2 years, and it ends after the last spawning event takes place; however, immediate post-spawning mortality seems not to occur on the spawning grounds investigated to date.

Interest to Fisheries: ***Loligo reynaudii***, commonly known as "chokka", it is the only cephalopod of major commercial importance in the South African fishing industry. The erratic fluctuations in catches have been the object of intensive research focused on the species distribution and spawning biology and the relationship of population composition with environmental constraints. Prior to 1980, the South African catch of squid was limited to bycatch from demersal trawlers that targeted fish species. Since then, however, increased demand has led to the establishment of a directed squid fishery that includes jig fishing. Commercial catches of chokka squid varied between a maximum of about 10 000 tonnes in 1989 to 2 500 tonnes in 1992. Catch values have risen dramatically, and chokka squid has become the most valuable South African fishery at USD 23 million in 1997. However, the high variability in squid catches can have devastating economic consequences to the fishing industry during years of reduced production. In an effort to forecast these fluctuations, quantitative models have been developed for prediction of spawning aggregations and spawning success in relation to environmental factors. Geographical Information Systems (GIS) are used to help understand the spatial and temporal biology of the chokka squid. Management measures are in place that control effort and designate a specified season for the directed jig fishery.

Remarks: Male specimens may display stripes similar to those typical of ***Loligo forbesii*** on the ventral sides of the mantle; however, these stripes are much smaller, less numerous and less intensely coloured than in ***L. forbesii***. ***Loligo reynaudii*** originally was differentiated from the closely related ***Loligo vulgaris*** by d'Orbigny (1839-1845) on the basis of morphological characters. Subsequently, Adam (1952) found the differences between the 2 species not to be significant, and additional studies based on the combination of morphological characters, meristic data on selected characters and electrophoresis lead to the conclusion that ***Loligo reynaudii*** was a subspecies of ***Loligo vulgaris*** (Augustyn and Grant, 1988). General consensus was reached in the 2003 CIAC meeting in Phuket that ***Loligo vulgaris*** and ***Loligo reynaudii*** are 2 distinct and separate species (Vecchione *et al*., 2005).

Literature: Adam (1952), Roper *et al*. (1984), Nesis (1982, 1987), Augustyn (1991a,b), Augustyn *et al*. (1994), Augustyn and Grant (1988), Lipinski *et al*. (1998a), Roeleveld (1998), Vecchione (2008e).

Afrololigo Brakoniecki, 1986

Afrololigo Brakoniecki, 1986, *Ph.D. Dissertation, University of Miami, Coral Gables, FL*, 163 pp. [92].

Type Species: *Afrololigo mercatoris* (Adam, 1941).

Diagnostic Features: Tentacular **clubs narrow**, small; suckers arranged in 4 series, 4 or 5 pairs of medial suckers on manus much larger than the lateral sukers; club sucker rings with 15 to 25 teeth. **Arms I extremely short** in comparison to the others. Arm sucker rings with square, plate-like teeth around entire margin. Left ventral arm of males hectocotylized, its proximal half with 6 to 12 pairs of normal suckers, its distal half with elongate papillae replacing the suckers, those of the dorsal row more strongly developed. Suckers on midsections of dorsolateral and ventrolateral arms (arms II, III) of males greatly enlarged. Head short; **buccal lappets without suckers**. **Mantle without posterior tail-like elongation**. **Fins rounded, short, broad with convex posterior margins**. Photophores absent.

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

Geographical Distribution: Atlantic coast of Africa.

Remarks: Brakoniecki established the genus ***Afrololigo*** in his Ph.D. Dissertation. Normally Dissertations do not have standing for systematic/nomenclatural purposes. However, Sweeney and Vecchione (1998:224) included a paragraph stating essentially that in F.M. Bayer's opinion, as a commissioner of ICZN, the way that Bakoniecki distributed his dissertation made the names available. Currently the genus is monotypic.

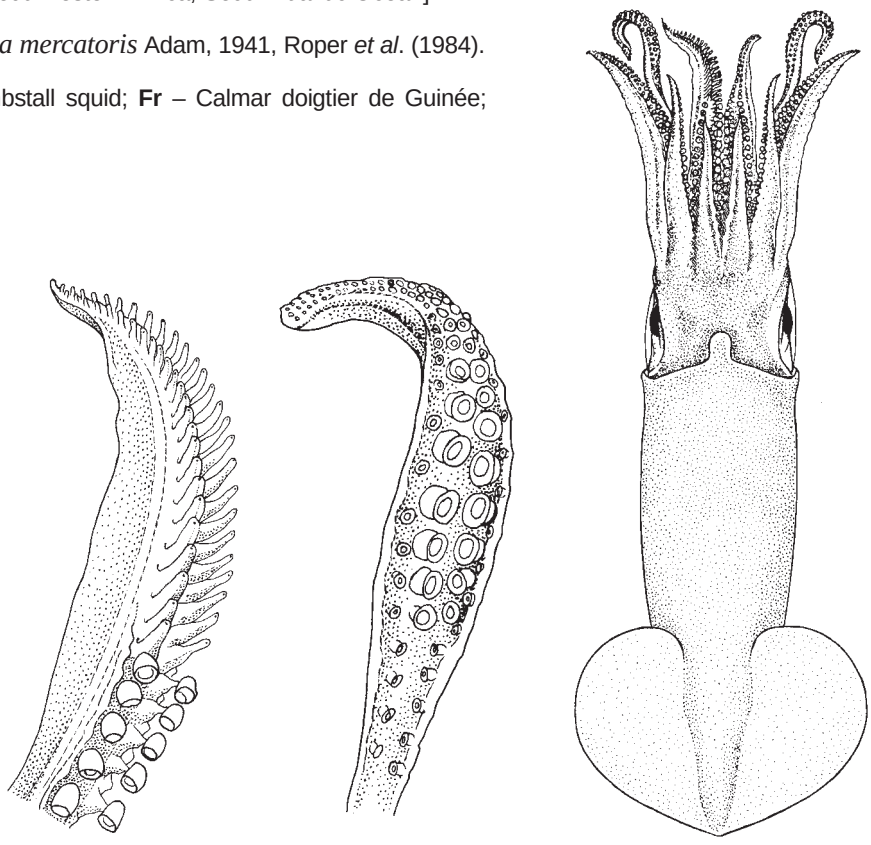
Afrololigo mercatoris (Adam, 1941) **Fig. 75**

Lolliguncula mercatoris Adam, 1941, *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, series 2, 21: 83–162. [125]. [Type locality: Luderitz Bay, southwestern Africa, South Atlantic Ocean].

Frequent Synonyms: *Lolliguncula mercatoris* Adam, 1941, Roper *et al*. (1984).

FAO Names: En – Guinean thumbstall squid; **Fr** – Calmar doigtier de Guinée; **Sp** – Calamar dedal de Guinea.

Diagnostic Features: Mantle broad (width about 35% of mantle length), and bluntly rounded posteriorly. **Fins rounded, short** (length 40 to 45% of mantle length), **broad** (width of both fins about 55 to 65% of mantle length) with convex posterior margins. Head short; buccal lappets without suckers. Tentacular **clubs narrow, small, with suckers arranged in 4 longitudinal series, 4 or 5 pairs of medial suckers on manus much larger than the lateral suckers**; club sucker rings with 15 to 25 more or less sharp teeth, larger and more pointed distally. Dorsal arms extremely short in comparison with the others; left ventral arm of males hectocotylized, its proximal half with 6 to 12 pairs of normal suckers, its distal half with elongate papillae that replace the suckers; the papillae of the dorsal row are more strongly developed.



hectocotylus **tentacular club** **dorsal view**

Fig. 75 ***Afrololigo mercatoris***

Size: Maximum mantle length 50 mm in females, 35 mm in males.

Geographical Distribution: Eastern central Atlantic Ocean: limited to the west coast of Africa from Rio de Oro (Mauritania) to Lüderitz Bay (Namibia) (Fig. 76).

Habitat and Biology: ***Afrololigo mercatoris*** is collected at depths of less than 50 m on mud and sandy-mud bottoms. Little information is available on its life cycle and biology. Eggs are small. Spermatophores have long cement bodies. Paralarvae are difficult to distinguish from early growth stages of ***Loligo reynaudii***.

Interest to Fisheries: This small species currently is not exploited.

Remarks: ***Afrololigo mercatoris*** shares many morphological characters with species of ***Lolliguncula***, the genus in which it was originally described by Adam (1941). However, based primarily on gladius characters (Alexeyev, 1989, 1991), DNA sequence data (Anderson, 2000a,b) and biogeography considerations, ***Afrololigo*** is recognized as a valid genus for this species (Vecchione *et al*., 2005). ***"Loligo" abulati*** Adam, 1955 in the Red Sea was thought to be related to ***A. mercatoris***, but currently it is placed in ***Uroteuthis (Photololigo)***.

Literature: Adam (1941), Roper *et al*. (1984), Brakoniecki (1986), Roeleveld (1998), Vecchione (2008a).

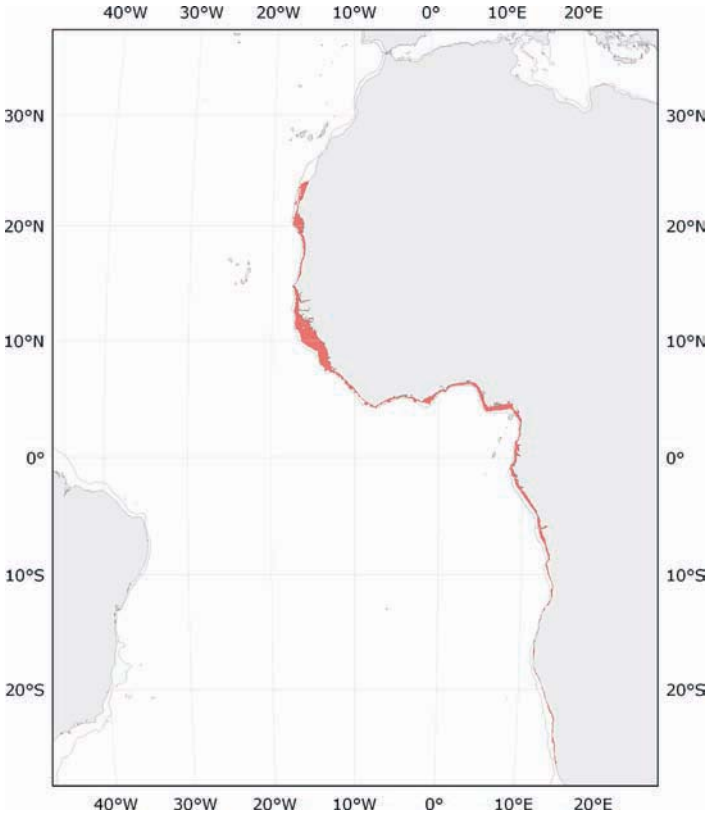


Fig. 76 ***Afrololigo mercatoris***

Alloteuthis Wülker, 1920

Alloteuthis Wülker, 1920, Senckenbergiana, 2(1): 48-58 [56].

Type Species: *Alloteuthis media* (Linnaeus, 1758).

Diagnostic Features: Tentacles long, robust; **clubs large, expanded**, with large suckers in the 2 median manal series. Hectocotylus without crest; proximal suckers unmodified, 10 to 12 (usually 11) normal suckers in ventral row followed distally by papillae. **Buccal suckers absent**. Mantle long, relatively narrow, **its posterior end drawn out into a narrow, pointed tail**, up to 60 mm long in adults. **Fins posterior, heart-shaped**, their lateral angles rounded, posterior borders concave, **extend posteriorly along tail**. Photophores absent.

Size: Small to medium-sized, maximum mantle length up to 205 mm.

Geographical Distribution: Eastern Atlantic Ocean and Mediterranean Sea.

Remarks: The close similarity between ***Alloteuthis*** and ***Loligo***, lead Vecchione *et al*. (1998b) to consider the former a subgenus of the latter. Subsequent molecular analyses, however (Anderson, 2000a,b), supported early morphological-anatomical considerations by Naef (1921b–1923) and Alexeyev (1989), that ***Alloteuthis*** should be a separate genus (Vecchione *et al*., 2005). The genus comprises 3 nominal species. Two species, ***A. media*** Linnaeus, 1758 and ***A. subulata*** Lamarck, 1798, occur in the eastern Atlantic Ocean, north of 20°N, and in the Mediterranean Sea. The third species, ***A. africana***, lives in the waters off West Africa, from southern Morocco to Namibia. In spite of the low level of species diversity, however, ***Alloteuthis*** taxonomy and systematics are confused and assignment of specimens to species may be difficult (e.g. Laptikhovsky *et al*., 2002b, 2005, Anderson *et al*., 2006, Anderson *et al*., 2008). Recent analyses of populations of

A. media and ***A. subulata*** from the eastern Mediterranean and the northwestern African waters indicate that a species complex probably exists that requires realignment of previous concepts of these 2 nominal species (Laptikhovsky *et al*., 2002b, 2005). Subsequent molecular phylogenetic studies (Anderson *et al*., 2006) reveal clades that do not correspond to the traditionally recognized ***Alloteuthis*** species; these clades include an Angolian/Mauritanian group (referable to ***A. africana***), a large eastern Atlantic/Mediterranean group (referable to ***A. media*** + ***A. subulata***) and a small group represented by specimens from the southwestern Adriatic Sea, morphologically indistinguishable from other specimens of ***A. media*** collected in the same area. It was suggested that this clade may represent a cryptic species. More recent data provide evidence that the character often used to distinguish ***Alloteuthis*** species (relative fin length) can be misleading (Anderson *et al*., 2008). Clearly, further studies are required to help define the whole species complex. Until the taxonomic situation with ***A. media*** and ***A. subulata*** is resolved, we retain them here as separate entities.

Literature: Naef (1921b, 1923), Roper *et al*. (1984), Vecchione *et al*. (1998b), Anderson (2000a,b), Anderson *et al*. (2006, 2008), Laptikhovsky *et al*. (2002b, 2005), Vecchione *et al*. (2005), Vecchione (2008b).

Alloteuthis media (Linnaeus, 1758) **Fig. 77**

Sepia media Linnaeus, 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*, 10(1): 824 p. [659]. [Type locality: “Pelago”].

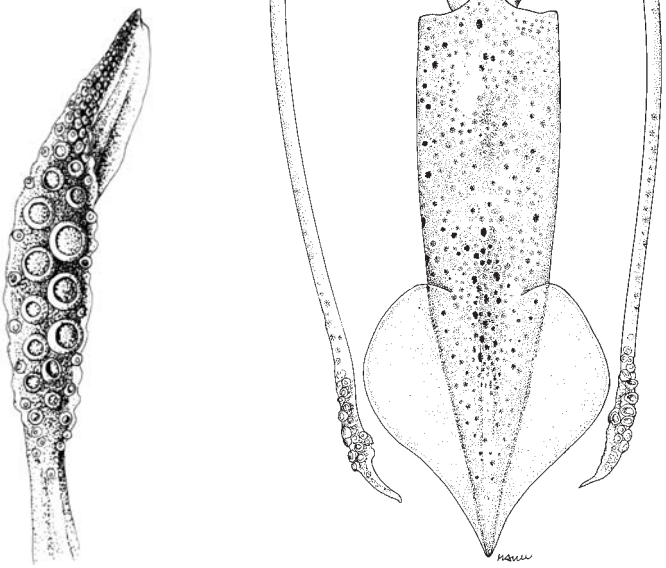
Frequent Synonyms: *Sepia media* Linnaeus, 1758, *Loligo parva* Leach, 1817, *Loligo marmorae* Verany, 1839, *Loligo urceolatus* Risso, 1854.

Misidentifications: *Loligo vulgaris*, *Alloteuthis subulata* (formerly, multiple authors).

FAO Names: En – Midsize squid; **Fr** – Casseron bambou; **Sp** – Calamarín menor.

Diagnostic Features: Mantle long, relatively narrow, its posterior end drawn out into a short, narrow, pointed tail, less than 10 mm long in adults. Fins heart-shaped, their lateral angles rounded, posterior borders concave, extend posteriorly along tail. Buccal suckers absent. Tentacles long, robust; **clubs large, expanded, median manal suckers large (9 to 14% of head width)**. Left ventral arm hectocotylized: 10 to 12 (usually 11) normal suckers in ventral row, followed distally by papillae.

Size: Small-sized squid; maximum mantle length 132 mm.



tentacular club **dorsal view**

Fig. 77 ***Alloteuthis media***

Geographical Distribution: Eastern North Atlantic Ocean and Mediterranean Sea: reported from about 20°N to 60°N in the eastern Atlantic. ***Alloteuthis media*** was considered very rare in the North Sea and, although old records from the Irish Sea and the English Channel do exist (late 1800s, early 1900s), recent reports on the presence of the species north of the Gibraltar Strait are limited to the northwestern Spanish coast. The species is widely distributed throughout the Mediterranean Sea, including the Sea of Marmara (Fig. 78).

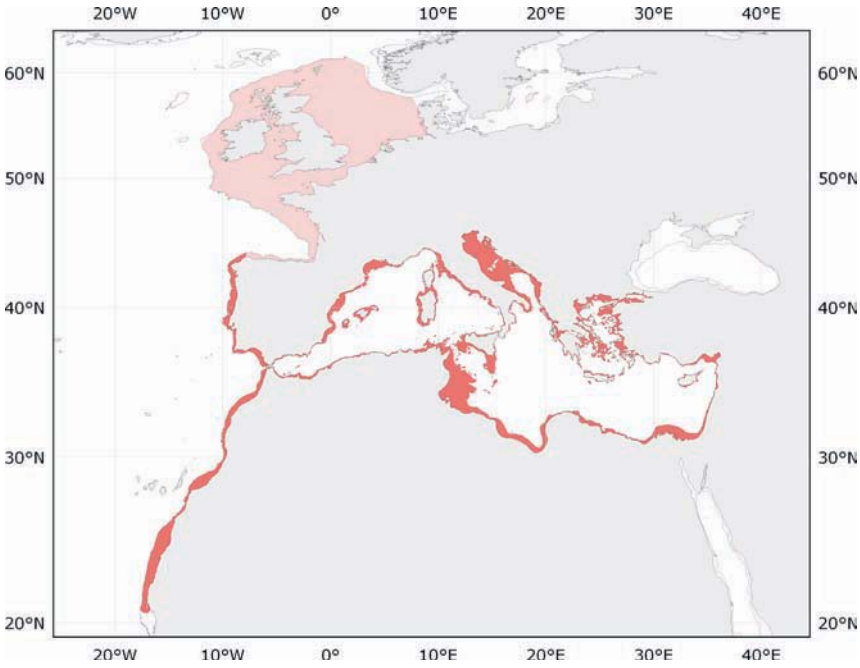


Fig. 78 ***Alloteuthis media***

Habitat and Biology: ***Alloteuthis media*** occurs on sandy and muddy grounds and preferentially inhabits coastal and shelf waters (from the surface to 200 m), even though it has been recorded down to about 500 m depth. Like other neritic squids, it performs seasonal migrations between offshore and inshore areas. In the western Mediterranean, spawning extends throughout the year, but 2 groups of spawners usually can be distinguished by size and time of peak spawning. Large individuals are encountered in February at depths between 150 and 200 m; from March to April, they start to migrate into shallower waters, where spawning takes place on sandy grounds and to a minor extent on Posidonia grass beds. The second group, composed of smaller individuals, migrates onshore in June and July and spawns later in the year. By late autumn, depending on environmental temperatures, they start returning to deeper waters. Also, 2 main reproductive peaks occur in the Northern Tyrrhenian Sea, in May and in September. Maturation occurs at a wide size range, both in the western and eastern Mediterranean, and a gradient of decreasing values in minimum mantle length at maturity from the western to the eastern basins, probably exists in the ***A. media*** populations, as seen in other Mediterranean cephalopods. The smallest mature females measure 80 mm mantle length, smallest mature males 50 mm mantle length in the western basin, and 37 mm mantle length and 32 mm mantle length in the eastern basin, respectively. The bulk of females mature at about 70 and 90 mm mantle length in the eastern and western Mediterranean, respectively and mantle length 50% was estimated to be about 60 mm mantle length in females and 50 mm mantle length in males in the Tyrrhenian Sea (Central Mediterranean). Females mature at 70 mm mantle length and males at 50 mm mantle length in the Adriatic Sea Central Mediterranean. Maximum length of ripe eggs varies between 1.4 and 1.6 mm in females from the western Mediterranean and from 1.5 to 2.3 mm in females from the eastern Mediterranean; also, fecundity is higher in females from the eastern basin compared to those from the western basin, i.e. 1 500 to 2 500 eggs versus 1 400 eggs. This suggests a higher reproductive potential in the eastern basin. Spermatophore length varies between 2.3 and 3.4 mm and the maximum number of spermatophores per male is 170. The eggs are laid in several batches and are encapsulated in short gelatinous capsules, like those of ***Loligo vulgaris***, but more fragile and transparent. The eggs are attached in batches or clusters to hard objects on the substrate (shells, corals, stones). ***Alloteuthis media*** feeds on crustaceans, molluscs and small fishes. The life cycle is estimated to be about one year in males and 1.5 years in females; females grow larger than males.

Interest to Fisheries: Generally ***A. media*** is captured as bycatch in the bottom trawl fishery throughout its distributional range. It is sold at most Mediterranean markets along with its congeneric species. An active, directed trawl fishery exists for this species in the western Mediterranean, where it is taken between 150 and 200 m depth in winter and in shallower waters of 50 to 150 m in spring, summer and autumn. Abundance of ***A. media*** along the Catalan coast, northwestern Mediterranean, varies significantly seasonally, but annual variations in abundance are minor. It is marketed fresh and frozen, and its commercial interest varies depending on the geographic location.

Local Names: FRANCE: Petit encornet; ITALY: Calamaretto comune; MONACO: Totanitu; SPAIN: Luria; UNITED KINGDOM: Little squid.

Remarks: Studies on the eastern Mediterranean ***Alloteuthis*** species populations suggested that those squids represent a single taxonomic unit and were considered to be ***A. media*** (Laptikovsky *et al*., 2002b). Subsequent morphological analyses indicated that ***A. media*** and ***A. subulata*** may represent extremes of a morphological gradient in a single species (Laptikhovsky, *et al*., 2005). More recent molecular data analysis support a sister-species relationship between ***A. media*** and ***A. subulata*** and reveal significant genetic differentiation between Atlantic and Mediterranean ***A. media*** (Anderson *et al*., 2008). Morphometric analyses by the same authors confirm that central club sucker size is a reliable character to separate ***A. media*** from ***A. subulata*** (Anderson *et al*., 2008).

Literature: Mangold Wirz (1963), Roper *et al*. (1984) Auteri *et al*. (1987), Nesis (1982, 1987), Guerra (1992), Belcari (1999a), Laptikovsky *et al*. (2002b, 2005), Anderson *et al*. (2006, 2008), Vecchione (2008b).

Alloteuthis africana Adam 1950

Alloteuthis africana Adam 1950a, *Bulletin du Institut Royal des Sciences naturelles de Belgique*, 26(45): 1–9. [1]. [Type locality: 0°03'S, 9°07'E, eastern South Atlantic].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – African squid; **Fr** – Casseron africain; **Sp** – Calamarin africano.

