

2.12 Family ENOPLOTEUTHIDAE Pfeffer, 1900

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Enoploteuthidae Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 145–198 [163].**Type Genus:** *Enoploteuthis* d'Orbigny in Rüppel, 1844: [129].**FAO Names:** **En** – Enope squids; **Fr** – Enoploloutènes; **Sp** – Enoplolurias.

Diagnostic Features: Funnel-mantle locking apparatus straight; biserial armature (except occasionally at the arm tips) with at least **some hooks on all the arms. Buccal crown with 8 supports; buccal connectives attached to dorsal margins of arms IV.** No secondary buccal connectives attached to ventral margins of arms I and II. (*Enoploteuthis dubia* Adam, 1960a, is unique in having connectives that attach dorsally to all arms). **Tentacular clubs with 1 or 2 series of hooks on manus** (arrangement varies with genus); armature on manus in 2 or 3 series. **Photophores present on mantle, funnel, head, eyeballs, and arms.** Photophores absent from tentacles, viscera, and most of fins. **Nidamental glands absent;** oviducal glands enlarged; oviducts unpaired. **Fins usually terminal; always lack posterior lobes.** Tail fleshy, extends well beyond conus of gladius. Photosensitive vesicles present. **Nuchal folds present.** Tentacles not modified near base; stalk “ligament” and vein leave tentacle at base in membrane. **Ink sac not embedded in digestive gland.** Gladius with small, blunt conus and elongate cone field; rostrum absent.

Size: Small-sized squid up to 130 mm mantle length.**Geographical Distribution:** Inhabitants of the tropical, subtropical and temperate oceans of the world.**Habitat and Biology:** Enoploteuthids are mesopelagic squids that undergo extensive diel vertical migrations. Paralarvae and juveniles are epipelagic and inhabit the upper 200 m.**Interest to Fisheries:** Generally enoploteuthids are not fished on a commercial basis. There are exceptions, however, most notably the intense, seasonal fishery for *Watasenia scintillans* in Japan, especially in Toyama Bay, where annual commercial landings approach 4 000 tonnes. *Enoploteuthis chunii* is sympatric with *W. scintillans* and also enters the fishery as bycatch with *Watasenia*. A third species is known to be used in Singapore, but no data currently are available.

Remarks: The Enoploteuthidae formerly was comprised of three long-established subfamilies: Enoploteuthinae (*Enoploteuthis*, *Abralia*, *Abraliopsis*, *Watasenia*); Pyroteuthinae (*Pyroteuthis*, *Pterygioteuthis*); and Ancistrocheirinae (*Ancistrocheirus*, *Theledioteuthis*). Now these are recognized as separate, closely-related families of the Enoploteuthid group (Clarke, 1988b; Young and Harman, 1998; Young *et al.*, 1998a). *Theledioteuthis* now is considered as an immature *Ancistrocheirus*, with which it is synonymized. The young of *Abralia* and *Enoploteuthis* are not easily distinguished: the presence of 2 photophores on the developing eyes of *Enoploteuthis* versus 3 enlarged photophores on *Abralia* seems to apply for most species but not necessarily all. *Abraliopsis* species generally are distinctive from other related genera from a very small size by the development of the bulbous photophores on the tips of the ventral arms (IV), by relatively longer arms (greater than or equal to the mantle length) and tentacles. Other characters useful for species discrimination include chromatophore patterns, size of largest club suckers versus arm suckers, relative sizes among club suckers, number of club suckers, photophore patterns and photophore sizes.

Key to the families of the Enoploteuthid Group^{1/}

- 1a. Photophores on mantle, surface of head and arms (>4 mm ML); not on viscera → **2**
 1b. Photophores on viscera, not on mantle or surface of head or arms **Pyroteuthidae**

- 2a. Photophores on mantle, head, eyes, and arms, not on tentacles **Enoploteuthidae**
 2b. Photophores on mantle, head, arms, and tentacles, but not on eyes (>5 to 7 mm ML) **Ancistrocheiridae**

Key to the Genera of the family Enoploteuthidae

- 1a. One or more enlarged photophores on distal tip of arms IV (>3 to 5 mm ML). → **2**
 1b. No enlarged photophores on distal tip of arms IV. → **4**

- 2a. Squid collected from seas around Japan. → **3**
 2b. Squid collected also from other geographic regions **Abraliopsis**

- 3a. Tentacle hooks in 2 rows (appear at about 5 to 10 mm ML). **Abraliopsis**
 3b. Tentacle hooks in 1 row (appear at about 5 mm ML). **Watasenia**

- 4a. Two enlarged photophores develop on eye (>2.5 mm ML). **Enoploteuthis**
 4b. Three enlarged photophores develop on eye (>2.0 to 2.5 mm ML). **Abralia**

Literature: Okiyama and Kasahara (1975), Roper and Young (1975), Kluchnik and Starobogatov (1978), Tsuchiya (1993), Young *et al.* (1998b), Bower *et al.* (1999c), Sweeney and Young (2003j), Tsuchiya and Young (2008).^{1/} Young *et al.* (1992). A more detailed key for genera is found in Dunning, 1998e.

***Enoploteuthis* d'Orbigny in Rüppell, 1844**

Enoploteuthis d'Orbigny in Rüppell, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135 [129].

Type Species: *Enoploteuthis leptura* (Leach, 1817).

Frequent Synonyms: None.

Diagnostic Features: Manus of club with 2 series of hooks; marginal suckers absent. No enlarged photophores at tips of arms IV. Fins subterminal. Buccal crown with typical chromatophores on aboral surface, possibly with light epithelial pigmentation on oral surface. Nine or 10 photophores on eyeball. Right arm IV hectocotylized. Suckers present distally on arms IV. Spermatophore receptacles at posterior junction of retractor muscles of funnel and head. Complex photophores of integument, in life, without red colour filters. Radula with heterodont rhachidian tooth. Large arm hooks with open apertures. Mantle with tail-like projection beyond posterior end of fin insertion. Anterior and posterior ocular photophores small, subequal.

Remarks: *Enoploteuthis* is a speciose genus with most species having been described in recent decades as a result of exploratory midwater trawling in the mesopelagic realm. While all *Enoploteuthis* species are important in the economy of the sea as abundant food sources for fishes and odontocetes, they have little commercial value at the present time, with the exception of *Enoploteuthis chunii* which is taken as bycatch in the Japanese fishery for *Watasenia scintillans*.

Literature: Roper (1964, 1966), Nesis (1982, 1987), Nesis (1993b), Young *et al.* (1998b), Jivaluk (2001), Tsuchiya (2009).

***Enoploteuthis leptura leptura* (Leach, 1817)**

(Type Species) Fig. 215

Loligo lepturo Leach, 1817, *Zoological Miscellany*, 3(30): 137–141 [141]. [Type locality: Not designated; 01°08'N, 07°26'E, Gulf of Guinea, eastern Atlantic Ocean, fide Lipinski *et al.* (2000: 107)].

Frequent Synonyms: None.

FAO Names: En – Hooked enope squid; Fr – Enoploloutène crochu; Sp – Enoploluria uncinada.

Diagnostic Features: Seven distinct light organ rows on ventral side of the mantle. Two rows of hooks extend along arm.

Size: Maximum mantle length to 92 mm.

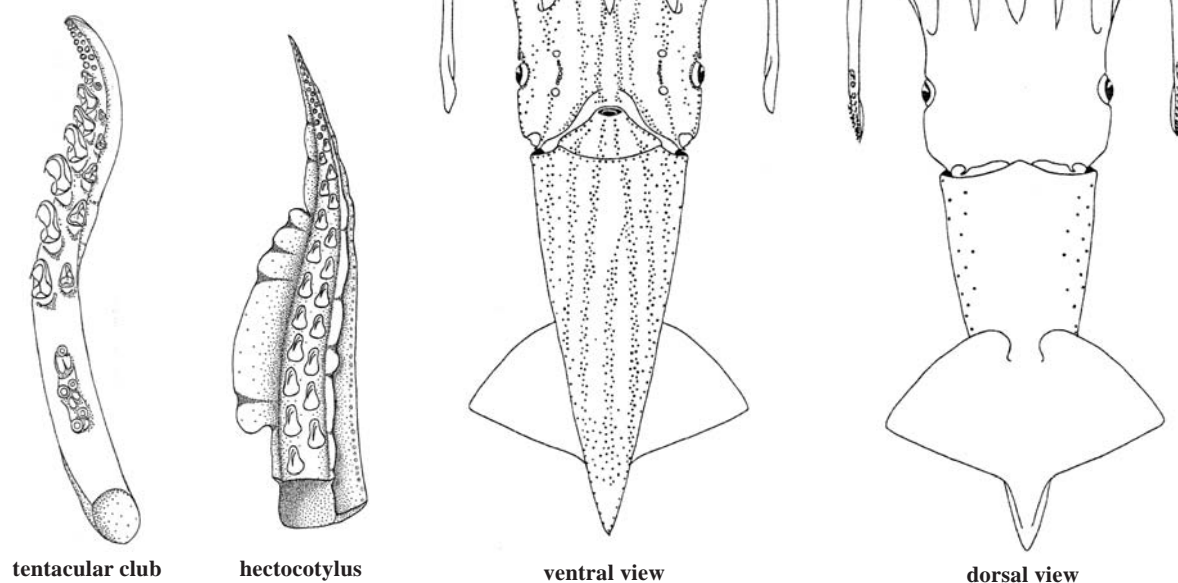


Fig. 215 *Enoploteuthis leptura leptura*

Geographical Distribution: Gulf of Guinea, eastern and western central Atlantic Ocean, Indo-West Pacific Ocean (Fig. 216).

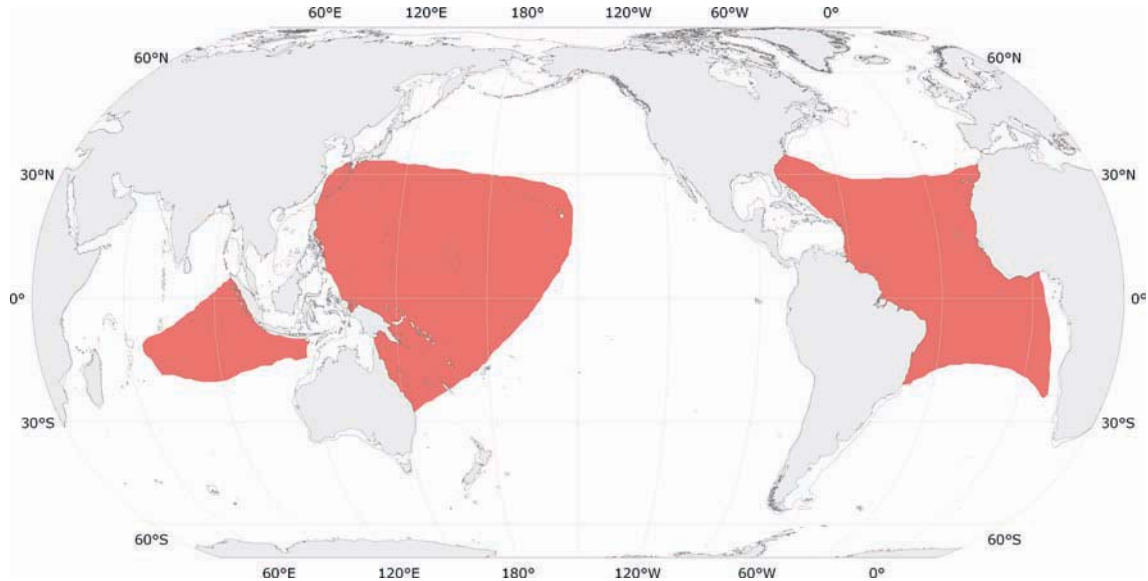


Fig. 216 *Enoplateuthis leptura leptura*

■ Known distribution

Habitat and Biology: Mesopelagic to epipelagic in tropical, subtropical (rarely temperate) waters as diel vertical migrators.

Remarks: Records from Pacific and Indian Oceans probably refer to subspecies *Enoplateuthis magnoceani* Nesis (1982, 1987).

Literature: Roper (1966), Arkhipkin (1994).

***Enoplateuthis leptura magnoceani* Nesis, 1982**

Enoplateuthis leptura magnoceani Nesis, 1982, *Light and Food Industry Publishing*, 358 pp. [162]. [Type locality: Pacific Ocean, exact locality unknown].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Tropical western and central Pacific Ocean and Indian Ocean; South China Sea; equatorial waters.

Habitat and Biology: Mesopelagic to epipelagic diel vertical migrator.

Literature: Tsuchiya (1993).

***Enoplateuthis anapsis* Roper, 1964**

Enoplateuthis anapsis Roper, 1964, *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1): 140–148 [140]. [Type locality: 16°55'N, 81°10'W, Caribbean Sea, western Atlantic].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Tropical and subtropical Atlantic Ocean; Gulf of Mexico and Caribbean Sea.

Habitat and Biology: Mesopelagic to epipelagic as diel vertical migrator.

Literature: Roper (1964, 1966), Laptikhovsky (1999b).

***Enoploteuthis chunii* Ishikawa, 1914**

Enoploteuthis chunii Ishikawa, 1914, *Journal of the College of Agriculture, Imperial University of Tokyo*, 4(7): 401–413 [401]. [Type locality: Toyama Bay, Etchu Province, Japan, western Pacific Ocean].

Frequent Synonyms: *Enoploteuthis theragrae* Taki, 1964.

Size: Mantle length to 100 mm.

Geographical Distribution: Western Pacific Ocean; Sea of Japan, off central and southern Japan, approximately 20°N to 40°N, 120°E to 150°E.

Habitat and Biology: A nerito-oceanic, mesopelagic boundary species that undergoes diel vertical migrations of the migrant pattern: day and night patterns are clearly separated with peak abundance deeper than 300 m during the day and shallower than 300 m at night. This species is restricted to warm Core Ring waters in the northwestern North Pacific Ocean. Captured as bycatch in the *Watasenia scintillans* fishery. Prey of odontocete whales and dolphins, walleye pollack.

Interest to fisheries: This species co-occurs with *Watasenia scintillans* and it constitutes a bycatch that is not sorted out from the target species.

Literature: Okiyama and Kasahara (1975), Okutani (1987, 1995), Hayashi (1991).

***Enoploteuthis galaxias* Berry, 1918**

Enoploteuthis galaxias Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavour, 1909–1914*, 4(5): 201–298 [211]. [Type locality: Victoria, Australia, Tasman Sea, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 110 mm.

Geographical Distribution: Southwestern South Pacific Ocean: southern, eastern Australia and northern New Zealand.

Habitat and Biology: A southern subtropical, nerito-oceanic mesopelagic and benthic-bathyal species.

Literature: Riddell (1985).

***Enoploteuthis higginsii* Burgess, 1982**

Enoploteuthis higginsii Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [718]. [Type locality: off Waianae, Oahu Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 60 mm.

Geographical Distribution: Hawaiian waters, equatorial region of central Pacific Ocean; Indian Ocean.

Habitat and Biology: Mesopelagic to epipelagic as a diel vertical migrator.

Literature: Tsuchiya (1993).

***Enoploteuthis jonesi* Burgess, 1982**

Enoploteuthis jonesi Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [713]. [Type locality: off Milolii, Hawaii Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 85 mm.

Geographical Distribution: Hawaiian waters and equatorial region of western central Pacific Ocean.

Habitat and Biology: Mesopelagic to epipelagic as a diel vertical migrator.

Remarks: Nesis (1982, 1987) considers *Enoploteuthis jonesi* to be a subspecies of *E. anapsis* Roper, 1964.

Literature: Roper (1966), Young *et al.* (1998b).

***Enoploteuthis obliqua* (Burgess, 1982)**

Enoploteuthis migrato Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [704]. [Type locality: 11°47'N, 144°47'W, central Pacific Ocean].

Frequent Synonyms: *Enoploteuthis migrato* Burgess, 1982.

Size: Mantle length to 60 mm.

Geographical Distribution: Eastern equatorial central Pacific Ocean from east of Line Islands eastward to Central American region.

Habitat and Biology: A mesopelagic to epipelagic species as a diel vertical migratory.

Literature: Young *et al.* (1998b).

***Enoploteuthis octolineata* Burgess, 1982**

Enoploteuthis octolineata Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [708]. [Type locality: 2°56'N, 150°03'W, central Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Equatorial region of the central Pacific Ocean.

Habitat and Biology: Presumed diel vertical migratory in mesopelagic to epipelagic waters.

Literature: Young *et al.* (1998b).

***Enoploteuthis reticulata* (Rancurel, 1970)**

Enoploteuthis migratory Rancurel, 1970, *Cahiers O.R.S.T.O.M., Océanographique*, 8(4): 3–87 [45]. [Type locality: 0°02'S, 135°48'W, central Pacific Ocean].

Frequent Synonyms: *Enoploteuthis migratory* Rancurel, 1970.

Size: Mantle length to 130 mm.

Geographical Distribution: Very broadly distributed in Indo-Pacific Ocean region, approximately 35°N to 30°S in western Pacific Ocean and 75°E to 90°E in Indo-Pacific Ocean; pantropical to subtropical.

Habitat and Biology: Mesopelagic to lower epipelagic, diel vertical migrator. Prey of lancet fishes and other mesopelagic fishes.

Literature: Rancurel (1970), Tsuchiya (1993).

***Enoploteuthis semilineata* Alexeyev, 1994**

Enoploteuthis semilineata Alexeyev, 1994b, *Ruthenica*, 4(2): 167–171 [167]. [Type locality: 40°10.7'S, 127°48.4'W – 40°03.5'S, 127°36.7'W, eastern South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 90 mm.

Geographical Distribution: Eastern South Pacific Ocean; holotype at 40°S, 127°W.

Habitat and Biology: Presumed diel vertical migrator from mesopelagic to lower epipelagic zones.

Literature: Alexeyev (1994b).

***Abralia* Gray, 1849**

Abralia Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum*, I: Cephalopoda Artepedia, 164 pp. [50].

Type Species: *Abralia armata* (Quoy and Gaimard, 1832).

Frequent Synonyms: *Enoploion* Pfeffer, 1912; *?Prodromoteuthis* Pfeffer, 1912; *Stenabralia* Grimpe, 1931; *Arabralia* Nesis, 1982, 1987.

Diagnostic Features: Manus of tentacular club with 1 series of hooks, 2 series of suckers. Enlarged photophores on tips of arms IV generally absent; when present, photophores not covered by black chromatophores. Fins terminal. Buccal crown with typical chromatophores on aboral surfaces, no other pigmentation present, only occasionally with silvery photophores smaller than the diameter of the arms. Five to 12 photophores of various sizes on eyeball. Right or left arm IV hectocotylized. Suckers present distally on arms IV. Spermatophore receptacle(s) located under collar, in median pocket at posterior end of nuchal cartilage, or between stellate ganglia. Complex photophores of integument, in life, without red colour filters. Radula with homodont teeth. Large arm hooks with closed apertures.

Geographical Distribution: Worldwide in tropical and subtropical waters.

Habitat and Biology: The species principally are epipelagic to mesopelagic. They are members of the midwater fauna of diel vertical migrators that ascend from daytime depths of around 600 m to nighttime depths of usually less than 200 m. Some species may occur at shallow depths when they inhabit waters where the mesopelagic zone intersects slopes of land masses, e.g. of oceanic islands, called the mesopelagic-boundary zone. Species are heavily preyed upon by tunas, billfishes, etc. and by the deeper-hunting odontocete cetaceans.

Remarks: *Abralia* is the most speciose genus in the Enoploteuthidae.

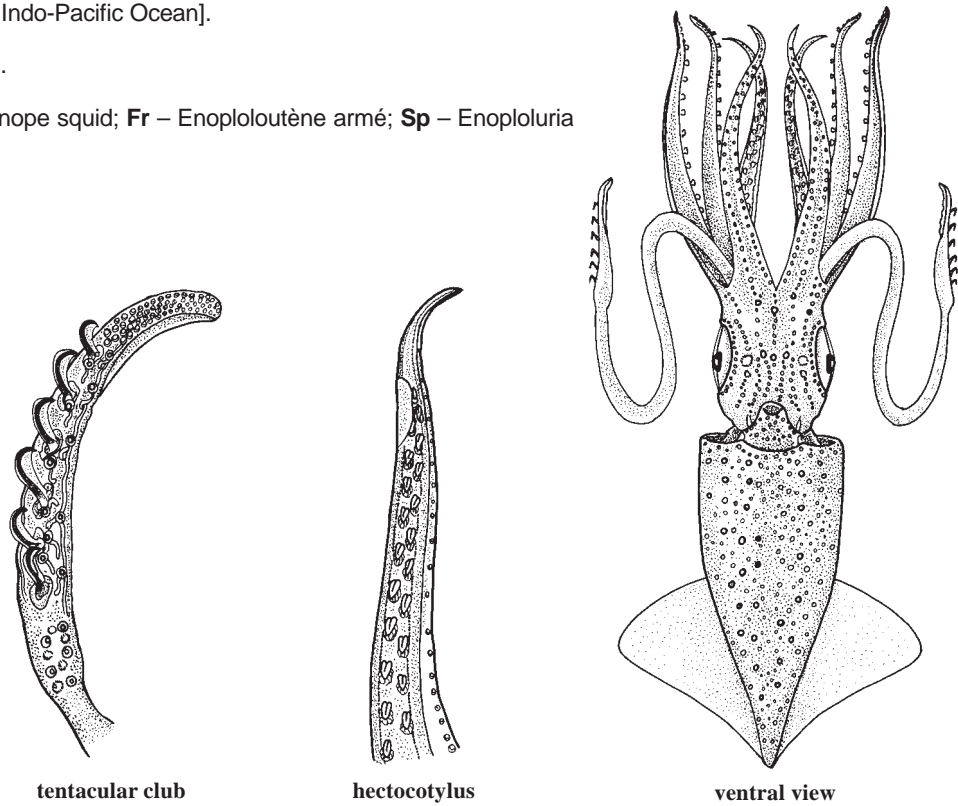
Literature: Roper and Young (1975), Tsuchiya and Okutani (1988), Young *et al.* (1998b), Burgess (1992 [1991], 1998), Young and Tsuchiya (2009a).

Abralia armata (Quoy and Gaimard, 1832)**Fig. 217**

Onychoteuthis armatus Quoy and Gaimard, 1832, *Voyage de découvertes de l'Astrolabe 1826–1829, Zoologie*, 2(1): 1–320 [84]. [Type locality: near Sulawesi (Celebes) Island, Indonesia, Indo-Pacific Ocean].

Frequent Synonyms: None.

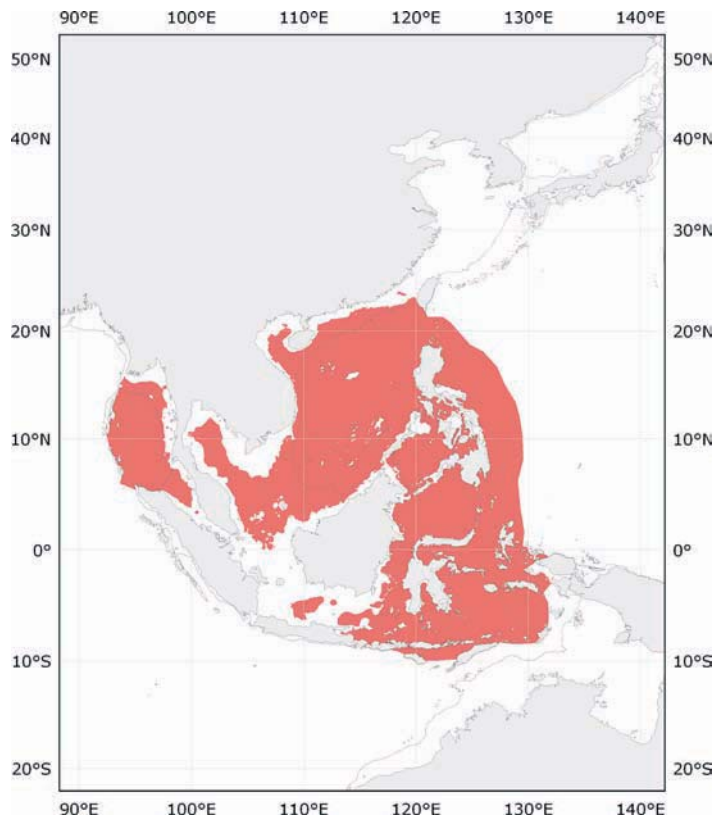
FAO Names: **En** – Armed enope squid; **Fr** – Enoploloutène armé; **Sp** – Enoploluria armada.

**Fig. 217** *Abralia armata*

Size: Mantle length to around 20 mm.

Geographical Distribution: Indo-Pacific Ocean: Indonesia, Philippines, Moluccas Islands, South China Sea (Fig. 218).

Literature: Young *et al.* (1998b).

**Fig. 218** *Abralia armata*

■ Known distribution

Abralia andamanica Goodrich, 1896

Abralia andamanica Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology*, 7(1): 1–24 [9]. [Type locality: Andaman Sea, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 60 mm.

Geographical Distribution: Indian and western Pacific Oceans: Arabian Sea and Seychelles, Philippines, Indonesia, off Japan to Tasman Sea, East China Sea, South China Sea, Yellow Sea, off Australian North West Shelf.

Habitat and Biology: A mesopelagic-boundary species that ascends from the mesopelagic zone to 100 to 300 m at night. Off Japan it exhibits a multimodal size distribution and spawns in late summer to early winter.

Remarks: This taxon as currently recognized may in fact represent several closely-related species.

Literature: Okutani (1974a), Yamamoto and Okutani (1975), Okutani *et al.* (1987), Okutani (1995).

Abralia astrolineata Berry, 1914

Abralia astrolineata Berry, 1914, *Transactions and Proceedings of the New Zealand Institute*, 46(24): 134–149 [145]. [Type locality: Kermadec Islands, off eastern Australia, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Southwestern Pacific Ocean; eastern Australia (off Queensland); off Kermadec Islands.

Habitat and Biology: A presumed mesopelagic-boundary species, with three discrete spawning periods during the year.

Literature: Nesis (1982, 1987).

Abralia astrostricta Berry, 1909

Abralia astrostricta Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 407–419 [412]. [Type locality: off Oahu Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Central and western Pacific Ocean; Hawaiian Islands to Philippine Sea, eastern Australia, off Japan, Kuroshio Current, South China Sea.

Habitat and Biology: This is a widely distributed tropical, subtropical species of the mesopelagic-boundary fauna.

Literature: Tsuchiya (1993), Young (1995).

Abralia dubia (Adam, 1960)

Enoploteuthis dubia Adam, 1960a, *Bulletin of the Sea Fisheries Research Station, Haifa*, 26: 1–26 [12]. [Type locality: Eylath, Gulf of Aqaba, Red Sea, northwestern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Red Sea.

Literature: Young *et al.* (1998b).

***Abralia fasciolata* Tsuchiya, 1991**

Abralia fasciolata Tsuchiya, 1991, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 17(2):69–79 [70]. [Type locality: 11°14'06"N, 47°38'12"E, Gulf of Aden, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Indian Ocean: Gulf of Aden.

Habitat and Biology: Midwater, mesopelagic to epipelagic at night.

Literature: Young *et al.* (1998b).

***Abralia grimpei* Voss, 1959**

Abralia grimpei Voss, 1959, *Bulletin of Marine Science of the Gulf and Caribbean*, 8(4): 369–389 [375]. [Type locality: 26°25'N, 79°45'W, western Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 27 mm.

Geographical Distribution: Western North Atlantic Ocean, Gulf Stream, Florida; probably Caribbean Sea; tropical, subtropical.

Habitat and Biology: Mesopelagic to epipelagic.

Literature: Young *et al.* (1998b).

***Abralia heminuchalis* Burgess, 1992**

Abralia heminuchalis Burgess, 1992, [1991], *Bulletin of Marine Science*, 49(1–2): 113–136 [120]. [Type locality: 0°44'S, 149°46'W, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Central equatorial Pacific Ocean; from 16°N to 15°S and from 144°W to 168°W.

Literature: Hidaka and Kubodera (2000).

***Abralia marisarabica* Okutani, 1983**

Abralia marisarabica Okutani, 1983b, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 9(4): 161–168 [162]. [Type locality: 24°48'N, 63°20'E, Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 25 mm.

