Marine Flora and Fauna of the Eastern United States Mollusca: Cephalopoda

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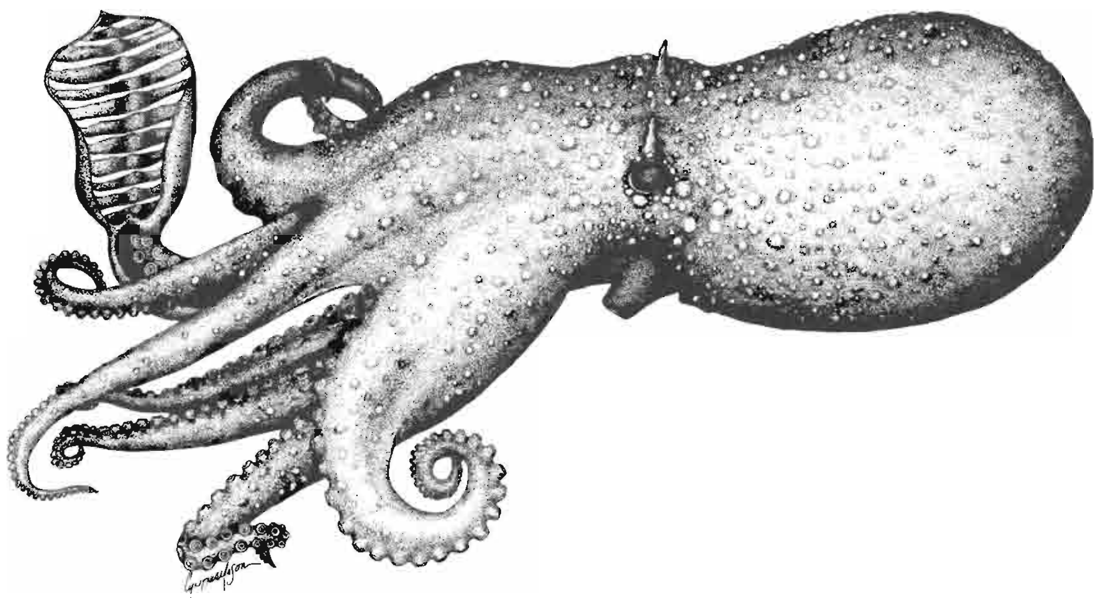

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U.S. DEPARTMENT OF COMMERCE
Robert Mosbacher, Secretary
National Oceanic and Atmospheric Administration
William E. Evans, Under Secretary for Oceans and Atmosphere
National Marine Fisheries Service
James Brennan, Assistant Administrator for Fisheries

Foreword

This NOAA Technical Report NMFS is part of the subseries ''Marine Flora and Fauna of the Eastern United States'' (formerly ''Marine Flora and Fauna of the Northeastern United States''), which consists of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the eastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation. These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used ''Keys to Marine Invertebrates of the Woods Hole Region,'' edited by R.I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the ''Marine Flora and Fauna of the Eastern United States'' is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but can vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The ''Marine Flora and Fauna of the Eastern United States'' is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

Manuals are available from the National Technical Information Service, United States Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161, either as a paper copy or microfiche, for a charge. Manuals are not copyrighted, and so can be photocopied from the NOAA Technical Report NMFS Circulars and Reports available in most major libraries and listed on p. 23 of this manual.

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Abstract

The cephalopods found in neritic waters of the northeastern United States include myopsid and oegopsid squids, sepiolid squids, and octopods. A key with diagnostic illustrations is provided to aid in identification of the eleven species common in the neritic waters between Cape Hatteras and Nova Scotia; included also is information on two oceanic species that occur over the continental shelf in this area and that can be confused with similar-looking neritic species. Other sections comprise a glossary of taxonomic characters used for identification of these species, an annotated systematic checklist, and checklists of the 89 other oceanic species and 18 Carolinian and subtropical neritic species that might occur occasionally off the northeastern United States.

'A pile of fresh squid lay on the deck, and the larger cod thinks very well of a little shiny piece of squid tentacle at the tip of a clam-baited hook. Next day they caught many fish, and met the "Carrie Pittman," to whom they shouted their luck, and she wanted to trade—seven cod for one fair-sized squid; but Disko would not agree at the price, and the "Carrie" dropped sullenly to leeward and anchored half a mile away, in hope of striking on to some for herself.'

Rudyard Kipling
Captains Courageous

Introduction

Cephalopods are very important, both to the marine ecosystem and to humans. They can be abundant predators that are large, active, and voracious; conversely, they are important as prey for many marine mammals, birds, and fishes, including economically important species. Substantial squid fisheries have existed in North America almost exclusively to provide bait for other fisheries. Cephalopods also are important as food for people in many parts of the world. Furthermore, they are important in biomedical research; much of what is known about neurophysiology results from experiments with the giant axon of squids, a contributing factor in the founding of the Marine Biological Laboratory at Woods Hole, Massachussetts.