Diagnostic Features: Mantle long and narrow; mantle width 20 to 25% mantle length in juveniles, 15% in adult females, 5% in adult males; anterior ventral mantle margin squarish in outline. Tail (fins and posterior mantle projection) very long and pointed in females (37% of dorsal mantle length in juveniles 58% in adults) and extremely long and spike-like in males (35% in juveniles, 73% in adults). Fins oval in outline, fin width index (width of both fins as a percentage of dorsal mantle length) 23% in adult females and 10% in adult males; posterior border of fins concave; arms very short; buccal lappets without suckers. **Diameter of club suckers of median 2 series 3 times greater than lateral suckers**. Club sucker rings with 20 to 30 blunt teeth. Left ventral arm hectocotylized by modification of distal 40% of length; 8 to 11 pairs of normal suckers proximally followed by 2 longitudinal series of elongate papillae that gradually decrease in size distally; arm suckers with 6 to 10 square teeth on distal half, smooth on proximal half.

Size: Medium-sized squid; maximum mantle length 205 mm in males, 175 mm in females.

Geographical Distribution: Eastern Atlantic: from 20°S to 25°N (Fig. 80).

Habitat and Biology: ***Alloteuthis africana*** is found on the continental shelf off the western African coasts, at depths of 20 to 100 m and temperatures of 16° to 26°C. It feeds on small fishes and reproduction apparently occurs year-round. Studies on age and growth of the species based on statolith analysis indicate a life span of less than 1 year, with males not older than 8 months and females about 6 months old. Growth is faster than that of the congener ***A. subulata*** in the same area.

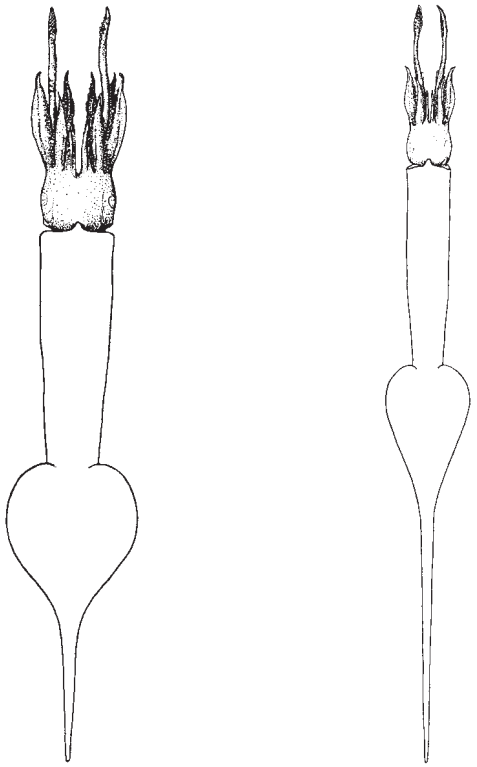
Interest to Fisheries: Captured only as bycatch in local trawl fisheries. Separate statistics are not reported for this species.

Local Names: None available.

Remarks: Analyses of morphometric data suggest that head width can be used to separate ***A. africana*** from the other 2 species (Anderson *et al*., 2008).

Literature: Adam (1950a), Roper *et al*. (1984), Arkhipkin and Nekludova (1993), Anderson (2000a), Anderson *et al*. (2008), Vecchione (2008b).

Fig. 79



dorsal view of female **dorsal view of male**

Fig. 79 ***Alloteuthis africana***

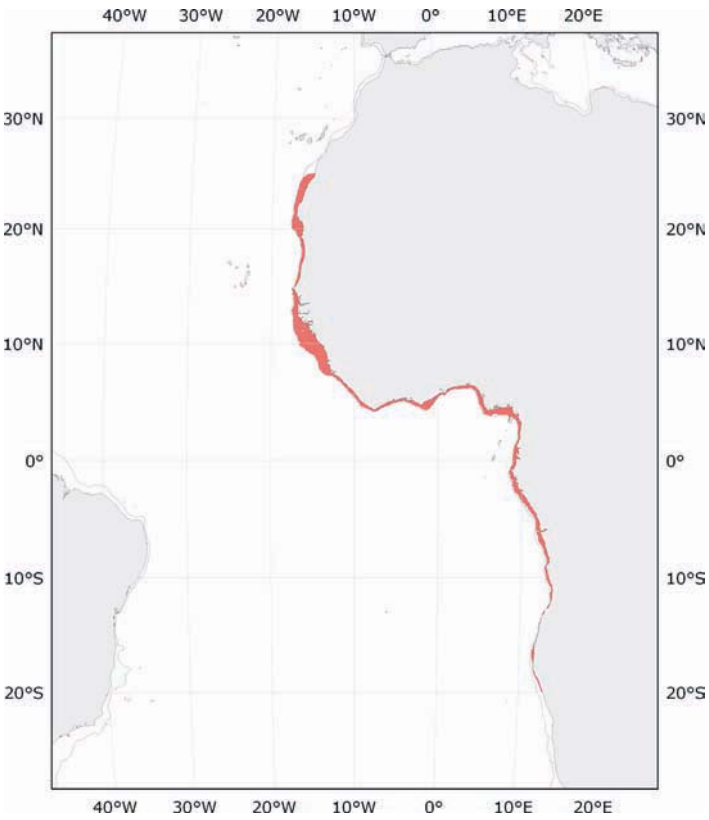


Fig. 80 ***Alloteuthis africana***

Known distribution

Alloteuthis subulata (Lamarck, 1798)

Fig. 81; Plate III, 17

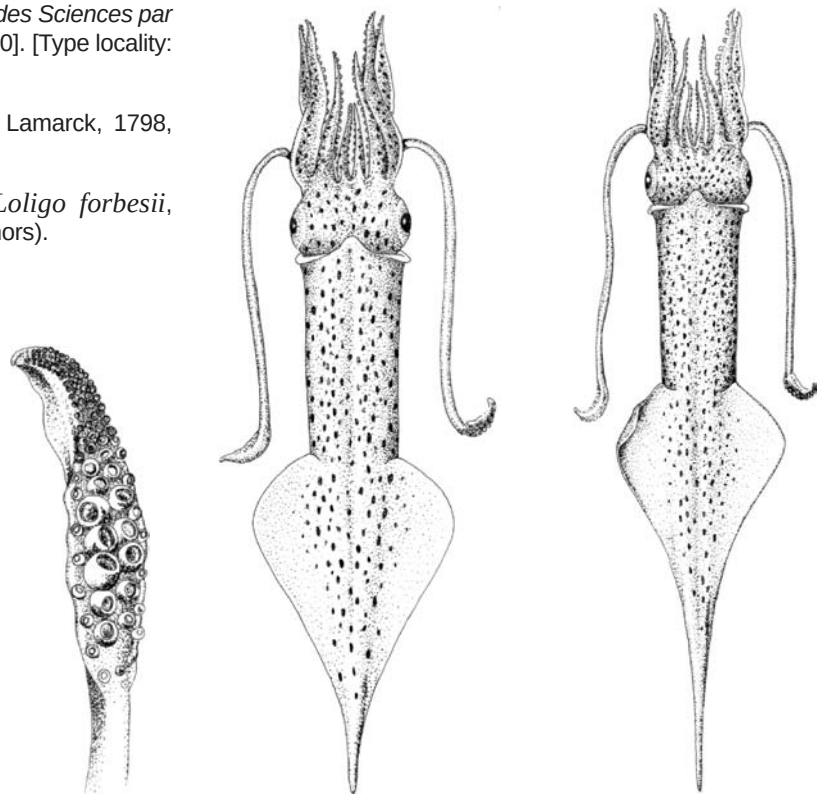
Loligo subulata Lamarck, 1798, *Bulletin des Sciences par la Societe Philomatique*, 2(5):129–131 [130]. [Type locality: Mediterranean Sea].

Frequent Synonyms: *Loligo subulata* Lamarck, 1798, *Sepia subulata* Bosc, 1802.

Misidentifications: *Loligo vulgaris*, *Loligo forbesii*, *Alloteuthis media* (formerly, multiple authors).

FAO Names: En – European common squid; **Fr** – Casseron commun; **Sp** – Calamarín picudo.

Diagnostic Features: Mantle long and narrow; anterior ventral mantle margin slightly curved; tail long (up to 20 mm) and pointed in adult females (length of posterior extension plus fins equals 66% of mantle length); tail very long (up to 50 to 60 mm) and spike-like in adult males (72% of mantle length). Fins rhombic, with pointed lateral angles, their posterior borders concave and they extend along the tail; fin length exceeds 50% of mantle length. Buccal lappets without suckers; tentacles short, delicate; **clubs small, narrow, median manal suckers small (6 to 8% of head width)**. Arms are medium to short; left ventral arm hectocotylized, with 6 to 8 pairs of normal suckers proximally, followed distally by 2 longitudinal series of fine papillae.



tentacular club **dorsal view of female** **dorsal view of male**

Fig. 81 ***Alloteuthis subulata***

Size: Small to medium-sized squid; maximum mantle length 184 mm in males, 140 mm in females.

Geographical Distribution: Eastern Atlantic Ocean, from approximately 60°N to 20°S: western Baltic Sea (sporadic), North Sea and Celtic Sea, to the western coast of Ireland, south to the Sahara Banks, where the limits of its distribution probably are located at Cape Blanc. Throughout the Mediterranean Sea, except its easternmost part, i. e. not represented in Turkish waters or the Sea of Marmara (Fig. 82).

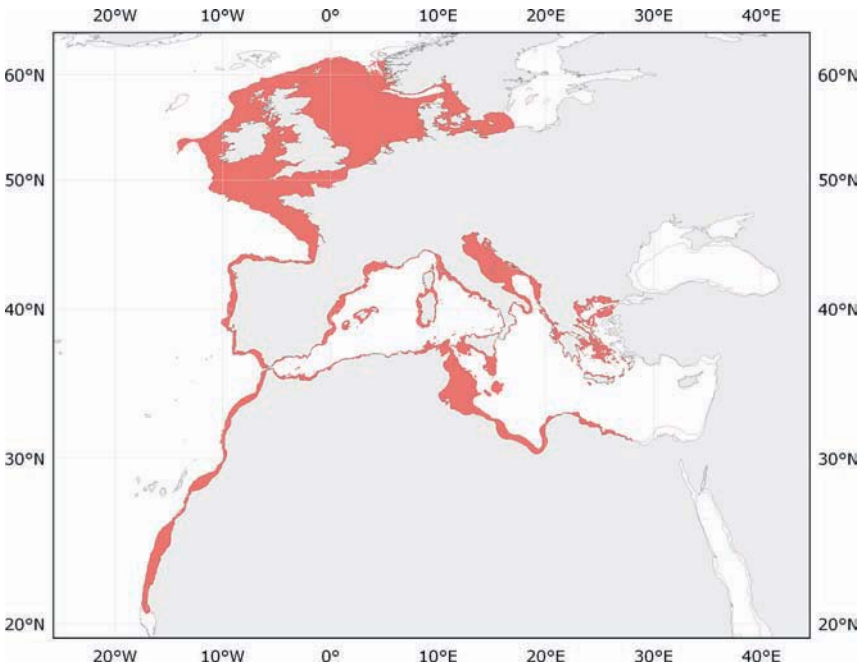


Fig. 82 ***Alloteuthis subulata***

Habitat and Biology: Associated mostly with sandy and muddy bottoms but also present on hard substrata, i.e. coralligen, ***Alloteuthis subulata*** occurs from coastal shallow waters (less than 50 m) down to about 500 m, even though captures below 300 m are sporadic. It is reported as the most abundant cephalopod in the North Sea and the adjacent Skagerrak, where it forms dense aggregations over sandy and muddy bottom in shallow areas. It also is recorded in high quantities in the Celtic Sea and Irish waters, where it concentrates in inshore areas; it is rather common in the English Channel coastal waters, and it often is reported as abundant in Portuguese waters. It is less common in the Mediterranean Sea, where it is considered rare in some areas, and it generally is less frequently caught than the congeneric and sympatric

A. media. Seasonal migrations occur in the North Sea, where mature males and females arrive together in inshore waters in spring/early summer and juveniles leave in autumn and early winter to migrate into the Atlantic Ocean.

Sexual dimorphism consists mainly of the longer tail that characterizes adult males. Maturation occurs at a wide size range, as in the congener ***A. media***, with males maturing earlier than females and probably living longer. Animals start to mature at about 30 to 50 mm mantle length and in Portuguese waters manle length at 50% maturity (ML 50%) is 75 to 80 mm in females and 70 to 75 mm in males. An extended spawning period characterizes the English Channel population, where three main spawning peaks occur in spring, summer and autumn. Once mature, males start to mate and release spermatophores and continue to do so for the rest of their life span; this implies the possibility to mate with females of different cohorts. Mating in the laboratory occurred only head-to-head (or buccal-crown-to-buccal-crown) and spermatophores usually were placed on the ventral portion of the buccal membrane.

Eggs are small. Also, egg capsules are small, 20 to 40 mm long, and balloon-shaped, attached by “stalks” to hard substrata. Embryonic development lasts 2 to 3 weeks at temperatures of 15° to 18°C, and the small hatchlings, 1.5 to 2.2 mm mantle length, have a planktonic life phase of a few weeks before they become demersal. Growth rates are slower than those of the congener ***A. africana***, and in general, both species are considered among the slowest growing, in terms of percentage increase of body weight per day, of the family Loliginidae.

Life span is estimated to be about 1 year in the English Channel, much longer than that on the West African shelf, where it is estimated to be about 6 months.

Interest to Fisheries: ***Alloteuthis subulata*** is a bycatch in trawl fisheries throughout its range; in the Mediterranean Sea it is taken at 20 to 120 m depths over sandy-muddy bottoms. It is sold at most Mediterranean seafood markets along with the congeneric species ***A. media***, marketed fresh and frozen. Separate statistics are not reported and the species is considered of variable commercial interest depending on the geographic location.

Local Names: ITALY: Calamaretto puntuto.

Remarks: Effective schooling behaviour in response to light, predators, food and other external stimuli was observed in the laboratory (Lima *et al*., 1995). Recent genetic analyses indicate that ***A. media*** and ***A. subulata*** may represent extremes of a morphological gradient in a single species, or perhaps that these entities, in a different taxonomic arrangement, will turn out to be a species complex (Laptikhovsky *et al*., 2005). More recent molecular analyses support a sister-species relationship between ***A. subulata*** and ***A. media*** (Anderson *et al*., 2008). Morphometric analyses by the same authors confirm that central club sucker size can be used to separate ***A. subulata*** from ***A. media*** (Andersen *et al*., 2008).

Literature: Roper *et al*. (1984), Nesis (1982, 1987), Guerra (1992), Arkhipkin and Nekludova (1993), Belcari (1999b), Laptikovsky *et al*. (2002b, 2005), Anderson *et al*. (2006, 2008), Hastie *et al*. (2009).

Doryteuthis Naef, 1912

Doryteuthis Naef, 1912b, *Zoologischer Anzeiger*, 39(25):741–745 [742].

Type Species: *Loligo plei* (Blainville, 1823).

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Hectocotylus on left ventral arm IV with proximal suckers unmodified; ventral crest absent; suckers of reduced size and sucker stalks elongated to form papillae on dorsal or both dorsal and ventral series. **Fins posterior**. **Eggs small to moderate sized, less than 4 mm long**. Spermatophore cement body short. Photophores absent.

Geographical Distribution: American waters of the western Atlantic and eastern Pacific Oceans.

Remarks: Two subgenera currently are recognized. Since the type species of the formerly monotyic genus belongs to the subgenus ***Doryteuthis***, the subgenus ***Doryteuthis*** is treated first in this work.

Literature: Vecchione *et al.* (2005), Vecchione (2008c).

Key to the subgenera of *Doryteuthis*

1a. Modified portion of hectocotylized arm extends to arm tip; edges of gladius vane thickened; . . . . . ***Doryteuthis (Doryteuthis)***

1b. Modified portion of hectocotylized arm does not extend to arm tip; edges of gladius vane not thickened . . . . . ***Doryteuthis (Amerigo)***

Subgenus ***Doryteuthis*** Naef, 1912

Doryteuthis Naef, 1912b, *Zoologischer Anzeiger*, 39(25): 741–745 [742].

Type Species: *Doryteuthis (Doryteuthis) plei* (Blainville, 1823).

Doryteuthis (Doryteuthis) plei (Blainville, 1823)

Fig. 83; Plate IV, 23; Plate V, 24–25

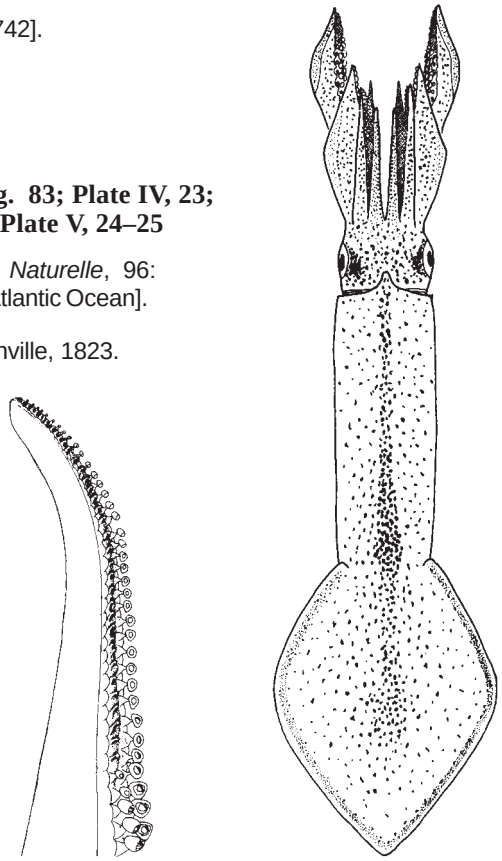
Loligo plei Blainville, 1823, *Journal Physique Chimie d'Histoire Naturelle*, 96: 116–135 [132]. [Type locality: Martinique, West Indies, western North Atlantic Ocean].

Frequent Synonyms: *Loligo plei* Blainville, 1823, *Loligo pleii* Blainville, 1823.

Misidentifications: *Loligo pealeii* (formerly, multiple authors).

FAO Names: En – Slender inshore squid; **Fr** – Calmar flèche; **Sp** – Calamar flecha.

Diagnostic Features: Mantle long, slender, cylindrical, the posterior end acutely pointed; fins rhomboidal, their sides fairly straight, widest point curved. Low, narrow, midventral ridge often present, particularly on males. **Left ventral arm hectocotylized in mature males by a modification of distal half to fourth of arm that extends to arm tip**; one half to three-fourths (42 to 82) of suckers in dorsal row much smaller than half the size of their ventral counterparts; modified (small) suckers on small, narrow, triangular pedicels. Gladius slender, feather-shaped; ratio of greatest width of vane of gladius to greatest width of rachis 1.5 to 2.7; edge of vane straight (often slightly curved in females), thick, and ribbed (especially mature males). **Suckers present on ventral buccal lappets**. Eye not unusually large; diameter of externally visible eyeball 14 to 19% of mantle length, diameter of dissected lens 2 to 7% of mantle length. **Colour**: (dark) reddish brown dorsally, darkest along dorsal midline of mantle; lighter, more yellowish background colour ventrally with reddish brown overlay; often with reddish brown longitudinal stripes on anterior ventrolateral mantle of males.



hectocotylus **dorsal view**

Fig. 83 ***Doryteuthis (Doryteuthis) plei***

Size: Medium-sized squid; maximum mantle length 370 mm in males, 260 mm in females.

Geographical Distribution: Western Atlantic Ocean, in continental shelf and upper slope waters from Cape Hatteras (36°N) (very rarely strays north to southern New England) to northern Argentina (35°S), often in association with the warm Brazil Current; this includes the Gulf of Mexico, the Caribbean Sea, Bermuda, Bahamian and Caribbean Islands (Fig. 84).

Habitat and Biology: This squid occurs from the surface to about 370 m depth, though it occurs mostly shallower than 200 m; apparently concentrates near the bottom during the day and disperses into the water column at night, when it can be dip-netted at the surface. Some sexual dimorphism is evident in the species: the gladius is wider in females, while male gladii usually have straighter margins with stronger lateral ribs. Ventral longitudinal ridges are more often present in males than females, and mature males often have ventrolateral stripes of chromatophores along the ventral mantle.

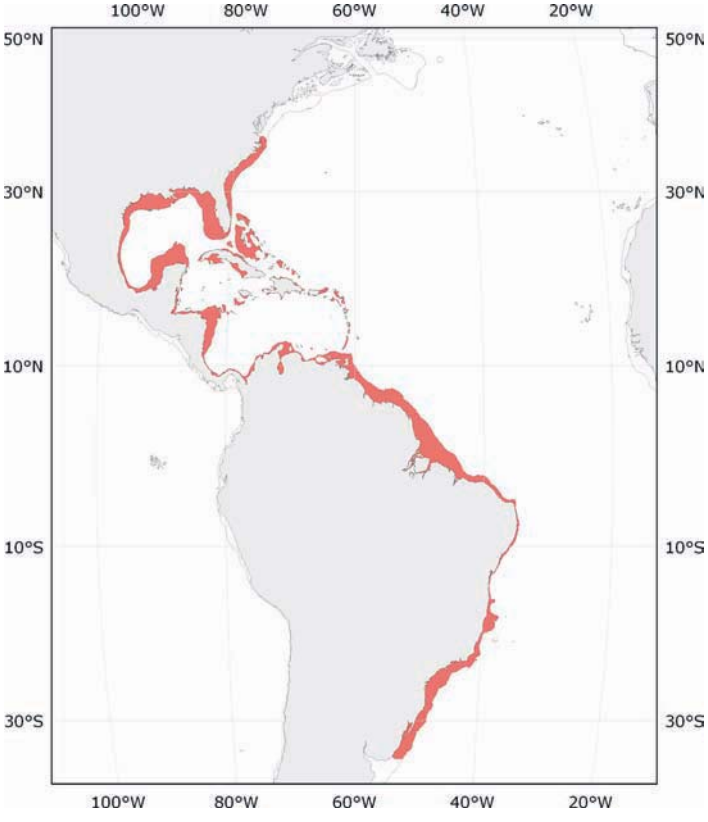


Fig. 84 ***Doryteuthis (Doryteuthis) plei***

Maturity occurs over a broad range of sizes depending on season and locality, the smallest mature males are 38 mm mantle length, the smallest females 42 mm mantle length, whereas they can remain immature up to 148 mm (males) and 143 mm (females); 50% maturity occurs at 175 and 155 mm mantle length in males and females of the northeastern Venezuelan waters, and at 194 and 141 mm mantle length for males and females off southern Brazil's offshore waters (Santa Catarina). In that area, however, studies on the coastal squid population give much lower values (i.e. 147 mm ML for males and 97 mm ML for females), suggesting the existence of a population distinct from the offshore squids. Immature and mature specimens of a broad range of sizes may be caught in the same net-haul. Mature squid are present throughout the year, but 2 seasonal peaks occur in the populations studied: in spring and autumn in the Caribbean Sea, in late spring-early summer and autumn off the northeastern Venezuelan coasts, and in summer and winter in the southern Brazilian waters. Mating and spawning occur year round, but observations on specimens kept in aquaria indicate post-spawning mortality. Underwater observations reveal no immediate mortality to occurr after spawning, while observations on the sex-ratio distribution of the southern Brazilian population after the spawning events indicate post-spawning mortality. It is probable, though, that the extent of the spawning phase varies depending on several different factors. Also, due to the wide geographical range covered, the duration of the species' life cycle may vary, depending on geographic location and the specific environmental constraints that affect growth. At present, reproductive patterns and size structure of ***D. plei*** landed along the southern Brazilian coasts indicate an annual cycle for the species there, in agreement with earlier estimates for populations farther north. However, statolith and age studies on the northwestern Gulf of Mexico population (i.e. on samples from a much warmer and more productive region) revealed a very rapid, non-asymptotic growth and a life span of about 6 months. Combined analyses of gladius and statoliths suggest a "compromise" of about nine months as the probable life span for this species off southern Brazil. ***Doryteuthis plei*** feeds on crustaceans, small fishes and squids. It is preyed upon by a variety of vertebrates, including fishes, dolphins, fur seals and penguins.