Geographical Distribution: Indian Ocean; Arabian Sea, Seychelles Islands.

Habitat and Biology: Presumed mesopelagic to epipelagic as diel vertical migrator at night.

Literature: Piatkowski and Welsch (1992 [1991]), Chesalin and Zuev (2002b).

***Abralia multihamata* Sasaki, 1929**

Abralia multihamata Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University, Supplement*, 20: 357pp. [245]. [Type locality: Akocho, Formosa, Taiwan, western North Pacific Ocean].

Frequent Synonyms: *Abralia (Stenabralia) lucens* Voss, 1963a.

Size: Mantle length to 32 mm.

Geographical Distribution: Far western Pacific Ocean; Taiwan, China; Philippines; northwest Pacific Ocean.

Habitat and Biology: A mesopelagic-boundary species.

Literature: Tsuchiya (1993), Young *et al.* (1998b).

***Abralia omiae* Hidaka and Kubodera, 2000**

Abralia omiae Hidaka and Kubodera, 2000, *Bulletin of Marine Science*, 66(2): 417–443 [419]. [Type locality: 05°00'N, 155°00'E, western tropical Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to about 30 mm.

Geographical Distribution: Western tropical Pacific Ocean; type locality: 05°00'N, 155°00'E.

Literature: Hidaka and Kubodera (2000).

***Abralia redfieldi* Voss, 1955**

Abralia redfieldi Voss, 1955, *Bulletin of Marine Science of the Gulf and Caribbean*, 5(2): 81–115 [99]. [Type locality: off Gun Cay, Bahamas Islands, western North Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 30 mm.

Geographical Distribution: Western Atlantic Ocean, tropical eastern Atlantic Ocean; Nova Scotia (43°N) to Argentina (45°S); most abundant in Bahamas, Bermuda, Greater and Lesser Antilles; western tropical Africa.

Habitat and Biology: This small species is mesopelagic-epipelagic and bathypelagic, neritic-oceanic in its vertical distribution.

Literature: Cairns (1976), Golub (2001).

***Abralia renschi* Grimpe, 1931**

Abralia renschi Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [149]. [Type locality: Sabang Harbour, Sumatra, Indonesia].

Frequent Synonyms: None.

Size: Mantle length to 45 mm.

Geographical Distribution: Indonesian region; off Sumatra, Java, Maldives Islands.

Habitat and Biology: Mesopelagic-epipelagic.

Literature: Young *et al.* (1998b).

***Abralia robsoni* Grimpe, 1931**

Abralia robsoni Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [156]. [Type locality: South of Bonomisaki, Japan, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 51 mm.

Geographical Distribution: Western Pacific Ocean; off Japan; open ocean.

Habitat and Biology: A mesopelagic to epipelagic diel vertical migrator.

Literature: Tsuchiya and Okutani (1988).

***Abralia siedleckyi* Lipinski, 1983**

Abralia siedleckyi, Lipinski, 1983, *Veliger*, 25(3): 255–265 [255]. [Type locality: 39°05'08"S, 13°43'E, South Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 33 mm.

Geographical Distribution: Southeastern Atlantic Ocean; off South Africa.

Habitat and Biology: Presumably a mesopelagic-epipelagic species.

Literature: Lipinski (1983), Hidaka and Kubodera (2000).

***Abralia similis* Okutani and Tsuchiya, 1987**

Abralia similis Okutani and Tsuchiya, 1987, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 13(4): 141–150 [141]. [Type locality: 30°03.2'N, 134°03.5'E, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 32 mm.

Geographical Distribution: Northwestern Pacific Ocean; Shikoku Basin, Japan, Tonga Islands, (possibly equatorial western Indian Ocean and eastern Pacific Ocean).

Habitat and Biology: Mesopelagic-epipelagic in subtropical waters, e.g. in Kuroshio Current; diel vertical migrations.

Literature: Tsuchiya and Okutani (1988), Hidaka and Kubodera (2000).

***Abralia spaercki* Grimpe, 1931**

Abralia spaercki Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [150]. [Type locality: near Amboina, Banda Sea, Indonesia].

Frequent Synonyms: None.

Size: Mantle length to 50 mm.

Geographical Distribution: Indonesia, Philippines, Banda Sea.

Habitat and Biology: Mesopelagic-epipelagic.

Literature: Voss (1963a), Young *et al.* (1998b).

***Abralia steindachneri* Weindl, 1912**

Abralia steindachneri Weindl, 1912, *Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 49(17): 270–275 [271]. [Type locality: Shadwan, Red Sea, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 55 mm.

Geographical Distribution: Red Sea; Indian Ocean; off eastern Africa, Seychelle Islands, Gulf of Aden.

Habitat and Biology: A mesopelagic boundary species.

Literature: Nesis and Nikitina (1987), Young *et al.* (1998b).

***Abralia trigonura* Berry, 1913**

Abralia trigonura Berry, 1913b, *Proceedings of the United States National Museum*, 45(1996): 563–566 [565]. [Type locality: Pailolo Channel, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 37 mm.

Geographical Distribution: Central and western North Pacific Ocean; Hawaiian Islands, off Japan.

Habitat and Biology: Mesopelagic to epipelagic diel vertical migrator. Prey of dolphins.

Literature: Young *et al.* (1979b), Vecchione (1992a [1991]), Bower *et al.* (1999c), Hidaka and Kubodera (2000).

***Abralia veranyi* (Rüppel, 1844)**

Enoplateuthis veranyi Rüppel, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135 [131]. [Type locality: off Messina, Sicily, Central Mediterranean Sea].

Frequent Synonyms: *Enoploion eustictum* Pfeffer, 1912.

Diagnostic Features: See general description.

Size: Mantle length to 50 mm.

Geographical Distribution: Mediterranean Sea, off Messina, Italy; Atlantic Ocean. Tropical and subtropical western and eastern Atlantic Ocean, from northeastern United States to the Gulf of Mexico and Suriname; from Mediterranean Sea to Madeira.

Habitat and Biology: At bottom in bathyal and in midwater above slopes, occasionally to surface (night time); absent in the open ocean far from the slopes and slope waters. A mesopelagic to epipelagic diel vertical migrator.

Literature: Berry (1926), Kluchnik and Starobogatov (1978), Herring *et al.* (1992b), Young *et al.* (1998b).

Abraliopsis* Joubin, 1896*Plate VII, 40**

Abraliopsis Joubin, 1896, *Bulletin de la Société Scientifique et Médicale de l'Quest*, 5(1): 19–35 [20].

Type Species: *Enoplateuthis hoylei* Pfeffer, 1884.

Frequent Synonyms: None.

Diagnostic Features: Manus of club with 2 series of hooks, 1 series of suckers. Two to 4 (mostly 3) large photophores covered by black chromatophores on tips of arms IV. Fins terminal. Buccal crown without typical chromatophores, with dark epithelial pigmentation on oral surface. **Eyeball with 5 photophores ventrally, anterior and posterior photophores enlarged**, the 3 remaining photophores small, subequal. **Right or left arm IV hectocotylized. Suckers absent from arms IV.** Spermatophore receptacle(s) located under collar or between stellate ganglia. Complex photophores of integument, in life, with red colour filters. Radula with homodont teeth. **Large arm hooks with apertures closed.**

Remarks: *Abraliopsis* species occupy similar habitats as *Abralia* species, both geographically and vertically. As well, they are heavily preyed upon by epipelagic and mesopelagic top-level predatory fishes and by odontocete cetaceans. Species of

Abraliopsis can be placed into three subgenera (i.e. *Abraliopsis*, *Micrabralia*, *Pfefferiteuthis*) but these may not all be natural groups (Young and Tsuchiya, 2009b).

Literature: Young (1973b), Young *et al.* (1979b), Moreno and Pereira (1998), Young *et al.* (1998b), Young and Tsuchiya (2009b).

***Abraliopsis hoylei* (Pfeffer, 1884) (Type Species) Fig. 219**

Enoploteuthis hoylei Pfeffer, 1884, *Abhandlung aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30 [17]. [Type locality: Mascarene Islands, southwestern Indian Ocean].

Frequent Synonyms: None.

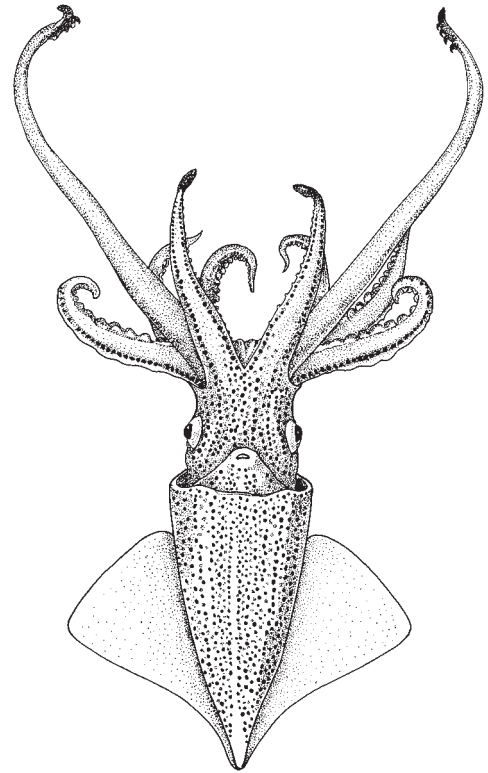
FAO Names: **En** – Hoyle's enope squid; **Fr** – Enoploloutène de Hoyle; **Sp** – Enoploluria de Hoyle.

Size: Mantle length to 30 mm.

Geographical Distribution: Indian Ocean, Mascarene Islands. Tropical and subtropical Indo-West Pacific Ocean from Hokkaido to the Tasman Sea and from eastern Africa to Hawaii; absent in Arabian Sea and Bay of Bengal (Fig. 220).

Habitat and Biology: Probably diel vertical migrator from mesopelagic zone to epipelagic waters at night.

Literature: Nesis (1974a).



ventral view

Fig. 219 *Abraliopsis hoylei*

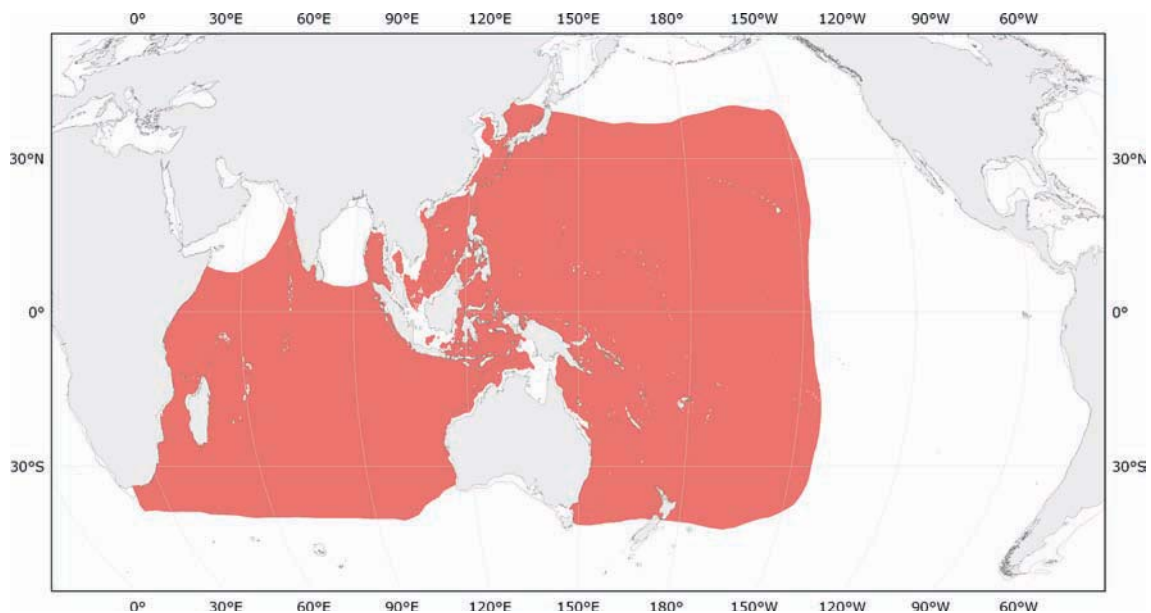


Fig. 220 *Abraliopsis hoylei*

■ Known distribution

Abraliopsis affinis (Pfeffer, 1912)

Abralia (Micrabralia) affinis Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [160]. [Type locality: eastern temperate North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Eastern tropical Pacific Ocean, off Mexico south to off Ecuador, approximately from 20°N to 30°S.

Habitat and Biology: A mesopelagic species that migrates to epipelagic zone at night. Prey of hammerhead shark.

Literature: Alexeyev (1994a), Okutani (1995).

Abraliopsis atlantica Nesis, 1982

Abraliopsis atlantica Nesis, 1982, *Light and Food Industry Publishing House*, 358 pp. [172, as footnote]. [Type locality: 01°51'N, 00°31'E, Gulf of Guinea, eastern tropical Atlantic].

Frequent Synonyms: None.

Size: Mantle length to 33 mm.

Geographical Distribution: Eastern tropical Atlantic Ocean, Gulf of Guinea.

Habitat and Biology: Assumed to be mesopelagic to epipelagic as a diel vertical migrator.

Literature: Cairns (1976), Laptikhovskiy (1999b).

Abraliopsis chuni Nesis, 1982

Abraliopsis chuni Nesis, 1982, *Light and Food Industry Publishing House*, 358 pp. [172, as footnote]. [Type locality: 01°49'N, 45°29'E, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 38 mm.

Geographical Distribution: Western Indian Ocean; tropical Indo-West Pacific Ocean, from eastern Africa to Line Islands.

Habitat and Biology: Presumed to be an equatorial, mesopelagic-epipelagic diel vertical migrator.

Literature: Chun (1910).

Abraliopsis falco Young, 1972

Abraliopsis falco Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 159 pp. [13]. [Type locality: 28°54'N, 118°08'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 46 mm.

Geographical Distribution: Eastern tropical Pacific Ocean; off Baja California to northern Chile from about 35°N to 20°S.

Habitat and Biology: Vertical migrator at night from mesopelagic into epipelagic zone.

Literature: Okutani (1974a, 1995).

***Abraliopsis felis* McGowan and Okutani, 1968**

Abraliopsis felis McGowan and Okutani, 1968, *Veliger*, 11(1): 72–79 [72]. [Type locality: 31°59'N, 122°24'W, Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 45 mm.

Geographical Distribution: Eastern North Pacific Ocean; off west coast North America, 27°N to 43°N; northwest Pacific Ocean off Japan.

Habitat and Biology: Strongly defined vertical migrator from 300 to 600 m (peak 400 to 500 m) during daytime, ascending to the upper 200 m (mean 100 m) at night. A dominant species in the Kuroshio-Oyashio transition zone, northwest Pacific Ocean. Prey of northern elephant seal, Pacific dolphins.

Literature: Young (1972a), Tsuchiya (1993), Mori *et al.* (2002).

***Abraliopsis gilchristi* (Robson, 1924)**

Abralia gilchristi Robson, 1924, *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3: 1–14 [3]. [Type locality: off Cape Town, South Africa, western South Atlantic Ocean].

Frequent Synonyms: *Enoploteuthis neozelanica* Dell, 1959.

Size: Mantle length to 40 mm.

Geographical Distribution: Eastern South Atlantic Ocean; Indian Ocean, off Cape Town; off New Zealand, central South Pacific Ocean (possibly circumglobal in southern subtropical belt).

Habitat and Biology: Probable diel vertical migrator.

Literature: Roeleveld *et al.* (1992), Lipinski (1992).

***Abraliopsis lineata* (Goodrich, 1896)**

Abralia lineata Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology*, 7(1): 1–24 [10]. [Type locality: Andaman Sea and off Ganjam coast, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 27 mm.

Geographical Distribution: Indian Ocean, Andaman Sea; Arabian Sea.

Habitat and Biology: Mesopelagic to epipelagic at night.

Literature: Tsuchiya *et al.* (1991), Young *et al.* (1998b).

***Abraliopsis morisii* (Verany, 1839)**

Onychoteuthis morisi Verany, 1839, *Memorie della Reale Accademia della Science di Torino*, series 2, 1: 99–101 [100]. [Type locality: 39°N, 20°W, eastern Atlantic Ocean].

Frequent Synonyms: *Abraliopsis pfefferi* Joubin, 1896, *Compsoteuthis lonnbergi* Pfeffer, 1900; *Abralia (Compsoteuthis) jattai* Pfeffer, 1912.

Size: Mantle length to 45 mm.

Geographical Distribution: This species is widely distributed in the tropical to warm-temperate eastern and western Atlantic Ocean; Gulf of Mexico, Mediterranean Sea.

Habitat and Biology: Inhabits epipelagic and mesopelagic zones; undergoes diel vertical migrations. Prey of giant red shrimp.

Remarks: The name *Abraliopsis pfefferi* Joubin, 1896, was used for this species for a while (Nesis, 1982/87). The name *A. morisii* was restored by Bello (2005), after the re-examination of the original description of the species given by Verany (1839). Therefore *A. pfefferi* Joubin, 1896 is a junior synonym of *A. morisii* (Verany, 1839).

Literature: Young *et al.* (1998b), Laptikhovskiy (1999b); Bello (2005).

***Abraliopsis pacificus* Tsuchiya and Okutani, 1990**

Abraliopsis pacificus Tsuchiya and Okutani, 1990, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 16(2): 47–60 [48]. [Type locality: 32°47'18"N, 147° 58'42"E, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 36 mm.

Geographical Distribution: Western North Pacific Basin, off Japan; Shikoku Basin, between latitudes 25°N and 35°N. Hawaiian waters.

Habitat and Biology: Probably a diel vertical migrator.

Literature: Young *et al.* (1998b).

***Abraliopsis tui* Riddell, 1985**

Abraliopsis tui Riddell, 1985, *Fisheries Research Bulletin, New Zealand*, 27: 1–52 [37]. [Type locality: Kermadec Islands, off eastern Australia, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 30 mm.

Geographical Distribution: South Pacific Ocean off New Zealand: 170°E, 20°S to 170°W, 40°S, north and south of the subtropical convergence.

Habitat and Biology: Presumed diel vertical migrator.

Literature: Young *et al.* (1998b).

***Watasenia* Ishikawa, 1914**

Watasenia Ishikawa, 1914, *Zoologischer Anzeiger*, 43(7): 336 [336].

Type Species: *Watasenia scintillans* (Berry, 1911a).

FAO names: En – Sparkling enope squids.

Diagnostic Features: Manus of club with hooks in 1 series (2 or 3 in number); 1 series of suckers. Two to 4 large photophores covered by black chromatophores on tips of arms IV. Fins terminal. Buccal crown without typical chromatophores, with dark epithelial pigmentation on oral surface. Five photophores on eyeball. Hectocotylus on right arm IV with 1 dorsal and 1 ventral flap. Suckers absent from arms IV. Spermatophore receptacles located under collar. Complex photophores of integument, in life, apparently with red colour filters. Radula with homodont teeth. Large arm hooks with closed apertures.

Remarks: Monotypic.

Watasenia scintillans* (Berry, 1911)*Fig. 221**

Abrialiopsis scintillans Berry, 1911a, *Nautilus*, 25(8): 93–94 [93]. [Type locality: Japan, exact locality unknown].

Frequent Synonyms: *Abrialiopsis joubini* Watase, 1906; *Abrialiopsis scintillans* Berry, 1911a; *Abrealia (Compsoteuthis) nishikawae* Pfeffer, 1912; *Abrealia japonica* Ishikawa, 1929.

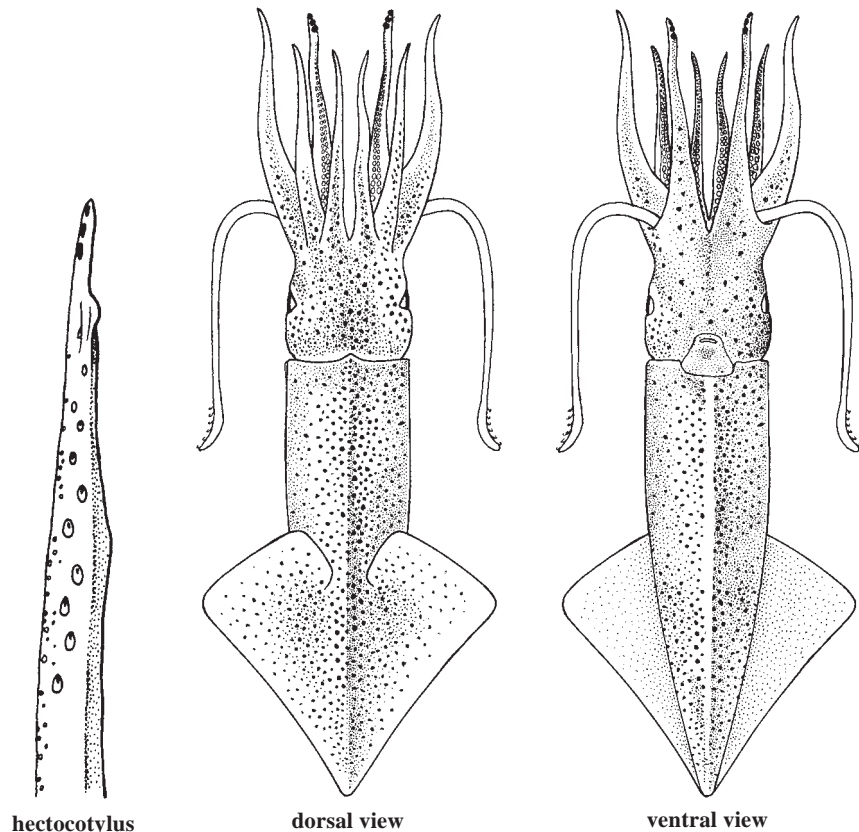
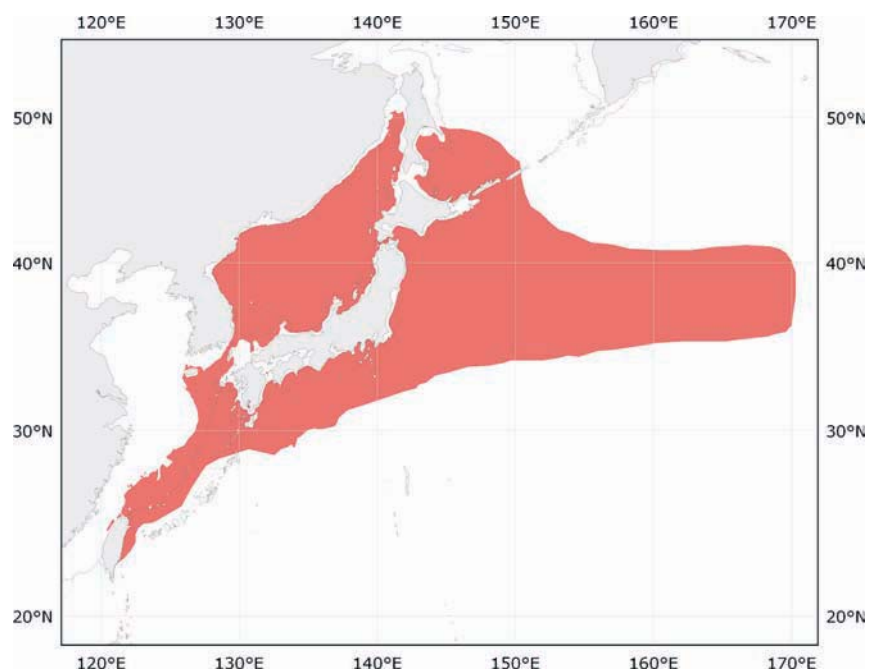
FAO names: **En** – Sparkling enope squid; **Fr** – Encornet lumiere; **Sp** – Enoploluria centellante.

Diagnostic Features: Mantle stocky; elongate, conical posteriorly. Only 2 (3) large hooks on ventral row of manus of club; 4 suckers, no hooks, on dorsal row. Arms with hooks. Mantle covered with numerous, minute photophores on ventral and lateral surfaces, but with ventral midline devoid of photophores. Fins rhomboidal, terminal, about 70 to 75% of mantle length. Minute photophores present in 4 indistinct rows on ventral surface of head; 5 photophores on ventral surface of eyeball, posterior and anterior ones enlarged; 3 (rarely 2, 4) bulbous black photophores on tips of arms IV. Right arm IV hectocotylized with 1 dorsal and 1 ventral flap. Male has a shorter mantle and fewer mantle photophores than the female.

Size: Small sized squid; maximum mantle length 70 mm in females and 60 mm in males.

Geographical Distribution: Western North Pacific Ocean; Kuroshio-Oyashio transition region; East China Sea, Sea of Japan and southern Sea of Okhotsk; South Kuriles, with occasional occurrence in the North Kuriles, to southern Japan; Japan and Korea; to about 170°E (Fig. 222).

Habitat and Biology: A primarily oceanic luminescent species, that inhabits depths between 100 and 600 m; a mesopelagic-boundary species that undergoes diel vertical migrations of the migrant type in which day and night habitats are clearly separated with peak abundance deeper than 300 m during the day and shallower than 300 m at night. It occurs in the warm core ring and cold water masses, avoiding the warm subtropical water in upper layers of the warm core ring. The species is most abundant in sub-Arctic waters with peak biomass of 32.9 tonnes per sq km and average biomass of 3.2 tonnes per sq km. It spawns in waters close to the shore, e.g. Toyama Bay, Sagami Bay, Suruga Bay, Japan. Spawning occurs year round, with a peak of activity in

**Fig. 221** *Watasenia scintillans***Fig. 222** *Watasenia scintillans*

■ Known distribution

spring (April-June). Eggs and juveniles are distributed in the subsurface waters down to 150 m; greatest abundance in the upper 70 m. Post-spawning mortality is complete and the life span is believed not to exceed 1 year. While in inshore waters and bays, *Watasenia scintillans* has been observed and photographed during its spectacular luminescent displays of blue greenish light. Diet varies from calanoid copepods in the paralarval stage to planktonic crustaceans (amphipods, copepods, euphausiids), fishes and squids during the subadult and adult stages. It is preyed upon by baleen whales and other marine mammals; it constitutes 8% by volume of the diet of the northern Pacific fur seal. The species also is significantly preyed upon by many species of demersal fishes and some sharks.

Interest to Fisheries: The annual catch fluctuates between 800 and 3 700 tonnes over a period of years, without any clear trend. However, recent evidence indicates a relationship between catch abundance and surface water temperature (and associated plankton biomass as an index of food availability) during early spring (April-May) of the same year. The species is taken regularly with set nets in Toyama Bay, Japan, between February and early July (peak April to May), as well as from Sagami Bay and Suruga Bay. During this period it aggregates near the surface, particularly at night. *Enoploteuthis chunii* is sympatric with this species in commercial catches.

Local Names: JAPAN: Hotaruika, Matsuika; USA: Japanese firefly squid.

Remarks: Also extensively used in research on bioluminescence.

Literature: Hayashi (1991, 1995a,b), Jivaluk (2001), Okutani (2005), Watanabe *et al.* (2006b), Zuev (2006), Tsuchiya (2007).

2.13 **Family GONATIDAE Hoyle, 1886** by Clyde F.E. Roper, Elaina M. Jorgensen, Oleg N. Katugin and Patrizia Jereb

Gonatidae Hoyle, 1886, *Report of the Scientific Results of the Voyage of the HMS Challenger, Zoology*, 16(44): 1–245 [173].

Type Genus: *Gonatus* Gray, 1849.

FAO Names: **En** – Gonate squids; **Fr** – Gonaleutènes; **Sp** – Gonaluras.