The classification of recent taxa of the molluscan Class Cephalopoda (see Voss 1977) includes the squids (Order Teuthoidea), the octopods (Order Octopoda), and the cuttlefishes and sepiolid or bobtailed squids (Order Sepioidea), as well as the bizarre vampire squid in the monotypic Order Vampyromorpha and the chambered nautilus in the separate subclass Nautiloidea. Teuthoid squids are further distinguished based on whether their eyes are covered by a transparent cornea (Suborder Myopsida) or are exposed (Suborder Oegopsida). The fauna of the northeastern United States lacks nautiloids and true cuttlefishes but does include myopsid and oegopsid squids, octopods, and sepiolid squids; the vampyromorph *Vampyroteuthis infernalis* occurs in this geographic area but is limited to the deep waters of the bathypelagic realm.

Although the cephalopods of the northeastern United States have not been reviewed since the works of Verrill (1880, 1881), considerable collecting has been done in this region. Many species of cephalopods have been collected off the northeastern United States and can be divided into two ecological groups:

1) Species of the neritic zone with life histories restricted to obligate relationships with the comparatively shallow waters of the continental shelf (some of these species can also be found on the continental slope); and

2) oceanic species found primarily in open oceanic waters away from the shelf and slope (some of these species can also be found in shelf and slope waters).

We discuss here the cephalopod species commonly found in neritic waters of the northeastern United States. This work is based largely upon extensive collections of cephalopods deposited throughout the last century in the National Museum of Natural History (NMNH). These collections are a result of efforts by fishermen, individual researchers, institutional research programs, and government agencies. The old U.S. Commission of Fish and Fisheries and its descendents, the Bureau of Commercial Fisheries and, finally, the National Marine Fisheries Service (NMFS) have conducted comprehensive trawling along the northeastern United States for groundfish surveys, and cephalopods from these surveys have been deposited at the National Museum. The area of coverage for this paper extends from Cape Hatteras to Nova Scotia.

The scope of this presentation does not include the many oceanic species of squids and octopods normally found in deep waters beyond the continental slope, although any of these species could move inshore to the slope or shelf under conditions such as impingement of a Gulf-Stream eddy onto the shelf. Examination of the NMNH collections demonstrates, however, that a few oceanic species are sufficiently common in neritic waters and similar enough to neritic species to cause confusion. Therefore, two of these oceanic species are included in the key, but this is not intended to be a comprehensive guide to all oceanic species that can be transported into neritic waters by Gulf-Stream eddies or other mechanisms.

Cephalopod morphology changes substantially during growth. Some species hatch as planktonic ''paralarvae'' (Young and Harman 1988), and the greatest morphological changes occur during the transition between the paralarval and juvenile phases of the life cycle. Paralarval morphology and ecology have not been determined for many species (Okutani 1987, Vecchione 1987). Thus, the key is designed for identification of adults and advanced juveniles but does not apply to paralarvae and early juveniles.

Glossary

This glossary is derived from a more complete illustrated listing of taxonomic characters presented by Roper et al. (1984). Interested readers also should consult Roper and Voss (1983).

Anal flaps Pair of fleshy palps that arise at the sides of the anus in teuthoid and sepioid squids (Fig. 1).

Anterior Toward the head end or toward the arm tips.

Carpal knobs Small rounded protuberances on the carpus of the tentacular club to which carpal suckers from the opposite club adhere during the locking-together of the clubs.

Carpus Proximal zone of the tentacular club which often has small suckers and/or knobs (Fig. 2).

Cartilaginous tubercles Semi-rigid to rigid structures in the skin of certain squids; can be overlapping and scale-like, or simple to multifaceted knobs or papillae.

Cirri Fleshy erectile protuberances of the skin, usually elongate and finger-like (Fig. 3).

Corneal membrane Thin, transparent skin that covers the eyes of myopsid and sepioid squids and octopods (Fig. 2).

Dactylus Distal, terminal zone of the tentacular club, often characterized by comparatively small suckers (Fig. 2).

Dorsal Uppermost surface, opposite the ventral surface where the funnel is located.

Fin angle Angle between the longitudinal axis of the mantle and the posterior border of one fin (Fig. 4).

Fins Pair of muscular flaps that arise along the dorsolateral surface of the mantle, usually in its posterior half (Fig. 2).

Foveola Transverse membranous fold of skin that forms a pocket in the funnel groove of some oegopsid squids (Fig. 5).