Interest to Fisheries: ***Doryteuthis plei*** is caught throughout its geographic range, but separate statistics are not kept where it may co-occur with ***D. pealeii***. The former species comprises most of the cephalopod fishery in Venezuela, and a small fishery occurs in Yucatan. In the Bahamian and Caribbean Islands undoubtedly it is the most frequently captured commercial species of Loliginidae, and it has been an important component of the trawl fishery bycatch in the southern Brazilian waters for many years; there, when the crisis in the shrimp fishery forced the fleet to find alternative target species in the bycatch to reduce operation costs, interest in squids increased and ***D. plei*** now is the subject of directed small-scale fisheries both inshore and offshore. The principle gear includes otter trawls and dipnets. It is used as food and bait.

Local Names: USA: Arrow squid; VENEZUELA: Luria.

Remarks: Whitaker (1978), Hixon (1980a) and Sanchez *et al*. (1996) computed several indices in order to separate ***D. plei*** from ***D. pealeii***; the most reliable is the ratio of gladius width to rachis width (GW/RW), combined with the overall shape of the gladius, including the presence or absence of marginal ribs (present in ***D. plei***). In particular, the GW/RW ratios range from 1.9 to 2.7 in ***D. plei*** and from 2.1 to 3.8 in ***D. pealeii***, and the separation of the 2 species is best accomplished with a GW/RW ratio of 2.7. However, the 2 species are so similar morphologically, that a very careful examination of the collected samples always is recommended, especially in the areas where they are sympatric. The broad geographic range of ***D. plei*** makes it an interesting candidate to investigate adaptations to different environmental/oceanographic regimes, such as plasticity in growth and reproduction rates among different populations. Available information indicates that a small, isolated population exists in Bermuda waters, and an investigation on ***D. plei*** in the Gulf of Mexico revealed a genetic break between the northwestern Gulf of Mexico and the northeastern Gulf-western Atlantic populations (Herke and Folz, 2002).

Literature: Cohen (1976), Roper *et al*. (1984), Arocha and Urosa (1991), Sanchez *et al*. (1996), Perez *et al*. (2002), Herke and Folz, (2002), Jackson and Forsythe (2002), Vecchione (2002, 2008c).

Doryteuthis (Doryteuthis) roperi (Cohen, 1976) **Fig. 85**

Loligo roperi Cohen, 1976, *Malacologia*, 15(2): 299–367, [346, figs 27-30]. [Type locality: 25°42'30"N, 79°20'W, Caribbean Sea, western North Atlantic Ocean].

Frequent Synonyms: *Loligo roperi* Cohen, 1976.

Misidentifications: *Doryteuthis plei*.

FAO Names: En – Island inshore squid; **Fr** – Calmar créole; **Sp** – Calamar insular.

Diagnostic Features: Mantle long, slender, cylindrical; tapers to an acute posterior point. Fins rhomboidal, with curved lateral and anterior margins, that give them a heart-shaped or oval appearance in some specimens; **fin length about 33 to 39% mantle length**. Tentacles short, robust; clubs expanded, about 14 to 21% mantle length, with <25 transverse series of suckers. **Left ventral arm hectocotylized for >50% of arm length** (57 to 62%); about 80% of suckers in dorsal series modified to minute size, set on broadly triangular bases. Reddish brown chromatophores over the entire mantle, larger and more closely spaced on posterior half of dorsal side.

Size: Small-sized species, maximum mantle length 72 mm.

Geographical Distribution: Western Atlantic Ocean: Caribbean Sea and Gulf of Mexico (Fig. 86).

Habitat and Biology: The island inshore squid probably is widely distributed on the continental shelf of the Caribbean Sea, but its vernacular name reflects its apparent association with the islands therein. The species has been repeatedly recorded on the Flower Garden Banks, in the northwest Gulf of Mexico. Here, seasonal aggregations of juvenile and adult squid are observed during the annual coral spawning event (about 7 to 10 days after the first full moon in August and in September if there is a split spawning). Ancillary observations suggest that squid may be attracted by coral spawning, or the squid may spawn then as well. Alternatively, they may aggregate to utilize the prolific food resources made available by the coral spawning event. Maturation occurs at a small size: the smallest mature males measure 44 mm mantle length, the smallest mature females are 43 mm mantle length. Some sexual dimorphism occurs: the margins of the vane of the gladius are straighter in males, more tapered in females; the fins of most males are more rhombic than those of most females and males have a midventral ridge on the mantle.

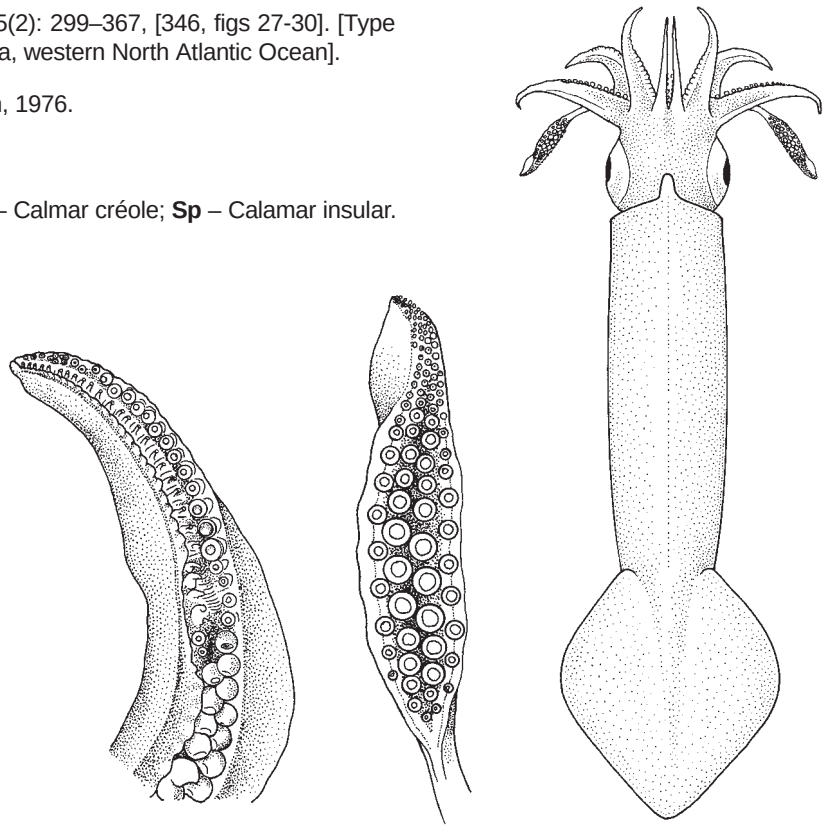


Fig. 85 ***Doryteuthis (Doryteuthis) roperi***

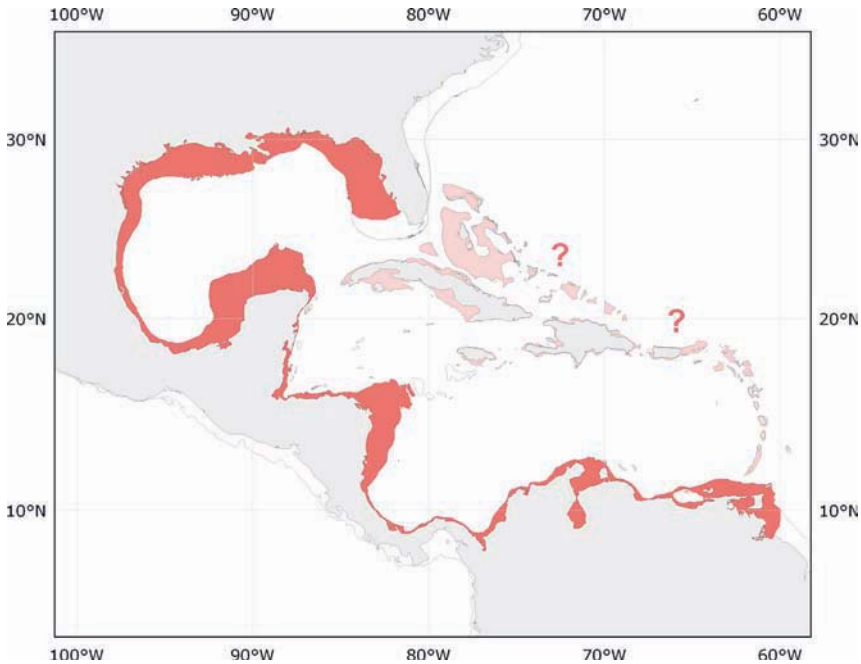


Fig. 86 ***Doryteuthis (Doryteuthis) roperi***

Known distribution Probable presence

Interest to Fisheries: The island inshore squid is taken by dip net at the surface at night, and it also is caught by trawl nets at depths between 50 and 300 m. However, its small size limits its interest to fisheries.

Local Names: None available.

Remarks: Because this small loliginid is easily confused with ***Loligo plei***, it may be more widespread than current records indicate.

Literature: Cohen (1976), Roper *et al*. (1984), Debose and Nevitt (2006), Vecchione (2002, 2008c).

Subgenus ***Amerigo*** Brakoniecki, 1986

Amerigo Brakoniecki, 1986, *Ph.D. Dissertation, University of Miami, Coral Gables, FL*, 163 p. [106].

Type Species: *Doryteuthis (Amerigo) gahi* (d'Orbigny, 1835).

Doryteuthis (Amerigo) gahi (d'Orbigny, 1835) **Fig. 87**

Loligo gahi d'Orbigny, 1835, *In* 1834-1847, *Voyage dans l'Amerique Meridionale*, 5(3): 1–758. [60, pl 3 figs 1–2]. [Type locality: Valparaiso, Chile, eastern South Pacific Ocean].

Frequent Synonyms: *Loligo gahi* d'Orbigny, 1835, *Loligo patagonica*, Smith, 1881.

Misidentifications: None.

FAO Names: En – Patagonian squid; **Fr** – Calmar patagon; **Sp** – Calamar patagónico.

Diagnostic Features: Mantle moderately elongate. **Fins** rhomboidal, **short, their length usually about 40% to 45%** (up to 53%) **of mantle length**. Tentacles long, slender; tentacular clubs narrow, unexpanded, with no distinguishable carpus and relatively small suckers on manus; median suckers about 2 times the diameter of the marginal suckers; teeth on club sucker rings regularly spaced, pointed, very numerous: 25 to 35 (possibly 45). Arms elongate, especially the ventral and ventrolateral arms; arm sucker rings with 6 or 7 broad, flat teeth in distal half, proximal half smooth; **left ventral arm hectocotylized in distal one-third**: suckers in dorsal series greatly reduced in size and set on elongated, triangular, swollen pedicles that grade smaller distally; ventral row unmodified. Chromatophores present on the oral/ventral surface of all arms, including hectocotylus. **Hatchling chromatophore general pattern**: 3 or 4 red chromatophores mixed with a similar number of yellow ones on each tentacle; 2 red chromatophores on each arm IV; 3 or 5 (generally 4), red chromatophores present on the "cheek patch" areas; 6 brown chromatophores arranged as a hexagon commonly found on dorsal head surface; 5 brown chromatophores form a pentagon in the centre, frequently present on the dorsal mantle surface, with yellow ones close to the posterior margins; numerous red chromatophores on the ventral surface of the mantle, arranged to form a more or less regular grid of oblique lines. However, variability occurs in chromatophore number and pattern, especially in the "cheek patch" area.

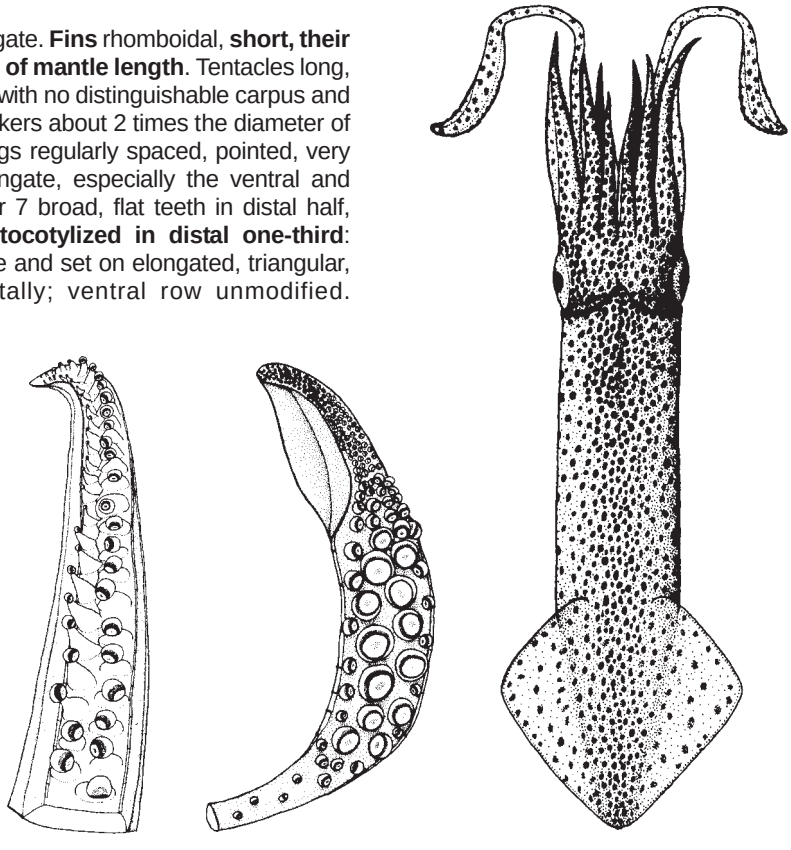


Fig. 87 ***Doryteuthis (Amerigo) gahi***

Size: Medium-sized squid; maximum reported mantle length 340 mm for females and 400 mm for males.

Geographical Distribution: Eastern Pacific Ocean, from northern Peru to southern Chile and southwestern Atlantic Ocean, from the Gulf of San Matias (Argentina, about 42°S) to Tierra del Fuego. The northern limits on both coasts are uncertain, but in the Pacific it is reported in the waters off Puerto Pizarro (about 4°S, southern Guayaquil Gulf, northern-most Peru), while in the Atlantic it extends on the continental slope to about 36°S, following the cold waters of the Malvinas (Falkland) currents (Fig. 88).

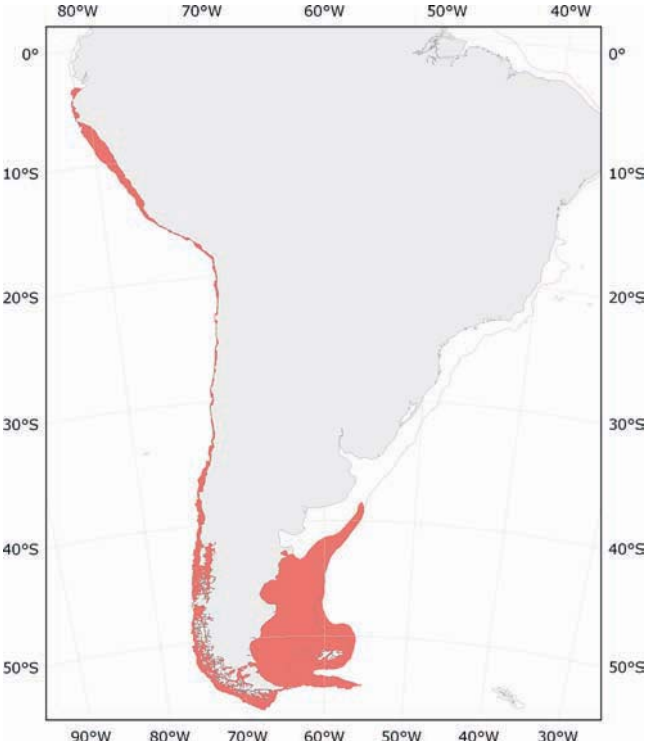


Fig. 88 ***Doryteuthis (Amerigo) gahi***
Known distribution

Habitat and Biology: ***Doryteuthis (Amerigo) gahi*** supports an important fishery on the Patagonian shelf. Due to the economic importance of the fishery, considerable research has focused on the populations that inhabit this area of the distributional range, and present knowledge on the biology of the species is derived mainly from data obtained in the Falkland Interim Conservation Zone (FICZ). Much less is known about the Pacific populations. The Patagonian squid occurs from the surface to about 600 m depth, but it is most commonly found within the 300 m isobath. Information on the Falkland population indicates that ontogenetic migrations occur in that area: the species spawns in shallow water and migrates down the continental shelf and slope after hatching for feeding and maturation. Animals then return to shallow water to spawn. Sexual segregation occurs during these migrations: while the greatest numbers of juveniles (<100 mm mantle length), both males and females, are consistently caught in waters of <100 m to the south and east of East Falkland, larger squid (>100 to 110 mm mantle length) on the feeding grounds are segregated by sex and depth, the females at 250 to 300 m, the males at 170 to 250 m. Males emigrate from their shallower feeding grounds to the spawning grounds earlier than the deeper-feeding females and the sex ratio evens out by the middle of the spawning season on the shallow spawning grounds (30 to 100 m). Interannual changes in the spatial distribution and abundance of the species also occur in relation to changes in the strength, oceanographic features and meander locations of the Falkland Current. This current meets the continental slope east of the Falkland Islands, causing a strong upwelling of the Sub-Antarctic Superficial water mass, where the main feeding grounds of the squids usually are located. However, in years of intensified current, a part of the population is displaced farther north and aggregates on the shelf at about 45°S to 47°S. Data about migrations in the Pacific waters off Peru and Chile are not available, but a migratory pattern for the species in the Callo area of Northern Peru has been hypothesized. In the Falkland population females have a larger mantle circumference than males, whereas only some differences in hard structures occur between males and female of the Peruvian population and no significant difference at all is evident between the 2 sexes in the Chilean population. Size at maturity is extremely variable; the observed range of mantle lengths at full maturity for males and females in the Falkland population is 80 to 380 mm and 70 to 300 mm mantle length respectively.

Maturation and growth of the reproductive organs seem to take place using energy derived from the squids' food, not at the expense of somatic tissue, and both processes continue during the migration from the feeding grounds to the spawning grounds. Mating first occurs on the feeding grounds where part of the male population remains after maturation, to meet with the maturing females on their way back to inshore waters. A 2-phase copulation seems to occur, with the first mating (sperm deposition in the sperm reservoirs on the buccal membrane) probably taking place on the feeding grounds and triggering the process of female maturation. Mature females then migrate to the spawning grounds, where the second mating occurs, with sperm deposition within the mantle cavity, thus allowing fertilization of eggs during spawning. Spawning is intermittent with egg deposition in batches as in other loliginids, and females remain on the spawning grounds until death. The number of ripe eggs in the oviducts of mature females varies with the size of the animals, from 90 to 200 in females of 80 to 100 mm mantle length to 4 000 to 4 500 in females of 280 to 300 mm mantle length. A high Potential Fecundity (PF) occurs with 1 800 and 35 000 eggs present (PF=0.56 ML 1.86). Actual fecundity is about 50% of total fecundity. Eggs are oval in shape and their size is intermediate for loliginids, those of the Atlantic populations are between 1.4 to 1.9 mm and 1.8 to 2.8 mm; the larger eggs are laid in winter. Eggs from the Chilean population are slightly larger, with diameters between 2.3 and 3.2 mm, as were those from 1 egg mass found in the Bridges Islands, Beagle Channel, Tierra del Fuego at 2.3 to 3.0 mm. Inshore spawning sites occur in shallow waters (0 to 20 m) all around the coastline of the South Falkland Islands and along the Patagonian Coast, from the Bridges Islands up to Gulf San Matias (about 42°S). However, collections of hatchlings in deeper waters (i.e. 86 miles, north of Nuevo Gulf, Argentina, at about 40°S), suggest that the spawning grounds may extend to greater depths, at least in the northern area of the distribution. Around the Falkland Islands, the eggs are found attached exclusively to kelp stipes of the species *Lessonia* spp. and *Macrocystis pyrifera*, preferably on short, solitary kelp strands, often at the outer (seaward) edge, with ambient water temperatures of 3.86° to 9 °C. Along the Patagonian coast eggs are found attached to various hard substrata, such as ropes, shells, fishing lines and gravel in sites where the SST ranges from 5°C (in the Beagle Channel in August) to close to 23°C (in the Nuevo Gulf in February). Freshly laid egg masses are bright white; egg capsules are mainly 50 to 60 mm in length and contain an average of 70 fertilized eggs. Egg masses are formed by a variable number of capsules, from less than 10 to more than 300; this variability depends on the size and condition of the female and on the deposition of multiple egg masses

on a common mass by more than one female, as observed in other loliginids. Year-round spawning occurs at the northern limit of the distribution in the Nuevo Gulf, while two main spawning seasons, in May to June and in October to November, exist around the Falkland Islands. ***Dorytheuthis gahi*** spawns in colder waters than any other loliginid species, with normal egg development active at a temperature as low as 3.86°C, considerably less than in other loliginid species and less than that observed under experimental conditions in the laboratory. The duration of the embryonic development is negatively correlated with water temperature in squids; it requires 125 days at a very low temperature (one of the longest times among loliginids), while it is much shorter at higher temperatures (30 to 35 days at about 13°C). Consequently, the 2 cohorts observed in the Falkland Islands area differ in the duration of the embryonic development, so that the 5 to 6 months difference in the spawning time diminishes to only about 2 to 4 months difference in hatching time. This strategy enables recruits from both cohorts to take advantage of the spring-early summer zooplankton bloom that occurs in the Southwest Atlantic Ocean. The mantle length of hatchlings incubated in an aquarium varied between 2.3 and 3.7 mm, being inversely correlated with the mean incubation temperature; the newly hatched squids display a marked positive phototaxis and swim actively. Studies on juvenile distribution in the Falkland Island waters show that juveniles aggregate close to the bottom and are more available to the sampling gear by night than by day. Data from statolith analysis indicate a life span of about 1 year for the species throughout the distributional range; males may live longer than females (up to about 15 months), and it is assumed that catastrophic mortality of most of the population occurs soon after spawning. As in most of the squid species studied to date, feeding is likely to be opportunistic, with the animals eating all possible pelagic prey, with an apparent preference for euphasiid crustaceans in the population of the Falkland Islands. Peak feeding activity takes place around mid-day and early afternoon. Predators include several fish species, other squids, albatrosses, penguins, mammals (dolphins and sea lions).