Diagnostic Features: The Gonatidae have a rather **narrow muscular body and medium to large rhomboid or heart-shaped fin**. In some species muscle tissues, particularly mantle, fin and arms, degenerate upon maturation and become watery and flaccid, which is associated with post-spawning egg-brooding, a unique feature among the order Teuthida. The Gonatidae is characterized by a **basic tetraserial armature on the arms. Arm tips may have more than 4 series of minute suckers. The 2 medial series on arms I to III typically consist of hooks along nearly the entire arm length**, except for the most basal and distal portions of the arms. However, in 1 species, *Berryteuthis anonychus*, several (usually 5 to 8) small hooks occur at the bases of arms I to III in females, while males have no hooks at all. All members of the family have a **simple, straight funnel-locking cartilage** that may flare slightly at the posterior end; **buccal connectives DDVV**; numerous series of suckers on the clubs: minute, crowded and almost equal-sized on *Eogonatus tinro* and *Berryteuthis anonychus*; larger in the centre and minute along the edges on *B. magister*; organized in rows with additional hooks on *Gonatus*. **Tentacles are equipped with a well-developed fixing apparatus along the dorsal margin**; this structure covers the proximal edge of the club and may extend well proximally along the club to occupy almost half of the tentacle length in *B. magister*, for example. The fixing apparatus consists of numerous alternating pads (or knobs) and minute toothless suckers in *B. magister*, and has evolved into a complex structure of several alternating ridges with knobs and grooves in *Gonatus* species. In species of *Gonatopsis* the tentacles are present only in the early life stages (from paralarvae to early juveniles), then completely lost by the late juvenile stages. Only 1 species in the family (*Gonatus pyros*) currently is confirmed to have photophores, present as oval patches located on the ventral surface of the eyes. **Most species of the Gonatidae do not have a true hectocotylus**; however, males of *B. magister* develop a notable modification of suckers in the middle portion of 1 ventral arm upon maturation, which is considered hectocotylization by some authors. Mature males of *Gonatus* and *Gonatopsis*, are known to have a long penis, which is used to transfer spermatophores onto the female's buccal membrane.

Size: Small- to medium- and large-sized squid; maximum mantle length to 550 mm.

Geographical Distribution: The family exhibits a bipolar distribution: the western arctic-boreal region, the boreal North Atlantic Ocean, the boreal (sub-Arctic) North Pacific Ocean (including the cool temperate California Current waters from California to Alaska) and the whole notalian (sub-Antarctic) belt. The vast subtropical and tropical zones of the world's oceans are devoid of gonatid species.

Habitat and Biology: Most species inhabit the upper water levels as paralarvae and juveniles, then they undergo significant ontogenetic descent as adulthood approaches. Adults of species can descend to great depths in the midwaters (mesopelagic) or to the deep-sea floor where they mate and spawn. Paralarvae and juveniles ascend to food-rich epipelagic waters to feed until ontogenetic growth begins. Spent females of *Gonatus* and *Gonatopsis* *sensu stricto* become degenerate and gelatinous and float, suspended in the meso- and bathypelagic layers or even in the surface waters. Some species also undergo diel vertical migrations during which they descend to the mesopelagic zone during the day, then ascend to the surface layers at night. Gonatid species are extremely important as prey for many fishes (including many commercially valuable species), seabirds, odontocete (toothed) whales and pinnipeds. Several species are fished commercially, most notably *Berryteuthis magister*, which is harvested by a specialized fishery and as a bycatch during other fisheries (e.g. for walleye pollock, *Atka mackeresl*, etc.). Up to 70 000 tonnes of this species are taken annually on the slope off the Kuril Islands in the Pacific Ocean and in the western Bering Sea by the Russian fishery alone.

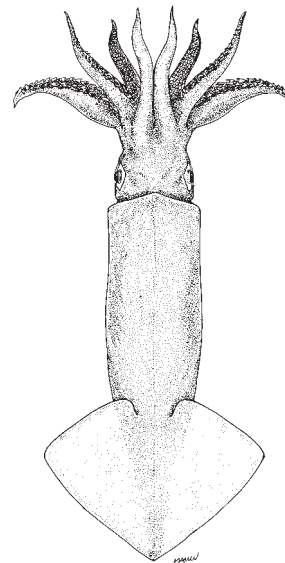
Remarks: Species in this family belong to 4 genera, *Berryteuthis*, *Eogonatus*, *Gonatopsis* and *Gonatus*. All genera inhabit the North Pacific, and only *Gonatus* has expanded its range far beyond the North Pacific Ocean into the Arctic, North Atlantic and southern oceans. All species of the Gonatidae are cold-water forms and are among the most abundant squids in higher latitudes, most especially in the sub-Arctic (boreal) North Pacific Ocean. Of the 19 currently described species in the family, 13 species of gonatids inhabit the sub-Arctic northwestern Pacific Ocean, and the Bering, Okhotsk and Japan seas, 3 species are endemic to the eastern North Pacific, 2 species inhabit the North Atlantic and 1 species dwells in the Southern Ocean. Differentiation occurs among populations of *Berryteuthis magister* from different areas, which ultimately led to the designation of 2 distinguished subspecies, *B. magister nipponensis* and *B. magister shevtsovi*. Therefore, 21 entities are listed and described in this Catalogue.

Local Names: USA: Armhook squids.

Literature: Jefferts (1983), Okutani *et al.* (1988), Arkhipkin and Bizikov (1997), Sweeney and Young (2003k), Katugin (2004), Katugin and Shevtsov (2006), Kubodera *et al.* (2006a,b,c,d), Jorgensen (2007).

Key to the genera of Gonatidae

- 1a. Tentacles present in adults → 2
 1b. Tentacles absent in adults (Fig. 223) *Gonatopsis*
- 2a. Tentacular club armed with suckers only → 3
 2b. Tentacular club armed with suckers and hooks (Fig. 224) *Gonatus*
- 3a. Radula with 5 longitudinal rows of teeth *Eogonatus*
 3b. Radula with 7 longitudinal rows of teeth *Berryteuthis*



dorsal view

Fig. 223 *Gonatopsis*



tentacular club

Fig. 224 *Gonatus*

Table 3

Ecological Characteristics of Gonatid Squids (from Nesis, 1997, 1999a, 2002; authors' data)

Species	Size	Horizontal Distribution	Spawning Habitat	Diurnal Vertical Migration	Ontogenetic Descent	Gelatinous Degeneration
<i>Beryteuthis anonychus</i>	Small	N P low-boreal	Pelagic	Yes; e	Late	No
<i>Beryteuthis magister</i>	Intermediate/ large	N P panboreal; bottom-associated	Bottom	Yes; (e)m-b	Early	No
<i>Eogonatus tinro</i>	Small	N P upper-boreal	Pelagic/ bottom?	Yes; e-m-b	Early	Yes
<i>Gonatopsis borealis</i>	Small/ intermediate	N P panboreal	Pelagic/ bottom	Yes; e-m	Late	No
<i>Gonatopsis japonicus</i>	Very large	Nw P panboreal	Pelagic/ bottom?	Yes; e-m	Intermediate	Yes
<i>Gonatopsis makko</i>	Large	Nw P low boreal	Pelagic/ Bottom	Unknown	Unknown	Yes
<i>Gonatopsis octopedatus</i>	Small	Nw P panboreal	Pelagic/ bottom?	Yes; e-m	Early	Yes
<i>Gonatus antarcticus</i>	Intermediate	S O notalian	Pelagic	Yes; e-m-b	Early	Yes
<i>Gonatus berryi</i>	Intermediate	N P panboreal	Pelagic	Yes; m-b	Very late	Yes
<i>Gonatus californiensis</i>	Small	Ne P low-boreal	Pelagic	Yes; (e)m-b	Early?	Yes
<i>Gonatus fabricii</i>	Intermediate	A N A boreal	Pelagic	Yes; e-m-b	Early	Yes
<i>Gonatus kamtschaticus</i>	Very large	N P upper-boreal; nerito-oceanic	Pelagic	Yes; e-m	Intermediate	Yes
<i>Gonatus madokai</i>	Large	N P upper-boreal	Pelagic	Yes; e-m-b	Intermediate	Yes
<i>Gonatus onyx</i>	Small	N P panboreal	Pelagic	Yes; e-m-b	Early	Yes
<i>Gonatus pyros</i>	Small	N P panboreal	Pelagic	Yes; (e)m-b	Early?	Yes
<i>Gonatus steenstrupi</i>	Small/ intermediate	Ne A boreal	Pelagic	Yes; e-m-b	Early?	Yes

Key:

Size: Small: dorsal-mantle length (DML) about 100 to 150 mm; intermediate: DML about 200 to 350 mm; large: DML from 350 to 500 mm; very large: DML larger than 500 mm.

Horizontal Distribution: N P = North Pacific; Nw P = Northwestern Pacific; Ne P = Northeastern Pacific; A N A = Arctic Northwestern Atlantic; Ne A = Northeastern Atlantic; S O = Southern Ocean.

Diurnal Vertical Migration: e = epipelagic; m = mesopelagic; b = bathypelagic.

***Gonatus* Gray, 1849**

Gonatus Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia*, 164 pp. [67].

Type Species: *Gonatus fabricii* Lichtenstein, 1818.

Frequent Synonyms: *Lestoteuthis* Verrill, 1880 (in 1879–1880); *Chiloteuthis* Verrill, 1881 (in 1880–1881).

Diagnostic Features: Tentacular club with at least 1 large central hook on manus and generally with additional hooks (large distally and small proximally) in median line. Club with distinctive locking (fixing) apparatus on dorsal border of manus that consists of a series of 4 to 6 large, thick, transverse pads with medial alternating oval pads and suckers; radula with 5 longitudinal rows of teeth. Hooks well developed in 2 medial series on arms from paralarval or immediate post-paralarval stages. Fins heart-shaped, extend posterior to end of mantle, attenuate into tail supported by cartilaginous rod.

Habitat and Biology: As adults, *Gonatus* species are typically mesopelagic and upper bathypelagic; however several species ascend to epipelagic layers at night. They are important prey for odontocete cetaceans, large oceanic and benthic fishes, e.g. gadoids, salmonids, coalfish, redfish.

Interest to Fisheries: *Gonatus* species currently do not support any significant commercial fishery, in spite of the good consistency of the flesh and the large size of some species. However, a good potential for future exploitation does exist.

Remarks: Currently the genus consists of 11 species. Eight of these species have been described since 1972 in coincidence with the development of concentrated sampling in deeper waters. Also responsible are the intense sampling and execution of exploratory fishing programmes in high-latitude seas, especially in the northern Pacific Ocean realm.

Literature: Nesis (1997), Katugin (2004), Lindgren *et al.* (2005), Kubodera *et al.* (2006d).

Gonatus fabricii (Lichtenstein, 1818)

Fig. 225

Onychoteuthis fabricii Lichtenstein, 1818, *Isis, oder Encyclopädische Zeitung*, 1818(9): 1591–1592. [1592]. [Type locality: Amerloq Fjord, West Greenland, Davis Strait, North Atlantic Ocean].

Frequent Synonyms: *Onychoteuthis fabricii* Lichtenstein, 1818; *Onychoteuthis amoena* Moller, 1842; *Cheloteuthis rapax* Verrill, 1881 (in 1880–1881).

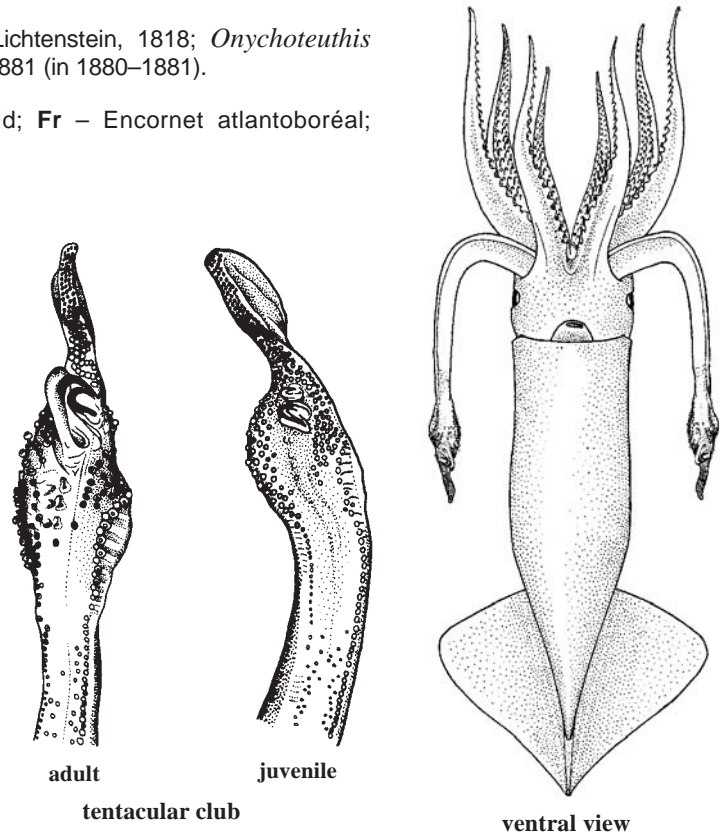
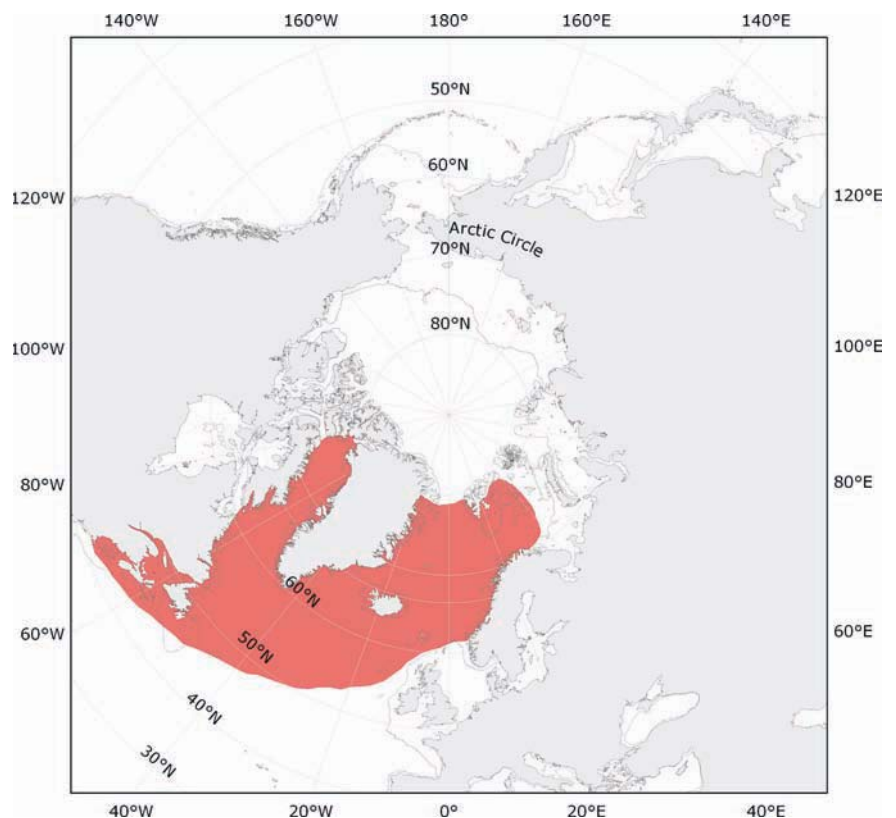
FAO Names: En – Boreoatlantic gonate squid; Fr – Encornet atlantoboréal; Sp – Gonalura atlantoboreal.

Diagnostic Features: Mantle long, slender, conical, slightly wider at midpoint, tapers to a sharp point posteriorly, its muscular part ends at the conus, but a fleshy, tapered column extends posteriorly as the tail. Fins sagittate with anterior lobes free, lateral margins rounded; fin length less than 50% of mantle length, fin width slightly less than the mantle length. **Tentacular clubs slender, small, their length about 12 to 20% of mantle length, with 1 very large, central hook, followed proximally by 3 small hooks and 1 small sucker, and distally by 1 moderate-sized sucker;** 9 to 13 transverse series of suckers and hooks on proximal half of arms III, 14 to 17 series of suckers (no hooks) on proximal half of arms IV. Arm hooks develop at about 20 to 40 mm dorsal mantle length, starting in the middle portion.

Size: Maximum mantle length attained is 400 mm.

Geographical Distribution: This boreo-Atlantic squid occurs in offshore arctic and subarctic waters of the northern North Atlantic Ocean from the Newfoundland Basin southward to south of Cape Cod (Georges Bank and various canyons and sea mounts) and northward from the Labrador Sea to Baffin Bay in the western North Atlantic Ocean; around Greenland and eastward to the western Barents Sea and Norway in the eastern North Atlantic Ocean (Fig. 226).

Habitat and Biology: *Gonatus fabricii* is an oceanic species that occurs between the surface and 500 to 700 m (records to 1 000 m) depth. It is the most abundant squid in the boreal Atlantic waters. Adults are common in midwater layers in arctic and subarctic waters of the North Atlantic Ocean, while juveniles inhabit near-surface waters in the northwestern North Atlantic Ocean. Females produce about 10 000 eggs that are laid in gelatinous masses at great depths. As typical for many gonatid species, maturing and spawning females undergo rapid degradation of tissue of the mantle and arms into a gelatinous consistency; tentacles and arm suckers are lost, and normal, active locomotion is reduced. Egg masses

Fig. 225 *Gonatus fabricii*Fig. 226 *Gonatus fabricii*

■ Known distribution

are held in the arms while the embryos develop. After eggs hatch into paralarvae, the female dies. Mating occurs head to head and the spermatophores are deposited on the buccal membrane of females. Spawning seems to extend from mid-April to December with a peak period in late May and June. The incubation period for some species may extend to 6 months. In the Norwegian Sea spawning appears to occur from winter to summer with hatching subsequently from late March to June or July; summer biomass of juveniles in the Norwegian Sea was calculated to be at least 1.5 million tonnes. Juveniles off west Greenland showed average growth rates of 4 to 5.5 mm per month from July to November. The life cycle is about 2 years. Juveniles feed on copepods, euphausiids, hyperiid amphipods, pteropods, and chaetognaths. Once the hooks have developed on juveniles, at a mantle length of about 20 to 40 mm, an important part of the diet is made up of fishes e.g. redfish, hake and small *Gonatus*; adults can feed on prey larger than themselves. *Gonatus fabricii* is preyed upon by the northern bottlenose whale, harp and hooded seals in the Norwegian Sea and extremely heavily by sperm whales off Iceland and in the North Atlantic Ocean. Northern bottlenose whales in the Norwegian Sea annually eat 480 000 tonnes of *G. fabricii*, while sperm whales consume 365 000 to 520 000 tonnes; total biomass here produced by a 2 year old cohort is about 20 million tonnes. Narwhals feed extensively on *G. fabricii* during all feeding seasons and exclusively during the autumn. Also, this species frequently is found in stomachs of other marine mammals, e.g. ringed harp and hooded seals, as well as in coalfish, Greenland halibut, salmon, various gadoids, blue ling, the redfish (*Sebastes marinus*) and others. Atlantic puffins in the Norwegian Sea prey heavily on *G. fabricii* in offshore waters in the winter, while northern fulmars prey primarily on this species in autumn through spring. Other predators include thick-billed murres, and ommastrephid squid *Todarodes sagittatus*.

Interest to Fisheries: This species is believed to have a significant fishery potential if sustainable yields and consumer interest can be developed. *Gonatus fabricii* is by far the most abundant "edible" squid in North Atlantic arctic and sub-Arctic waters. Because females undergo significant tissue degradation at maturity, pre-spawning aggregations will need to be targeted. The flesh has a good pre-spawning consistency and the species attains a desirable size. Greenland Eskimos use it as bait in the cod (*Gadus morhua callarias*) and halibut (*Hippoglossus hippoglossus*) hook-and-line fishery and for human food. It is taken as by catch in shrimp trawl and other benthic otter trawl fisheries.

Local Names: GERMANY: Nordische Köder Kalmar.

Literature: Young (1973a), Wiborg (1979b), Kristensen (1980a, b), Bjoerke (1995), Arkhipkin and Bjoerke (1999), Falcon, *et al.* (2000), Piatkowski *et al.* (2001a), Hastie *et al.* (2009).

Gonatus kamtschaticus (Middendorff, 1849)

Onychoteuthis kamtschatica Middendorff, 1849, *Memoires de l'Academie Imperiale des Sciences de Saint-Petersbourg*, series 6(6): 329–610 [515]. [Type locality: Schumschu Island, Kuril Islands, Northwest Pacific Ocean].

Frequent Synonyms: *Onychoteuthis kamtschatica* Middendorff, 1849 (generic misspelling); *Gonatus middendorffi* Kubodera and Okutani, 1981.

FAO Names: En – Shortarm gonate squid; Fr – Encornet bras courts; Sp – Gonalura bracicorta.

Diagnostic Features: Mantle long, muscular, very slender, its width from 18% of mantle length in young individuals to 24% of mantle length in maturing individuals, tapers posteriorly to a sharp, long, choroidal tail. Fins muscular, relatively long (43 to 52% of mantle length) and narrow (their width 40 to 43% of mantle length), sharply pointed posteriorly; fin angle 50° for both fins. Tentacular stalks relatively long; tentacular clubs small, their length less than 13% of mantle length; manus with a single large central hook, 1 medium-sized distal hook and up to 6 small proximal suckers (in young specimens), which are modified into hooks as the animal grows. Arms rather short, arms III equal to 50% of mantle length in young animals and to 77% in maturing individuals.

Size: The maximum mantle length attained is 550 mm.

Fig. 227

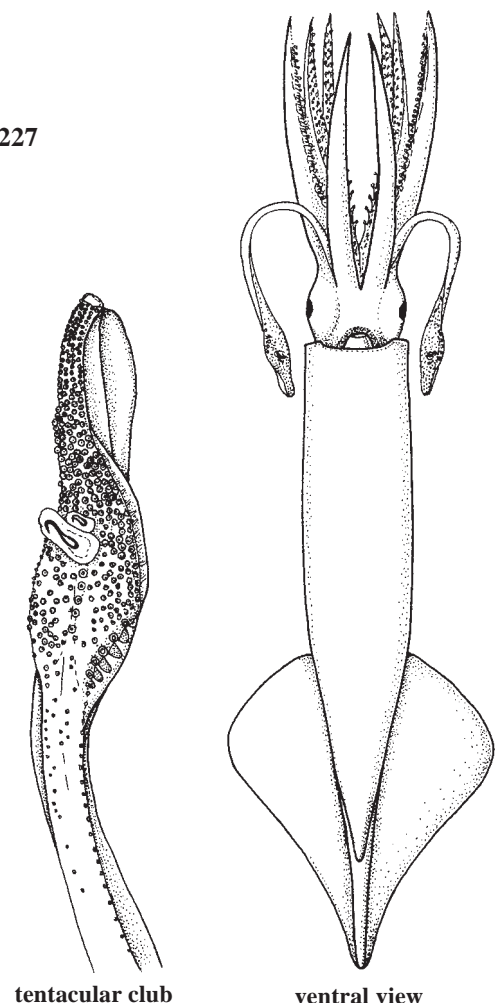
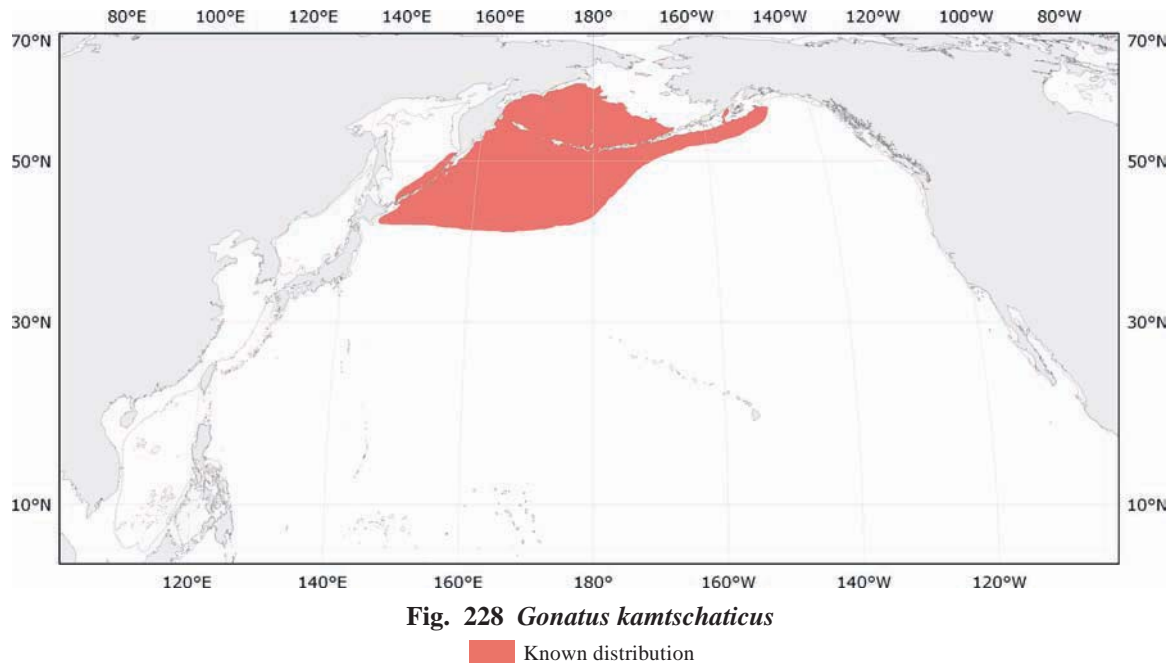


Fig. 227 *Gonatus kamtschaticus*

Geographical Distribution: This species occurs in the far North Pacific Ocean from the Bering Sea southwest along the Kuril Islands into the southeastern Okhotsk Sea and south to Japan, and eastward along the Aleutian Islands Chain (Fig. 228).



Habitat and Biology: *Gonatus kamtschaticus* is an oceanic species that undergoes diel vertical migrations as adults from approximately 400 to 800 m in daytime to less than 200 m at night. The paralarvae occur near the surface at night. Juveniles occur in the upper layers, and do not conduct extensive diel vertical migrations. As the squid grow and mature, they tend to descend to deeper layers, and mature animals of over 300 mm mantle length occur in deep waters along the continental slope. In the Pacific Ocean off the Kuril Islands, the species is most frequently observed in the epipelagic zone throughout the year; in the Okhotsk Sea, animals occur mainly in the meso- and bathypelagic layers from January through June, and mainly in the epipelagic layer from July through December. The species is an important prey item in the diet of sperm whales, northern fur seal, pomfret and Pacific salmon (especially *Oncorhynchus nerka* and *O. kisutch*). Young squids consume mainly crustaceans (*Themisto japonica*, *Primno macropa*, *Thysanoessa longipes*, *T. raschii*), and as they grow they start feeding more intensively upon fish and juvenile gonatid squids.

Interest to Fisheries: This species may have a fishery potential in pre-adult stages, both because of its size and its relatively muscular consistency prior to maturity. However, only juvenile animals are known to swarm in dense aggregations, while maturing adults and especially adults are usually very rare in trawl catches.

Local Names: JAPAN: Kamchatka-Takagiika.

Remarks: After its description in 1849, *Gonatus kamtschaticus* was synonymized with *G. fabricii* by both Steenstrup (1880) and Hoyle (1886). The name was declared nomen dubium by Kubodera and Okutani (1981) when they described *Gonatus middendorffi*, citing lack of type specimens and subsequent literature on *G. kamtschaticus*. Nesis (1982, 1987, 1997) re-elevated *G. kamtschaticus* to species status, declaring *G. middendorffi* a junior synonym.

Literature: Kubodera and Jefferts (1984a,b), Nesis (1997), Shevtsov *et al.* (2004a), Jorgensen (2007), Katugin and Zuev (2007).

Gonatus madokai* Kubodera and Okutani, 1977*Fig. 229**

Gonatus madokai Kubodera and Okutani, 1977, *Venus*, 36(3): 123–151. [124]. [Type locality: 49°32'N, 168°50'E, Northwest Pacific Ocean].

Frequent Synonyms: None.