Interest to Fisheries: ***Doryteuthis gahi*** is the second most important loliginid squid in the commercial fisheries world wide. The Falkland Islands international fishery is mainly concentrated in the south and east of the Falkland Island Interim Conservation and Management Zone. It was the world's largest fishery for a loliginid species until 1996, when it was overtaken by the Californian fishery for ***D. opalescens***. In the Falkland fishery there are 2 fishing seasons each year, from February to June and August to October. The 2 seasons result from the presence of the 2 main spawning groups. Squid from each spawning group recruit into the fishery at an age of about 6 months and are fished during the second half of their life cycle. At least 2, and more usually 3, cohorts of squid recruit to the fishery each year. Squid recruit in February, April/May, and August/September. The extensive commercial fishery concentrates mainly on the feeding grounds, at different depths according to season; consequently, the sexes are targeted differently at depths and in areas where the commercial fishery operates. The fishery has been regulated since the beginning of 1987, by using a target proportional escapement policy, which allows a level of fishing effort compatible with yearly conservation targets. Joint management by Argentina and the United Kingdom ensures that the fishery is closed at about the escapement limit.

Recent studies showed a strong negative relationship between sea surface temperature and recruitment intensity, and management strategies taking this relationship into account were proposed. Also, inverse patterns in abundance of ***Illex argentinus*** and ***D. gahi*** around the Falkland area were analysed and related to possible interspecific competition, in which ***I. argentinus*** likely represents a "limiting" factor ***D. gahi*** in some years, months and zones, either by direct (as a predator) or indirect (as a food competitor) impact. Undoubtedly, predicting squid recruitment using factors such as environmental data and predator abundance offers the potential to refine the licensed effort based on likely abundance.

Doryteuthis gahi also is fished by small-scale and industrial fisheries in Chilean waters, mainly in the southern area. Here the species is caught year-round, with maximum catches in summer and autumn. Also off the Peruvian coast landings of ***D. gahi*** are reported throughout the year, with 2 main seasons in spring (peak in March) and late summer (peak in September). In this region the catches are influenced by El Niño and La Niña events, where El Niño (associated rise in sea temperature) has a negative effect, while La Niña (lowered sea temperature) a positive one.

Local Names: ARGENTINA, CHILE, PERU: Calamar.

Remarks: The systematic position of ***Doryteuthis gahi*** (type locality: Valparaiso, Chile) had been long controversial. Considered the same species as ***Loligo patagonica*** Smith, 1881 (type locality: Alert Harbor, West coast of Patagonia) by several authors (e.g. Castellanos and Cazzaniga, 1979; Brakoniecki 1984b), the species were both considered to be valid species by other authors (e.g. Nesis, 1982, 1987). Observations on the egg size revealed that small differences exist between the Chilean and the southwestern Atlantic populations (e.g. Arkhipkin *et al*., 2000b, Baron, 2001, Guerra *et al*., 2001). Studies on morphological differences between ***D. gahi*** from the 2 oceans revealed significant differences between the Peruvian, Chilean and Patagonian populations. Differences were more accentuated between the population from the Falkland Islands and those from Peru and Chile than those between the 2 latter localities (Vega *et al*., 2002). Genetic studies also demonstrated that differences between the South East Pacific and South West Atlantic populations exist, supporting the suggestion that the 2 populations may represent distinct subspecies (Shaw *et al*., 2004).

As for the southwestern Atlantic populations, the similarity between ***D. gahi*** and ***D. sanpaulensis***, makes the identification of the 2 species difficult/uncertain, especially for juveniles and in the area where the 2 species overlap, i.e. between 42°S and 46°S. Recent morphological and meristic analyses indicate that indices of relative fin width (FW/ML) and relative gladius (GW/ML) are useful tools for the identification of the species. FW/ML can be used alone as a rapid and easy tool in the field: index values lower than 0.53 correspond to ***D. gahi***, while those higher are ***D. sanpaulensis*** (Pineda *et al*., 2002). Other characters useful on fresh, undamaged specimens are the body coloration and the pattern of chromatophores on the oral surface of arms IV: ***D. gahi*** is brownish dorsally and reddish ventrally, while ***D. sanpaulensis*** is reddish on both surfaces; no chromatophores are present on the arms of ***D. sanpaulensis***, while both sexes and all sizes of ***D. gahi*** possess chromatophores, even on the hectocotylus (Pineda *et al*., 2002). Less easily used but very useful nonetheless are statolith size and proportions in the 2 species: the statoliths of ***D. gahi*** are significantly larger than those of ***D. sanpaulensis***, and they have a

very prominent dorsal dome and a comparatively long and thin rostrum (Pineda *et al*., 1998b). Additional observations on the the relative growth of beaks in the 2 species indicate differences that and can be used to discriminate between the 2 species, whereas the beak morphometry is similar (Pineda *et al*., 1996).

Literature: Brakoniecki (1984b), Roper *et al*. (1984), Hatfield and Rodhouse (1991), Pineda *et al*.(1998a, b), Brunetti *et al*. (1999), Villegas (2001), Vega *et al*. (2002), Arkhipkin *et al*. (2006).

Doryteuthis (Amerigo) ocula (Cohen, 1976)

Fig. 89

Loligo ocula Cohen, 1976, *Malacologia*, 15(2): 299–367. [330, figs 15-30]. [Type locality: 22°59'N, 78°43'W, Caribbean Sea, western Atlantic Ocean].

Frequent Synonyms: *Loligo ocula* Cohen, 1976.

Misidentifications: *Doryteuthis pealei*.

FAO Names: En – Bigeye inshore squid; **Fr** – Calmar à gros yeux; **Sp** – Calamar ojigrande.

Diagnostic Features: Mantle bluntly pointed posteriorly. Fins rhomboidal, their lateral angles rounded, anterior lobes well developed; **fin length about 45 to 55% of mantle length**. **Eyes very large; visible part 15 to 21% of mantle length**. **Left ventral arm hectocotylized, modified in distal one-third to one-fourth but not to tip**; 10 to 12 suckers in dorsal series <1/2 diameter of ventral counterparts; 2 to 5 suckers proximal to reduced suckers are enlarged; all modified suckers on swollen, triangular bases. Tentacles robust; clubs expanded, about 24 to 35% of mantle length.

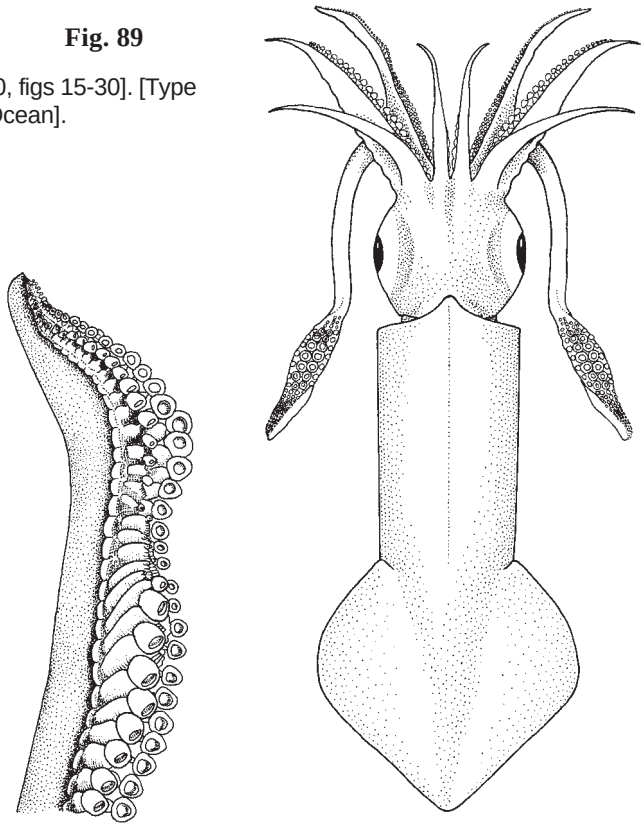
Size: Small-sized species; maximum reported mantle length 127 mm.

Geographical Distribution: Western Atlantic: Caribbean Sea around Cuba (Fig. 90).

Habitat and Biology: Found in depths of 250 to 360 m. Its biology is unknown.

Remarks: This small loliginid is known only from the original description, but because it is easily confused with ***Loligo pealeii*** it may be more widespread than current records indicate.

Literature: Cohen (1976), Roper *et al*. (1984), Vecchione (2002, 2008c).



hectocotylus **dorsal view**

Fig. 89 ***Doryteuthis (Amerigo) ocula***

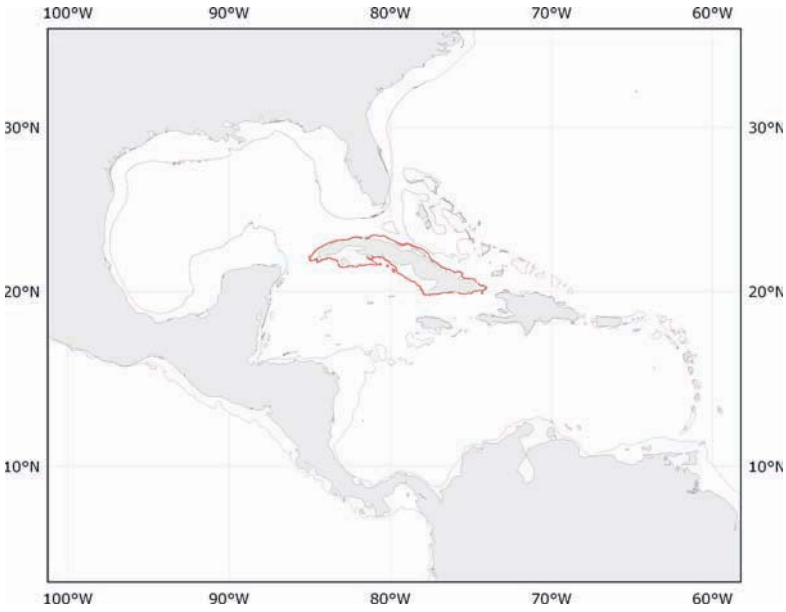


Fig. 90 ***Doryteuthis (Amerigo) ocula***
Known distribution

Doryteuthis (Amerigo) opalescens (Berry, 1911) **Fig. 91; Plate IV, 18–19**

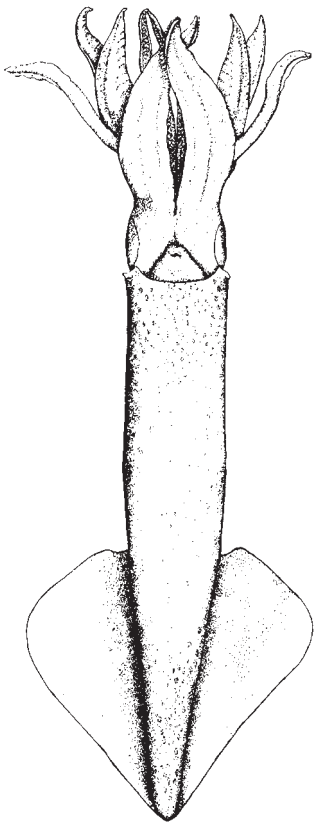
Loligo opalescens Berry, 1911b, *Proceedings of the United States National Museum*, 40(1838): 589–592. [591]. [Type locality: Puget Sound, Washington, USA, eastern North Pacific].

Frequent Synonyms: *Loligo opalescens* Berry, 1911, *Loligo stearnsii*, Hemphill, 1892.

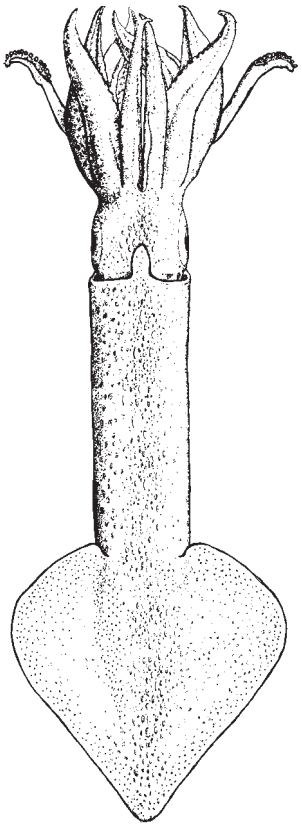
Misidentifications: None.

FAO Names: En – Opalescent inshore squid; **Fr** – Calmar opale; **Sp** – Calamar opalescente.

tentacular club



ventral view



dorsal view

Fig. 91 ***Doryteuthis (Amerigo) opalescens***

Diagnostic Features: Mantle slender, width 20 to 33% of mantle length. **Fin length and width approximately equal, 38 to 52% of mantle length**. Tentacular **clubs narrow, unexpanded**; sucker rings with about 30 blunt teeth. Arms short; arm sucker rings with 9 to 12 blunt teeth. **Left ventral arm hectocotylized along distal one-third** by great reduction in sucker size and enlargement of stalks into papillae. Ink sac elongate.

Size: Small to medium-sized squid; most commonly reported sizes range between 130 and 190 mm mantle length, averaging between 140 and 170 mm mantle length. Maximum reported total length 305 mm.

Geographical Distribution: Endemic to the California Current region. Range from southeastern Alaska (58°N) to southern tip of Baja California, Mexico (22°N). However, abundance is generally low north of Vancouver Island, British Columbia, Canada (Fig. 92).

Habitat and Biology: ***Doryteuthis opalescens***, also known as the California market squid, inhabits most of the coastal waters over the continental shelf off western North America, from the surface to depths of 500 m within 200 miles off shore. Adult squid move to deep waters during the day, but return to the surface at night, mostly to hunt. Squid distribution, growth and life cycle success in this geographic

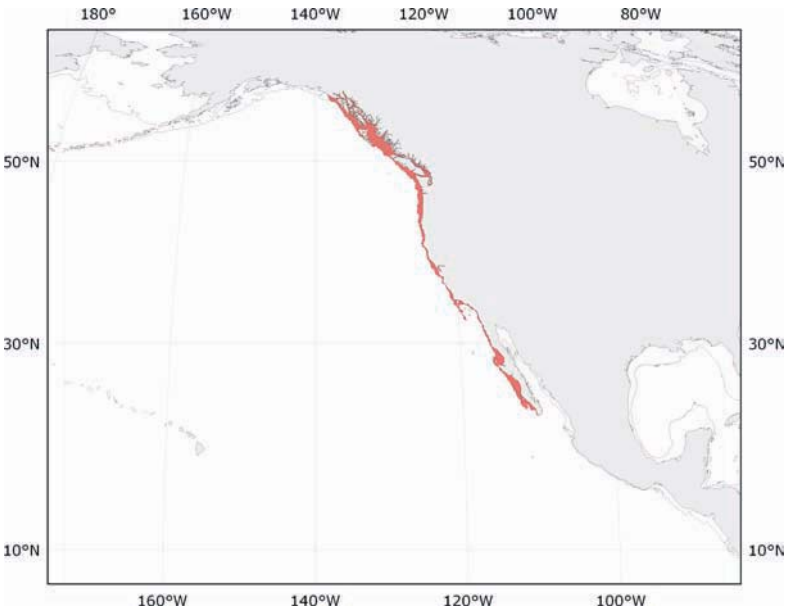


Fig. 92 ***Doryteuthis (Amerigo) opalescens***

area are related to the oceanography of the eastern Pacific Ocean, in which warmer, oxygen-rich surface waters lie above the deep zone of cold, nutrient-rich but oxygen-poor waters transported into the Pacific Basin from Antarctic origins. The very complex California Current System extends from Oregon to Baja California and generates eddies and meanders that affect the distribution of paralarval and juveniles. Upwelling of cold, rich water along the coast affect squid growth and abundance. This system, in turn, is affected by the El-Niño and La Niña events that occur farther south, both resulting in strong fluctuations of squid abundance and distribution.

Sexual dimorphism exists: females have distinctly shorter and thinner arms and tentacles than males, and smaller heads; this results in a more massive appearance of males, that enables easy indentification of adult males and females. Males grow larger than females and squid size is positively correlated with La Niña (colder waters-lower metabolic rates) and upwelling (high productivity-rich food resources available) events. Conversely, during the El Niño events, squid are smaller and less abundant due to the combined effects of high metabolic rates (increased temperatures) and lower levels of available prey (decreased ocean productivity). Size at maturity varies; the smallest mature female observed in the field mesured 81 mm mantle length, the smallest mature male 72 mm mantle length; even smaller sizes are noted for animals cultured in the laboratory (i.e. 60 mm mantle length for females and 71 mm for males). However, female and male squid may remain immature to a mantle length of 140 and 130 mm, respectively.

Maturation and growth of the reproductive organs seem to occur from energy derived directly from food, not at the expense of somatic tissue, judging from the excellent condition of the squid entering the spawning areas, with animals described as “fat and heavy, with glossy, unmarked skin and thick and firm mantles” (Fields, 1950). Reproduction is seasonal and spawning takes place at different seasons within the distributional range. In southern California spawning occurs in winter, from approximately December to March; farther north, in Monterey Bay, the spawning season extends from April to November, with a major peak in April; off Central California a main spawning peak occurs in October. Off Bamfield, British Columbia, spawning peaks occur in spring. Even farther north off Vancuver Island, spawning does not occur every year, but, when it does, it takes place in late summer.

Spawning aggregations may result in millions of individuals aggregating on the spawning grounds. In Monterey Bay, however, small spawning groups (about 30 to 200 squids) commonly are formed from the much larger schools aggregated above in the water column (i.e. thousands or tens of thousands of squid). In situ observations indicate that this particular spawning activity occurs during daytime, and no mass die-off seems to occur after spawning; instead, squids actively rejoin the larger schools aggregated above. These animals apparently are in excellent condition, corroborating results of other studies on loliginids that spawn intermittently. This phenomenon of daytime spawning and absence of mass die-off of spawned-out loliginid squid is contrary to earlier perceptions. Mating behaviour is unique among loliginid squids: the male grasps the female from her ventral side and holds her for minutes or hours in a nearly vertical position; both copulation and deposition of egg capsules occur in this posture, with the paired animals lowering themselves together to the egg bed. In living animals tissues are milky and translucent, with a faintly bluish tone. When mating, the male’s mantle is pale but the arms and some of the head are dark red, while the female’s colour does not vary. Mottled gold and brown is a common colour pattern for excited animals and squids become very dark if disturbed.

In the laboratory, ***Doryteuthis opalescens*** exhibits dominance behaviour during spawning. A single dominant male prevents other males from approaching the egg mass he guards. Females are allowed to approach the egg mass. The dominant male uses postural and colour displays directed toward the intruding male. Similar dominance behaviour and displays have not yet been observed in the ocean.

Eggs are oval, about 2.0 to 2.5 mm in length, 1.3 to 1.6 mm in width; sizes usually are proportional to the female size, and the eggs are enveloped in a thick corion. Eggs are arranged irregularly in elongated capsules, the outer layer of which is an acellular matrix 1 to 2 mm thick that contains a dense culture of bacteria, the probable source of which are the nidamental glands. These bacteria may aid in carotenoid production and egg protection by forming antibiotics and toxic products. This may partly explain why such low predation occurs on the readily accessible and highly visible egg masses attached to the substrate. Average capsule length is about 80 mm and each capsule is anchored by a thin, transparent stalk to the substrate (sandy bottom) or to other capsules. The number of eggs per capsule varies, but mean values number between 150 and 200 eggs. Freshly laid capsules are white, but they soon become brown, infested with worms and debris, and often have damaged sheaths. Often mixed masses of older brown capsules occur later in the centre of a mass surrounded by more recently deposited white capsules; this confirms that aggregate egg masses are formed over an extended interval of time.

Egg development requires 30 to 35 days at 13.6°C but shortens to as little as 21 days at 16°C. Oxygen levels are critical for embryonic development. Hatching occurs mainly at night and newly hatched squid (2.5 to 3.2 mm mantle length) are active swimmers and display a positive phototaxis in the laboratory. In the natural environment paralarvae are most abundant adjacent to oceanic fronts associated with uplifted isotherms, and their distribution is strongly affected by tidal currents; this keeps them within 3 kilometers of shore long enough to allow them to feed on the abundant coastal plankton.

Growth is highly influenced by environmental constraints, with males responding quicker to changes in the environment than females, most probably due to the much greater reproductive investment of females in terms of relative body weight percentages. Individuals reach maturity at 6 to 9 months, and even though, spawning activity may be prolonged, contrary to previous belief, their lifespan is completed within less than one year.

Opalescent squids are active predators that feed upon a wide range of prey, including crustaceans, fishes, polychaetes and cephalopods. Slight differences in prey preference may occur, depending on growth, habitat, sex and maturity stage, but these squids are basically opportunistic feeders. The diet, therefore, changes in relation to water depths and location.

Market squid are preyed upon by a variety of fishes and higher-level predators and are the principal forage items for several species of fishes, birds and mammals. Therefore they are very important in the food web off California.

Interest to Fisheries: The California market squid has been harvested since the 1860s, and since 1993 it has become the largest fishery in California, both in terms of tonnage and value. In the 1999–2000 season fishermen landed 105 005 tonnes of California market squid, with an ex-vessel (wholesale) revenue of USD 36 million, the highest ever attained in the California fisheries. After the decline of the anchovy fishery decades ago, ***Doryteuthis opalescens*** probably constitutes the largest biomass of marketable species off California. They typically are harvested on shallow nearshore spawning grounds; specialized light boats shine high intensity lights on the water to attract and congregate the squids near the surface, then seiner boats capture them with purse-seine nets. The fishery originated in Monterey Bay, and has expanded to southern California, where the majority of squid captures currently occur around the California Channel Islands, from Pt. Dume to Santa Monica Bay and in southern Monterey Bay. Landings continued to increase in recent decades, as the fishing activity intensified, with fishermen from Alaska, Washington and Oregon also participating. A strong relationship between total landings and important El Niño events has been noted. Squid landings collapsed twice, following strong El Niño events in 1982–83 and 1997–98, whereas only slight decreases occurred after weak ones.

Due to the paramount importance of this fishery some management measures have been enacted, but they have been limited only to weekend closures, to allow a weekly 48-hours period of undisturbed spawning. In addition, since 2000, light boat and seine vessel operators have been required to complete logbooks for the California Department of Fish and Game, so that Catch Per Unit Effort (CPUE) for the market squid can be estimated. Due to (1) the increasing market demand, (2) the fact that the fishery is concentrated on the spawning grounds and (3) the knowledge that spawning represents the final phase of the squids life and that squid abundance is strictly related to environmental conditions, unwarranted concern about effective management actions recently has increased. Spatial closures have been suggested to protect at least a few spawning sites and guarantee some undisturbed reproduction. The recent establishment of the marine reserve system in the Channel Islands should protect about 13% of initial squid spawning grounds. Paralarval density index was found to correlate strongly with subsequent adult squid abundance on the spawning grounds. Therefore, catch limits for the fishery could be set according to paralarval abundance surveyed about nine months prior to spawning and fishing.

Local Names: USA: California market squid.

Remarks: Information on the extent of genetic differentiation among exploited populations is crucial for the conservation of the species. Due to the extensive distribution of ***Doryteuthis opalescens*** the existence of more than one population or genetically distinct stocks, isolated by seasonal or geographical spawning differences, has been postulated (e.g. Ally and Keck, 1978, Kashiwada and Recksiek, 1978a,b, Bettinger *et al*., 1985, Hixon, 1983). However, recent observations indicate that no significant difference was detected within the sampled population over about 2 500 km of the North American west coast, suggesting that unrestricted gene flow prevents population differentiation in the market squid (Reichow and Smith, 1999, 2001). This may be due to the relatively narrow continental shelf in the area, which restricts inshore/offshore migrations and expands north/south movements and distribution.

Literature: Fields (1965), Karpov and Caillet (1978, 1979), Kashiwada and Recksiek (1978a,b), Hixon (1983), Yang *et al*. (1986), Vojkovich (1998), Reichow and Smith (2001), Zeidberg and Hamner (2002), Jackson and Domeier (2003), Forsythe *et al*. (2004), Zeidberg *et al*.(2004, 2006), Vecchione (2008c).

Doryteuthis (Amerigo) pealeii (Lesueur, 1821) **Fig. 93; Plate IV, 20–22**

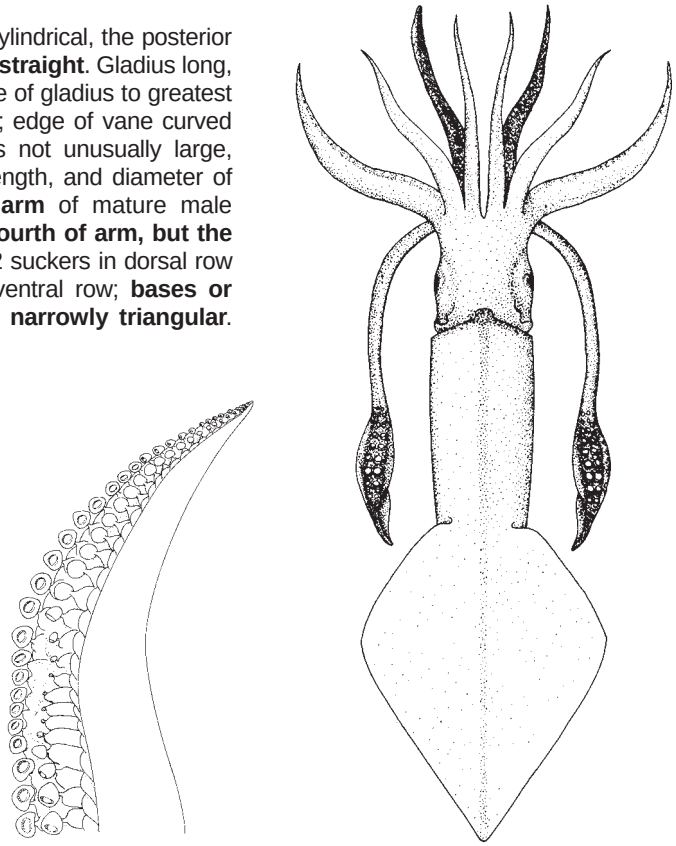
Loligo pealeii Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, 7 pls, [92, pl 8]. [Type locality: South Carolina, western North Atlantic Ocean].

Frequent Synonyms: *Loligo pealeii* Lesueur, 1821, *Loligo punctata* DeKay, 1843, *Loligo pallida* Verrill, 1873, *Loligo pealii* Verrill 1874, *Loligo pealeii* var. *borealis* Verrill, 1880, *Loligo pealeii* var. *pallida* Verrill, 1881.

Misidentifications: *Doryteuthis plei*, particularly in the southern end of the geographic range of *D. pealeii*.

FAO Names: En – Long-finned inshore squid; **Fr** – Calmar totam; **Sp** – Calamar comun.

Diagnostic Features: Mantle long, moderately slender, cylindrical, the posterior end acutely pointed; **fins rhomboidal, their sides nearly straight**. Gladius long, rather wide, feather-shaped, ratio of greatest width of vane of gladius to greatest width of rachis 2.7 to 3.7 in females, 2.4 to 2.9 in males; edge of vane curved (sometimes straight in males), thin, rarely ribbed. Eyes not unusually large, diameter of externally visible eyeball 8 to 18% mantle length, and diameter of dissected lens 2 to 6% mantle length. **Left ventral arm** of mature male **hectocotylized by modification of the distal third to fourth of arm, but the modification does not extend to arm tip**; fewer than 12 suckers in dorsal row smaller than half the size of their counterparts in the ventral row; **bases or pedicels of some of the modified suckers rounded, narrowly triangular**. **Colour**: reddish brown, darker and more vivid dorsally, lighter, less pigmented ventrally.



tentacular club **dorsal view**

Fig. 93 ***Doryteuthis (Amerigo) pealeii***

Size: Medium- to large-sized squid; maximum mantle length 465 mm for males and 303 mm for females. However, sizes in the western central Atlantic are considerably smaller than in northern waters: males do not exceed 300 mm mantle length (less than 200 mm average), and females do not exceed 130 mm mantle length.

Geographical Distribution: Western Atlantic Ocean continental shelf and upper slope waters, from Newfoundland (Holyrood, 47° 30'N, 53° 06'W) to the Gulf of Venezuela, including the Gulf of Mexico and the Caribbean Sea. (Does not occur around islands, except as rare strays to islands close to continental shelf or slope) (Fig. 94).

Habitat and Biology: ***Doryteuthis pealeii*** distribution represents the second broadest geographical distribution and greatest range of environmental temperature adaptation of any loliginids in the northwest Atlantic, after that of ***Doryteuthis plei***. Typically neritic, in the northwest Atlantic, North of Cape Hatteras, ***D. pealeii*** migrates inshore and northward in late spring and early summer into shallow coastal waters to spawn; by late autumn to early winter the squid migrate southward and into deeper waters along the edge of the continental shelf, where they over-winter. These inshore-offshore and north-south movements are mainly related to the avoidance of water temperatures of 8°C or below. Large concentrations of squid are associated with frontal zones with strong temperature gradients, and they are concentrated mostly along the warm-water side. Hence the definition of "member of the migratory, warm-water group of species, centred primarily in mid-Atlantic waters" (Murawski, 1993), which makes seasonal migrations. Along with water temperature, variations in atmospheric forcing associated with the North Atlantic Oscillation (NAO) also affects the species distribution. Conspicuous in the Mid Atlantic Bight from Cape Cod to Cape Hatteras, offshore and to the north, ***D. pealeii*** coexists with the short finned squid, ***Illex illecebrosus***. Inshore, from Delaware Bay south, it shares waters with the thumbstall squid, ***Lolliguncula brevis*** and with the island inshore squid, ***Doryteuthis plei***, with which it often is confused and misidentified. Conflicting information exist on depth segregation of the three loliginids in the areas where they co-occur.

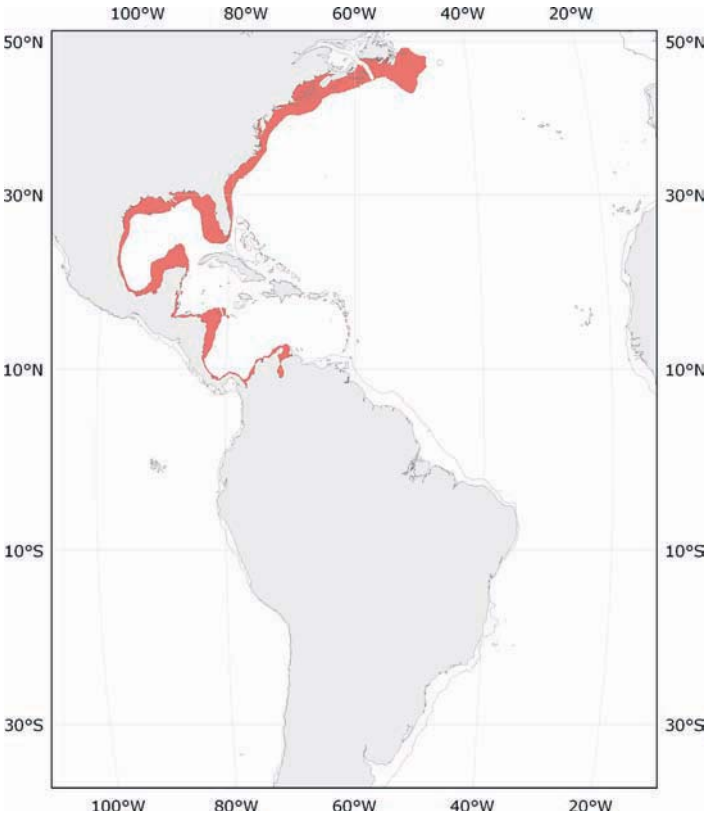


Fig. 94 ***Doryteuthis (Amerigo) pealeii***

Known distribution

The depth distribution of ***D. pealeii*** ranges from shallow surface waters (i.e. 0 to 10 m) down to 393 m, about the maximum acknowledged depth for most loliginids. Generally demersal, ***D. pealeii*** disperses upward into the water colum at night, and daily movements off the sea bottom are known from trawl samples at all depths and seasons.

Sex ratio in the studied populations is consistently close to 1:1, although males and females are not necessarily equally represented in older age groups. Males grow larger than females, and a distinctive sexual dimorphism has been documented frequently. More males than females have a midventral ridge on the mantle, and this is is more pronounced in males; also, some large mature males have longitudinal reddish brown chromatophore stripes along the ventrolateral margins of the mantle. However, even though the 2 sexes are significantly different statistically in many characters, the differences are small; aside from size, these differences are distinctive only in 2 characters: females have a broader gladius vane and fewer gill filaments than males.

The size at which 50% of the North Atlantic population reaches maturity is about 200 mm mantle length. However, sexual maturity is relatively independent of size and more “environmentally controlled”. Minimum mantle length of mature males and females was 61 and 73 mm, respectively, for specimens from the Caribbean, while the largest immature specimens came from Martha’s Vineyard, Massachussets, and measured 219 and 208 mm, respectively. These and other observations support the hypothesis that latitude and environment affect maturation and spawning. Mating and egg laying have been observed frequently in aquaria. Prior to copulation there is a notworthy mating behaviour to establish a hierarchy, with bright, conspicuous colour displays and arm movements. Males engage in agonistic bouts to gain females, and egg masses play a role in this behaviour. Visual detection of eggs and physical contact stimulate male-to-male aggression, probably through a heat labile factor embedded within squid egg capsules that acts as a chemosensory cue. Mating occurs both in the head-to-head posture, which results in the transfer of spermatophores to the female buccal area, and in a parallel posture; in the latter case males pick up bundles of spermatophores from the muscular penis with the hectocotylus and transfer them inside the female mantle cavity, near the opening of the oviduct. Spawning observations in the field report a complex social structure associated with the egg laying behaviour. After mating, ***D. pealeii*** males and females remain paired and several pairs form a semicircle; 1 pair at a time proceeds with the egg laying process, where the male interwines arms with the female then actually delicately moves both of them over and among the egg fingers, while the female produces the egg capsules. No agonistic behaviour occurs after the pairs are formed. However, field video reveals that smaller, non-consort, “sneaker” males obtain extra-pair copulations, thus participating in the egg fertilization event. The high potential of multiple paternity within eggs capsules derives from such a behaviour, and the subsequent high degree of genetic mixing, result in a stronger sexual selection within the population.

Spawning occurs year-round, with 2 major spawning seasons: 1 in winter, the majority of which occurs in the southern end of the species’ range, in near-shore waters on the continental shelf south of Cape Hatteras, North Carolina; another in spring-summer, on the shelf waters off southern New England, north of Cape Hatteras, usually as far as George’s Bank and Cape Cod. However, unusual environmental conditions may favour northern extention of distribution and spawning (e.g. into the Gulf of Maine and to Newfoundland, as in 2002).

Actual reproductive output varies greatly in wild-caught females kept in an aquarium, with a maximum of 53 000 eggs laid, with the highest mean number over 15 000. Neither size nor age consistently affect fecundity, and multi-ovipositing occurs, where females can lay realtively small clutches of eggs at short intervals or large clutches several weeks apart. Females maintained in isolation from males can lay fertilized eggs, demonstrating the use of stored sperm and deposition lasting over periods of 15 or more days. All these elements indicate that ***D. pealeii*** is a multiple spawner, with ovideposition extending over weeks or months.

Eggs are yolky and ovate, about 1.0 to 1.6 mm long. They are laid in gelatinous finger-like strands or capsules, each one about 8 to 10 cm long, 3.5 to 5.0 cm in diameter, and amber coloured; each capsule contains up to 180 eggs arranged in spiral arrays. Capsules are provided with a sticky filament on one end, which females use to attach them together in masses (“sea mops”), typically anchored to a solid substrate (rock, shells, man-made objects) at depths from a few to 250 m. These egg masses frequently are found on anchor lines, in fish traps and other places that indicate that they are deposited over a short period of time, often overnight.

Normal embryonic development occurs at temperatures between 12º and 23°C, with mean hatching times of 27 to 10 days, respectively. Hatching is nearly synchronous. Newly hatched ***D. pealeii*** measure about 1.8 mm mantle length and they immediately swim to the water’s surface, regardless of illumination intensity. Planktonic paralarvae and juveniles are abundant in surface waters of the Mid-Atlantic Bight in spring, summer and autumn and usually are confined to coastal waters, except when current conditions result in offshore transport. The appearance of schooling behaviour at a size of 5 to 8 mm mantle length may indicate the transition from the planktonic to the juvenile and adult neritic phase of the life cycle.

Laboratory growth in the first phase of the life cycle is fast, and the increase of body mass per day is significantly higher in squid reared at a higher temperature, providing strong evidence of phase-specific temperature sensitivity in squid growth. Thus, wild squid hatched in early summer would be 2 and 3 times the weight, at the same age, of squid hatched in spring and early autumn, because of their exposure to warmer summer temperatures. This temperature-differential mechanism allows later-hatched cohorts to catch up with older squid in size and maturity through seasonally increasing water temperature.

Until recently, ***D. pealeii*** was thought to have a life span of up to 3 years and several different models were used to describe growth from field data (e.g. length frequency distributions); these included linear, cyclic, von Bertalannfy and exponential models and more than 1 growth phase was suggested by some authors. Subsequent application of statolith aging techniques

indicates that the species grows more rapidly than previously thought and has a life span of less than 1 year . Growth in length and weight is exponential, and males grow faster and achieve larger sizes than females.

As is the case for many other squid species, the long finned squid feeds on a variety of prey, including fishes, cephalopods, crustaceans and other invertebrates. Diet changes with the ontogenetic development; the smallest juveniles (10 to 40 mm mantle length) feed mainly on copepods, while larger ones (40 to 80 mm mantle length) eat macroplankton (e.g. euphausids) and begin to feed on fish larvae. Young crabs, shrimps and polychaetes are eaten by squid larger than 80 mm mantle length, then young fishes (e.g. silver hake, mackerel, herring, manhaden) and other squids start to dominate, and become the major prey items in adult squid. The highest feeding activity occurs in daylight, and seasonal variation in the feeding rate was observed, with highest feeding activity in the summer. Also, seasonal and geographic variation occurs in the diet composition, depending on the availability of prey items at specific times and places. Size-structured patterns of food consumption were observed, wherein each size-group of squid has its own optimum size of prey (i.e. from 4 to 24% of predator length), piscivory being greater in larger squid. In turn, ***D. pealeii*** is preyed upon by many vertebrates, including fishes (e.g. gadids, skates, lambrids, tunas, sharks) as well as marine mammals and seabirds.

Recent studies indicate that ***D. pealeii*** is a major component in the flow of biomass from pelagic species to predator fish species on the continental shelf off the eastern United States and southeastern Canada, which in turn is a large fraction of the overall energy budget of the shelf ecosystem off the northeast coast of the United States. The tonnage of squid consumed by predatory fishes approaches or exceeds fishery landings, and may even approach and exceed the current estimates of maximum sustainable yield. Therefore, composition and abundance of predators may have important implications on long-term fishery yields of squid.

Interest to Fisheries: ***Doryteuthis pealeii*** is one of the five important commercial species of squids of the northeastern fisheries region of the United States. Small coastal fisheries expanded with the entry of distant waters fleets during the late 1960s and 1970s and catch quotas were established in 1974 by the International Commission for Northwest Atlantic Fisheries–ICNAF. It is caught principally by otter trawls and inshore trapnets. Utilized as food and for bait, it is fished primarily north of Cape Hatteras, although catches also occur in the northern Gulf of Mexico, Yucatan, Columbia and Venezuela. Currently, this is one of the few loliginid species for which specific fishery statistics exist (Jereb and Roper, 2005).

Local Names: None available.

Remarks: Whitaker (1978), Hixon (1980a) and Sanchez *et al*. (1996) computed several indices in order to separate ***D. pealeii*** and ***D. plei***, the most reliable of which is the ratio of gladius width to rachis width (GW/RW) combined with the overall shape of the gladius, including the presence or absence of marginal ribs (absent in ***D. pealeii***). In particular, the GW/RW ratios range from 1.9 to 2.7 for ***D. plei***, and from 2.1 to 3.8 for ***D. pealeii***, and the separation of the two species is best accomplished with a GW/RW ratio of 2.7. However, the 2 species are so similar morphologically that a very careful examination of the collected samples always is recommended, especially in the areas where they are sympatric.

Long considered to be a unit stock, although heterogeneous populations were known to exist (Garthwaite *et al*., 1989), the ***D. pealeii*** fishery was conducted, assessed and managed accordingly (e.g. Sissenwine and Tibbets, 1977, Lange, 1981, Lange and Sissenwine, 1983, Lange *et al*., 1984, Brodziak and Rosenberg, 1993). Recently, however, a genetic break between the northern Gulf of Mexico and the Atlantic Ocean populations was demonstrated (Herke and Foltz, 2002) and subsequently the existence of multiple genetic stocks within the Atlantic population was confirmed (Buresch *et al*., 2006). This phenomenon, along with the rapidly developing offshore fisheries (up to 90% of total landings), the development of a new export market for juveniles (< 50 mm mantle length) and the discovery that this species grows very rapidly and completes its life cycle in less than 1 year, requires that a more cautionary and comprehensive population-based management policy be implemented to ensure a sustainable fishery. Once based on total annual allowable catch and already considered inadequate in the late 1990s (e.g. Macy, 1995a,b, Brodziak, 1998), concise management clearly will need special attention from now on.

As one of the best-studied loliginid species, the literature on ***D. pealeii*** is substantial and includes studies on anatomy, physiology, morphology, biology, behaviour, life cycle and fishery, as well as medical applications (see the Appendix).

Literature: Drew (1911, 1919), Mesnil (1977), Cohen (1976), Summers (1983), Roper *et al*. (1984), Brodziak and Rosenberg (1993), Macy (1995a), Brodziak and Hendrickson (1999), Dawe *et al*. (2001), Hatfield *et al*. (2001), Hatfield and Cadrin (2002), Herke and Foltz (2002), Buresch *et al*. (2006), Dawe *et al*. (2007), Vecchione (2008c).

Doryteuthis (Amerigo) surinamensis (Voss, 1974) **Fig. 95**

Loligo surinamensis Voss, 1974, *Zoologische Mededelingen Rijksmuseum van Natuurlijke Historie et Leiden*, 48(6): 43–53. [43, figs 1–3]. [Type locality: 30 miles northeast of lightship "Suriname River", off the coast of Suriname, western South Atlantic Ocean].

Frequent Synonyms: *Loligo surinamensis* Voss, 1974.

Misidentifications: *Doryteuthis pealeii*.

FAO Names: En – Suriname inshore squid; **Fr** – Calmar du Surinam; **Sp** – Calamar Surinamés.

Diagnostic Features: Mantle moderately broad, about 25% of mantle length. **Fins broadly rhombic**, with rounded lateral angles; **fin length about 50% of mantle length**. Tentacular **clubs expanded, about 30 % of of tentacle length**. Arms of moderate length, about 45% of mantle length. **Left ventral arm of males hectocotylized in distal portion** beginning at 22nd to 24th dorsal sucker pair; suckers at arm tip unmodified; modified suckers reduced in size and set on enlarged, transversely flattened bases. Sucker rings on unmodified ventral arms with sharply pointed teeth. Numerous small to large brown and reddish brown chromatophores on mantle and head, both dorsally and ventrally, more numerous on dorsal side.

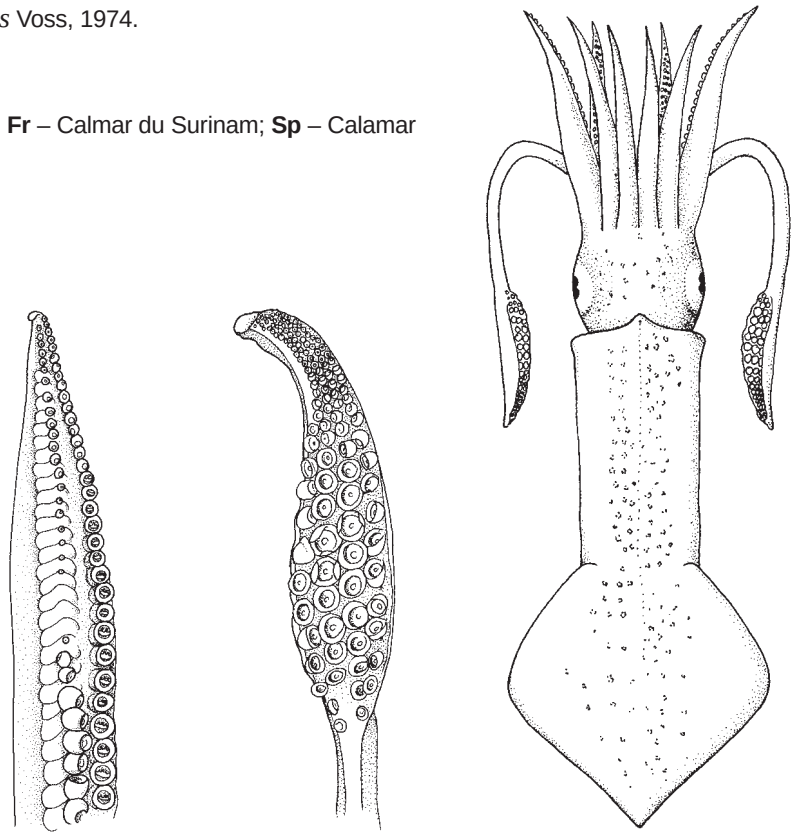


Fig. 95 ***Doryteuthis (Amerigo) surinamensis***

Size: Small-sized squid: maximum reported mantle length 118 mm.

Geographical Distribution: Southern Caribbean Sea: currently, reported only from around the mouth of the Suriname River, Suriname (Fig. 96).

Habitat and Biology: Apparently a shallow living species; known depth range 27 to 37 m.

Remarks: Because this squid is easily confused with ***Doryteuthis pealeii***, its range may be more extensive than indicated by the limited published reports.

Literature: Voss (1974), Roper *et al*. (1984), Vecchione (2002, 2008c).