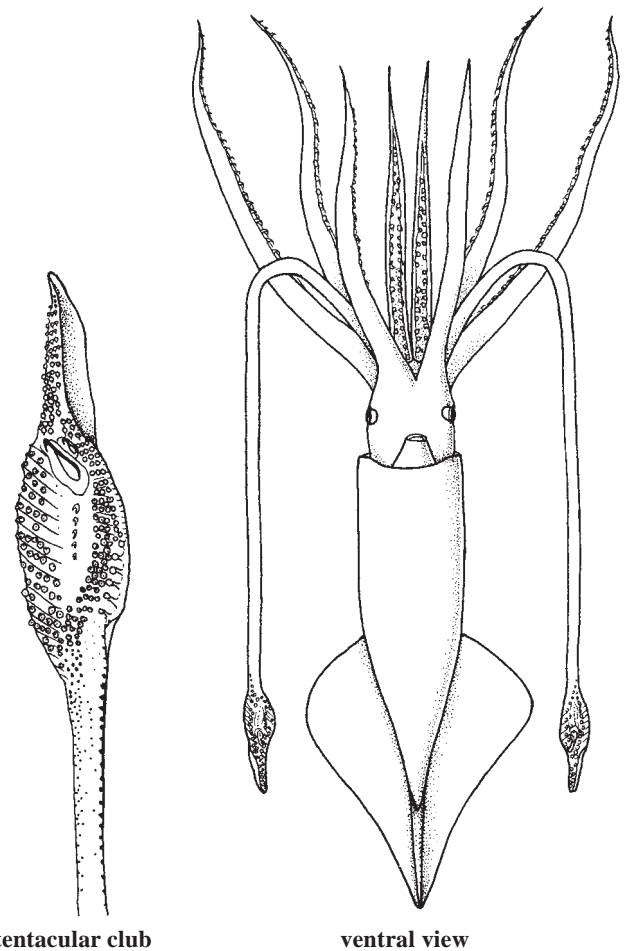
Misidentifications: *Gonatopsis okutanii* (Nesis, 1972b).

FAO Names: **En** – Madoka's gonate squid; **Fr** – Encornet madokai; **Sp** – Gonalura madokai.

Diagnostic Features: **Mantle moderately broad, soft-fleshed**, extends posteriorly into a long, pointed tail (20% of mantle length); the posterior part non-muscular posterior to the conus. Fins sagittate, their length 60 to 65% of mantle length, their width 50 to 75% of mantle length. **Tentacular clubs long** (20% of mantle length), with **1 very large central hook, 1 moderate-sized hook distally**, and **4 to 7 very small suckers and hooks proximally** (these develop at greater than 70 mm mantle length). **Arms very long, the longest (III) equal to mantle length**; 11 or 12 transverse series of suckers and hooks on proximal half of arms III; 16 series of suckers proximally on arms IV.

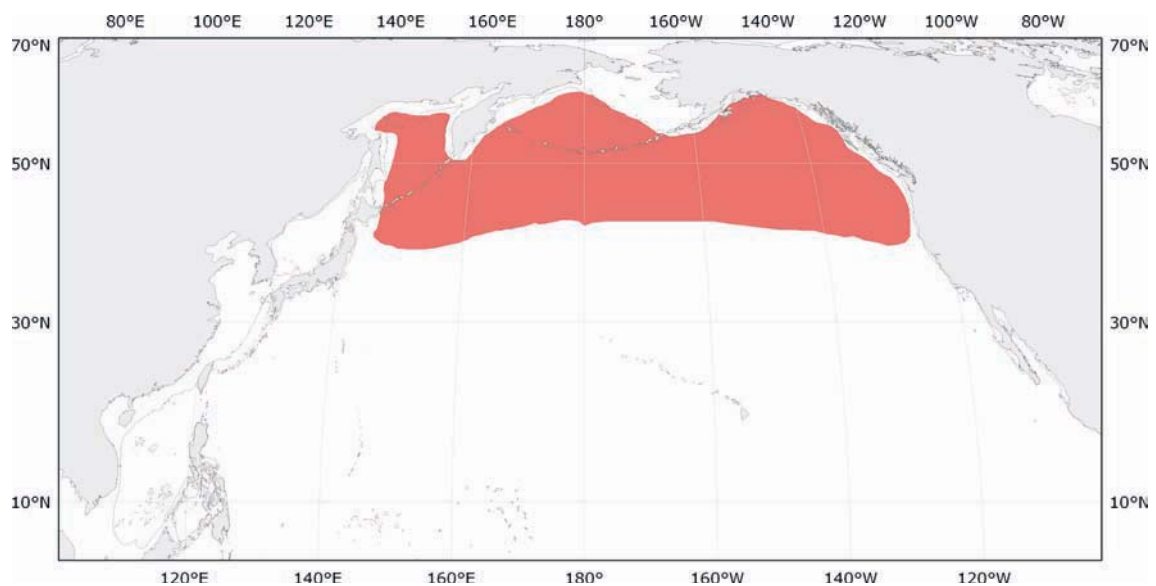
Size: This species attains a maximum mantle length of 470 mm.

Geographical Distribution: *Gonatus madokai* is widely distributed in the northern North Pacific Ocean: northern Japan Sea (only 1 reliable record of juveniles off southwestern Sakhalin), Bering Sea (rare), around the Kamchatka Peninsula and the Kuril and Aleutian Islands, the Gulf of Alaska, southward to about 42°N. It is especially abundant in the Okhotsk Sea where it is 1 of the most common of all squids (Fig. 230).



tentacular club

ventral view

Fig. 229 *Gonatus madokai***Fig. 230** *Gonatus madokai*

■ Known distribution

Habitat and Biology: This large species is an epipelagic to meso-bathypelagic species that descends to mesopelagic depths in daytime (but not exclusively). *Gonatus madokai* has been captured to 1 500 m in midwater and possibly as deep as 400 to 3 400 m on the bottom. It has been recorded in association with the Oyashio Current, sub-Arctic Front Zone. The paralarvae are consistently abundant shallower than 300 m in the Okhotsk Sea, where spawning occurs in spring (March to June) and paralarvae are common from June to September. They occur earlier in the season in the Gulf of Alaska. Both diel vertical migration and ontogenetic descent are characteristic. In females, tentacles autotomize during maturation and they break off a short distance from the base, leaving a short but distinctive stem or stump. Muscle tissues become very gelatinous in mature individuals. The life span appears to be at least 2 years. Adult *G. madokai* consume mainly fish (most commonly *Leuroglossus schmidti*), euphausiids (*Thysanoessa raschii* and *T. longipes*) and juvenile gonatid squid. Juveniles prey predominantly upon amphipods (*Themisto japonica* and *Primno macropa*), and some have had salps and chaetognaths in their stomachs. Adults are heavily preyed upon by toothed whales, walleye pollock (*Theragra chalcogramma*), Pacific salmon, pomfret and northern fur seals.

Interest to Fisheries: While this is a very abundant species, it has no potential for the development of a fishery because, even in the pre-spawning stage, the flesh is watery and jelly-like, which make the squid unacceptable as a food product.

Local Names: JAPAN: Sasaki-Takagiika.

Literature: Kubodera and Jefferts (1984a,b), Katugin and Merzlyakov (2002), Katugin *et al.* (2004b,c), Jorgensen (2007).

***Gonatus steenstrupi* Kristensen, 1981**

Fig. 231

Gonatus steenstrupi Kristensen, 1981, *Steenstrupia*, 7(4): 61–99 [78]. [Type locality: between 53°24' – 51°52' – 8°29'W, Northeast Atlantic Ocean].

Frequent Synonyms: *Gonatus fabricii* (Lichtenstein, 1818), in part.

FAO Names: En – Atlantic gonate squid; Fr – Encornet atlantique; Sp – Gonalura atlántica.

Diagnostic Features: Mantle long, very slender, thick-walled but muscular; widest at anterior margin then tapers evenly to the posterior pointed tip; muscular part of mantle ends at conus, but a fleshy column extends posteriorly as a short tail. Fins sagittate, their length about 45% of mantle length, their width 52% of mantle length. Tentacles strong and moderately long with tentacular clubs large, expanded, their length about 25 to 36% of mantle length; **1 very large central hook on manus**, with **1 immediately distal, moderate-sized hook** and **4 or 5 progressively smaller hooks proximal to it** (fifth hook sometimes a sucker). Arms III with 8 or 11 transverse series of 31 to 42 suckers and hooks on proximal half; arms IV with 12 to 14 transverse series of 46 to 57 suckers (no hooks) on proximal half.

Size: The species attains a maximum mantle length of 150 mm, possibly to 190 mm.

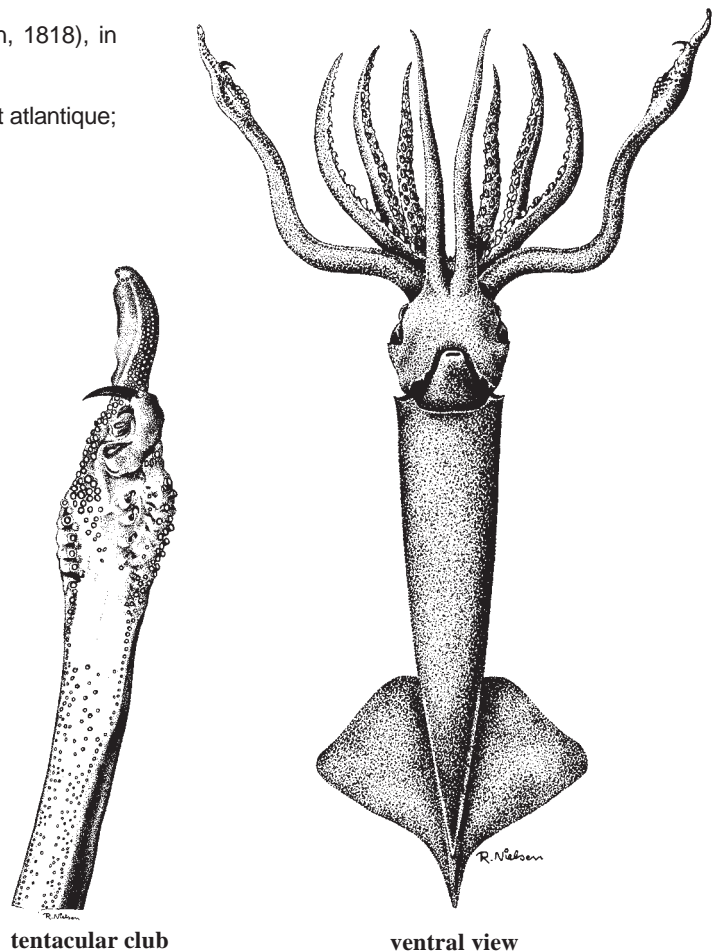


Fig. 231 *Gonatus steenstrupi*

Geographical Distribution: *Gonatus steenstrupi* occurs in the North Atlantic Ocean from 45°N to 63°N. It is widely distributed in the temperate (Bay of Biscay) to boreal (Irminger Sea-East Greenland) waters, east of the Grand Banks of Newfoundland (Fig. 232).

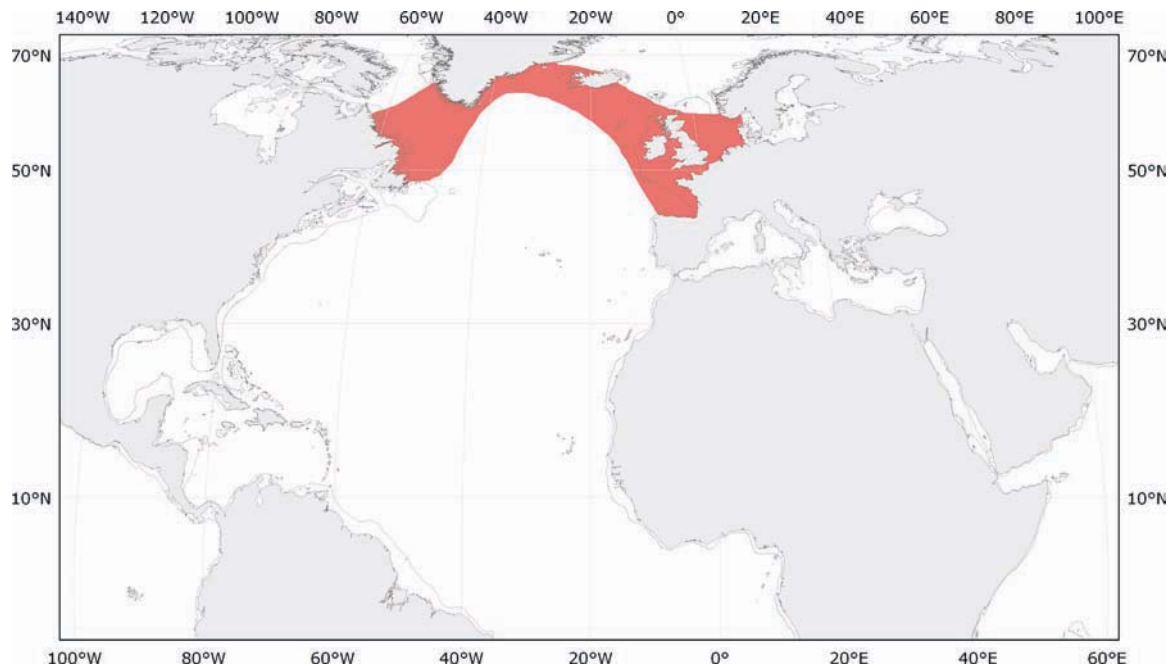


Fig. 232 *Gonatus steenstrupi*

■ Known distribution

Habitat and Biology: This species is an oceanic, mesopelagic species that occurs to 1 000 m depth. Paralarvae up to 20 mm mantle length occur shallower than 200 m, while juveniles larger than 20 mm mantle length occur at depths of 250 to 1 000 m, thus demonstrating a strong ontogenetic descent during development. Young specimens occur only in spring and summer. The species is preyed upon by numerous odontocete cetaceans, e.g. northern bottlenose whale, striped dolphin, Atlantic white-sided dolphin, Risso's dolphin, killer whale, sperm whale.

Interest to Fisheries: Currently no fisheries are directed at this species, but its desirable size and consistency of flesh make it a good potential resource. It is possible that estimates of huge population size and biomass of *G. fabricii* might also involve a component of *G. steenstrupi*.

Local Names: None.

Remarks: *Gonatus steenstrupi* was confused with *G. fabricii* for decades until it was recognized and separated by Kristensen in 1981. While the distributions of the 2 species overlap considerably, *G. steenstrupi* occurs slightly more southerly into Bay of Biscay and beyond in offshore waters and around Newfoundland and into the Gulf of St. Lawrence. *Gonatus fabricii* extends much further north into high Arctic waters.

Literature: Kristensen (1981), Falcon *et al.* (2000).

***Berryteuthis* Naef, 1921**

Berryteuthis Naef, 1921a, *Mitteilungen aus der Zoologischen Station zu Neapel*, (22)16: 527–542 [535].

Type Species: *Berryteuthis magister* (Berry, 1913a).

Frequent Synonyms: *Pfefferiopsis* Ishikawa, 1924; *Berryiteuthis* Grimpe, 1922; *Berryteuthis* Thiele, 1934.

Diagnostic Features: **Tentacular club with suckers only, no hooks; suckers in central part of manus are notably larger than marginal suckers. Fixing apparatus on club consists of suckers and knob-like tubercles, without transverse ridges and grooves.** One ventral arm of adult male bears modified suckers, which may serve to transfer spermatophores to female. Radula with 7 longitudinal rows of teeth. Mantle and body firm, muscular. Fins large, rhomboidal, do not extend to posterior end of mantle as a tail; fin length 54 to 56% and fin width 64 to 80% of mantle length.

Remarks: *Berryteuthis magister* is the object of a major fishery, the only directed fishery for the Gonatidae, versus those species caught as by catch. Consequently, a large body of research and publications exists for this species.

Literature: Okutani *et al.* (1988), Okutani and Kubodera (1987), Katugin (2004), Kubodera *et al.* (2006a).

Berryteuthis magister* (Berry, 1913)*Fig. 233**

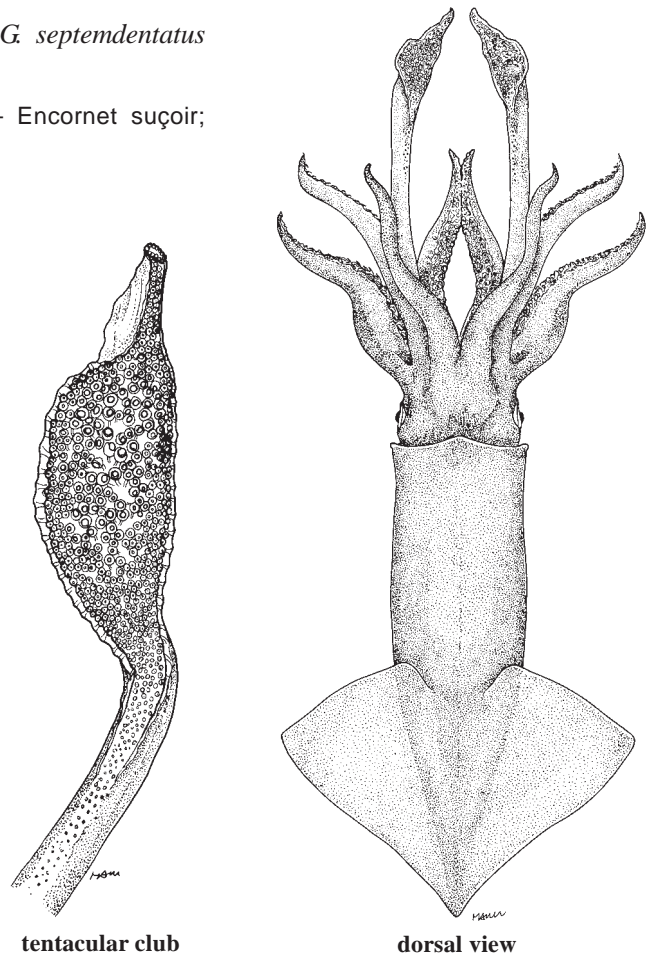
Gonatus magister Berry, 1913a, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77. [76]. [Type locality: Puget Sound, Washington, Northeast Pacific Ocean].

Frequent Synonyms: *Gonatus magister* Berry, 1913a; *G. septemdentatus* Sasaki, 1915a.

FAO Names: **En** – Schoolmaster gonate squid; **Fr** – Encornet suçoir; **Sp** – Gonalura magister.

Diagnostic Features: **Mantle large, robust, muscular**, mantle width 35 to 37% of mantle length. Fins large, rhomboidal, broadly sagittate, thick, straight anterior and posterior margins, relatively long (length up to 55% of mantle length) and broad (width 70 to 80% of mantle length). **Tentacles strong, long** when extended in dead animal, 120 to 160% of mantle length; in live animal they are usually as long as the arms; **tentacular clubs expanded, long, with no hooks but with extremely numerous, long-stemmed minute suckers, that occur in 20 or more transverse series; suckers in central part of manus noticeably larger than others.** Club sucker rings with 20 to 22 sharp teeth. No obvious boundary exists between manus and carpal region, except that the number of transverse series of suckers and sucker size tend to decrease proximally. Arms relatively long, 62 to 67% of mantle length, formula III = II, I, IV. Arms I to III with well-developed hooks in the medial 2 series that emerge at about 75 mm mantle length; hooks in adults occupy all but the distal part of the arms; sucker-hook series number 50 to 55. Arms IV have 4 series of suckers arranged in 60 transverse series. Arm sucker rings with 11 to 18 sharp teeth along distal margin. One ventral arm is modified in males into a hectocotylus-like structure. Seven rows of teeth on radula.

Size: The maximum mantle length of this species is reported to be 430 mm, while its weight can reach to 2.6 kg; normally, however, mantle length is up to 340 mm.

**Fig. 233** *Berryteuthis magister*

Geographical Distribution: *Berryteuthis magister* is a conspicuous inhabitant of the North Pacific Ocean. It is panboreal and it occurs in the Japan, Okhotsk and Bering seas, along the Kuril, Commander and Aleutian islands, then southward in the eastern North Pacific Ocean as far south as central or southern California waters (Fig. 234).

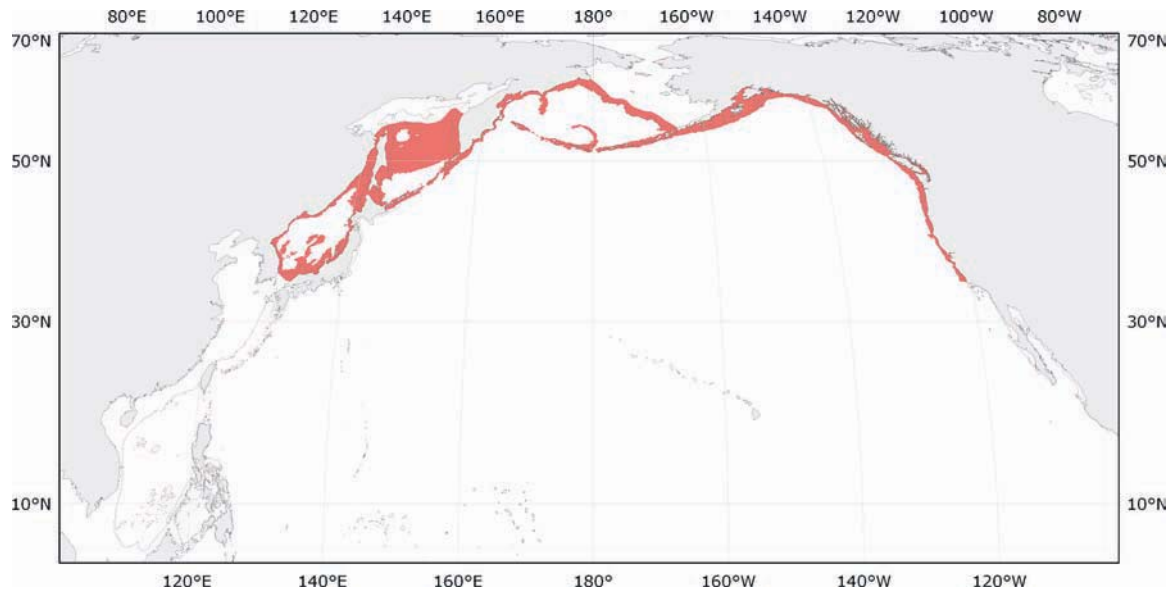


Fig. 234 *Berryteuthis magister*

■ Known distribution

Habitat and Biology: A demersal oceanic pelagic species, *B. magister* is recorded from the surface to about 1 500 m depth, but its greatest abundance is near the bottom on the continental slope and in the mesopelagic zone. In the epipelagic zone it occurs occasionally and is much less abundant than most other species of gonatids in the North Pacific Ocean. In spite of extremely high abundance of adults of this species throughout the North Pacific rim, newly hatched/paralarval *B. magister* had been reported only once, from about 400 m deep in the Strait of Georgia. Recently, paralarvae have been reported to be common in the epipelagic zone of the slope region of the Gulf of Alaska, where hatchlings with internal yolk sacs were captured at 0 to 200 m in Bongo tows during March. Juveniles with mantle length ranging from 40 to 120 mm regularly occur near the bottom at depths 300 to 450 m in the Bering Sea, and may occur in epi- and mesopelagic waters. However, diel vertical migrations of young *B. magister* are much less extensive than, e.g. in *Gonatopsis borealis*, and even at night, juvenile *B. magister* are rarely found in the upper epipelagic waters. Finally, immature squid descend to the benthic habitat where they aggregate and concentrate during the day; at night they disperse into the near-bottom waters, and occasionally into the mesopelagic zone to feed. Because of the extensive geographical range of *B. magister*, spawning can occur at various locations throughout the year. Aggregations of males and females begin to increase intensely as spawning time approaches. Mating takes place immediately prior to spawning, with only mature stage V females being mated. Penis in *B. magister* is rather short, and does not show up out of the mantle edge in mature male; we may suggest that in the absence of distensible penis male uses a modified ventral arm (hectocotylus) to transfer spermatophores into the mantle cavity of the female, where they are attached most frequently to the mantle wall adjacent to the openings of the oviducal glands, or occasionally onto the midgut gland or the gills. Judging from the number of implanted sperm bulbs, most females copulate 2 times, rarely 1 or 3 times. In the Bering Sea, females produce 20 000 to 96 000 eggs (40 000 eggs, on the average), while males produce up to 700 to 1 000 spermatophores in total. In the Japan Sea, where squid are much smaller and produce larger eggs, individual fecundity is only about 4 000 eggs. The incubation period is thought to last for about 6 months. Spawning occurs on the bottom presumably at 400 to 1 000 m, depending on locality. The age estimates for *B. magister* vary, depending on aging technique and locality, but most recent analyses favour a 2-year life cycle. The analyses of growth using statoliths and gladii suggest that the 2-year life cycle of *B. magister* in the western Bering Sea includes 6 months of embryonic development and 18 months of post-embryonic growth. Several different seasonal groups may exist within a geographic location, apparently related to several spawning events during a year, or different places of origin. Juvenile and maturing squid feed voraciously during their pelagic phases, with younger forms eating euphausiids, hyperiid amphipods and small mesopelagic shrimps, while larger individuals switch to fishes and squids. Cannibalism is common in *B. magister* of all sizes and large quantities of squids are consumed, mostly conspecifics. During this feeding phase, the digestive gland ("liver") becomes enormous, up to 25 to 40% of total wet body weight, with enough reserves to supply all energetic needs during final maturation and spawning. During this final benthic stage, feeding activity is very low, then ceases in 92% of mature males and 100% of mature females. The number and variety of predators is enormous and includes, but is not limited to, the following: fishes (walleye pollock, Pacific cod, chinook, chum, coho, pink and sockeye salmon, Pacific pomfret, Greenland turbot, Pacific halibut, sablefish, various grenadiers, liparids, blacksmelts, rockfishes); odontocete cetaceans (Baird's beaked whale, short-finned pilot whale, Dall's porpoise, sperm whale, false killer whale); northern fur seal, thick-billed murre, albatrosses and *Berryteuthis magister* itself.

Interest to Fisheries: *Berryteuthis magister* is the only species of gonatid squid fished in commercial quantities in the Pacific Ocean and adjacent seas; consequently it has been intensively studied. The commercial fishery production of *B. magister* is

supported by enormous populations throughout much of its range, but determining actual biomass, either by region or in total, is difficult. Nonetheless, a summary of biomass calculations from different areas (some with different techniques) totals 677 000 tonnes. Of course, annual fluctuations are the norm in squid populations, so this value cannot be used to validate quota expectations. The Russian fishery began in the 1960s off the Commander Islands as by catch in the walleye pollock bottom trawl fishery. By the 1970s and 1980s the fishery included species-directed trawling and was greatly expanded to the northern Kuril Islands and into the Bering Sea, then into the Japan Sea. The total catch of the Russian fishery in 1985 reached approximately 65 700 tonnes; production plummeted in 1986 to 13 000 tonnes, and through the 1990s did not exceed 20 000 tonnes. Russian estimates for a sustainable annual fishery in the western Bering Sea, northwestern Pacific Ocean off the Kuril Islands and in the Russian Exclusive Economic Zone of the Japan Sea, Kita-Yamato Bank, total up to 98 000 tonnes. FAO fisheries statistics report about 49 000 tonnes landed in 2007, for this species. The unique biological features among all gonatid species make *B. magister* the best candidate for a significant, sustained fishery: it aggregates on the bottom in the adult stage, following a relatively early-stage ontogenetic descent; it spawns on the bottom; it does not become gelatinous in maturing and spawning stages, consequently, it is accessible to benthic trawling. The meat is judged tasty and it contains high levels of beneficial proteins. Finally, potential is developing for use of the species for valuable biologically active compounds and pharmaceutical preparations, especially from the gonads, digestive gland and optic ganglia.

Local Names: JAPAN: Dosuika; RUSSIA: Commander squid; USA: Commander armhook squid, Red squid.

Remarks: Genetic studies (allozymes using starch and polyacrylamide gel electrophoresis) have shown that differentiation occurs among populations of *Berryteuthis magister* from 3 different geographical regions: the Japan Sea, the northwestern Pacific Ocean (including Okhotsk and Bering seas), and the Gulf of Alaska. Genetic differences detected were both temporal and spatial. Subsequently, the form from the Japan Sea has been designated a subspecies of *B. magister*, *B. m. shevtsovi* (see below). In waters around Japan, a subspecies, *B. m. nipponensis*, has been distinguished based on such external characters as small mantle opening, small fin and less pronounced differences in size between central and marginal club suckers. The more muscular body of this extremely rare form suggests that it is more powerful swimmer than the typical *B. magister*, whose representatives are quasi-benthic the greater part of their lives.

Literature: Okutani *et al.* (1988), Nesis (1995), Arkhipkin *et al.* (1998a), Katugin (1999, 2000a, 2002), Arkhipkin (2003b), Starovoytov *et al.* (2004), Katugin and Shevtsov (2006), Jorgensen (2007).

***Berryteuthis anonychus* (Pearcy and Voss, 1963)**

Fig. 235

Gonatus anonychus Pearcy and Voss, 1963, *Proceedings of the Biological Society of Washington*, 76: 105–112 [105]. [Type locality: 45°26.8'N, 125°08.1'W, Northeast Pacific Ocean].

Frequent Synonyms: *Gonatus anonychus* Pearcy and Voss, 1963.

FAO Names: En – Smallfin gonate squid; Fr – Encornet ailes courtes; Sp – Gonalura alicorta.

Diagnostic Features: Mantle muscular, elongate, narrow, with a deep funnel depression on the ventral edge of mantle between the locking cartilages. Fins small, oval, extend to posterior end of mantle in a short gelatinous tail; fins short (length 22 to 27% of mantle length); narrow (width 49 to 55% of mantle length). Tentacular clubs narrow and long (about one-half of tentacle length), with numerous minute almost equal-sized suckers in 12 to 15 transverse series; no hooks. Club sucker rings with 3 or 4 teeth. Arms with 4 transverse series of suckers and very few (about 6 to 8) small hooks in the medial 2 series on the basal part of arms I to III in maturing and mature females; no hooks in males. Radula with 7 longitudinal rows of teeth.

Size: This species attains a maximum mantle length of possibly 150 mm.

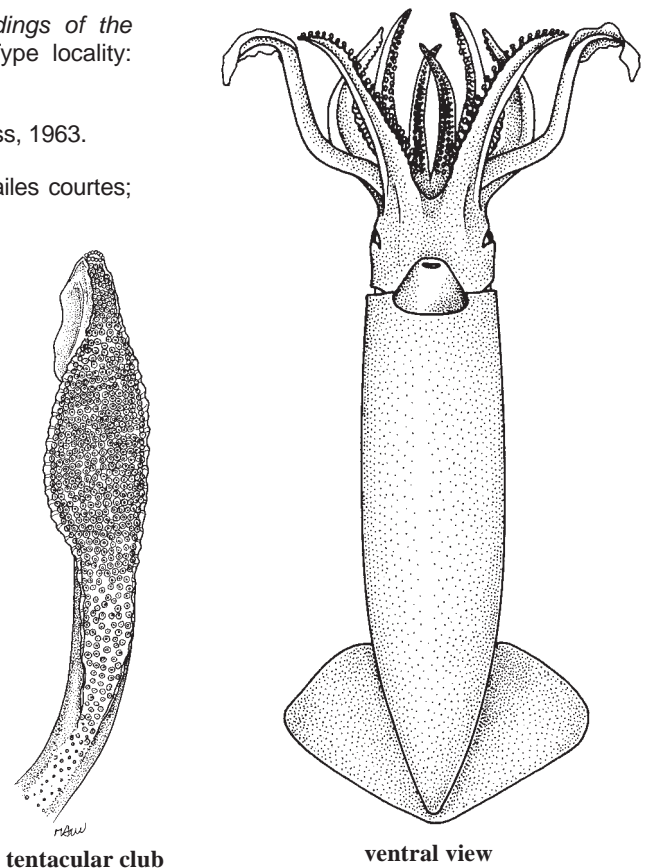


Fig. 235 *Berryteuthis anonychus*

Geographical Distribution: *Berryteuthis anonychus* is widely distributed in the North Pacific Ocean, from the Kuril Islands and southeastern Okhotsk Sea to the east, encompassing the Aleutian Islands, the southern Bering Sea and the Gulf of Alaska southward to Oregon (Fig. 236).

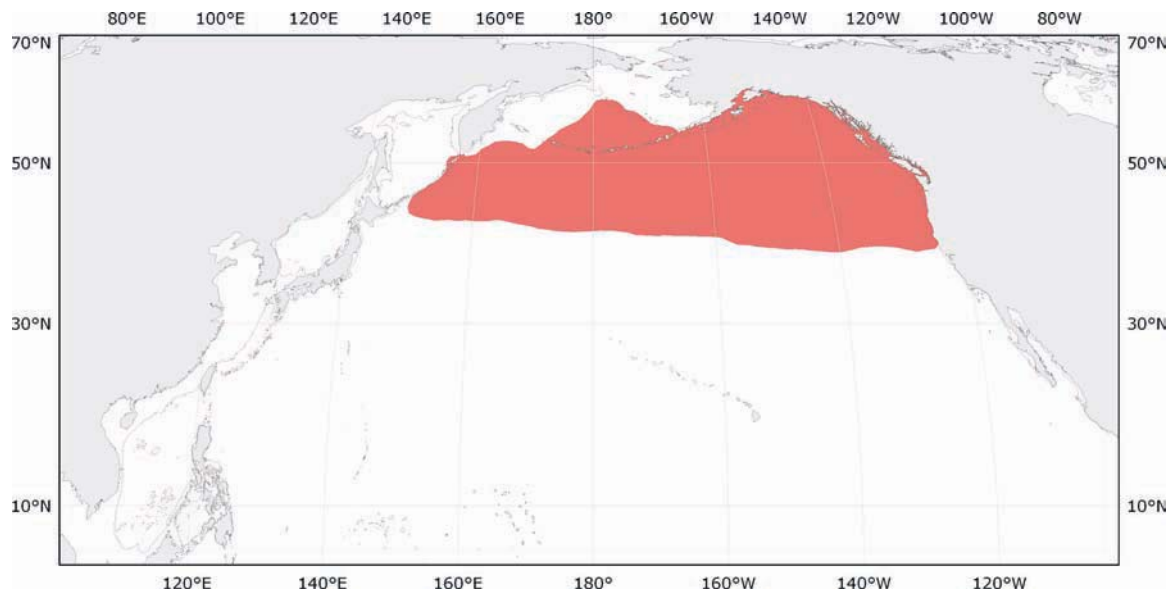


Fig. 236 *Berryteuthis anonychus*

■ Known distribution

Habitat and Biology: *Berryteuthis anonychus* is a low-boreal distant-neritic species that occurs from the surface at night to about 1 500 m deep in offshore waters. The exact distribution pattern is unknown. It is most abundant in the Gulf of Alaska and the open sub-Arctic domain to the south and southwest of the Gulf. It is rare south of Oregon and to southern Baja California. The species occurs in open ocean over great depths, but it is most common over the slopes and seamounts, e.g. Eikelberg Ridge, and seamounts Warwich, Miller and Morton. Juveniles are gregarious and broadly dispersed over the northern Pacific Ocean and the southern Bering Sea. While specimens have been reported as deep as 1 000 to 1 500 m, most adults actually are captured in the epipelagic zone, 0 to 200 m; they are concentrated mostly over the seamounts and slopes. No gelatinous degeneration seems to occur at maturity, which begins at 70 to 90 mm mantle length, i.e. at 80 to 90 mm in females and 70 to 80 mm in males. Spawning occurs year-round, with peaks in February to April and again in late June to September; life span is approximately 1 year. The species is a first-order diel vertical migrator in the epipelagic zone; it occurs at 50 to 200 m during the day and at night it ascends to 150 m to the surface. Squids aggregate in areas of oceanic rings (eddies) and vortices where high concentrations of medium- and large-sized zooplankton occur. Food consists mainly of copepods, hyperiid amphipods, pteropods, chaetognaths, and euphausiids. This macroplanktophagous squid in turn is preyed upon by many species of fishes (pomfret, salmonids (pink, coho, chum, sockeye), albacore, lancetfish; neon squid (*Ommastrephes bartramii*); seabirds (murre, short-tailed shearwater, albatross); marine mammals (northern fur seal, fin whale, Dall's porpoise and other odontocete whales).

Interest to Fisheries: Currently the status of any potential fishery is undetermined. However, the firm consistency of the flesh, the convenient size of the species and its dense aggregations in certain oceanic areas seem to indicate a potentially appropriate target species for a fishery.

Local Names: JAPAN: Hime-Dosuika; USA: No-hook armhook squid.

Literature: Pearcy and Voss (1963), Katugin *et al.* (2002), Bower *et al.* (2002), Katugin (2004), Katugin *et al.* (2005), Shimura *et al.* (2006), Jorgensen (2007).

Gonatopsis Sasaki, 1920

Gonatopsis Sasaki, 1920, *Proceedings of the United States National Museum*, 57: 163–203 [198].

Type Species: *Gonatopsis octopedatus* Sasaki, 1920.

Frequent Synonyms: None.

Diagnostic Features: **Tentacles absent in individuals larger than juveniles of about 30 mm mantle length.** Juveniles smaller than 30 mm mantle length possess small rod-like tentacles about the same size as arms IV; (in *Gonatopsis borealis* tentacles disappear at 9 to 20 mm mantle length). **Radula with 5 or 7 longitudinal rows of teeth.** Mantle muscular, becomes flabby, gelatinous in mature and spent females; *G borealis* does not degenerate at maturation. Fins heart-shaped with a posterior short or long tail supported by cartilaginous rod, except in *G borealis*.

Remarks: In 1971, Nesis divided the genus *Gonatopsis* into 2 subgenera. *Boreoteuthis*, with 7 longitudinal rows of teeth on the radula (*Gonatopsis borealis*), and *Gonatopsis sensu stricto*, with 5 longitudinal rows of teeth on the radula (*Gonatopsis octopedatus* and *G japonicus*). A new species (*Gonatopsis okutanii*) was assigned to *Gonatopsis sensu stricto*, since it possessed a 5-rowed radula (Nesis, 1972). In 1973, Nesis suggested that *Gonatopsis makko* belongs to the subgenus *Boreoteuthis*; however, the type specimens from sperm whale stomachs lacked radulas, and it was impossible to determine whether they had 5 or 7 longitudinal rows of teeth (Okutani and Nemoto, 1964). In 1978, Okutani and Satake, based on personal information from Okiyama, reported that *G makko* has a 5-toothed radula. Confusion about the systematic status of *G makko* remains. In 1997, in one of the latest reviews on the Gonatidae, Nesis used this name as a junior synonym to *Gonatopsis japonicus*. Recent studies using genetic analyses suggested that *Boreoteuthis*, which comprises 8-armed gonatids with a 7-toothed radula, might be elevated from subgenus to genus level. However, at the present state of knowledge, and to maintain stability of the generally accepted classification, *Boreoteuthis* remains a subgenus in this Catalogue.

Literature: Okiyama (1969, 1970), Kubodera and Jefferts (1984a,b), Shevtsov and Bessmertnaya (1996), Lindgren *et al.* (2005), Kubodera *et al.* (2006c).

Gonatopsis octopedatus Sasaki, 1920

Fig. 237

Gonatopsis octopedatus Sasaki, 1920, *Proceedings of the United States National Museum*, 57: 163–203 [198]. [Type locality: 48°22'30"N, 145°43'30"E, near Cape Patience, Sakhalin, Okhotsk Sea].

Frequent Synonyms: None.

FAO Names: **En** – Eight-armed gonate squid; **Fr** – Gonaleutène huit-bras; **Sp** – Gonalura ocho-brazos.

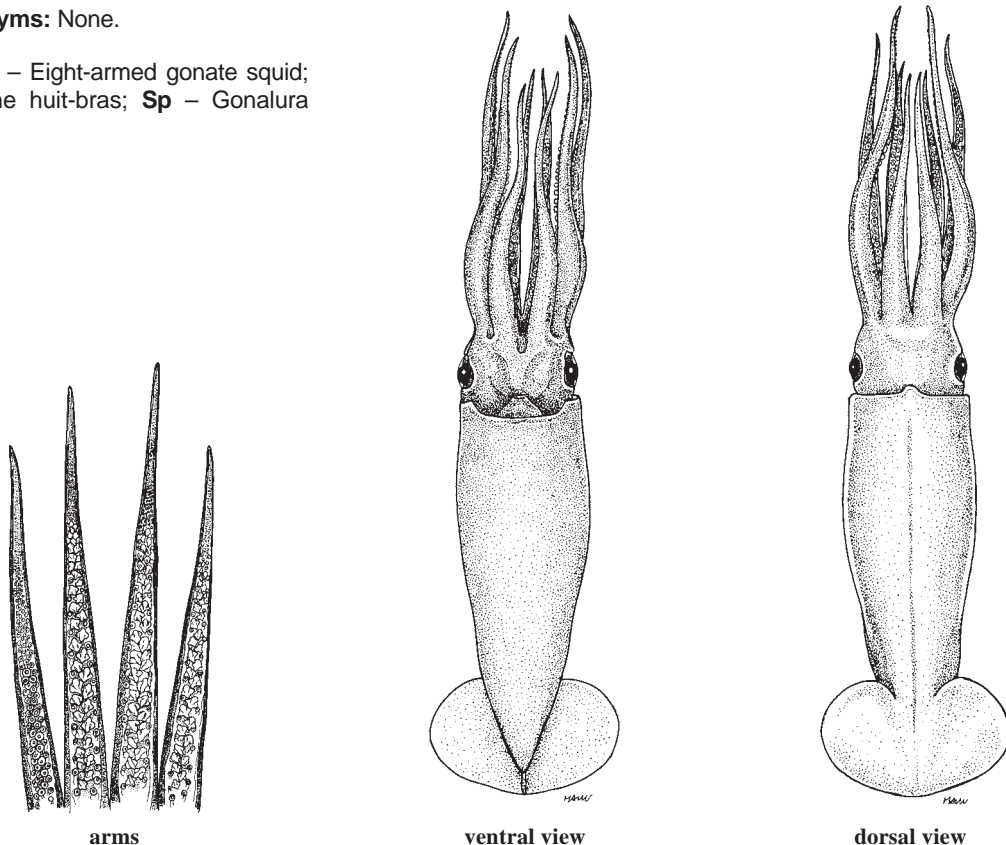


Fig. 237 *Gonatopsis octopedatus*

Diagnostic Features: See generic section.

Size: Small-sized species that attains a maximum mantle length of 175 mm.

Geographical Distribution: This species occurs in the western North Pacific Ocean (from northeastern Honshu, along the Kuril Islands and Kamchatka), in the Japan Sea, Okhotsk Sea, and central western Bering Sea (Fig. 238).

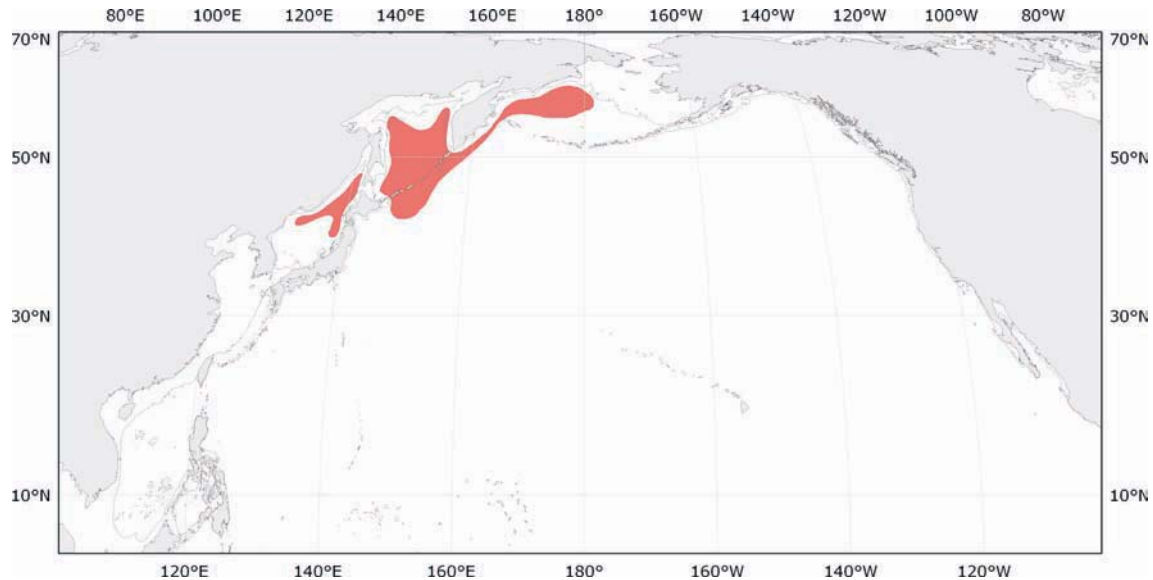


Fig. 238 *Gonatopsis octopedatus*

■ Known distribution

Habitat and Biology: *Gonatopsis octopedatus* is a common species that at various times occupies epi-, meso- and bathypelagic zones and descends close to the bottom on the slope. It occurs over a very broad depth range from the surface to 2 000 m. In the Okhotsk and western Bering Sea, the species abundance increases with depth. In the northwestern Japan Sea in winter and spring, it is the most commonly occurring cephalopod species in the pelagic zone down to 1 000 m. Spawning occurs in deep water. This species is known to have the largest ripe eggs among all gonatids, up to 6.5 mm in diameter. Consequently, the individual fecundity is very low, and ranges from 297 to 414 oocytes. Post-paralarvae and juvenile squid occur in the epipelagic zone and conduct diel vertical migrations. Ontogenetic descent occurs early in the life cycle. Maturation starts at about 100 mm mantle length in deep layers, where maturing animals become very gelatinous.

Interest to Fisheries: This species is found in large quantities in the mesopelagic layers over deep-water basins and slope in the Japan and Okhotsk seas, and plays a significant role in trophic structure of local deep-water pelagic communities. However, small size and weak consistency of flesh does not make it a good potential resource for fishery.

Local Names: JAPAN: Tenaga-Takoika.

Remarks: Very large senescent individuals of up to 390 mm mantle length from the Okhotsk Sea, identified as *Gonatopsis octopedatus*, were most likely another gonatid species (Nesis, 1993a); incorrect species identifications of mature and post-spawning gelatinous gonatids frequently occur due to significant degeneration of their tissues, tentacle autotomy, and significant body damage in trawl nets (loss of fins, arm armature, arm tips and entire arms, breaking into separate pieces, etc.).

Literature: Kubodera and Jefferts (1984b), Okutani *et al.* (1988), Nesis and Nikitina (1996), Katugin (2004), Shevtsov and Mokrin (1998), Hochberg (2006), Katugin and Shevtsov (2006).

Gonatopsis borealis* Sasaki, 1923*Fig. 239**

Gonatopsis borealis Sasaki, 1923, *Annotationes Zoologicae Japonenses*, 10: 203–207 [203]. [Type locality: Kushiro, Nemuro, Tokachi; all on eastern Hokkaido, Japan].

Frequent Synonyms: None.

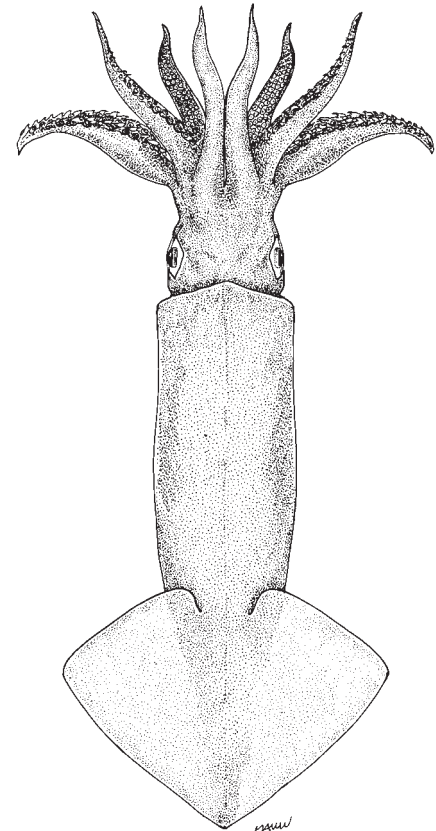
FAO Names: **En** – Boreopacific gonate squid; **Fr** – Encornet boréopacifique; **Sp** – Gonalura pacificoboreal.

Diagnostic Features: Mantle stout (width 25% of mantle length), thick, muscular; reddish purple coloration. Fins muscular, relatively short (40 to 45% of mantle length) and broad (65 to 80% of mantle length), not attenuate into tail posteriorly. Tentacles absent (present only in larvae and disappear at 12 to 15 mm mantle length). Arms robust, muscular, short; length 40 to 50% of mantle length; arms I to III with 2 medial series of hooks and 2 marginal series of suckers; arm IV with 4 series of suckers, no hooks. Hooks develop on arms at 35 to 45 mm mantle length. Radula with 7 rows of teeth.

Size: The maximum mantle length of this species attains 280 mm in males and 300 mm in females.

Geographical Distribution: *Gonatopsis borealis* inhabits the northern Pacific Ocean. It is a panboreal species from northern Japan (37°N to 40°N) throughout the Okhotsk Sea, Bering Sea slope waters, along the Aleutian Islands and Gulf of Alaska, and southward to California, even to Baja California (20°N) (Fig. 240).

Habitat and Biology: An oceanic species, *G. borealis* is one of the most abundant and widely distributed gonatid species. It occurs in cold temperate waters, where it is extremely eurybathic: it ranges from the surface to mesopelagic depths and even into the bathypelagic zone. It is known to undertake diel vertical migrations and to form increasingly large aggregations between April and early autumn, particularly in the eastern and western parts of the North Pacific Ocean. This species may account for up to 68% of squid catches in the Okhotsk Sea in summer. Biomass estimates reach 278 000 tonnes in the Okhotsk Sea (up to 0.5 million tonnes according to some estimates), 209 000 tonnes in the western Bering Sea, 285 000 tonnes along the western Kamchatka slopes and 100 000 tonnes off the Kuril Islands. *Gonatopsis borealis* occurs in epipelagic, mesopelagic and bathypelagic depths from the surface to 1 500 m and is benthic at 200 to 1 375 m, but it is much more abundant in the midwater realm (captured in 95% of midwater tows versus 19% of benthic trawl tows). Maximum abundance occurs at 300 to 500 m, while only single specimens are caught below 1 000 m (consequently probably were caught in much shallower depth while the open nets were hauled back through the zone of abundance). The very pronounced diel vertical migrations involve



dorsal view

Fig. 239 *Gonatopsis borealis*

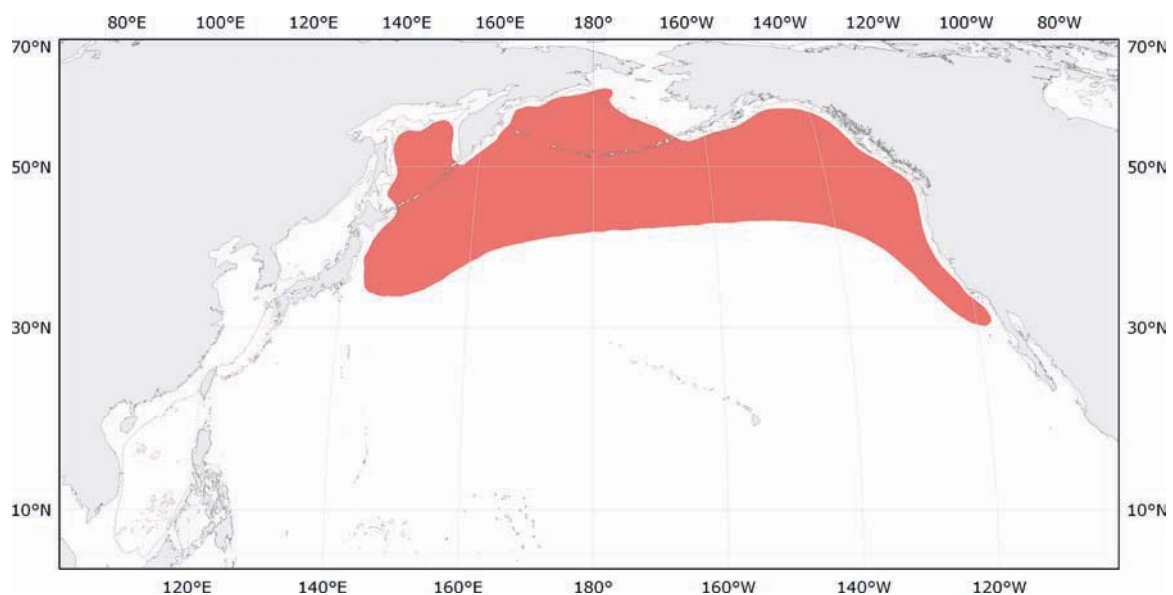


Fig. 240 *Gonatopsis borealis*

Known distribution

both adults and young. For example, off California, no specimens occurred during daytime in less than 300 m, even 16 mm mantle length juveniles; 90% of daytime captures were at 400 to 700 m. At night, specimens occurred principally at 100 to 500 m, mostly 300 to 400 m. In the upper epipelagic western Bering Sea in autumn, *G. borealis* was the most numerous cephalopod species and occurred in 27% of the hauls (in 44% hauls over deep Commander Basin) exclusively during night hours; it appeared that smaller individuals migrated to the surface layers and descended to deeper layers earlier than larger animals, showing possible behavioural adaptation that helps smaller squid to avoid the presence of larger cannibalistic relatives. *Gonatopsis borealis* preys on a great variety of pelagic crustaceans (euphausiids, hyperiid amphipods, copepods), fishes (mostly myctophids) and squids. The life span is presumably 1 year or slightly longer. Predators include fishes (e.g. salmonids, walleye pollock, pomfret, albacore, grenadiers); squids (*Berryteuthis magister*, *G. borealis*); seabirds (murre); seals, sea lions, dolphins, toothed whales (sperm, pilot, etc).

Interest to Fisheries: *Gonatopsis borealis* (mostly representatives of the large-sized cohort) is captured as bycatch with jigs and in substantial numbers in drift gillnets set for salmonids and the neon squid, *Ommastrephes bartramii*. It is believed to have some significant fishery potential because of its massive abundance and the consistency of its flesh. Its meat is delicious. However, its role as principal prey for dozens of commercially valuable fishes perhaps is more important at this juncture than a heavily developed fishery.

Local Names: JAPAN: Takoika.

Remarks: In the northwestern Pacific Ocean, 2 populations occur, 1 more northerly, maturing at small size (less than 180 mm mantle length); another one to the south of 45°N to 47°N, maturing at large size (larger than 220 mm mantle length). These populations or size cohorts occur sympatrically along the Kuril Islands.

Literature: Nesis (1972b), Kubodera and Jefferts (1984a, b), Okutani *et al.* (1988), Nesis and Nezlin (1993), Bower and Takagi (2004), Katugin (2004), Shevtsov *et al.* (2004b), Katugin and Zuev (2007), Jorgensen (2007).

***Gonatopsis japonicus* Okiyama, 1969**

Fig. 241

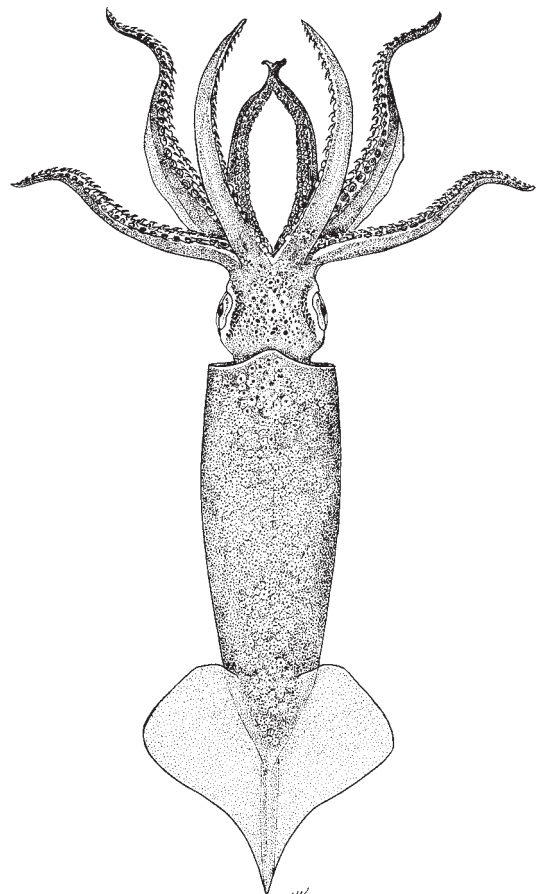
Gonatopsis japonicus Okiyama, 1969, *Publications of the Seto Marine Biological Laboratory*, (17)1: 19–32. [20]. [Type locality: 41°02'N, 138°11'E, Northwest Pacific Ocean].