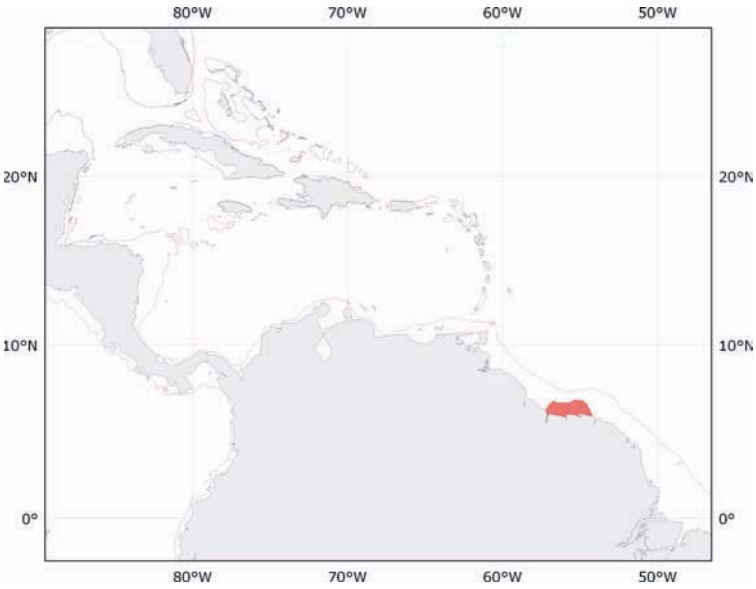


Fig. 96 ***Doryteuthis (Amerigo) surinamensis***

Subgenus undescribed

Doryteuthis sanpaulensis (Brakoniecki, 1984) **Fig. 97**

Loligo sanpaulensis Brakoniecki, 1984b, *FAO Fisheries Synopsis*, 125(3): 1– 277. [102, text-figs 3–5]. [Type locality: 41°47'S, 63°35'W, western South Atlantic Ocean].

Frequent Synonyms: *Loligo brasiliensis* Blainville, 1823.

Misidentifications: *Doryteuthis plei*, *Doryteuthis gahi*.

FAO Names: En – Sao Paulo squid; **Fr** – Calmar de Sao Paulo; **Sp** – Calamar de Sao Paulo.

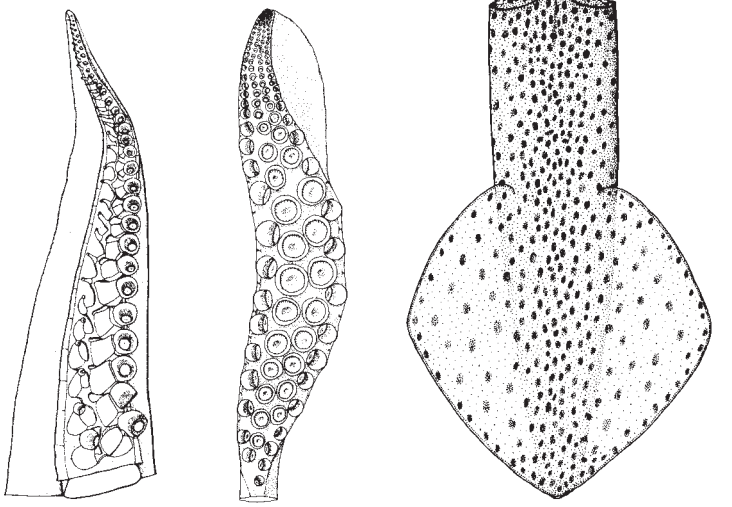


Fig. 97 ***Doryteuthis sanpaulensis***

Diagnostic Features: Mantle moderately long. **Fins rhombic, relatively long, 55% of mantle length** (exceptionally **to 65%**), widest at midpoint; anterior and posterior margins nearly straight; lateral angles rounded. Tentacles long; clubs expanded, distinct manus and dactylus present, but no distinguishable carpus; marginal suckers relatively large, median manal suckers only about one-third larger than marginal suckers; club sucker rings with about 25 pointed, separated teeth, smaller and more widely spaced proximally. Arms moderately long, arm length indices larger in females than in males; arm sucker rings with 5 to 7 broad truncate teeth distally, smooth proximally. **Left ventral arm hectocotylized along distal 45% of arm length** by great reduction in size of suckers in dorsal row that are set on conical to elongate thickened pedicels; suckers on ventral row normal but pedicels are slightly elongate and thickened. Gladius long and slender; edges of vanes with no lateral thickening or at most broad, diffuse thickenings. **Hatchling chromatophoric features**: 4 chromatophores on each tentacle, 2 red interspersed with 2 yellow, up to 3 red ones observed in largest hatchlings; only 1 red on each arm IV; cheek patch areas: 2 red commonly present, up to 3 observed. Other chromatophore arragements: ventral mantle – numerous red chromatophores (from 20 to 40) arranged in 6 horizontal rows, 3 or 4 yellow ones in a longitudinal row on each side; dorsal mantle – always devoided of dark chromatophores, 3 yellow ones arranged in an "arrow" pointing out to the posterior end, and 1 yellow chromatic phase frequently present at one of the lateral margins.

Size: Medium-sized squid; maximum reported mantle length 220 mm (specimen from Argentinian waters, sex unknown); common size 160 mm mantle length for females, 200 mm mantle length for males.

Geographical Distribution: Southwestern Atlantic Ocean: from southern Brazil to northern Patagonia (Argentina), approximately from 20°S to 46°S but precise limits are unknown (Fig. 98).

Habitat and Biology: ***Doryteuthis sanpaulensis*** is widely distributed in coastal waters off southern Brazil and Argentina, where it is the most abundant loliginid squid. It ranges in depth down to about 120 m. Inshore abundance is greater in less saline waters, while offshore higher concentrations are consistently coupled with the cold and food-rich areas of water mass fronts, such as the Subtropical Convergence off southern Brazil, where Subtropical Waters and the northern part of the Malvinas Current

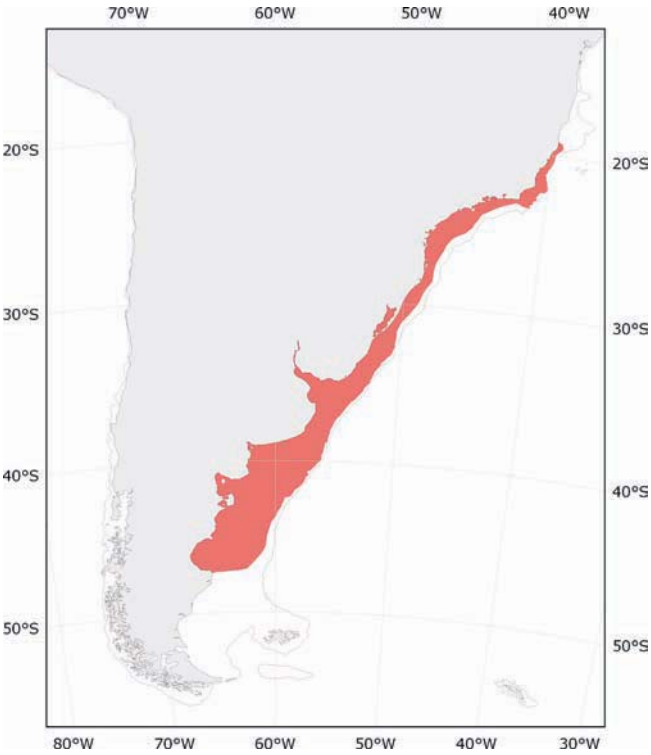


Fig. 98 ***Doryteuthis sanpaulensis***

(i.e. Subantarctic Waters) converge, as well as in the upwelling area of the South Atlantic Central waters off Cabo Frio, Brazil, the northern limit of known distribution.

Size at 50% maturity is very variable along the species distributional range, ranging between 40 mm and 78 to 80 mm for females in southern Brazil and northern Patagonia and between 23 and 90 mm for males from southern Brazil. However, no geographic gradient is evident. Spawning duration also is variable, and probably is related to latitude. Northern populations have long, almost year-round spawning seasons, with 2 peaks, in winter or winter/spring and summer. The midrange population of Mar del Plata (Argentina) spawns from spring to autumn, with highest activity in spring/summer in some years and early winter in other years. In northern Patagonia, the southernmost distribution area, low water temperatures restrict spawning to late spring-summer (occasionally early autumn) and to shallow-water bottoms, when the monthly average of the SST ranges between 15° and 17°C. Spermatophores are small and slender (SpLI between 3.7 and 7.4) with a smooth, slender cement body. Eggs are small, 1.2 to 1.3 mm maximum length and approximately oval in shape. They are laid in typical loliginid capsules on sandy or muddy bottoms. The number of capsules in egg masses varies between 10 and 400. Embryonic development occurs normally at temperatures between 16° and 19°C, whereas below 13° and above 23°C all embryos die after hatching. These observations that temperatures below 13°C are fatal to the embryos, agree with the egg mass findings from January to April/May in coastal shallow waters, when water temperature of the mixed upper layer (tens of meters thick) is about the same as that of the surface level. Embryonic development in captivity was completed in 16 days at 19°C. Newly hatched paralarvae measure between 1.4 and 1.7 mm mantle length and display a marked positive phototaxis, swimming actively with swinging movements. The paralarval chromatophore pattern is characteristic and enables species identification. Hatchling abundance/concentration is higher in coastal areas where upwelling occurs.

Doryteuthis sanpaulensis feeds mainly on fishes and crustaceans, but also cephalopods, including conspecifics. Predators include a wide range of fishes, squids, both conspecifics and ***Illex argentinus***, and marine mammals, birds and sharks. The Sao Paulo squid is particularly important in the diet of the La Plata and Franciscana dolphins, several fur seal species, the Magellanic penguin and the benthic dog shark.

Interest to Fisheries: This species is commonly taken as bycatch in trawl fisheries that target ***Loligo plei*** in its northern area of distribution and ***Loligo gahi*** in the southern area. Also, it is a common bycatch component of artisanal fish trapping and trawling that target coastal fishes and shrimps.

Local Names: ARGENTINA, BRAZIL, URAGUAY: Calamar.

Remarks: The similarity of ***Doryteuthis sanpaulensis*** with ***D. gahi*** makes the identification of the 2 species difficult and uncertain, especially in the case of juveniles and in the area where the 2 squids are sympatric, i.e. between 42°S and 46°S. Morphological and meristic analyses indicate that indices of fin width over mantle length (FW/ML) and gladius width over mantle length (GW/ML) are useful to help identify the species. FW/ML can be used alone as a rapid, easy differentiation tool in the field: index values lower than 0.53 correspond to ***D. gahi***, while those higher are ***D. sanpaulensis*** (Pineda *et al*., 2002). Other characters useful on fresh, less damaged specimens are the body coloration and the pattern of chromatophores on the oral surface of arms IV: ***D. gahi*** is brownish dorsally and reddish ventrally, while ***D. sanpaulensis*** is reddish on both surfaces; no chromatophores are present on ***D. sanpaulensis*** arms IV, while in both sexes and all size ranges studied chromatophores are found on ventral arms in ***D. gahi***, even on the hectocotylus (Pineda *et al*., 2002). Statolith morphology is less easy to use but useful nonetheless to distinguish the 2 species: the statoliths of ***D. sanpaulensis*** are significantly smaller than those of ***D. gahi*** at a given mantle length; they have a rounded dorsal dome and a short rostrum, whereas those of ***D. gahi*** have a very prominent dorsal dome and a comparatively long and thin rostrum (Pineda *et al*., 1998b).

Literature: Brakoniecki (1984a,b), Andriguetto and Haimovici (1991, 1996, 1997) Pineda *et al*.(1998a,b, 2002), Baron (2001, 2003a,b), Baron and Re (2002a,b), Vidal (2006a,b), Martins and Perez (2006a,b, 2007), Vecchione (2008c).

Heterololigo Natsukari, 1984

Heterololigo Natsukari, 1984a, *Venus, Japanese Journal of Malacology*, 43(3): 229–239 [234].

Type Species: *Loligo bleekeri* Keferstein, 1866.

Diagnostic Features: Tentacular **clubs narrow, with small, nearly uniform suckers in 4 series**. **Arms very short**; suckers with blunt teeth around distal ring. Hectocotylus with proximal suckers unmodified; suckers of reduced size and sucker stalks elongated to form papillae in dorsal series; **dorsal series of papillae and trabeculae at distal tip of modified hectocotylus form bicuspid lamelliform flaps** separated from ventral series of suckers by serrated membrane; no fusion between papillae and protective membrane in the modified portion. **Eggs small to moderate sized, less than 4 mm long**. Spermatophore cement body short. Photophores absent.

Size: Medium to large-sized; maximum recorded mantle length 380 mm.

Geographical Distribution: Northwestern Pacific.

Remarks: Currently monotypic.

Heterololigo bleekeri (Keferstein, 1866) **Fig. 99**

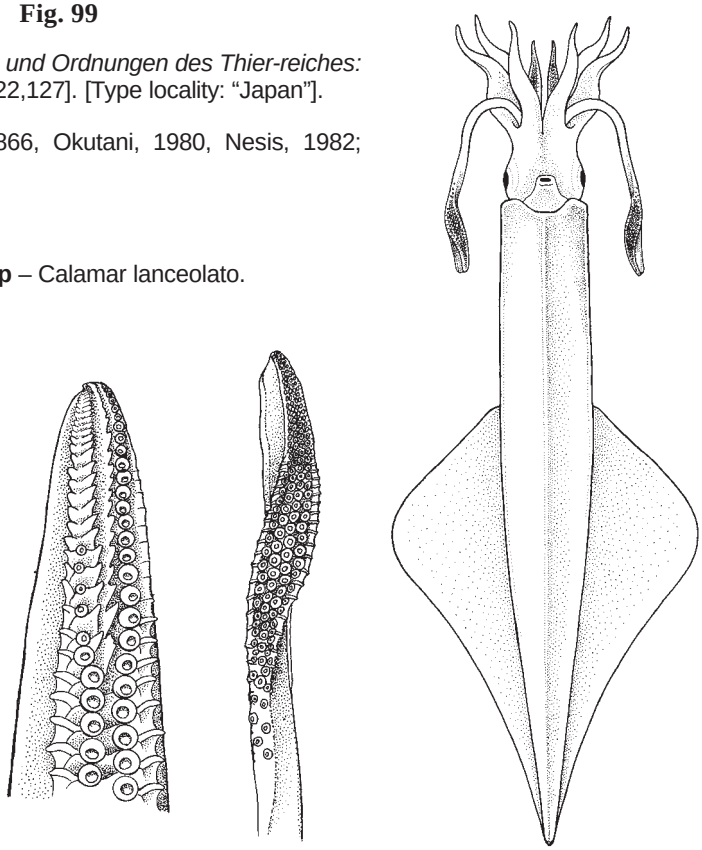
Loligo bleekeri Keferstein, 1866, *In* Bronn, *Die Klassen und Ordnungen des Thier-reiches: Weichthiere (Malacozoa)*, 1 500 p., 136 pls. [1402, pls.122,127]. [Type locality: "Japan"].

Frequent Synonyms: *Loligo bleekeri* Keferstein, 1866, Okutani, 1980, Nesis, 1982; *Doryteuthis bleekeri* Naef, 1912, Okutani, 1973.

Misidentifications: None.

FAO Names: En – Spear squid; **Fr** – Calmar lancette; **Sp** – Calamar lanceolato.

Diagnostic Features: Mantle very elongate, narrow, a fleshy ridge along ventral midline, indistinct in females. **Fins** posterior, **large, thick, length two-thirds of mantle length**. Tentacles short; tentacular clubs narrow, suckers small, nearly uniform in size, those of medial 2 series of manus only slightly larger than marginal series; manal sucker rings with about 30 long blunt, separate teeth, the 10 to 14 distal ones the largest. **Arms very short and small in relation to body size; left arm IV hectocotylized in distal one-third to one-fourth** where arm tip is thickened and blunt; modified sucker stalks become longer with thicker bases towards tip; suckers become very minute and rudimentary in the modified section, especially in the dorsal row, with very thickened basal papillae; dorsal basal papillae very greatly thickened, then transformed into tightly arranged, bicuspid, lamelliform flaps; a narrow, serrated membranous fleshy crest separates the 2 series of modified sucker papillae. **Hatchling dorsal chromatophore arrangement very characteristic**: a hexagon of red chromatophores surrounds a yellow one on the dorsal surface of the head and 6 red chromatophores are arranged in a rhombic design on the dorsal surface of the mantle.



hectocotylus **tentacular club** **ventral view**

Fig. 99 ***Heterololigo bleekeri***

Size: Medium to large-sized squid; maximum recorded length 380 mm mantle length for males and 301 mm mantle length for females. Commonly at 200 to 250 mm mantle length.

Geographical Distribution: Japan: from southern Kyushu (about 30°N) to the Kuril Strait (about 51°N); however, its northern limit commonly is located off Hokkaido waters (about 43ºN to 44°N). Present along the coast of Korea and in the East China Sea and Yellow Sea.Then it is not endemic to Japan (Fig. 100).

Habitat and Biology: The spear squid occurs from surface waters to depths of approximately 150 m; it has never been recorded beyond the continental shelf. However, where its distribution overlaps with that of ***Photololigo edulis***, ***H. bleekeri*** is distributed farther offshore in deeper waters. The centre of the distribution occurs in the northern Sea of Japan off the Aomori Prefecture. Adult squid migrate southward following water temperatures between 7º and 15°C, optimal for spawning.

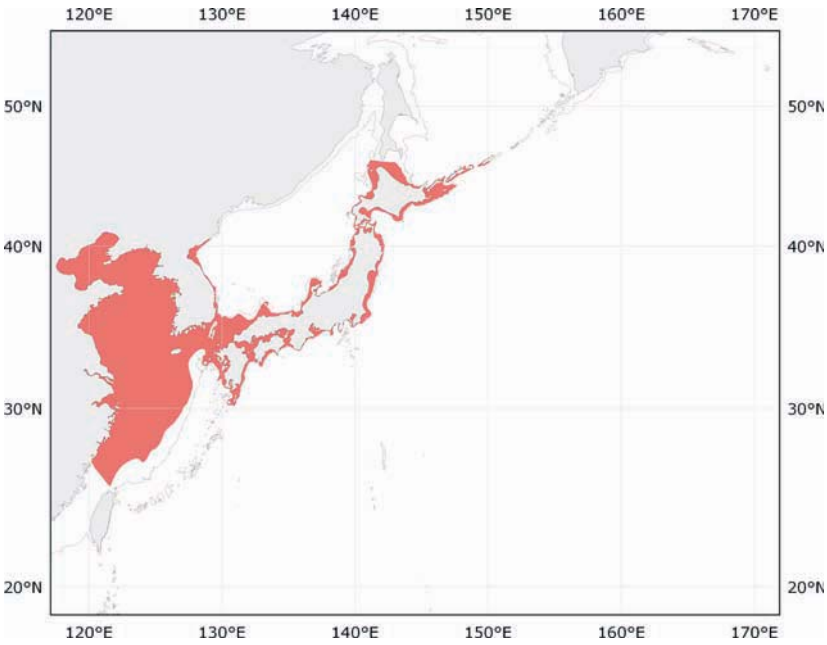


Fig. 100 ***Heterololigo bleekeri***

Known distribution

A slight sexual dimorphism occurs in adult squid. Males have a slightly more slender mantle, smaller heads and shorter arms than females of the same mantle length. Males grow larger than females and mature earlier; the smallest mature males recorded measured 100 mm mantle length, the smallest females 130 mm mantle length; all males and females are mature at 250 mm and 200 mm mantle length, respectively.

With the onset of maturity, squids migrate from the offshore areas to shallow waters near-shore, for mating and spawning. The spawning season extends over a rather long period, beginning earlier in the southern portion of the distribution area, where squid start spawning in December and continue spawning until May, whereas in the north, spawning starts in April and may last until October-November. The water temperature during the spawning season ranges between 7º and 15°C. Mating occurs mainly in the side-to-side position and occasionally in the head-to-head position. Spermatophores are attached to the buccal membrane and, more conspicuously, in the mantle cavity close to the opening of the oviduct.

Eggs are laid in clusters attached to seaweeds or the surface or undersurface of various hard substrates such as rocks, artificial reefs, wreckage, etc. at about 20 to 30 m depth. In the presence of these substrates, spawning also may occur in waters deeper than usual, to 60 to 70 m. While a record of egg cases being laid on the sand of an experimental tank also exists, in the natural environment eggs of the spear squid are never found on sandy bottom. Observations in aquaria indicate that females lay between 500 and 2 000 eggs per spawning event, and they spawn at least 2 to 4 times before they die. Newly laid eggs are ovate, amber coloured and measure 2.5 to 3.1 mm in length, and 1.8 to 2.1 mm in width. Eggs are arranged in typical loliginid egg cases, between 50 and 140 mm long and 5 to 10 mm wide. The mean number of eggs per egg case varies between 50 to 60 and 100. Data from the west coast of Kyushu as well as observations in captivity indicate that embryonic development lasts 83 days at 10°C, 38 days at 15°C, and 21 days at 22°C; development is inhibited below 7°C and above 25°C. Newly hatched paralarvae have a mean mantle length of 3.4 mm and a mean total length of 6.5 mm and undergo a short planktonic life before acquiring the demersal life-style.

Age determination by statolith analysis indicates a maximum life span of 351 days for females and 385 days for males.

Heterololigo bleekeri feeds opportunistically on crustaceans, fishes and molluscs; however, ontogenetic differences occur, with juveniles eating mostly copepods, young squids between 50 and 90 mm mantle length preying mostly on crustaceans, and adult squid over 200 mm mantle length feeding on fishes and other cephalopods.

Observations on differences in the spawning season peaks and migration routes lead to the hypothesis of the existence of 2 different populations in northern Japan. However, studies on population genetics indicate a low level of genetic diversity, that confirms the existence of a single population in the waters around Japan.

Interest to Fisheries: ***Heterololigo bleekeri*** is the most extensively utilized loliginid squid in Japan. It is caught by bottom trawl, set nets, trap nets, jigging, hand-held dip nets, gill nets and blanket nets. While trawlers are not selective, other fishery techniques target mainly mature, spawning squid, so that fishing seasons coincide more or less with the time of maturation and spawning and fishing varies according to location and fishing method. This species is widely caught in most Japanese coastal waters except south of Kyushu (i.e. in Okinawa seas), in the Inland Sea and east of Hokkaido. Catches fluctuate widely in relation to climatic conditions because the species prefers cool water regimes. In the southwestern Japan Sea, in particular, catches decreased sharply after the late 1980s, due to a climatic shift from cool to warm conditions in the Tshushima Warm Current and to the increased exploitation rate of the last decade, such that concern about a possible collapse of the stock exists. Management measures have been considered, including closures of some areas to the fishery and construction of artificial spawning beds to increase spawning yield and to create a favourable environment for newly hatched squid. The feasibility of aquaculture presently is under intensive study and the species has been reared in captivity for up to two months.

Local Names: JAPAN: Sasaika, Chiyokl, Sayanaga, Shakuhachiika, Tenashi, Teppo, Tsutsuika, Yariika.