Frequent Synonyms: *Gonatopsis makko* (Okutani and Nemoto, 1964), in part.

FAO Names: **En** – Japanese gonate squid; **Fr** – Gonaleutène japonais; **Sp** – Gonalura japonés.

Diagnostic Features: Mantle slender, muscular, fins relatively large and narrow; fin length slightly longer than width, about one-half mantle length. Tail long, attenuate, about one-half fin length. Head large, broader than mantle opening. Funnel relatively small, dorsal funnel organ inverted V-shaped. Funnel cartilage lanceolate and slightly curved inward. **Radula with 5 teeth per row.** Arms robust, subequal, the longest about 55% of mantle length. Hooks on arm I-III well developed, 57 to 61 in number. **Tentacles absent in adults.**

Size: The maximum mantle length of this very large gonatid species extends to 620 mm.



dorsal view

Fig. 241 *Gonatopsis japonicus*

Geographical Distribution: *Gonatopsis japonicus* is a northern North Pacific Ocean species that is distributed off eastern Honshu, Japan, in the Japan Sea, in the Okhotsk Sea and along the Kuril Chain north to the central eastern Bering Sea (Fig. 242).

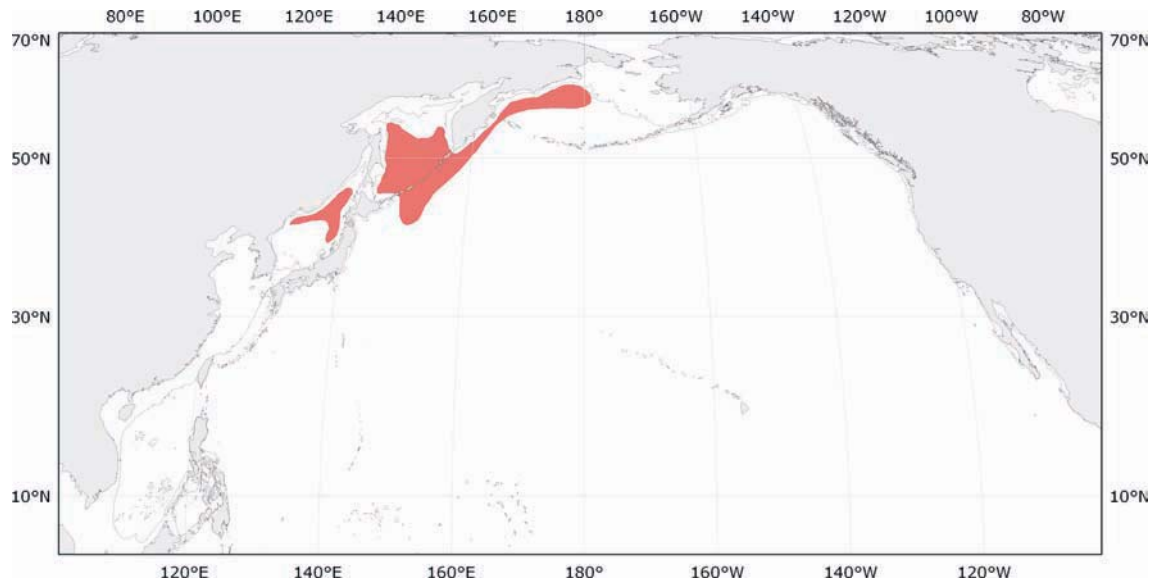


Fig. 242 *Gonatopsis japonicus*

■ Known distribution

Habitat and Biology: This is a panboreal species. It occurs from the epipelagic and down into the meso- and bathypelagic zones, having been captured at pelagic depths from the surface to 1 000 m and on the bottom at 400 to 2 000 m. In the Japan Sea, *G. japonicus* was most common in the upper 140 m, and its occurrence decreased rapidly with depth. Regular occurrence of juveniles and immature adults in the upper layers suggests that the species is active vertical migrant, and that ontogenetic descent occurs rather late in the life cycle. Most animals captured to date were immature, or at the onset of maturation. In the meso- and bathypelagic Okhotsk Sea, mature and pre-spawning males had mantle lengths from 278 to 478 mm, and immature and maturing females from 398 to 582 mm; the largest animal with mantle length of 620 mm was not dissected. Muscle tissues become gelatinous in mature individuals.

Interest to Fisheries: This species is found in large quantities in the pelagic layers over deep-water basins and slope in the Japan and Okhotsk seas, and plays a significant role in trophic structure of local pelagic communities. Rather weak consistency of flesh, especially in mature animals, does not make it a good potential resource for fishery.

Local Names: JAPAN: Nippon-Takoika.

Remarks: *Gonatopsis japonicus* is frequently confused with *Gonatopsis makko*, particularly, animals from the Japan and Okhotsk seas, mentioned under the name *G. makko*, belong to *G. japonicus* (see Remarks for *Gonatopsis makko*).

Literature: Okutani *et al.* (1988), Okutani *et al.* (1995), Shevtsov and Mokrin (1998), Lindgren *et al.* (2005), Katugin and Shevtsov (2006), Kubodera (2006a), Katugin *et al.* (2008).

Gonatopsis makko Okutani and Nemoto, 1964**Fig. 243**

Gonatopsis makko Okutani and Nemoto, 1964, *Scientific Reports of the Whales Research Institute*, Tokyo, 18: 111–121 [113].
[Type locality: from sperm whale stomach, Southern Bering Sea].

Frequent Synonyms: None.

Misidentifications: *Gonatopsis japonicus* Okiyama, 1969.

FAO Names: En – Makko gonate squid; Fr – Encornet mako; Sp – Gonalura mako.

Diagnostic Features: Mantle elongate, slender, conical, width about 20% of mantle length; soft and flabby. Fins very small, short (about 33% or less of mantle length); narrow (width from 45 to 50% of mantle length). **Tentacles absent in adults.** Arms I to III very long, robust, attenuate, up to 80% of mantle length. Arm hooks strong in medial 2 series; 2 series of marginal suckers. **Arms IV short, with 4 series of suckers, no hooks.**

Size: This species reaches a maximum mantle length of 350 mm, possibly larger.

Geographical Distribution: *Gonatopsis makko* occurs in the eastern North Pacific Ocean, from the northeastern coast of Honshu and the Japan Sea, along the Kuril Chain and eastward to the western Aleutian Islands (Fig. 244).

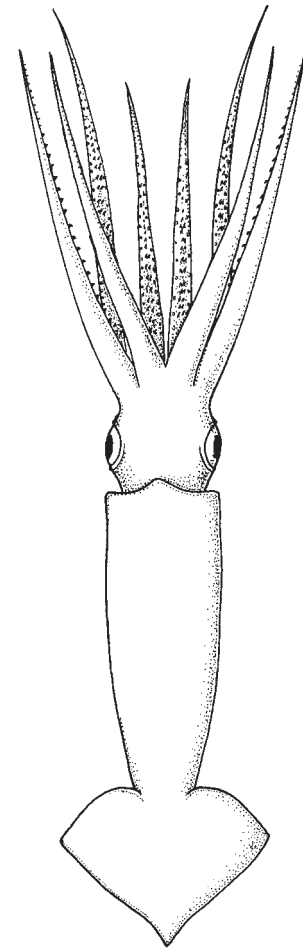
Habitat and Biology: An oceanic species, *G. makko* occurs rather frequently in midwater layers and to the bottom (650 to 1 200 m) in the Japan Sea and the northern North Pacific Ocean. It is preyed upon extensively by sperm whales.

Interest to Fisheries: This species is occasionally captured in the mesopelagic zone in the Okhotsk Sea.

Local Names: JAPAN: Makko-Takoika.

Remarks: Some authors consider that *Gonatopsis makko* might be the adult of *Gonatopsis japonicus* (e.g. Nesis, 1997), but only those specimens from the Japan and Okhotsk Seas. The validity of the name has been questioned by some authors because the species was described based on 3 individuals from sperm whale stomachs; these animals were notably damaged, partly digested and lacked buccal masses with radulas. Therefore, real body proportions and consistency of type specimens could have changed in whale stomachs, and what is more important, it remains uncertain how many rows of radular teeth (5 or 7, a basic systematic character state in the gonatid squid) were in *G. makko* type specimens.

Literature: Okutani *et al.* (1988), Nesis (1997), Kubodera (2006b).



dorsal view

Fig. 243 *Gonatopsis makko*

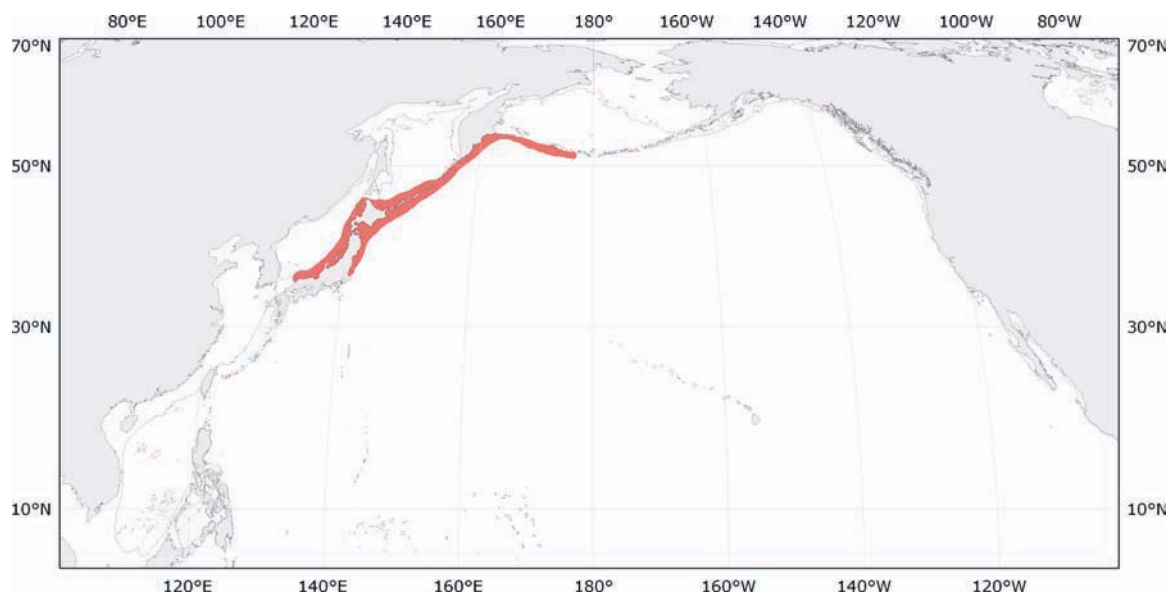


Fig. 244 *Gonatopsis makko*

Known distribution

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

***Gonatus antarcticus* Lönnerberg, 1898**

Gonatus antarcticus Lönnerberg, 1898, *Svenska Expeditionen till Magellansländerna*, 2(4): 49–64 [51]. [Type locality: on the beach, Punta Arenas, Chile].

Frequent Synonyms: None.

Size: This species grows to a maximum mantle length of 350 mm.

Geographical Distribution: *Gonatus antarcticus* is a notalian circumpolar species in the Southern Hemisphere, reaching Antarctic waters (south of 40°S). It also is distributed around South Georgia and along the Scotia Arc, north to southernmost South Africa, the Cook Strait and Peru (possibly well north on Peru–Chile current).

Habitat and Biology: Paralarvae and juveniles of *G. antarcticus* live in epipelagic and mesopelagic zones, adults in mesopelagic and bathypelagic zones. It is prey of numerous other species, e.g. white-chinned petrel, Magellanic penguin, king penguin, southern bottlenose whale, black-browed albatross, hake, rattail, southern elephant seal, Patagonian toothfish.

Literature: Okutani and Clarke (1992), Rodhouse *et al.* (1992a), Arkhipkin and Laptikhovskiy (2006).

***Gonatus berryi* Naef, 1923**

Gonatus berryi Naef, 1923, *Fauna e Flora de Golfo di Napoli, Monograph*, 35, 1(1) part 2: 149–863 [245]. [Type locality: Monterey Bay, California, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 190 mm.

Geographical Distribution: *Gonatus berryi* occurs in the North Pacific Ocean, from northern Honshu, eastern Hokkaido, the Bering Sea, through the Aleutian Island chain and the Gulf of Alaska and south to northern Baja California.

Habitat and Biology: A common panboreal meso-bathypelagic species, *G. berryi* occurs at 400 to 700 m in daytime and at 100 to 700 m (mostly to 500 m) at night. Paralarvae and early juveniles are known from the upper layers in the central and northeastern Pacific Ocean. One specimen has been observed from a deep-diving submersible at 915 m. Diel vertical migrations are not characteristic for this species. *Gonatus berryi* undergoes ontogenetic descent to deep waters early in ontogeny. Hooks on arms and tentacular club are developed at very small size, of about 6 to 8 and 12 to 34 mm gladius length, respectively. Muscle tissues become gelatinous in mature individuals. This species is preyed upon by pomfret, swordfish, *Ommastrephes bartramii*, Dall's porpoise, sperm whale, northern fur seal, and northern elephant seal.

Local Names: JAPAN: Berryi-Tekagiika.

Literature: Young (1972a), Kubodera and Jefferts (1984a, b), Katugin and Shevtsov (2006).

***Gonatus californiensis* Young, 1972**

Gonatus californiensis Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [51]. [Type locality: 33°32'N, 118°24'W, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: This species attains a maximum mantle length of 120 mm.

Geographical Distribution: *Gonatus californiensis* seems limited to the eastern North Pacific Ocean from Vancouver Island, Canada, to Baja California, Mexico, and possibly to the Gulf of Panama.

Habitat and Biology: A muscular, low-boreal, pseudo-oceanic, meso-bathypelagic species. No paralarvae of this species have been recorded in the surface layers. A vertical shifter early in ontogeny, *G. californiensis* may have a total depth range of 100 to 1 200 m with peak abundance at 400 to 700 m in daytime and dispersal to 100 to 500 m at night. This species has been recorded in the diet of sperm whale and beaked whale.

Local Names: JAPAN: California-Tekagiika

Literature: Young (1972a), Okutani *et al.* (1988), Okutani and Clarke (1992).

***Gonatus onyx* Young, 1972**

Gonatus onyx Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [43]. [Type locality: 33°19'N, 118°45'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: *Gonatus onyx* reaches a maximum mantle length of 150 mm.

Geographical Distribution: *Gonatus onyx* is a North Pacific Ocean panboreal species that is distributed from southern Honshu, Japan, to the southern Okhotsk Sea and Bering Sea, the Aleutian Islands, and Gulf of Alaska, then southward to northern Baja California.

Habitat and Biology: This extremely abundant panboreal species is epipelagic in its paralarval and early juvenile stages, then it becomes mesopelagic to bathypelagic in adult stages. Egg incubation requires from 6 to 9 months. Its daytime distribution shows bimodal peaks at 400 and 800 m, and at nighttime it undergoes diel vertical migration to 100 to 500 m, mostly concentrated at 300 to 500 m. Egg-brooding females, holding egg masses in their arms, have been observed at depths between 1 250 and 2 522 m off California. Egg mass contains about 2 000 to 3 000 ovoid eggs, each 2 to 3 mm in length and 1.8 to 2.1 mm in width. Mantle length of hatchlings ranges from 3.2 to 3.5 mm. Predators include chinook salmon (our data), walleye pollock, pomfret lancetfish, Dall's porpoise, Cuvier's beaked whale.

Literature: Young (1972a), Kubodera and Jefferts (1984a,b), Seibel *et al.* (1997), Seibel *et al.* (2000a, 2005), Katugin and Shevtsov (2006), Jorgensen (2007).

***Gonatus oregonensis* Jefferts, 1985**

Gonatus oregonensis Jefferts, 1985, *Veliger*, 28(2): 159–174 [167]. [Type locality: off Oregon, USA, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: This species reaches a maximum mantle length of 50 mm.

Geographical Distribution: *Gonatus oregonensis* occurs in the eastern North Pacific Ocean off Oregon, USA.

Habitat and Biology: It is confined to the California Current where it occurs shallower than 400 m at night.

Remarks: *Gonatus oregonensis* was described based on post-paralarval and juvenile individuals with mantle length ranging from 24 to 46 mm, and has not been recognized since its first description. In his review of the Gonatidae in 1997, Nesis suggested that it is very close to, and may represent a northern subspecies or a form of *Gonatus californiensis*, from which *G. oregonensis* is less easily separable (compared to other *Gonatus* spp.). Subtle differences between these 2 species are in fin dimensions, in sucker counts on the club and distribution of suckers on the dactylus.

Literature: Okutani *et al.* (1988), Okutani and Clarke (1992), Nesis (1997).

***Gonatus pyros* Young, 1972**

Gonatus pyros Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [49]. [Type locality: 33°37'N, 118°26'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: *Gonatus pyros* grows to a maximum mantle length of 130 mm.

Geographical Distribution: *Gonatus pyros* is distributed in the eastern North Pacific Ocean from the Bering Sea, Aleutian Islands, and Gulf of Alaska southward to northern Baja California; it is also known from the western North Pacific Ocean off Japan and Kuril Islands.

Habitat and Biology: *Gonatus pyros* predominantly is a meso-bathypelagic species. Paralarvae and juveniles rarely occur in epipelagic zone. Juveniles occur by day deeper than 300 to 400 m, mostly at 300 to 700 m; at night they disperse to 100 to 700 m, mostly to 300 to 500 m. The species is a diel vertical migrator. Mature females have mantle length about 130 mm, and undergo gelatinous degeneration; mature eggs are ovoid, 3.0 x 1.7 mm in size. The descent to deep layers presumably begins early in ontogeny. This squid is preyed on by pomfret, salmon, northern fur seal, Dall's porpoise and sperm whale.

Literature: Young (1972a), Okutani *et al.* (1988), Nesis (1997), Katugin and Shevtsov (2006).

***Gonatus ursabrunae* Jefferts, 1985**

Gonatus ursabrunae Jefferts, 1985, *Veliger*, 28(2): 159–174. [160]. [Type locality: South of Alaska Peninsula, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: Known only from paralarvae and juveniles; maximum reported mantle length 24 mm.

Geographical Distribution: *Gonatus ursabrunae* has a narrow distribution in the eastern North Pacific Ocean in the Bering Sea and the Gulf of Alaska; it is confined to the Alaskan gyre.

Remarks: *Gonatus ursabrunae* was described based on post-paralarval and juvenile individuals with mantle length ranging from 12 to 24 mm, and has not been recognized since its first description. In his review of the Gonatidae in 1997, Nesis suggested that it is either a species, as yet not recognized in adult stage, or a juvenile form of a known species, probably *Gonatus kamtschaticus*, from which *G. ursabrunae* is separable by its mantle width index and the size at which club hooks develop.

Literature: Kubodera and Jefferts (1984a,b), Okutani *et al.* (1988), Nesis (1997).

***Berryteuthis magister nipponensis* Okutani and Kubodera, 1987**

Berryteuthis magister nipponensis Okutani and Kubodera, in Okutani *et al.*, 1987, *Cephalopods from Continental Shelf and Slope Around Japan*, 194 pp. [133]. [Type locality: Okirai Bay, Iwate, northeastern Honshu, Japan].

Frequent Synonyms: None.

Size: This subspecies has a reported maximum mantle length of 180 mm.

Geographical Distribution: *Berryteuthis magister nipponensis* is recorded only from around Japan: the Japan Sea, off eastern Honshu and southern Hokkaido.

Remarks: According to authors of the original description, this subspecies is distinguishable from the typical *B. magister* in having narrower mantle, somewhat smaller fin and less evident size differences between central and marginal club suckers. In addition, they mature at a considerably smaller size.

Literature: Okutani *et al.* (1987), Okutani and Clarke (1992), Katugin (2000a).

***Berryteuthis magister shevtsovi* Katugin, 2000**

Berryteuthis magister shevtsovi Katugin, 2000a, *Veliger*, 43(1): 82–97 [91]. [Type locality: 42°30'N, 113°42'E, Japan Sea western Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length of fully mature females is 320 mm, that of fully mature males is 200 mm; however, smaller size are most common, i.e. 200 mm for females and 170 mm for males.

Geographical Distribution: *Berryteuthis magister shevtsovi* lives in the Japan Sea.

Habitat and Biology: This subspecies inhabits bathypelagic waters of very low temperatures. The total depth range for all maturity stages is 50 to 1 200 m, with the peak zone for adults at 300 to 500 m.

Remarks: This subspecies is differentiated on genetic, morphological, distributional, reproductive and ecological characteristics. (See *B. magister* section for additional information).

Literature: Katugin (2000a).

***Eogonatus* Nesis, 1972**

Gonatus (Eogonatus) Nesis, 1972b, *Zoologicheskij Zhurnal*, 51(9): 1300–1307 [1300].

Type Species: *Gonatus (Eogonatus) tinro* Nesis, 1972b.

Frequent Synonyms: None.

Diagnostic Features: Tentacles slender, weak. Tentacular clubs with no hooks, only numerous, very crowded, minute, equal-sized suckers. The 5 or 6 ridges and grooves of club fixing apparatus are short. Radula with 5 transverse rows of teeth. Head enlarged by large, bulbous eyes. Mantle not muscular. Fins ovate, not sagittate.

Size: Small-sized squid; maximum mantle length 140 mm.

Remarks: This taxon was elevated to generic status because of the absence of any hooks on the tentacular club, combined with 5 rows of teeth on the radula. However, genetic studies using allozymes and mitochondrial DNA suggested that this species is within the *Gonatus* s. str. group.

Literature: Nesis (1972b, 1985, 1997), Katugin (2004), Kubodera *et al.* (2006d).

***Eogonatus tinro* Nesis, 1972**

Eogonatus tinro Nesis, 1972b, *Zoologicheskij Zhurnal*, 51(9): 1300–1307 [1300]. [Typed locality: 58°22.2'N, 174°55', Bering Sea Northwest Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length recorded for this species is 140 mm.

Geographical Distribution: *Eogonatus tinro* occurs in the northern North Pacific Ocean from northeastern Hokkaido, Japan, the Okhotsk Sea and southern Kuril Islands, to the Bering Sea, the Aleutian Islands, and the Gulf of Alaska, south to British Columbia, Canada.

Habitat and Biology: This species is an upper-boreal, meso-bathypelagic species that undergoes ontogenetic descent and diel vertical migration. It spawns mainly in the summer; paralarvae and juveniles are described.

Local Names: JAPAN: Nise-Tekagiika.

Remarks: Mostly early ontogenetic stages of this species are known. See also Remarks for *Gonatopsis okutanii*.

Literature: Nesis (1972b), Okutani *et al.* (1988), Katugin and Shevtsov (2006).

***Gonatopsis okutanii* Nesis, 1972**

Gonatopsis okutanii Nesis, 1972b, *Zoologicheskij Zhurnal*, 51(9): 1300–1307 [1304]. [Type locality: 44°06.4'N, 150°28.2'E, Northwest Pacific Ocean].

Frequent Synonyms: None.

Size: *Gonatopsis okutanii* attains a maximum mantle length of 250 mm.

Geographical Distribution: *Gonatopsis okutanii* occurs in the North Pacific Ocean from the southern Kuril Islands to the northern slope of the Okhotsk Sea, the Bering Sea and the Gulf of Alaska.

Habitat and Biology: This is a mesopelagic, bathypelagic and abyssal species. It has relatively large eggs, and mates presumably "head to head", then dies after spawning.

Remarks: The validity of this species name has been questioned. Nesis (1997) suggested that it probably is a synonym of *Gonatus madokai*. However, *G. madokai* is easily distinguishable from *Gonatopsis okutanii* by its much larger fin, longer ventral arms and larger size-at-maturity. Katugin (unpublished) suggest that *G. okutanii* may represent an adult form of *Eogonatus tinro*. Usually tentacles of all collected individuals of *G. okutanii* appear broken at the bases, as in the holotype. However, several individuals of *G. okutanii*, collected by Katugin in the Okhotsk Sea, possessed intact slim tentacles with tentacular clubs like those in *E. tinro* (no hooks on the club, only minute suckers, and fixing apparatus with small ridges and grooves). There is one notable difference between these 2 species. In small *E. tinro*, the ventral arms are almost the same length or slightly longer than the other arms; in *G. okutanii*, the ventral arms are somewhat shorter and thinner than the other arms. However, individuals identified as *E. tinro* are usually small juveniles, while those assigned to *G. okutanii* are much larger adults, and observed differences in relative lengths of arms could be due to their asymmetric growth in ontogeny. Clearly, if this entity possesses tentacles, it does not belong in the genus *Gonatopsis*.

Literature: Nesis (1972b, 1997), Okutani and Clarke (1992).

2.14 Family HISTIOTEUTHIDAE Verrill, 1881

by Clyde F.E. Roper and Patrizia Jereb

Histioteuthidae Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 259–446. [431].

Type Genus: *Histioteuthis* d'Orbigny, 1841

FAO Names: En – Jewel squids; Fr – Loutènes bijou; Sp – Joyelurias

Diagnostic Features: Species are easily distinguished by **numerous** (usually), **anteriorly directed, complex photophores over the surface of the mantle, head and arms, especially on the vental and ventrolateral surfaces**; a broad head, with usually **asymmetrically developed eyes**, the left eye usually considerably larger than the right. Buccal membrane with 6 or 7 buccal lappets; **buccal connectives attach to the dorsal border of arms IV**; straight or slightly curved and slightly broad, simple, funnel-mantle locking elements; **suckers on the tentacular clubs arranged in 5 to 8 irregular series**; suckers on the arms biserial. Gladius with ventrally inrolled, cupped cone at posterior end. **Fins terminal, medium to large, together transversely oval in outline, unite posteriorly with a median notch**. An inner web connects arms and extends to greater than 60% of length of arms. A **hectocotylus is absent in males**, but both arms I have secondary sexual modifications: terminal suckers abruptly reduced in size set on elongate, palisaded pedestals; basal (or all normal) suckers enlarged, with swollen, fleshy collars; arms I often become more elongate, robust. Tentacles long with expanded club; distinct dactylus, manus and carpal adhesive apparatus, with alternating suckers and pads in a single row that extends proximally on the tentacular stalk for 1 to 3 club lengths. Sucker rings on manus are toothed around entire circumference.

Size: Small- to medium-sized squid; maximum mantle length 350 mm.

Geographical Distribution: As a group, the members of the Histioteuthidae occur in all oceans and marine seas of the world.

Habitat and Biology: Members of the cosmopolitan family Histioteuthidae are very broadly distributed throughout the world's oceans and seas in epipelagic (undergo diel vertical migration at night), mesopelagic and bathypelagic, even bathybenthic, habitats. Species range from the tropics to the polar seas. Closing-net data on a few species of *Histioteuthis* indicate the strong likelihood that diel vertical migration is common among the family members. For example, in an intensive open-net survey of the eastern Pacific Ocean off California no specimens of *H. heteropsis* were captured in the upper 300 m during the day; only 16% of daytime captures were caught at 300 to 500 m, while 62% were caught at 500 to 700 m. In contrast, at night, 69% of *H. heteropsis* captured were taken in the upper 400 m, with a peak at 300 to 400 m. The shallowest nighttime capture for specimens larger than 20 mm mantle length was 200 m and most were concentrated at 300 to 400 m. Some species are extremely abundant, and they appear to aggregate in "schools", even at great depths. Some species are quite large and attain mantle lengths of at least 350 mm, but the total length can be 4 to 5 times longer than mantle length. Most species are major components in the diets of sperm whales (up to 62% in some regions), other odontocete cetaceans, pinnipeds; albatrosses, penguins, other seabirds; sharks, tunas, lancetfishes; other squids.

Interest to Fisheries: While there are no large-scale directed fisheries for any species of *Histioteuthis*, it is possible that a small bycatch interest could develop as commercial fishery trawling probes increasingly deeper, to 1 500 m and beyond. The flesh on the mantle and arms of histioteuthids is firm and thick in adults of pre-spawning condition. At full maturation of both males and females, however, the tissue of the mantle, head and arms begins to soften, and by full spawning and post-spawning stages, the tissues of the mantle, head and arms soften to a semi-gelatinous consistency. A further impediment to development of a consistent fishery would be the suspected ammoniacal composition of the flesh.

Remarks: Following Voss *et al.* (1998a) the family is monotypic and all species are quite easily recognized as members of *Histioteuthis*. To date, 13 species are recognized, 2 of which have 1 and 3 subspecies, respectively, for a total of 17 currently recognized specific and subspecific entities. The first systematic monograph of the family was by N. Voss (1969). A comprehensive monograph was produced by Voss, Nesis and Rodhouse (1998), to which the reader is referred for detailed aspects of systematics, distribution, morphology, ecology, predation, etc. The family also has been treated on the "Tree of Life" website for Cephalopoda by Young and Vecchione (2000, 2008b,c,d). This site presents valuable information on and comparisons of specific taxonomic characters in tabular form. Most significantly, all subspecies that we list here, have been elevated to species level in ToL, a judgement with which we agree. A valuable adjunct to the contribution by Young and Vecchione is a comprehensive list of nominal genera and species named in the Histioteuthidae, with notations on their status (e.g. validity, synonyms, etc.) by Sweeney and Young (2003l).

The nomenclature and classification used herein is based on Voss *et al.* (1998a). Subsequently, different interpretations have been introduced that depart from the earlier classification (see Young and Vecchione, 2000, 2008h,i,j).

Local Names: USA: Umbrella squids.

Literature: Voss (1969), Voss *et al.* (1992a), Rodhouse *et al.* (1992a,c), Young and Vecchione (2000, 2008h,i,j); Voss *et al.* (1998a), Sweeney and Young (2003l).

Key to the species and subspecies of Histioteuthidae (from Voss *et al.* 1998a)

- 1a. Median row of tubercles on dorsal surface of mantle and basal portions of arms I–III present → 2
- 1b. Median row of tubercles on mantle and arms absent → 4
- 2a. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8 or 9 longitudinal rows on basal portions of arms IV, in cirlet of 19 to 22 around right eye *Histioteuthis meleagroteuthis*
(Atlantic, Pacific, and Indian oceans, tropical-subtropical)
- 2b. Photophores of uniformly medium size, arranged in moderately dense pattern on ventral surfaces of mantle and head, in 4 to 6 longitudinal rows on basal portions of arms IV, in cirlet of 16 or 17 (rarely 15 or 18) around right eye → 3
- 3a. Median row of tubercles occupies 19 to 39% of arm length in adults and subadults, 24 to 47% in juveniles of 17 to 38 mm mantle length; numerous photophores in diagonal rows on basal half of arms IV, 5 photophores in first 2 or 3 rows, 4 in subsequent rows *Histioteuthis miranda*
(southern Benguela Current, western Indian Ocean, subtropical waters of Australia-New Zealand)
- 3b. Median row of tubercles occupies 46 to 83% of arm length in adults and subadults; 65 to 92% in juveniles of 12 to 22 mm mantle length; numerous photophores in diagonal rows on basal half of arms IV, 6 photophores in first 2 or 3 rows, 5 in subsequent rows. *Histioteuthis oceani*
(equatorial Pacific Ocean and certain adjoining areas of North and South Pacific Oceans, ? tropical Indian Ocean)
- 4a. Single, large terminal photophore present on arms I to III or I to IV; inner web connecting basal portions of arms deep: 50% or more of arm length in adults, subadults, and large juveniles → 5
- 4b. Single, large terminal photophore absent on arms; inner web vestigial to moderate in depth: 30% or less of arm length in adults, subadults, and juveniles → 6
- 5a. Buccal membrane with 6 lappets and 1 connective to arms IV; segment of inner web absent between right and left junctures of web segments from arms III and IV *Histioteuthis bonnellii*^{1/}
(sub-Arctic, north temperate, and eastern tropical Atlantic Ocean; Mediterranean Sea; Benguela Current; nearly circumglobal in southern half of south subtropical regions)
- 5b. Buccal membrane with 7 lappets and 2 connectives to arms IV; segment of inner web present between right and left junctures of web segments from arms III and IV. *Histioteuthis macrohista*
(nearly circumglobal in Southern Subtropical Convergence, Benguela Current)
- 6a. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8 to 10 longitudinal rows on arms IV, in cirlet of about 19 to 21 (range 17 to 23) around right eye *Histioteuthis heteropsis*
(California Current, Peru-Chile Current)
- 6b. Photophores large or intermixed large and small, arranged in widely spaced to moderately dense pattern on ventral surfaces of mantle and head, in 3 or 4 longitudinal rows on arms IV, in cirlet of 16 to 18 (? rarely 15) around right eye. → 7
- 7a. Photophores large, arranged in widely to moderately widely spaced pattern on anterior one-third to one-half of ventral surface of mantle; cirlet around right eye composed of 16 or 17 (rarely 18 or ?15) large photophores. → 8
- 7b. Photophores intermixed large and small, arranged in moderately dense pattern on ventral surface of mantle; cirlet around right eye composed of 17 large and 1 small photophores → 15
- 8a. Photophores in widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ with 2 lateral flaps; male genitalia paired; skin conspicuously papillated (except in small juveniles) → 9
- 8b. Photophores in moderately widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ unsculptured; male genitalia single; skin not papillated. → 10

^{1/} Probably comprises more than 1 taxon.

- 9a. Spermatophore 5 to 6% of mantle length, with single loop in ejaculatory apparatus; large adult males with midportions of arms I with moderately increased robustness, median keel moderately expanded, protective membranes low *Histioteuthis hoylei*^{2/}
(Pacific and Indian Oceans, tropical-subtropical)
- 9b. Spermatophore 13 to 21% of mantle length, with numerous loops in ejaculatory apparatus; large adult males with midportions of arms I with greatly increased robustness, median keel greatly expanded, protective membranes high. *Histioteuthis arcturi, new combination*^{2/}
(Atlantic Ocean, tropical-subtropical)
- 10a. Terminal group of normal photophores on arms I to IV present, except in mature specimens (? mature male of *Histioteuthis celetaria celetaria* and mature female of *H. celetaria pacifica*), where terminal groups on arms I to III replaced by single, long, narrow, darkly pigmented photophore; denticulate collars of club suckers in ventral marginal rows on manus asymmetrically broadened → 11
- 10b. Terminal group of photophores on arms absent; denticulate collars of club suckers in ventral marginal rows on manus not asymmetrically broadened → 12
- 11a. Suckers in median 2 or 3 rows of club manus slightly enlarged and approximately coequally enlarged; gladius with shoulders of vanes somewhat flaring and angular *Histioteuthis celetaria celetaria*
(Atlantic Ocean, tropical-subtropical)
- 11b. Suckers of median 3 rows of club manus moderately enlarged to 1½ times ventral marginals (except in small juveniles), decreasing in size from ventral to dorsalmost rows; gladius with shoulders of vanes broadly rounded. *Histioteuthis celetaria pacifica*
(Pacific and Indian Oceans, primarily equatorial/tropical)
- 12a. Four longitudinal rows of photophores on arms IV *Histioteuthis corona berryi*
(North Pacific Ocean, subtropical, California Current)
- 12b. Three longitudinal rows of photophores on arms IV → 13
- 13a. Sucker rings on arms IV smooth; 20 to 27 teeth on rings of large suckers of club manus *Histioteuthis corona inermis*
(northwestern Pacific Ocean, subtropical)
- 13b. Sucker rings on arms IV with teeth; 30 to 60 teeth on rings of large suckers of club manus. → 14
- 14a. Thirty-three to 38 teeth on rings of large suckers of club manus *Histioteuthis corona corona*
(Atlantic Ocean, tropical-north subtropical)
- 14b. Fifty to 60 teeth on rings of large suckers of club manus *Histioteuthis corona cerasina*
(eastern and central equatorial Pacific Ocean, Peru-Chile Current)
- 15a. Three longitudinal rows of photophores on arms IV (of large organs) *Histioteuthis eltaninae*
(sub-Antarctic waters, circumglobal)
- 15b. Four longitudinal rows of photophores on arms IV (3 rows of large organs, 1 row of small or mixed-size organs) → 16
- 16a. Terminal group of enlarged photophores on arms I to III present; inner web moderately developed, 17 to 30% of longest arm length *Histioteuthis atlantica*
(southern Subtropical Convergence and northern half of sub-Antarctic waters, circumglobal)
- 16b. Terminal group of enlarged photophores on arms absent; inner web vestigial to low, less than 8% of longest arm length *Histioteuthis reversa*
(north temperate Atlantic Ocean and fringing sub-Arctic waters, north subtropical, tropical; Mediterranean Sea)

^{2/} At present, females and immature males of *Histioteuthis hoylei* and *Histioteuthis arcturi* can be separated confidently only by geographic location.

***Histioteuthis* d'Orbigny, 1841**

Histioteuthis d'Orbigny, 1841, in Ferussac and d'Orbigny, 1834–1848, *Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères Vivants et Fossiles*, 1vi and 361pp., 144 pl. [xxxvii].

Type Species: *Histioteuthis bonnellii* (Férussac, 1834).

Frequent Synonyms: *Calliteuthis* Verrill, 1880b; *Histiopsis* Hoyle, 1885a; *Histiotauma* Robson, 1948; *Lolidona* Risso, 1854; *Meleagroteuthis* Pfeffer, 1900; *Stigmatoteuthis* Pfeffer, 1900.

Diagnostic Features: Following Voss *et al.* (1998a) *Histioteuthis* is the sole genus in the monotypic family Histioteuthidae. Consequently, the diagnostic characters are the same as those given for the family.

Remarks: Species of *Histioteuthis* are extremely important in the diets of many toothed whales and dolphins, as well as fishes, sharks, albatrosses, other sea birds and other squids. Frequently, however, the remains from the stomachs of predators can not be identified to species level, so the food items are identified only to the generic level.

Literature: (see Family Literature) Roper *et al.* (1984), Santos and Haimovici (2002), Okutani (2005).

Histioteuthis bonnellii* (Ferussac, 1834)*Species Group****Fig. 245**

Cranchia bonnellii Ferussac, 1834, *L'Institut, Journal General des Societes et Travaux Scientifiques de la France et de l'Etranger*, 2(77): 355. [355]. [Type locality: off Nice, Mediterranean Sea].

Frequent Synonyms: *Cranchia bonnellii* Ferussac, 1834; *C. bonnelliana* Ferussac, 1834; *Histioteuthis bonnelliana* d'Orbigny, 1835–1848; *H. rüppelli* Verany, 1846; *Lolidona euphosina* Risso, 1854; *Histioteuthis collinsi* Verrill, 1879; *H. bonnellii corpuscula* Clarke, 1980.

FAO Names: En – Umbrella squid; Fr – Loutène bonnet; Sp – Joyeluria membranosa.

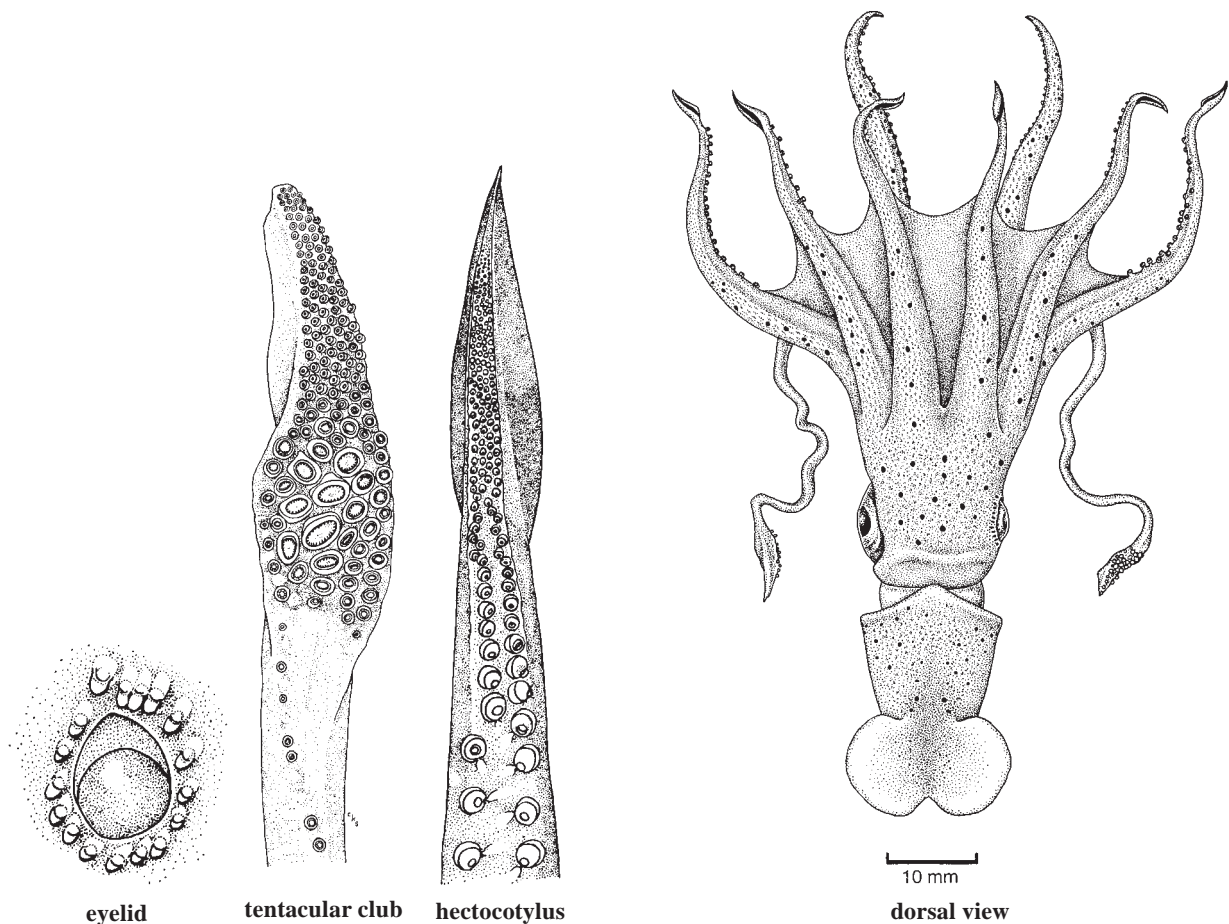
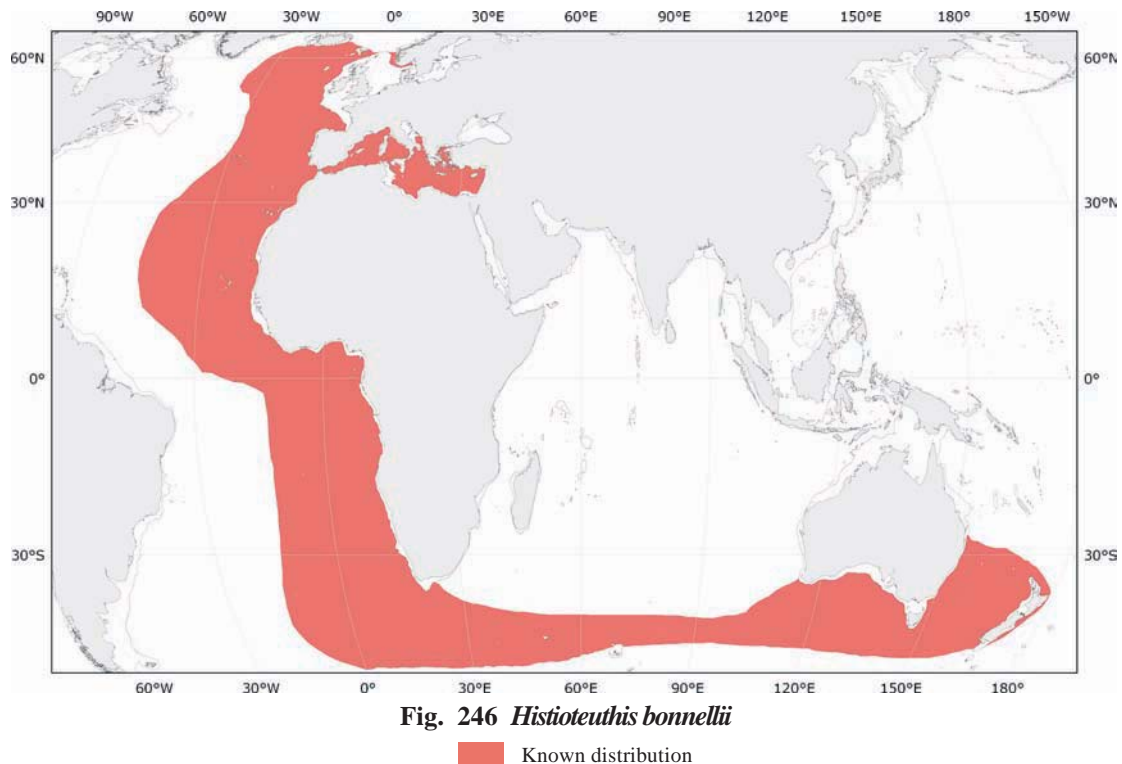


Fig. 245 *Histioteuthis bonnellii*

Diagnostic Features: Mantle conical, relatively short, broad, covered with dark, elongate compound photophores in 7 or 8 diagonal rows on ventral surface (lateral surfaces of mantle and ventral and lateral surfaces of head and arms also covered with these photophores). Fins oval, medium to large, length about 40 to 60% of mantle length, width about 70 to 90% of mantle length. **Head large, with 1 nuchal fold. Arms long, 130 to 300% of mantle length, connected with a very broad, deep, maroon-coloured web;** arm formula typically II=III>I=IV. A distinct, single, enlarged, elongate, dark, simple photophore on each arm tip (I to IV). **Buccal membrane 6-membered. Seventeen (rarely 16 or 18) small, oval photophores** around periphery of right eye-lid.

Size: This species attains a maximum mantle length of 330 mm, reported on a mature female from the sub-Arctic; males also reach about 330 mm mantle length.

Geographical Distribution: This species is very broadly distributed in the North Atlantic Ocean and Mediterranean Sea; from the eastern central North Atlantic Ocean and western Mediterranean, to the southeastern Atlantic Ocean and southwestern Pacific Ocean between Australia and New Zealand, and the southern Indian Ocean (Fig. 246).



Habitat and Biology: An oceanic species, *Histioteuthis bonnellii* is reported to occur usually in depths between 500 and 1 500 m, occasionally to over 2 000 m, sometimes associated with the bottom. Growth seems to be isometric and even juvenile specimens have the proportions of adults. Although they usually are taken singly or in pairs in sampling nets, it is suspected, from evidence in sperm whale stomachs and from very large midwater trawls, that it is a schooling species. Apart from sperm whales and other odontocetes, it is preyed upon by lancetfish (*Alepisaurus ferox*), scabardfish (*Aphanopus carbo*), albacore (*Thunnus alalunga*), swordfish (*Xiphias gladius*), blue shark (*Prionace glauca*).

Interest to Fisheries: The species is believed to have some fishery potential. Important prey for commercially exploited fish species.

Local Names: ITALY: Totano ingioiellato palmato.

Remarks: This is the largest *Histioteuthis* species.

Literature: Voss *et al.* (1992a), Tursi *et al.* (1994), Voss *et al.* (1998a), Lefkaditou *et al.* (1999), Quetglas *et al.* (2000), Okutani (2005), Lansdell and Young (2007).

Histioteuthis hoylei (Goodrich, 1896)

Species Group Fig. 247; Plate VII, 43

Histiopsis hoylei Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology*, 7(1): 1–24 [15]. [Type locality: Fonseca Bay, West coast of Central America].

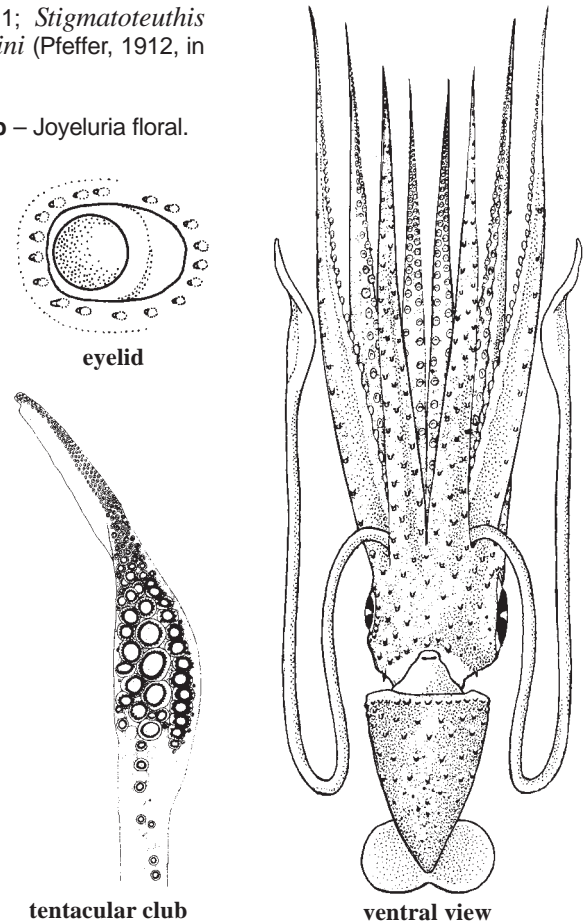
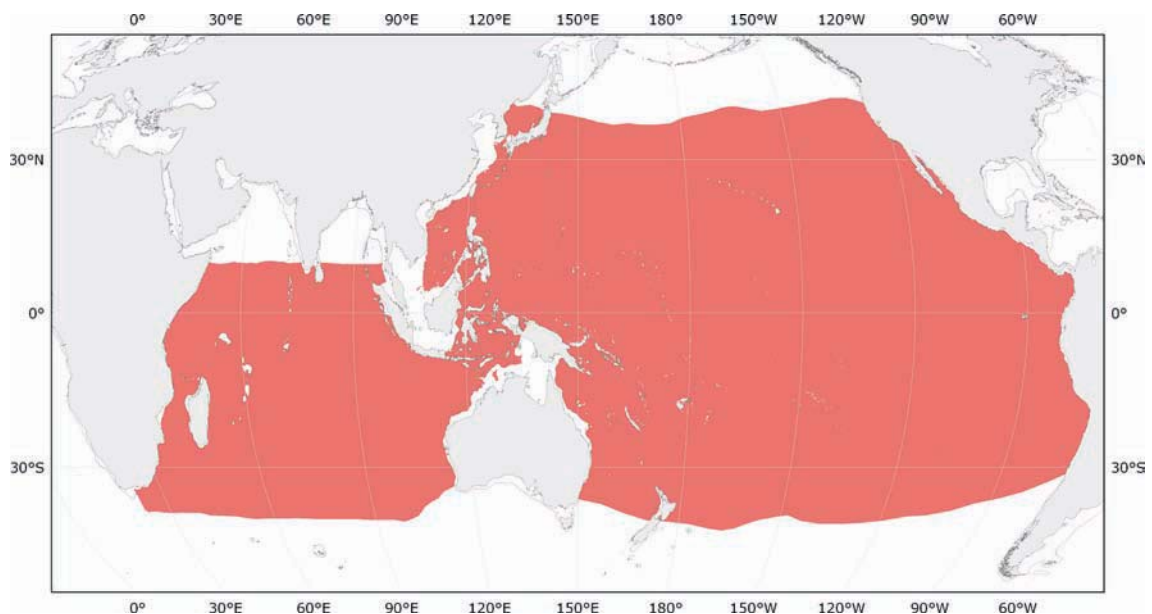
Frequent Synonyms: *Meleagroteuthis hoylei* Pfeffer, 1908a¹; *Stigmatoteuthis chuni* Pfeffer, 1912; *S. dofleini* Pfeffer, 1912; *Histioteuthis dofleini* (Pfeffer, 1912, in part).

FAO Names: En – Flowervase jewell squid; Fr – Loutène vase; Sp – Joyeluria floral.

Diagnostic Features: Males with paired genitalia. Mantle conical, relatively thick-walled, relatively short, moderately stout; skin of whole body (mantle, head, arms and basal half of fins) covered with thickly spaced, low, fleshy papillae, giving a rough, textured appearance; fins medium-sized, round, length about 30 to 40% of mantle length, width about 45 to 70% of mantle length. Head without nuchal folds. **Arms long, 160 to 250% of mantle length; mature males with arms I very elongate, greater than 400% of mantle length; no photophores on arm tips.** Ventral and lateral surfaces of mantle, head, arms covered with elongate, compound photophores; widely spaced on ventrum of mantle and arranged in about 6 diagonal rows; photophores progressively decrease in size on posterior two-thirds of mantle. Head large. Web between arms very low, indistinct. **Seventeen large photophores around right eyelid.** Dorsal pad of funnel organ with strong median ridge from apical papilla posteriorly along each lateral arm; expand posteriorly to form 2 broad flaps.

Size: The maximum mantle length attained in females is 240 mm in females, and to 210 mm in males.

Geographical Distribution: *Histioteuthis hoylei* (*dofleini*) is widely distributed in the tropical-subtropical waters of the Pacific Ocean between about 45°N and 45°S and in the Indian Ocean between about 10°N and the southern Subtropical Convergence (Fig. 248).

Fig. 247 *Histioteuthis hoylei*Fig. 248 *Histioteuthis hoylei*

Known distribution

Habitat and Biology: Off Hawaii, *Histioteuthis hoylei* occurs between depths of 100 and 850 m; in daytime it concentrates at 500 to 700 m (range 355 to 850 m) and at night it vertically migrates to depths of 100 to 500 m with 85% concentrated at 150 to 300 m. In the transitional waters of the northwestern North Pacific Ocean warm core rings and cold water this species is a non-migrant, remaining below 400 m. Analysis of stomach contents from sperm whales off Japan suggests that mature females occur in a dense aggregation adjacent to an isolated oceanic rise. This species is extremely important prey for sperm whales and other odontocete whales, including short-finned pilot whales and Hubb's beaked whale. Other predators include blue sharks in the western North Pacific Ocean. It is reported from the stomachs of swordfish of the west coast of Baja California, Mexico. Analysis of the dimorphic eyes suggests that the large left eye points upward and the small right eye points ventrolaterally when the animal is in its normal oblique, arms downward, position. This enables the squid in its daytime depth of 500 to 700 m, to use its large eye to utilize the dim daylight from above, while the small right eye perceives bioluminescent light from the side and below.

Interest to Fisheries: Undetermined. This species is an important prey for commercial species of fishes.

Local Names: JAPAN: Kuragedako.

Remarks: Voss *et al.* (1992), after the examination of the type of *Histiopsis hoylei* Goodrich, 1896, placed all specimens previously known as *Histioteuthis dofleini* in the synonymy of this earlier named species, as *H. hoylei* (Goodrich, 1896). Then Voss *et al.* (1998a), recognized that the Atlantic form was different and should be called *H. arcturi* (Robson, 1948). Young and Vecchione (2007b) consider members of the Histioteuthidae with paired secondary reproductive organs (penis, spermatophore gland complex, Needham's sac) distinctive and place them in a separate clade. Both *Histioteuthis hoylei* and *H. arcturi* are placed in this separate clade. The males that originally represented *H. hoylei* (Voss *et al.*, 1998a) came from north temperate waters off California and Japan. After the examination of material from off Hawaii, Young and Vecchione (2008i,j) consider the Pacific forms as divided into 2 different species, a temperate north Pacific one, for which they keep the name *H. dofleini* and a more southern species, *H. hoylei*. The same authors then consider the generic name *Stigmatoteuthis* Pfeffer 1900 as the valid designated genus name for this separate clade of histioteuthids (see Young and Vecchione, 2008h,i,j).

Literature: Okutani (1974a), Muntz (1976), Voss *et al.* (1992a, 1998a), Nesis (1994), Bower *et al.* (1999c), Okutani (2005), Watanabe *et al.* (2006b), Young and Vecchione (2007b, 2008h,i,j).

Histioteuthis miranda (Berry, 1918)

Species Group

Fig. 249

Calliteuthis miranda Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavor, 1909–1914*, 4(5): 201–298. [221]. [Type locality: 37°54'S, 178°56'E, western South Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Wondrous jewel squid; Fr – Loutènes bijou merveilleux; Sp – Joyeluria maravillosa.