Remarks: The eggs and egg cases of ***Heterololigo bleekeri*** resemble those of ***Photololigo edulis***. However, other than always being attached to hard substrates, the eggs of ***H. bleekeri*** are larger and the egg cases are smaller, less transparent and contain fewer eggs. Accordingly, newly hatched spear squid also are considerably larger than hatchlings of ***P. edulis***. Studies on the embryonic development of the spear squid indicate that the major developmental pattern is essentially identical to that of ***Doryteuthis pealeii*** and ***Loligo forbesii*** (Baeg *et al*., 1992) and similar to that of ***Doryteuthis gahi*** (Guerra *et al*., 2001), though the latter has smaller embryos. Records of the species from Ambon (Indonesia) exist (Joubin, 1894), but the spear squid never has been reported in Taiwan and/or the South China Sea; (e.g. Voss and Williamson, 1971, Dong, 1978, Tung, 1978 in Natsukari and Tashiro, 1991); therefore, these records are doubtful.

Literature: McConathy *et al*.(1980), Roper *et al*. (1984), Natsukari and Tashiro (1991), Reichov and Smith (2001), Ito (2002), Ikeda *et al*. (2005), Okutani (2005), Tian (2007), Vecchione (2008d).

Loliolus Steenstrup, 1856

Loliolus Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4: 185–216. [193].

Type Species: *Loliolus hardwickei* (Gray, 1849).

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Arm sucker rings with square plate-like teeth around entire margin. **Hectocotylus with ventral crest** formed by fusion of protective membrane with ventral row of papillae; original form of conical papillae completely obscured. Mantle **without posterior tail-like elongation**. **Fins posterior**. **Eggs small**. Spermatophore cement body short. Photophores absent.

Size: Small-sized squid; mantle length up to 150 mm.

Geographical Distribution: Indo-West Pacific waters.

Remarks: Two subgenera currently are recognized. Since the type species of the formerly monotypic genus belongs to the subgenus ***Loliolus***, the subgenus ***Loliolus*** is treated first in this work.

Literature: Vecchione *et al*. (2005), Vecchione (2008f).

Key to the subgenera of *Loliolus*

1a. Suckers along entire length of hectocotylized arm modified, no unmodified suckers on proximal arm . . . . . ***Loliolus (Loliolus)***

1b. Less than entire arm modified by hectocotylization, proximal part with unmodified suckers . . . . . ***Loliolus (Nipponololigo)***

Subgenus ***Loliolus*** Steenstrup, 1856

Loliolus Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4: 185–216. [193].

Type Species: *Loliolus (Loliolus) hardwickei* (Gray, 1849).

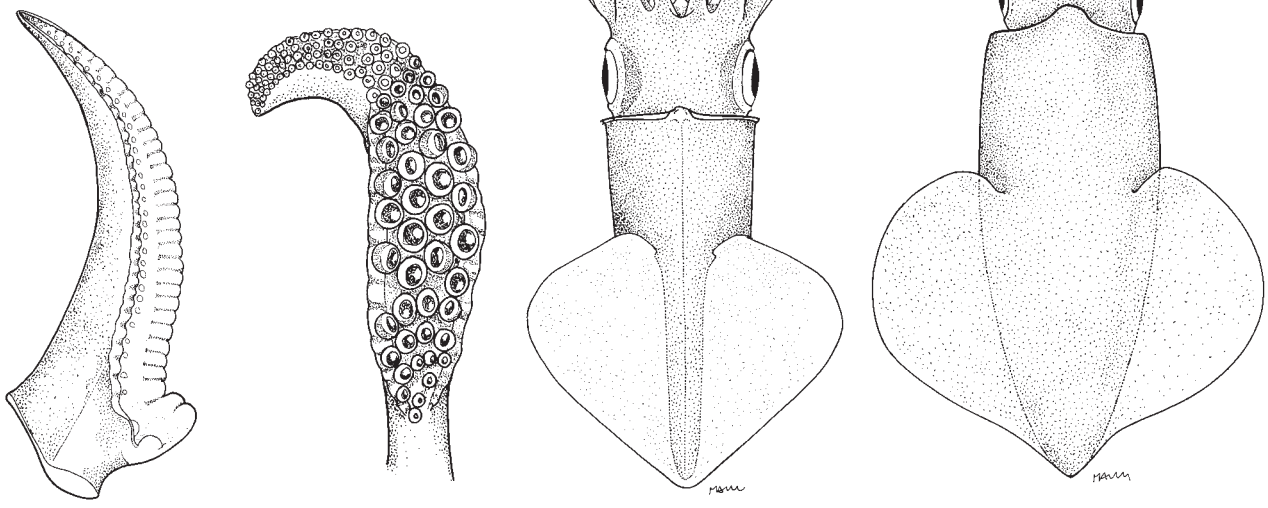
Loliolus (Loliolus) hardwickei (Gray, 1849) **Fig. 101**

Loligo hardwickei Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Artepedia*, 164 pages, London. [69]. [Type locality: India].

Frequent Synonyms: *Loliolus typus* Steenstrup, 1856; *Loliolus investigatoris* Goodrich, 1896, Massy, 1916, Adam, 1954, Silas, 1968, 1986, Jothinayagam, 1987, Nesis, 1987; *Loliolus buitendijki*, Grimpe, 1932.

Misidentifications: *Loliolus affinis*.

FAO Names: En – Little Indian squid; **Fr** – Petite encornet indien; **Sp** – Calamareto indico.



hectocotylus **tentacular club** **dorsal view of male** **dorsal view of female**

Fig. 101 ***Loliolus (Loliolus) hardwickei***

Diagnostic Features: Mantle short, stout; **fins large, heart-shaped**, with anterior and lateral edges rounded, **width up to 76% of mantle length**; head short, a little narrower than the mantle width. Arms rather short, subequal, usually shorter in females than males. Arm sucker rings with only 2 to 7 large, low, stout, broad teeth on the distal margin, their number varies depending on the arm and the sex of the specimen. **Left ventral arm hectocotylized in males by the modification of both ventral and dorsal series of suckers along its entire length**: suckers are missing, except at the very tip where 2 or 3 minute suckers may be present; ventral sucker stalks enlarged and fused entirely with the ventral trabeculate membrane to form a fleshy ridge. Modified suckers on dorsolateral and ventrolateral arms of males larger in dorsal series than in ventral series. Tentacles short. Clubs small, scarcely expanded; club suckers subequal; largest club sucker rings with 20 to 40 small, acute or bluntly triangular teeth around the entire margin. One pair of small papillae on the ink sac in males, absent in females.

Size: Small-sized squid; maximum reported size 88 mm mantle length (a male captured at the mouth of the River Hughli, India). Common at about 30 mm mantle length in males and over 60 mm mantle length in females.

Geographical Distribution: A tropical species of the Indian Ocean waters, from the Northern Persian Gulf, along the coasts of India and Burma (Myanmar), and throughout Indonesia. A single specimen was reported from the Chinese coast, opposite Taiwan. Never recorded in either northern or southern subtropical waters (Fig. 102).

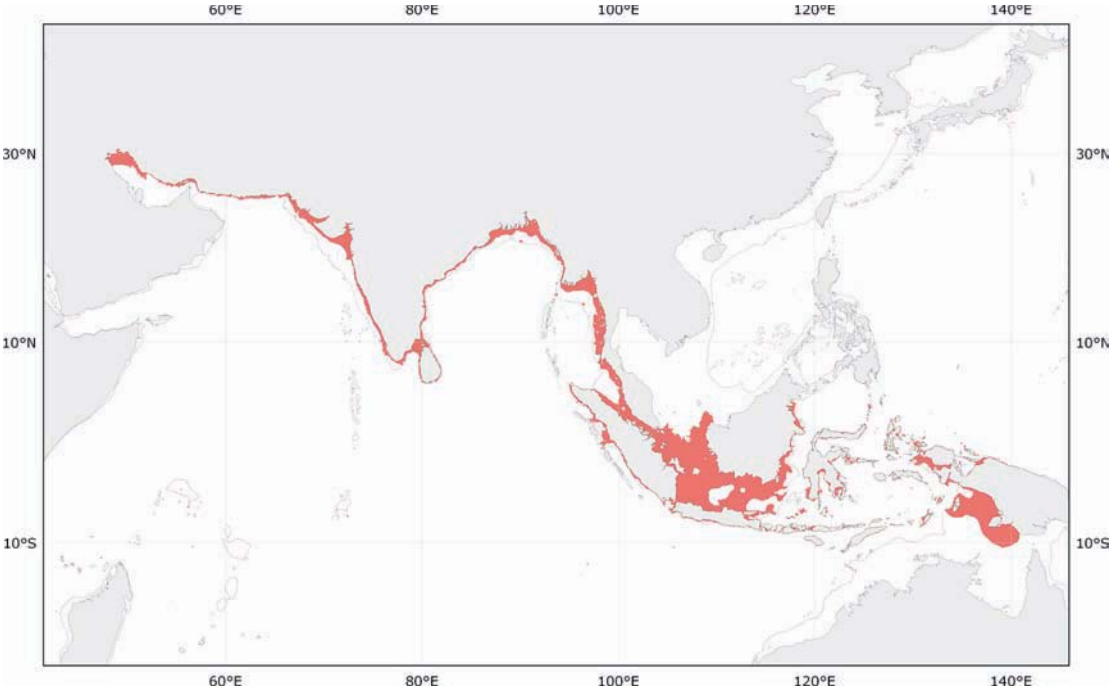


Fig. 102 ***Loliolus (Loliolus) hardwickei***

Known distribution

Habitat and Biology: Very little information is available on the biology of ***Loliolus hardwickei***, which is not considered by the major available references on Indian Ocean squid biology. This probably is because this species has little importance for the commercial fisheries, in spite of its common occurrence in the area. ***Loliolus hardwickei*** is known to inhabit estuarine and coastal waters to a maximum recorded depth of 30 m. Males and females reach sexual maturity at a size of about 30 to 40 mm mantle length.

Interest to Fisheries: In spite of its common occurrence in the Indo-Pacific region, few data on catch statistics are available; artisanal fisheries may occur in local situations. ***Loliolus hardwickei*** (as ***L. investigatoris***) is reported among the cephalopod resources of the northern part of the Arabian Sea, i.e. the Guajarat coast, and the eastern coast of India.

Local Names: None available.

Remarks: None.

Literature: Massy (1916), Silas (1986), Lu *et al*. (1985), Norman & Lu (2000), Jereb and Roper (2006), Vecchione (2008f).

Loliolus (Loliolus) affinis Steenstrup, 1856 **Fig. 103**

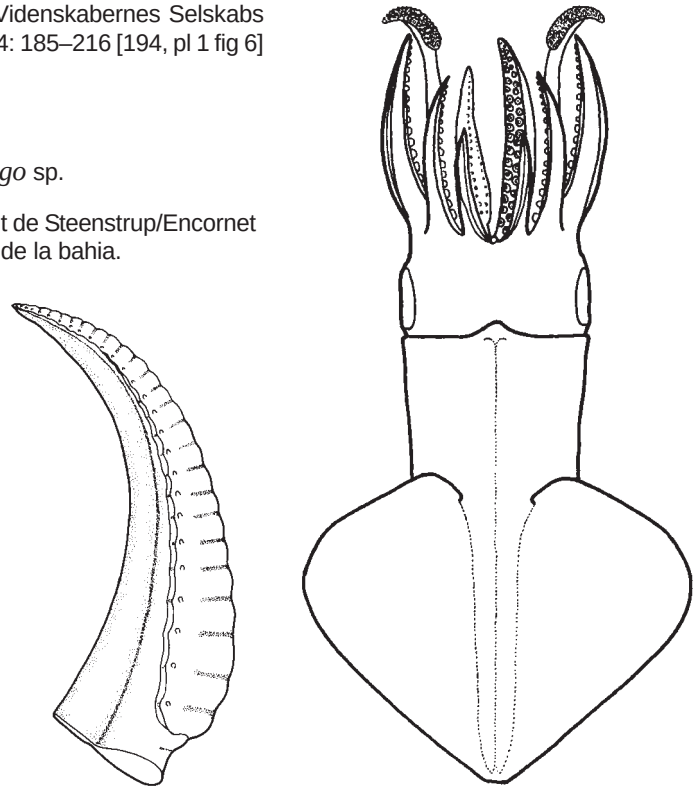
Loliolus affinis Steenstrup, 1856, Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk, 4: 185–216 [194, pl 1 fig 6] [Type locality: Indian Ocean].

Frequent Synonyms: None.

Misidentifications: *Loliolus hardwickei*, *Nipponololigo* sp.

FAO Names: En – Steenstrup's bay squid; **Fr** – Encornet de Steenstrup/Encornet de la baie; **Sp** – Calamareto de Steenstrup/Calamareto de la bahia.

Diagnostic Features: Mantle slightly flattened dorsoventrally, with a bluntly rounded tip. **Fins large, heart-shaped, width up to 98% of mantle length**. Head broad, short, as wide as mantle width, eyes large. Arms short; arm suckers larger in males. Modified suckers on dorsolateral and ventrolateral arms of males larger in ventral series than in dorsal series. Arm I largest suckers show 3 or 4 truncate teeth on distal margin; proximal margin smooth or irregular. **Left ventral arm hectocotylized in males, generally equal to or shorter than right ventral arm**; suckers and sucker stalks entirely absent in ventral row; ventral protective membrane broad, thickened; trabeculae on ventral row greatly thickened, fused by the broad, fleshy, ventral protective membrane. Tentacles relatively short, clubs small, slightly expanded, carpal suckers absent. Club sucker dentition shows truncate, conical teeth in juveniles, that change to square, plate-like teeth in adults. Medial manal suckers with 15 to 20 small, blunt, well-spaced teeth on entire margin. One pair of small papillae on the ink sac in males, absent in females.



hectocotylus **dorsal view**

Fig. 103 ***Loliolus (Loliolus) affinis***

Size: Small-sized squid; maximum mantle length 47 mm.

Geographical Distribution: Widely distributed in coastal waters of the Indo-Malayan region, from the eastern Bay of Bengal to the Andaman Sea, Thailand, Indonesia, and Cambodia. Confined to tropical areas; never extends to northern or southern subtropical zones (Fig. 104).

Habitat and Biology: This species occurs in shallow coastal habitats to depths of 13 to 15 m. It probably is a schooling species. Smallest mature males measure 22 mm mantle length; size at maturity of females uncertain. A general statement about mature individual size of 35 mm mantle length in the waters of Thailand, may include females as well as males, since females are larger than males.

Interest to Fisheries: Occasionally caught in demersal trawl catches in the Gulf of Thailand among larger loliginids; it may be confused with juveniles of other larger, more commercially important, species.

Local Names: None available.

Remarks: None.

Literature: Lu *et al*. (1985), Chotiyaputta (1993a,b), Okutani (2005), Vecchione (2008f).

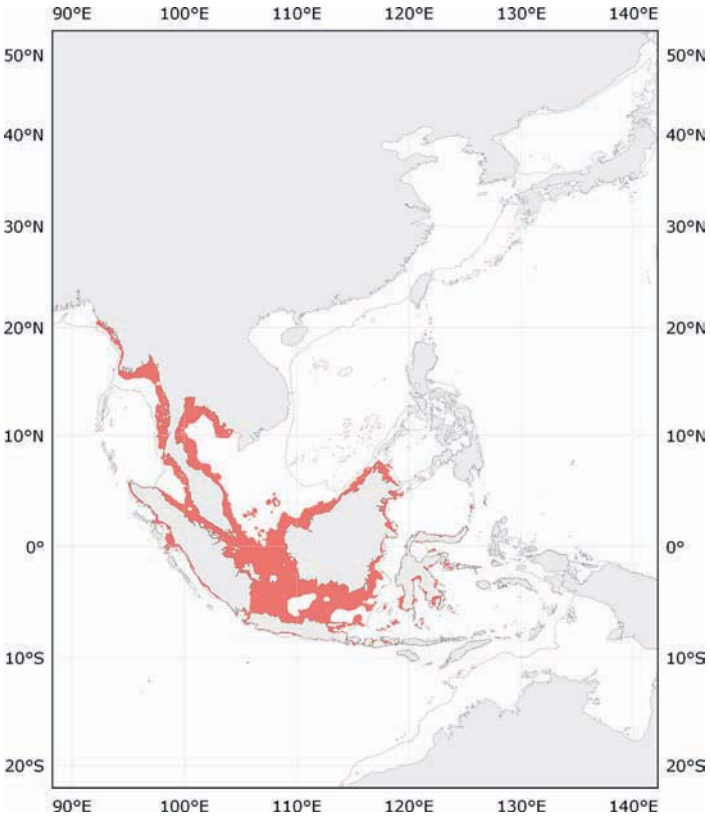


Fig. 104 ***Loliolus (Loliolus) affinis***

Known distribution

Subgenus ***Nipponololigo*** Natsukari, 1983

Nipponololigo Natsukari, 1983. *Venus*, 42(4):313-318, 6 figures. [313].

Type Species: *Loliolus (Nipponololigo) beka* (Sasaki, 1929).

Loliolus (Nipponololigo) beka (Sasaki, 1929) **Fig. 105**

Loligo beka Sasaki, 1929, J*ournal of the College of Agriculture, Hokkaido Imperial University*, 20 (supplement):1–357 [121, text-figs 70–72, pl 13 fig 5]. [Type locality: Kojima Bay, western Honshu, Japan, western North Pacific Ocean].

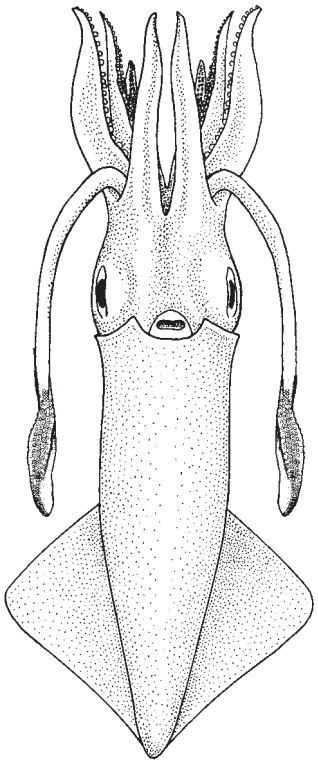
Frequent Synonyms: *Loligo sumatrensis*, Appellöf, 1886 (non Orbigny, 1839).

Misidentifications: *Loliolus uyii* (Wakiya and Ishikawa, 1921).

FAO Names: En – Beka squid; **Fr** – Calmar cracheur; **Sp** – Calamar beka.

Diagnostic Features: Mantle short, slender; f**ins rhomboidal with round lateral angles, both fin length and width more than 50% of mantle length, up to 60%**. Arms slightly longer in males than in females, with larger suckers; arm sucker rings with a smooth plate-like tooth extending up to one-third of the proximal margin and 2 to 7, wide, broad squared teeth along the distal margin. **Left ventral arm hectocotylized in males with about 6 to 9 pairs of normal suckers on the proximal end and the distinctive ventral row of palisade-like, fused, fleshy papillae that form a wall-like crest on the distal portion** (about two-third of the arm length). Tentacular clubs expanded, lanceolate; medial manal suckers twice the diameter of the lateral suckers, with 18 to 20 (30) sharp teeth on the sucker rings.

Size: Small-sized squid; maximum mantle length 87 mm (female).



ventral view

Fig. 105 ***Loliolus (Nipponololigo) beka***

Geographical Distribution: Temperate to tropical western Pacific Ocean; all along the southeast Asian coastal waters, from southern Japan and Hainan Island to the Gulf of Thailand and the Andaman Sea (Fig. 106).

Habitat and Biology: The depth distribution is undetermined. This species occurs in coastal and estuarine waters, particularly bays. Studies on the diet indicate that the Beka squid feeds mainly on benthic species of crustaceans and on juveniles of the small yellow croaker, *Pseudosciaena polyactis*. It is preyed upon by several fish species that inhabit estuarine waters.

Interest to Fisheries: The Beka squid is captured in trawls and light-luring nets in the Gulf of Thailand, and it is mentioned as one of the main fishery resources of the estuarine waters of the Pearl River, northeast of Hainan, East China Sea.

Local Names: INDIA (Tamil Nadu): Oosikanava; JAPAN: Beka.

Remarks: This is the smallest species within the subgenus ***Nipponololigo***.

Literature: Natsukari (1983), Okutani *et al*. (1987), Nateewathana (1992), Li *et al*. (1995), Yang and Tan (2000), Li *et al*. (2000), Norman and Lu (2000), Okutani (2005), Vecchione (2008f).

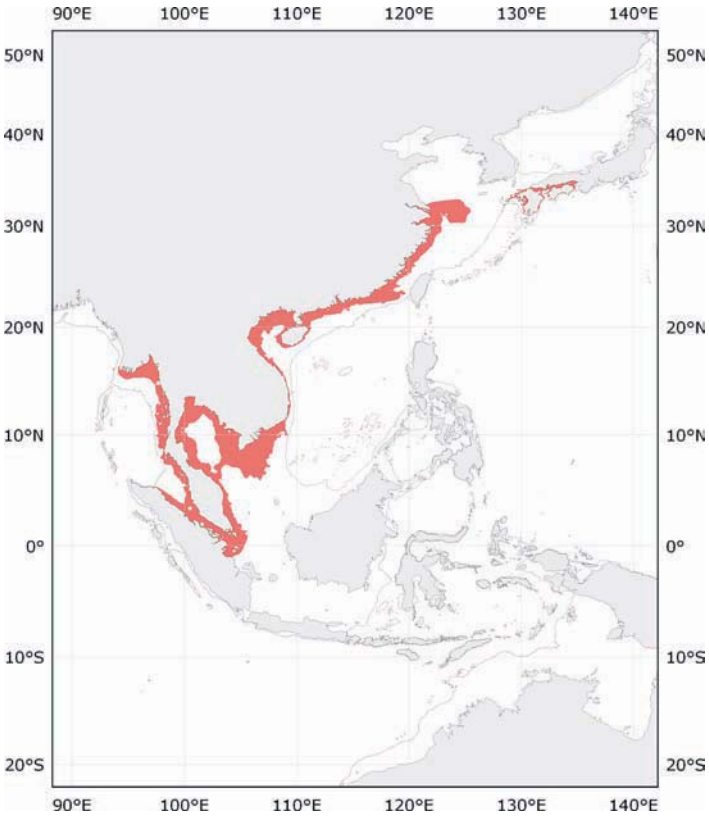


Fig. 106 ***Loliolus (Nipponololigo) beka***

Known distribution

Loliolus (Nipponololigo) japonica (Hoyle, 1885)

Fig. 107

Loligo japonica Hoyle, 1885, *Annals and Magazine of Natural History, Series*, 5(16):181–203. [187]. [Type locality: purchased at market, Yokohama, Japan].

Frequent Synonyms: *Loligo tetradynamia*, Ortmann, 1888.

Misidentifications: None.

FAO Names: En – Japanese squid; **Fr** – Calmar japonais; **Sp** – Calamar japonés.

Diagnostic Features: Mantle relatively small, stout, conico-cylindrical. **Fins rhomboidal, about 50% of mantle length**. Tentacular clubs expanded, lanceolate, **the 12 enlarged medial manus suckers 2 or 3 times the diameter of marginal ones**, with 20 to 30 closely set, low, rounded teeth. Arms II and III enlarged, thickened, largest sucker rings large, with 7 to 13 low, broad, blunt teeth. **Left ventral arm hectocotylized in distal half to two-thirds**, by sucker stalks modified into papillae, **most with minute, rudimentary suckers on tips**; papillae of ventral row especially swollen, somewhat flattened, fused together forming a wall-like crest; papillae of dorsal row more elongate, separate, conical. Several normal suckers on proximal, non-modified portion. Distalmost section of the arm not modified.