Diagnostic Features: Mantle robust, moderately elongate; wall thick; **ridge of low tubercles extends along dorsal midline of mantle on anterior half, well developed in medium-sized and large juveniles, but hidden beneath mantle tissue in large subadults and adults.** Fins medium-sized, oblong, length about 31 to 44% of mantle length, width about 44 to 57% of mantle length. Head relatively large; 1 nuchal fold present in juveniles, absent in adults. Arms of moderate length, about 100 to 150% of mantle length; arm formula I=II=III>IV. Basal one-third to one-half of arms I to III with median row of low tubercles. Inner web connects basal 16 to 25% of arms I to III; outer web only slightly developed. **Buccal membrane 7-membered.** Tentacles long, 150 to 260% of mantle length. Tentacular club without longitudinal cleft on aboral surface. Suckers on manus closely packed in 6 or 7 series; median suckers enlarged twice the diameter of ventral marginal suckers. Compound photophores numerous, of nearly uniform medium size, moderately widely spaced, arranged in 9 or 10 diagonal

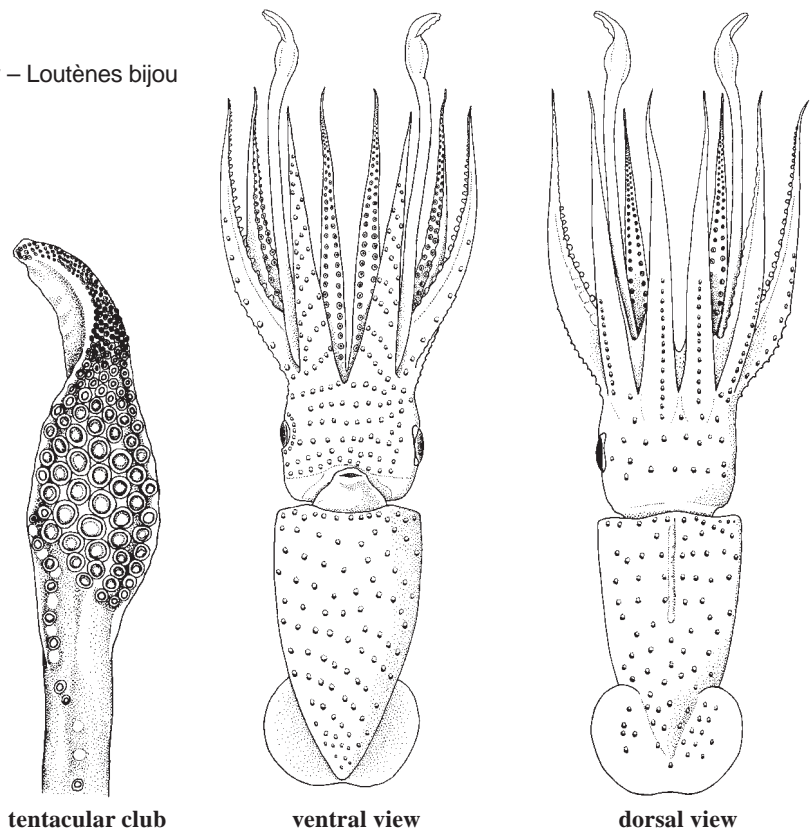


Fig. 249 *Histioteuthis miranda*

rows across ventral mantle; **16 or 17 (rarely 15) moderately large photophores encircle the right eye-lid**. Skin colour a dark grey-blue to purple.

Size: A large- to medium-sized squid. The maximum mantle length of mature females is 270 mm, of mature males is 260 mm.

Geographical Distribution: *Histioteuthis miranda* occurs in the Pacific and Indian Oceans but it is absent from the Atlantic Ocean, except off extreme southern South Africa in the Agulhas Current (about 33°S). It occurs in the Indian Ocean southern subtropical waters from southeastern South Africa eastward to Australian/New Zealand waters (Fig. 250).

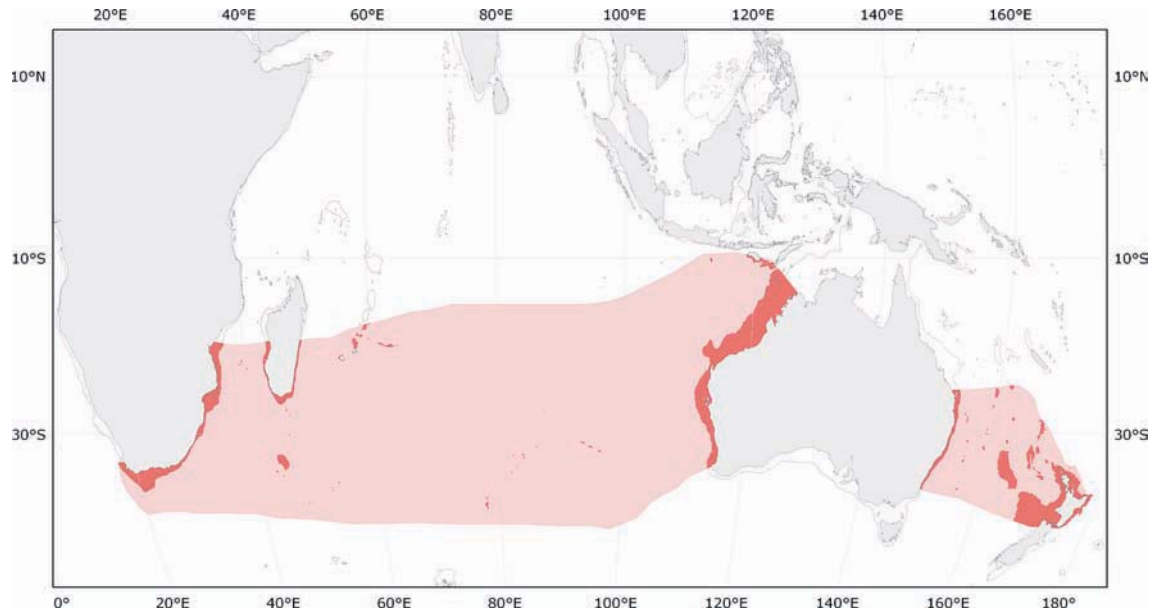


Fig. 250 *Histioteuthis miranda*

■ Known distribution ■ Probable presence

Habitat and Biology: This species occurs in close association with the slopes of continental masses and their offshore islands and submarine rises. Capture data suggest that this is the most abundant histioteuthid species encountered throughout most of its normal range. It occurs abundantly at 700 to 900 m off South Africa, where a large breeding population is located. It ranges from subsurface waters to at least 1 200 m; ontogenetic descent exists as larger subadults and adults generally are captured deeper than juveniles, 700 to 1 200 m on or close to the bottom; elsewhere subadults and mature males and females were taken both day and night at or near the bottom at 400 to 1 200 m. Many specimens of *H. miranda* have been caught frequently in deep-water, bottom-fishing, lobster trawls at 300 to 600 m off the North West Shelf of Australia and the Great Barrier Reef, suggesting an association with the sea floor at some time during their life cycle. This species is preyed upon by swordfish off eastern Australia and by pygmy sperm whale off New Zealand.

Interest to Fisheries: There is no direct interest to fisheries, but the species is important as prey of commercially harvested fishes.

Local Names: None available.

Literature: Clarke (1980), Roeleveld *et al.* (1992), Voss *et al.* (1998a), Dunning and Lu (1998), Okutani (2005).

Histioteuthis reversa (Verrill, 1880)

Species Group

Fig. 251

Calliteuthis reversa Verrill, 1880b, *American Journal of Science*, 20(41): 390–403 [393]. [Type locality: 39°53'N, 70°58'W, western North Atlantic Ocean].

Frequent Synonyms: *Stigmatoteuthis verrilli* Pfeffer, 1912; *Calliteuthis reversa mediterranea* Naef, 1921a; *C. r. atlantica* Grimpe, 1922; *C. elongata* Voss and Voss, 1962; *Histioteuthis elongata* (Voss and Voss, 1962).

FAO Names: **En** – Reverse jewell squid; **Fr** – Loutène retournée; **Sp** – Joyeluria invertida.

Diagnostic Features: Mantle **elongate to very elongate**, especially in **mature females**. Mantle **covered** (especially on ventral and lateral surfaces) **with intermixed large and small compound photophores**. Fins medium-sized, rounded; their length about 35 to 50% of mantle length, width about 40 to 60% of mantle length (proportionally smaller in mature females). Head large, wider than mantle (except in mature females). Usually 1 or 2 weak nuchal folds. Arms robust, no distinct photophores on tips; arms of moderate length, about 100 to 150% of mantle length; web between arms vestigial to low. **Eighteen photophores around right eyelid, 17 large and 1 small. Buccal membrane 7-membered.** Tentacles 100 to 200% of mantle length; club with deep longitudinal cleft on aboral surface of manus; manus suckers in about 6 diagonal series, markedly enlarged in median ventral series to 3 to 4 times diameter of ventral marginals.

Size: The maximum mantle length is 200 mm in mature females, smaller in males.

Geographical Distribution: *Histioteuthis reversa* is distributed in the Atlantic Ocean and Mediterranean Sea. It is confined to temperate, subtropical and tropical waters including the eastern and western Mediterranean Sea. It extends northward to the sub-Arctic in the Atlantic Ocean to at least 52°N and south into the eastern South Atlantic. Apparently it is excluded from the Gulf of Mexico, Caribbean Sea and South Atlantic Central water mass (Fig. 252).

Habitat and Biology: An oceanic species, *Histioteuthis reversa* is taken between the surface and 1 000 m depth with closing nets. Juveniles (up to 15 mm mantle length) occur in the upper 200 m both day and night; all juvenile/subadult sizes were captured in closing nets at 50 to 630 m during the day and 10 to 260 m at night. Consequently, a diel vertical migration is confirmed in this species, following the ontogenetic descent of post-paralarval juveniles. Both closing-net and open net captures, at daytime and night, of mature males and females in mid-water and near the bottom occurred at 500 to 1 000 m; this suggests that maturation immediately prior to spawning occurs in

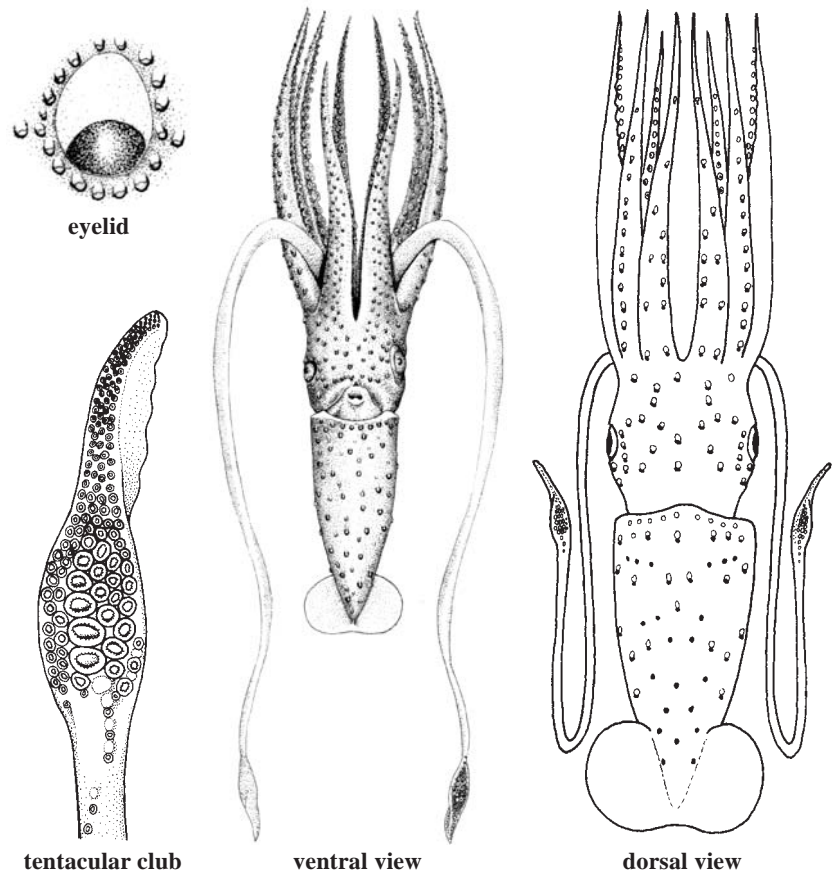


Fig. 251 *Histioteuthis reversa*

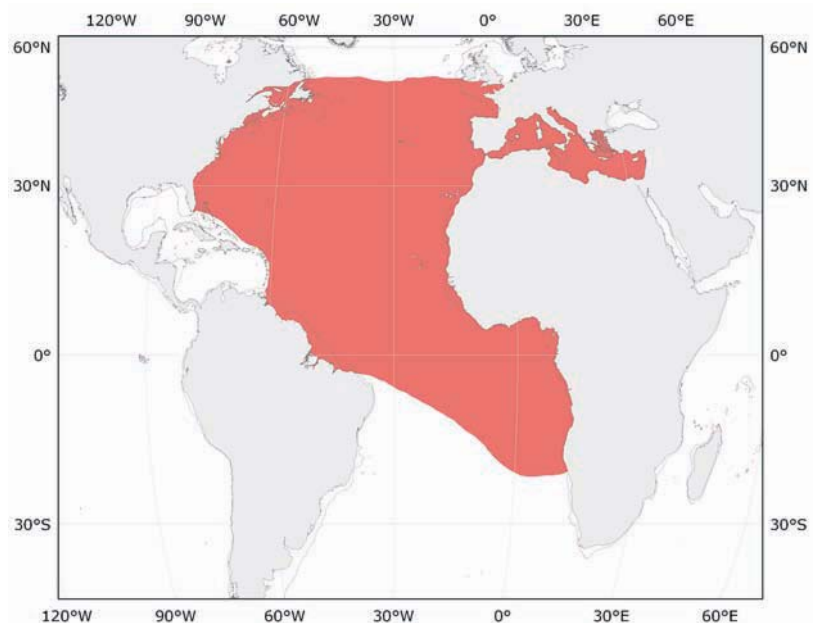


Fig. 252 *Histioteuthis reversa*

Known distribution

deep water. Captures of spent (spawning) dead or dying females at the surface suggest that females ascend through the water column to spawn in food-rich surface waters, then die. Specimens from the western North Atlantic were found to have concentrations of persistent organic pollutants and tributyltin, which has implications for trophic level transfer, e.g. to sperm whales and other toothed whales and pelagic predators. The species is preyed upon by sperm whales, pygmy sperm whales, northern bottlenose whales, Risso's dolphins, blue sharks and swordfish.

Interest to Fisheries: Currently no interest to fisheries exists, but this species is important prey for many exploited fish species.

Local Names: ITALY: Totano ingioiellato.

Literature: Voss (1969), Mangold (1974), Lu and Clarke (1975a,b), Voss *et al.* (1992a, 1998a), Lefkaditou *et al.* (1999), Giordano *et al.* (2001), Vecchione and Pohle (2002), Okutani (2005).

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

Note: The species listed here are presented in the order of their species group, as defined in Voss *et al.* (1998a), but arranged alphabetically.

Histioteuthis arcturi (Robson, 1948)

Stigmatoteuthis arcturi Robson, 1948, *Zoologica*, 33(3): 115–132. [122]. [Type locality: 26°54'N, 51°15'W, south Sargasso Sea, central North Atlantic Ocean, 0–3 000m].

Frequent Synonyms: *Histioteuthis dofleini* (Pfeffer, 1912).

Size: The maximum mantle length is 210 mm in females and 130 mm in males.

Geographical Distribution: *Histioteuthis arcturi* occurs in the Atlantic Ocean; it is tropical-subtropical between about 40°N and 30°S, to its southern limit just north of southern Subtropical Convergence. It is very abundant in the Gulf of Mexico, Gulf Stream, Sargasso Sea, central North Atlantic Ocean subtropical waters, the North African Subtropical Sea and sparsely distributed in the South Atlantic Ocean.

Habitat and Biology: Its vertical distribution extends from surface waters to depths below 1 000 m. Shallower living juveniles change to a diel vertical distribution pattern of 450 to 750 m during the day and between the surface and 400 m at night.

Remarks: *H. arcturi* has been reported in the literature as *H. reversa*, until the species was separated into the new combination by Voss *et al.* (1998a).

Literature: Nesis (1974a), Clarke and Lu (1974, 1975), Roper and Young (1975), Voss *et al.* (1998a).

Histioteuthis atlantica (Hoyle, 1885)

Histiopsis atlantica Hoyle, 1885a, *Annals and Magazine of Natural History*, (series 5) 16: 181–203. [201]. [Type locality: Messing [Würzburg Museum], Germany, and no locality [Leipzig Museum], fide Pfeffer (1912: 251)].

Frequent Synonyms: *Histioteuthis cookiana* Dell, 1951.

Size: The maximum mantle length reaches 260 mm in mature males and 150 mm in immature females.

Geographical Distribution: *Histioteuthis atlantica* is circumglobal in distribution between about 30°S to 33°S and 50°S, normally in the southern Subtropical Convergence, as well as in the fringes of the subtropical and the sub-Antarctic waters, over oceanic basins, plateaus and shelf areas.

Habitat and Biology: Maximum depth range about 40 to 2 000 m. Juveniles are taken in open nets at 100 to 200 m at night and at 500 to 1 000 m both day and night. Adults and subadults have been captured with open nets between 300 and 2 000 m at night and between 900 to 1 000 m during the day; subadults have been caught on the bottom at night between 700 to 850 m. It is prey of swordfish off eastern Australia.

Literature: Voss *et al.* (1992a), Rodhouse *et al.* (1992a), Voss *et al.* (1998a), Jackson *et al.* (2002), Okutani (2005).

***Histioteuthis celetaria celetaria* (Voss, 1960)**

Calliteuthis celetaria celetaria Voss, 1960, *Fieldiana, Zoology*, 39(40): 419–446. [424]. [Type locality: 32°10'N, 64°45'W, western North Atlantic Ocean [fide Voss (1969: 763)]; originally published incorrectly as 34°45'W].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 260 mm in mature females and 90 mm in mature males.

Geographical Distribution: *Histioteuthis celetaria celetaria* lives in the Atlantic Ocean in north subtropical and tropical waters and in the south subtropical region. It is absent from the Gulf of Mexico and the Caribbean Sea, between about 33°N and 19°S.

Habitat and Biology: The vertical distribution is not well established, because so few specimens are available; the species occurs from the upper 40 to 1 000 m.

Literature: Amelekhina *et al.* (1990), Voss *et al.* (1998a), Okutani (2005).

***Histioteuthis celetaria pacifica* (Voss, 1962)**

Calliteuthis celetaria pacifica Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 169–176. [174]. [Type locality: Dammi Island, between Jolo and Tawi Tawi, Philippine Islands].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 280 mm in mature males, and 230 mm in immature females.

Geographical Distribution: *Histioteuthis celetaria pacifica* occurs in the Pacific and Indian Oceans, primarily associated with tropical and equatorial waters. In Indian Ocean equatorial waters it extends from 8°N to 10°S and in the western part of the southern gyre to 35°S. In Indo-West Pacific Ocean it is very common along the northwest slope and shelf of Australia, northward through the Philippines.

Habitat and Biology: The species occurs throughout the Hawaiian Island chain eastward into the California Current. Most captures of this species are from on or near continental and island slopes and submarine rises. Juveniles occur in the upper 200 m but are capable of descending with growth to increasingly deeper depths, possibly to 1 000 m. Subadult and adult males have been found during day and night in midwaters and near bottom in shelf and slope waters at 250 to 1 000 m.

Literature: Nesis (1977c), Nateewathana (1995), Voss *et al.* (1998a), Okutani (2005).

***Histioteuthis corona berryi* Voss, 1969**

Histioteuthis corona berryi Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867 [781]. [Type locality: 29°17'N 125°41'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length recorded is 50 mm; all known specimens are juveniles.

Geographical Distribution: *Histioteuthis corona berryi* occurs exclusively in the eastern Pacific Ocean, between 26°N and 37°N, 115°W and 138°W in the California Current and the fringing waters to the westward.

Habitat and Biology: This may be a species that is more normally found in subtropical waters to the west of the California Current. Its vertical range is 300 to 800 m.

Literature: Jefferts (1983), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona cerasina Nesis, 1971

Plate VII, 41

Histioteuthis corona cerasina Nesis, 1971, *Zoologicheskij Zhurnal*, 50(10): 1463–1471. [1463]. [Type locality: 00°01'S, 84°59'W, eastern Central Pacific Ocean].

Frequent Synonyms: None.

Size: The species is known only from juveniles, the largest of which is 57 mm mantle length.

Geographical Distribution: *Histioteuthis corona cerasina* occurs in the eastern Pacific Ocean; it is concentrated in the equatorial waters and Peru-Chile Current between 00° and 24°S, 70°W and 85°W, but records indicate its extension to at least 155°W in equatorial waters.

Habitat and Biology: The species is caught in the open ocean and in the vicinity of submarine ridges and continental slopes. Open nets have caught early juveniles in the upper 300 m (to the surface) and late juveniles at 200 to 1 000 m at night and 500 to 1 500 m in the daytime.

Literature: Nesis (1971), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona corona (Voss and Voss, 1962)

Calliteuthis corona Voss and Voss, 1962, *Bulletin of Marine Science of the Gulf and Caribbean*, 12(2): 169–200. [191]. [Type locality: 29°10'N, 88°00'W, Gulf of Mexico, western Central Atlantic Ocean].

Frequent Synonyms: None.

Size: A maximum mantle length of 190 mm is reported in mature males and 170 mm in immature females.

Geographical Distribution: *Histioteuthis corona corona* is limited to the Atlantic Ocean exclusively. Principally it occurs from tropical and north subtropical waters in the Gulf of Mexico and Caribbean Sea and in the eastern Atlantic Ocean, in the tropical waters from the Azores, the Gulf of Guinea to well off South Africa; the Gulf Stream distributes it well into the northern and eastern Atlantic Ocean.

Habitat and Biology: The vertical distribution of this subspecies extends from the upper 100 m to in excess of 1 500 m.

Literature: Clarke and Lu (1974, 1975), Arkhipkin and Shchetinnikov (1989), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona inermis (Taki, 1964)

Calliteuthis inermis Taki, 1964, *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 5(2): 297–343 [297]. [Type locality: off Kambara, Suruga Bay, Japan].

Frequent Synonyms: None.

Size: This species is known only from juveniles, the largest of which is 53 mm mantle length.

Geographical Distribution: *Histioteuthis corona inermis* lives in the northwestern North Pacific Ocean off the east coast of Japan between 33°N and 35°N in Tosa, Suruga and Sagami Bays and off the Kii Peninsula.

Habitat and Biology: This species has been collected at depths of about 420 to 600 m. It is a non-vertical migrator at depths below 400 m where it is restricted to warm core ring waters in the northwestern North Pacific Ocean. It is prey of odontocete whales and blue sharks.

Literature: Okutani *et al.* (1987), Voss *et al.* (1998a), Okutani (2005), Watanabe *et al.* (2006b)

***Histioteuthis eltaninae* Voss, 1969**

Histioteuthis eltaninae Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867. [755]. [Type locality: 40°05'S, 149°55'W, South Pacific Ocean].

Frequent Synonyms: None.

Size: This small species attains a maximum mantle length of 110 mm.

Geographical Distribution: *Histioteuthis eltaninae* is circumglobal in sub-Antarctic waters. Its normal northern boundary is the southern Subtropical Convergence and its normal southern boundary is the Antarctic Polar Front; a few captures have been made around the Antarctic Peninsula and Scotia Sea. It also has been taken in the East Australian Current to about 33°S, and in the northeastern Tasman Sea.

Habitat and Biology: While the species occurs over oceanic basins, its greatest abundance occurs in the higher-productivity waters associated with submarine ridges and continental shelves. It occurs from the upper 100 m to in excess of 1 000 m, perhaps to 2 000 m. It is a dominant prey of southern elephant seals.

Literature: Nesis (1974a), Rodhouse *et al.* (1992a), Rodhouse and Piatkowski (1995), Voss *et al.* (1998a), Okutani (2005).

***Histioteuthis heteropsis* (Berry, 1913)**

Calliteuthis (Meleagroteuthis) heteropsis Berry, 1913a, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77. [75]. [Type locality: off Santa Barbara, California, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 90 mm in males and 130 mm in females.

Geographical Distribution: *Histioteuthis heteropsis* occurs in the eastern Pacific Ocean, including transitional waters of the California Current and the Chile-Peru Current. It is considered to be an eastern Pacific Ocean transitional species.

Habitat and Biology: The known vertical distribution of this species is derived from open nets off California and indicates daytime depths of 300 to 800 m with 62% of the specimens at 500 to 700 m. At night, 69% of the specimens were taken at 0 to 400 m, with a peak at 300 to 400 m. The species clearly undergoes a diel vertical migration of 300 to 400 m in extent. *Histioteuthis heteropsis* is prey for swordfish off northern Baja California and for hammerhead sharks in the southern part of the Gulf of California (24°N).

Literature: Young (1972a), Voss *et al.* (1998a), Seibel *et al.* (2004), Okutani (2005).

***Histioteuthis macrohista* Voss, 1969**

Histioteuthis macrohista Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867. [845]. [Type locality: 45°10'S, 160°10'E, Tasman Sea].

Frequent Synonyms: None.

Size: The maximum mantle length is 65 mm in females and 55 mm in males.

Geographical Distribution: *Histioteuthis macrohista* is broadly distributed in the Atlantic, Indian and western Pacific Oceans; it occurs primarily in fringing and transitional waters of the southern Subtropical Convergence between about 33°S and 47°S (where it is sympatric with *H. atlantica*). It is absent from the eastern Pacific waters.

Habitat and Biology: This species occurs close to continental slopes as well as oceanic basins. The vertical distribution of the species extends between the surface 100 m to over 1 000 m; both juveniles and subadults have been caught over the entire known vertical range at night, so a diel vertical migration is not confirmed. It is prey of swordfish off eastern Australia and pygmy sperm whales off New Zealand.

Literature: Lipinski and Turoboyski (1983), Roeleveld *et al.* (1992), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis meleagroteuthis (Chun, 1910)

Calliteuthis meleagroteuthis Chun, 1910, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition dem Dampfer Valdivia, 1898–1899*, 18: 1–401. [170]. [Type locality: 35°45'S, 176°20'E, western South Pacific Ocean].

Frequent Synonyms: *Meleagroteuthis separata* Sasaki, 1915b; *Histioteuthis bruuni* Voss, 1969.

Size: The maximum recorded mantle length is 114 mm in mature females and 102 mm in mature males.

Geographical Distribution: *Histioteuthis meleagroteuthis* has a circumglobal distribution in tropical and subtropical waters between approximately 35°N to 45°N and 45°S. The southern limit of occurrence is sharply defined by the southern Subtropical Convergence; the species does not normally inhabit the convergence transition waters. It is widespread in the tropical and subtropical Atlantic Ocean, but it does not occur in the Caribbean Sea or the Gulf of Mexico. It is a pan-Pacific Ocean species with many records concentrated in New Zealand and Australian warm waters, northward through the islands to southern Japan. Records in the Indian Ocean are scattered from about 65°E to the tip of South Africa.

Habitat and Biology: The species, throughout its range, appears to reach greatest abundance in the zones of higher productivity, particularly those waters associated with bottom slopes and submarine rises. The vertical distribution extends from the surface to in excess of 1 000 m. Closing nets have recorded juveniles at 210 to 300 m in daytime, with larger subadults at 610 to 700 m. At night juveniles were captured at 100 to 360 m. Open nets have captured specimens to 1 950 m in midwaters and to 1 250 m near the bottom. It is preyed upon by the deep sea shark, *Galeus melastomus* on the continental slope.

Literature: Okutani (1974a), Muntz (1976), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis oceani (Robson, 1948)

Histiothauma oceani Robson, 1948, *Zoologica*, 33(3): 115–132. [123]. [Type locality: 2°33'S, 89°44'W, eastern Central Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 70 mm, (possibly 100 mm). The species is known from only 19 specimens.

Geographical Distribution: *Histioteuthis oceani* occurs in the Pacific Ocean. It exhibits a broad equatorial distribution from the Galapagos Islands northward to the Hawaiian Islands, then westward to the Indo-West Pacific Ocean off New Guinea and the Philippines.

Habitat and Biology: The species occurs around islands, above submarine rises and in the open ocean.

Literature: Young (1978), Voss *et al.* (1998a), Okutani (2005).