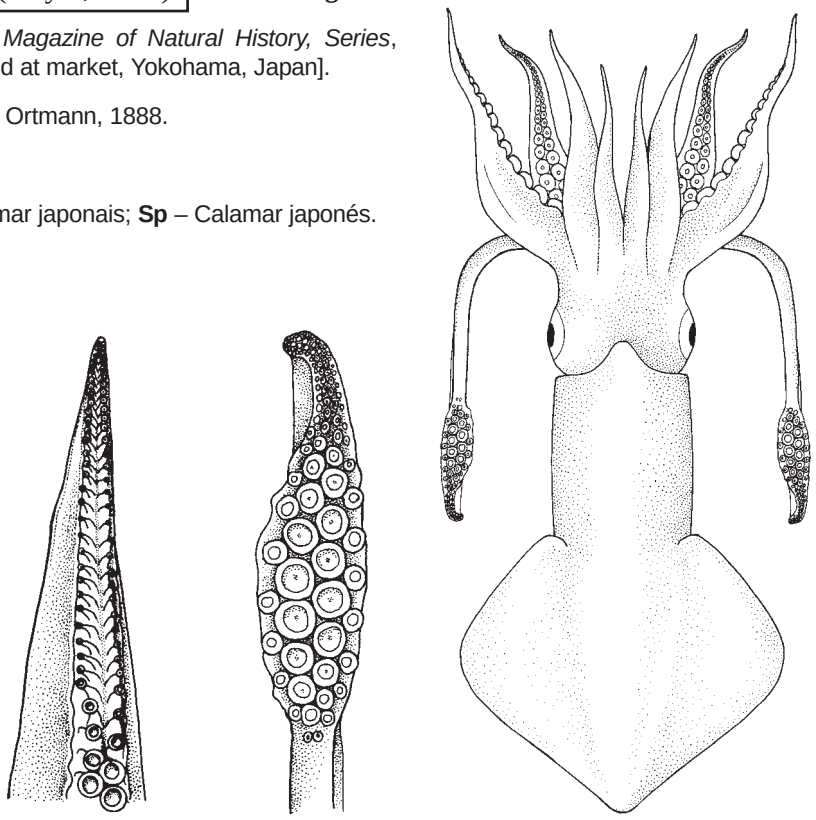


Fig. 107 ***Loliolus (Nipponololigo) japonica***

Size: Small-sized squid; maximum recorded mantle length 130 mm (female, northeastern Honsu) and 150 mm (sex not reported, Yellow Sea).

Geographical Distribution: Temperate to tropical western Pacific Ocean, from the Yellow Sea and East China Sea to southern Vietnamese waters and northward around Japan, to southern Hokkaido (Fig. 108).

Habitat and Biology: This species is most abundant in shallow waters. Spawning takes place during summer and autumn in depths between 1 and 10 m. During this period the squid form large aggregations.

Interest to Fisheries: This species supports local fisheries during spring and summer north of mid-Honshu, Japan, as well as in China and Viet Nam. It is reported as one of the most abundant species in the catches off Quingdao (Sangdon Province), China, East Yellow Sea, and, occasionally, off the southeastern coast of Honshu, Japan, Pacific Ocean. It is taken with set nets and small trawls, but it is uncertain whether small individuals can be attracted with light and then jigged. The squid is marketed fresh and frozen. The flesh is of excellent quality and often is eaten raw.

Local Names: JAPAN: Bouzuika, Hiika, Jhindouika, Koika.

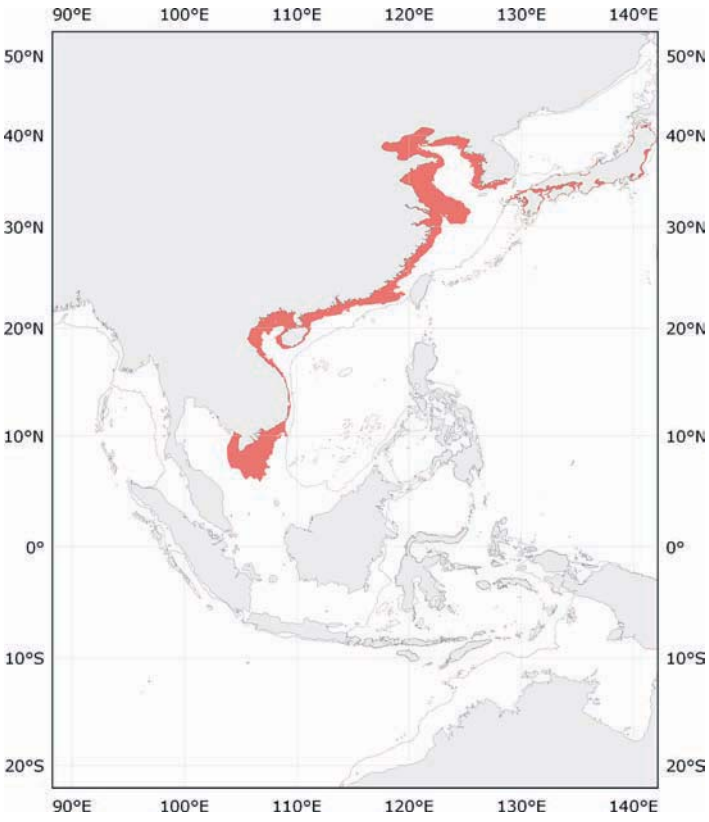


Fig. 108 ***Loliolus (Nipponololigo) japonica***

Remarks: The gladius length index (GLI: gladius width/gladius length x 100) was found to be the most useful character to discriminate juveniles of ***Loliolus japonica*** and ***Uroteuthis edulis*** smaller than 12 mm mantle length, in the areas where the 2 species co-occur (Okutani *et al*., 1975). Due the importance of this species to local fisheries, preliminary considerations were made on the methods of forecasting catches in the Yellow Sea and Bohai Sea (Ge and Qiu, 1991).

Literature: Natsukari (1983), Okutani *et al*. (1976a, 1987), Norman and Lu (2000), Okutani (2005), Ren *et al*. (2005), Vecchione (2008f).

Loliolus (Nipponololigo) sumatrensis (D'Orbigny, 1835) **Fig. 109**

Loligo sumatrensis D'Orbigny, 1835 *In* Ferussac and D'Orbigny, 1834-1848, *Histoire Naturelle Generale et Particuliere Cephalopodes Acetabuliferes Vivants et Fossiles*, 96 pages + lvi pages + 361 pages, Atlas with 144 plates. Paris. [317, Calmar pl. 13, figs 1-3]. [fide Tillier and Boucher-Rodoni (1994:101); taxon dated from plate]. [Type locality: Sumatra Island, Indonesia, eastern Indian Ocean].

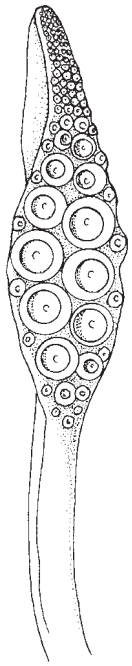
Frequent Synonyms: *Loligo kobiensis*, Hoyle, 1885, Roper *et al*. 1984, *Loligo yokoyae*, Ishikawa, 1926, *Loliolus rhomboidalis*, Burgess, 1967, *Nipponololigo kobiensis*, Natsukari, 1983.

Misidentifications: *Loliolus beka*, *Loliolus uyii*.

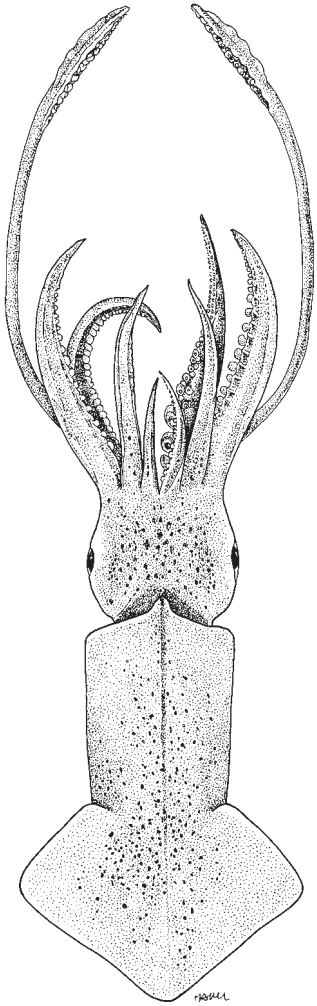
FAO Names: En – Kobi squid; **Fr** – Calmar kobì; **Sp** – Calamar kobí.

Diagnostic Features: Mantle short, slender, subcylindrical, gradually tapers posteriorly into a blunt point. **Fins rhomboidal** with round lateral angles, **length about 60 to 65% of mantle length, width slightly larger, 60 to 70% of mantle length**. Head small, with large eyes. Arms moderately long, slightly shorter in females; arm sucker rings with 6 to 9 low broad squared teeth. Arm III sucker rings with 5 to 10 low plate-like teeth; diameters less than those of the largest tentacular sucker rings which are smooth or have low serrations around only part of their diameter. **Left and right ventral arms modified in males**. **Most of the left ventral arm is hectocotylized, up to 87% distal to the first 3 pairs of normal suckers**, sucker stalks of the left arm modified as low stump-like papillae in the dorsal series and broad thick palisade-like papillae in the ventral series, reducing in size distally. **Right ventral arm with 3 or 4 pairs of much enlarged suckers proximally.** Suckers on the other arms are similar in shape and size in males and females, except the proximal suckers in arm III of males, enlarged at sexual maturity. Tentacles weak, tentacular clubs expanded and rather strong in comparison; 6 to 8 medial manal suckers up to 4 to 5 times the diameter of lateral suckers and with smooth sucker rings; smaller marginal suckers with 6 to 15 small, sharp teeth.

Size: Small-sized species, maximum mantle length 120 mm; common in catches at 20 to 70 mm mantle length.



tentacular club



ventral view

Fig. 109 ***Loliolus (Nipponololigo) sumatrensis***

Geographical Distribution: Temperate and tropical western Pacific, from the southern Japanese and South Korean waters southwestward to Sumatra, China, Thailand, Philippines and Indonesia, westward to the Bay of Bengal, from the Andaman Sea to the east coast of India and the Maldive Islands (Fig. 110).

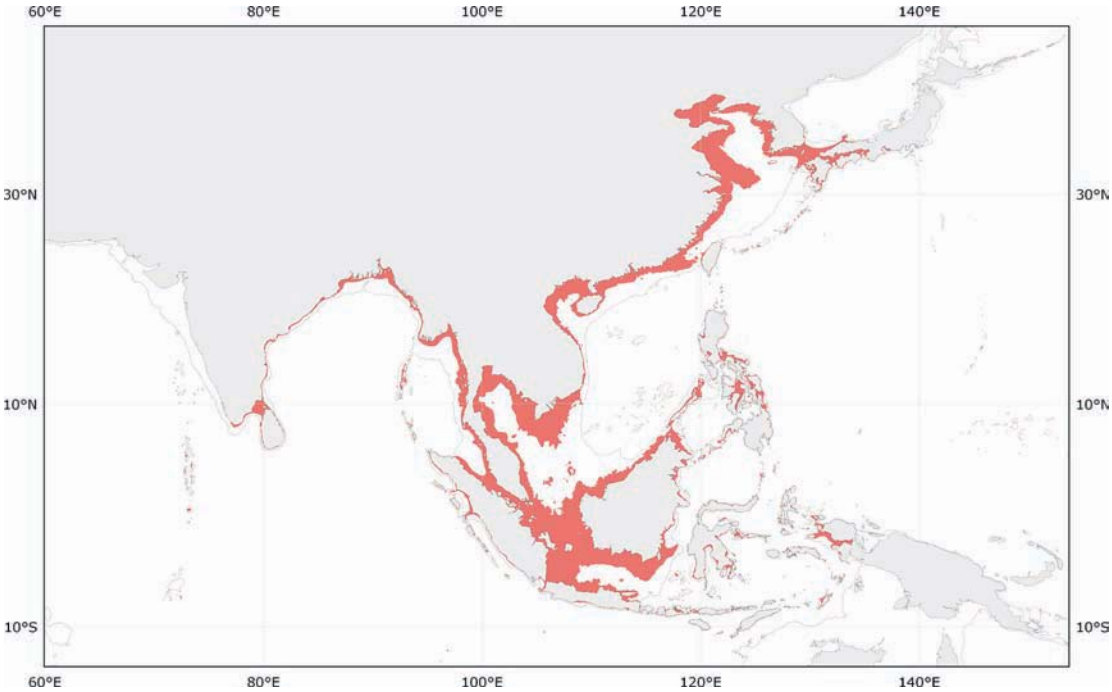


Fig. 110 ***Loliolus (Nipponololigo) sumatrensis***

Known distribution

Habitat and Biology: ***Loliolus (Nipponololigo) sumatrensis*** commonly inhabits coastal waters all loliginids are neritic and coastal waters. Its biology has not been specifically investigated, probably because of its marginal interest to fisheries. A synopsis of the available biological knowledge, however, is available for the Gulf of Thailand and the Andaman Sea populations where ***L. sumatrensis*** is common at sizes that range between 20 and 70 mm mantle length, and its spawning period extends year round. Egg capsules are leaf-like and contain about 100 eggs; hatchlings, 1.5 mm mantle length, are planktonic.

Interest to Fisheries: Taken as bycatch in trawl and light-luring fisheries for other squids in most of its distributional area (e.g. southwestern Japanese waters), the Kobi squid is highly abundant in the Gulf of Thailand and in the Andaman Sea, whereas it appears to be scarce in the Bay of Bengal. Attempts to rear this species in a large-scale culture system in Thailand provided initial data useful for potential commercial aquaculture production.

Local Names: THAILAND: Katoy squid.

Remarks: According to Manoch (1998) ***Loliolus uyii*** from the eastern side of the Gulf of Thailand is synonymous with ***L. sumatrensis***.

Literature: Burgess (1967), Natsukari (1983, 1984b), Okutani *et al*. (1987), Chotiyaputta (1993a), Okutani (2005), Jereb and Roper (2006), Vecchione (2008f).

Loliolus (Nipponololigo) uyii (Wakiya and Ishikawa, 1921)

Fig. 111

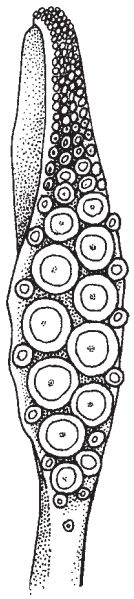
Loligo uyii Wakiya and Ishikawa, 1921, *Dobutsu-Gaku Zasshi [Zoological Magazine, Tokyo]*, 33:279–292, 12 figures [286, fig. 12a–h]. [Type locality: Bay of Kagoshima, Kii, Japan, western North Pacific Ocean].

Frequent Synonyms: *Loligo gotoi* Sasaki, 1929, *Loligo tago*, Sasaki, 1929, *Loligo aspera* Ortmann, 1888.

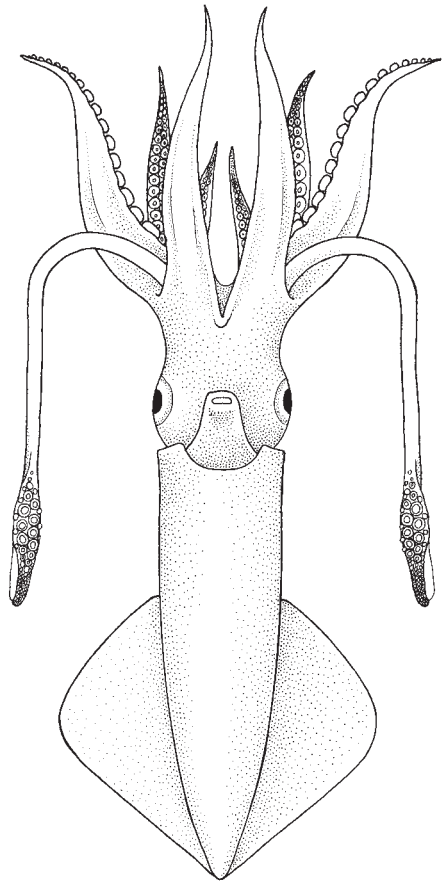
Misidentifications: None.

FAO Names: En – Little squid; **Fr** – Calmar mignon; **Sp** – Calamar balilla.

Diagnostic Features: Mantle short, moderately stout, its width about 25% of the mantle length. **Fins rhomboidal**, their angles rounded, length **about 60% of mantle length**. Tentacular clubs slightly expanded, about 8 suckers in 2 median manal series greatly enlarged with smooth rings; medial and distal rings with 7 to 10 very low, broad, plate-like or semilunar teeth. **Arm III sucker rings with 3 to 6 low plate-like teeth**; diameters approximately equal to those of the largest tentacular sucker rings which are smooth. **Left ventral arm hectocotylized along distal two-thirds with about 75 suckerless papillae**, those in dorsal series small, rounded, separate, but the ones on ventral row greatly swollen and connected into a ridge.



tentacular club



ventral view

Fig. 111 ***Loliolus (Nipponololigo) uyii***

Size: Small-sized squid; maximum mantle length 113 mm (female).

Geographical Distribution: Temperate and tropical Indo-West Pacific Ocean: southwestern Japan, to the East and South China Seas, including Taiwan (Province of China) (Fig. 112).

Habitat and Biology: This species occurs to about 50 m depth.

Interest to Fisheries: Unknown.

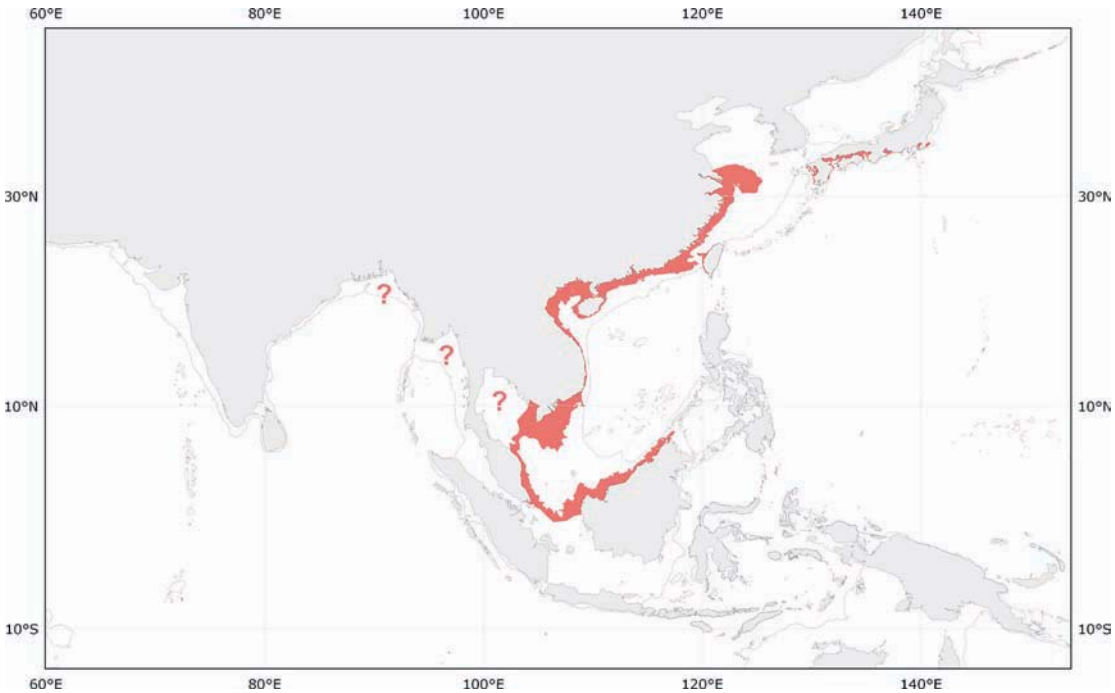


Fig. 112 ***Loliolus (Nipponololigo) uyii***

Known distribution

Local Names: CHINA: Yau jai.

Remarks: Norman and Lu (2000) report the species distribution to extend to the gulf of Thailand. According to Manoch, 1998, records from the Gulf of Thailand should be attributed to ***Loliolus sumatrensis***. Records of this species from the Bay of Bengal also exist (Yothinayagam, 1987).

Literature: Natsukari (1983), Nesis (1982, 1987), Manoch (1998), Vecchione, *et al*. (1998b), Norman and Lu (2000), Okutani (2005), Vecchione (2008f).

Lolliguncula Steenstrup, 1881

Lolliguncula Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 211–242. [242].

Type Species: *Lolliguncula brevis*.

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Arm sucker rings with square, plate-like teeth around entire margin. **Hectocotylus without crest**; suckers reduced, sucker stalks elongated to form papillae on either dorsal or both dorsal and ventral rows. Mantle without posterior tail-like elongation. Posterior of **fins broadly rounded; fins wider than long in adults**. Eggs small. Spermatophores with **long cement body**. Photophores absent.

Size: Small-sized species; maximum mantle length 120 mm.

Geographical Distribution: Tropical and subtropical West Atlantic, and tropical eastern Pacific Ocean.

Remarks: The genus ***Lolliguncula*** was established to distinguish ***L. brevis*** from the species of ***Loligo*** then known, based on body and fin shape and spermatophore deposition site. These characters have since proven to exhibit considerable variability, both within and among species. However, all of the species in this genus are united and distinguished from all other loliginids by the long cement body of their spermatophores. Variability exists in hectocotylus morphology, and this led Berry (1929) to erect the genus ***Loliolopsis*** and Brakoniecki (1986) to erect ***Afrololigo***. This variability is extreme in ***L. diomedeae***, but Brakoniecki (1986) has pointed out the similarities in hectocotylization between this species and the other species of ***Lolliguncula***. Many of the morphological characters of ***Afrololigo mercatoris*** are shared with species of ***Lolliguncula***, the genus in which it was originally described. However, DNA sequence analysis by Anderson (2000a) supports Brakoniecki's (1986) conclusion based on hectocotylus morphology that ***Afrololigo*** is a distinct genus (Vecchione, 2008a). Two subgenera currently are recognized. Since the type species of the formerly monotypic genus belongs to the subgenus ***Lolliguncula***, the subgenus ***Lolliguncula*** is treated first in this work.

Literature: Brakoniechi (1986), Anderson (2002a), Vecchione *et al*. (2005), Vecchione (2008g).

Key to the subgenera of *Lolliguncula*

1a. Modified portion of hectocotylus less than entire arm, proximal portion not modified . ***Lolliguncula (Lolliguncula)***
1b. Hectocotylus modified along entire arm . . . . . ***Lolliguncula (Loliolopsis)***

Subgenus ***Lolliguncula*** Steenstrup, 1881

Lolliguncula Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 211–242. [242].

Type Species: *Lolliguncula (Lolliguncula) brevis* (Blainville, 1823).

Lolliguncula (Lolliguncula) brevis (Blainville, 1823) **Fig. 113**

Loligo brevis Blainville, 1823, *Journal Physique Chimie d'Histoire Naturelle*, 96:116–135. [133]. [Type locality: Japan, western North Pacific Ocean].

Frequent Synonyms: *Loligo brevipinna* Lesueur, 1824, *Loligo hemiptera* Howell, 1867.

Misidentifications: *Loligo* spp.