Funnel Ventral tube through which water is expelled from the mantle cavity (Fig. 2).

Funnel organ Glandular structures on the internal dorsal and ventral surfaces of the funnel (Fig. 6).

Gladius Feather- or rod-shaped chitinous supporting structure in the dorsal mantle of squids (Fig. 7).

Hectocotylus One or more arms in males of some cephalopod species, modified for transferring spermatophores to the female; modifications can involve the suckers, sucker stalks, protective membranes, and/or trabeculae (Fig. 8).

Hooks Chitinous claw-like structures derived from the suckers on the arms and/or tentacles of some oegopsid squids (Fig. 2).

Light organ Simple or complex structure that produces bioluminescence (also termed photophore).

Ligula Spatulate, or spoon-shaped, terminal structure of the hectocotylus of octopods (Fig. 9).

Mantle Tubular or sac-like muscular body of cephalopods (Fig. 2).

Mantle length Standard measure of size, is abbreviated ML (Fig. 10).

Posterior Toward the closed end of the mantle, away from the head and arms.

Rachis Thickened central axis that usually extends the entire length of the gladius. The free rachis is the portion that does not support vanes (Fig. 7).

Side pockets Structures formed by small membranous folds of integument lateral to the foveola in the funnel groove of some oegopsids (Fig. 5).

Suckers Muscular suction-cups on the arms and tentacles and occasionally on the the membrane around the mouth. Suckers of squids are mounted on thin muscular stalks and include chitinous rings with teeth (Fig. 11).

Tentacles Elongate pair of appendages located between the ventral and ventrolateral arms (Arms III and IV) of squids and cuttlefishes (Fig. 2); with a proximal stalk usually devoid of suckers or hooks, and with a distal club armed with suckers and occasionally hooks.

Tentacular club Terminal, usually expanded, portion of tentacle, armed with suckers or, in some groups, with suckers and/or hooks (Fig. 11).

Trabeculae Muscular rods that support the protective membranes on the arms and tentacular clubs; occasionally the membranes are reduced and trabeculae are elongated so they project beyond the edge of the membrane as papillae (Fig. 8).

Vane Thin lateral expansion of the gladius that arises from the rachis (Fig. 7).

Ventral Lower surface of the animal; side on which the funnel is located.

Water pores Small orifices in the integument at the bases of some arms on some pelagic octopods (Fig. 12).

Web Membrane that extends between the arms of many octopods and sepiolid squids (Fig. 13).

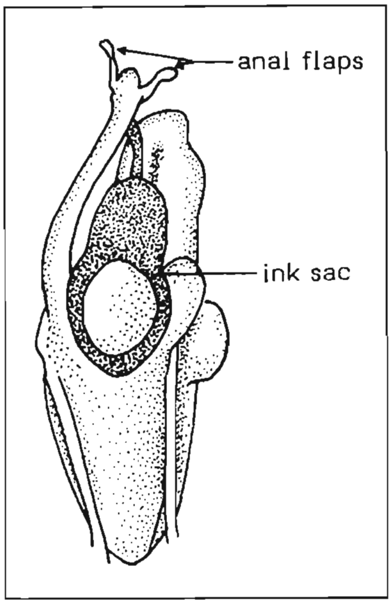

Figure 1
Ventral aspect of a squid visceral mass (schematic).

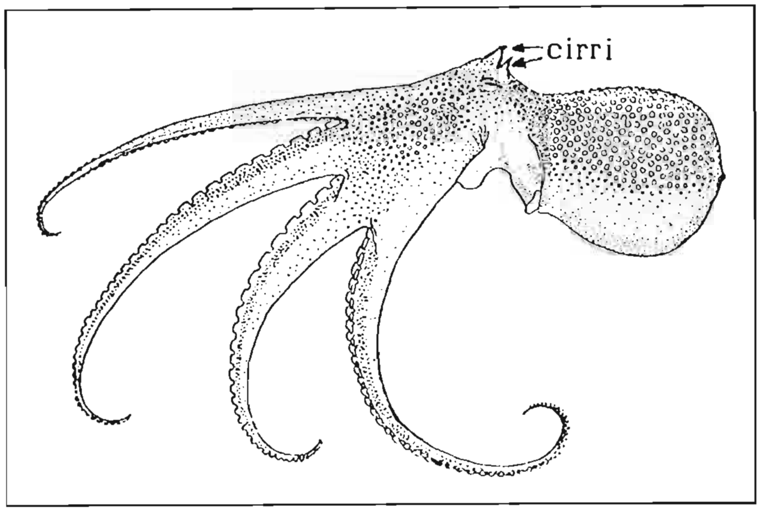

Figure 3
Lateral aspect of an octopod.

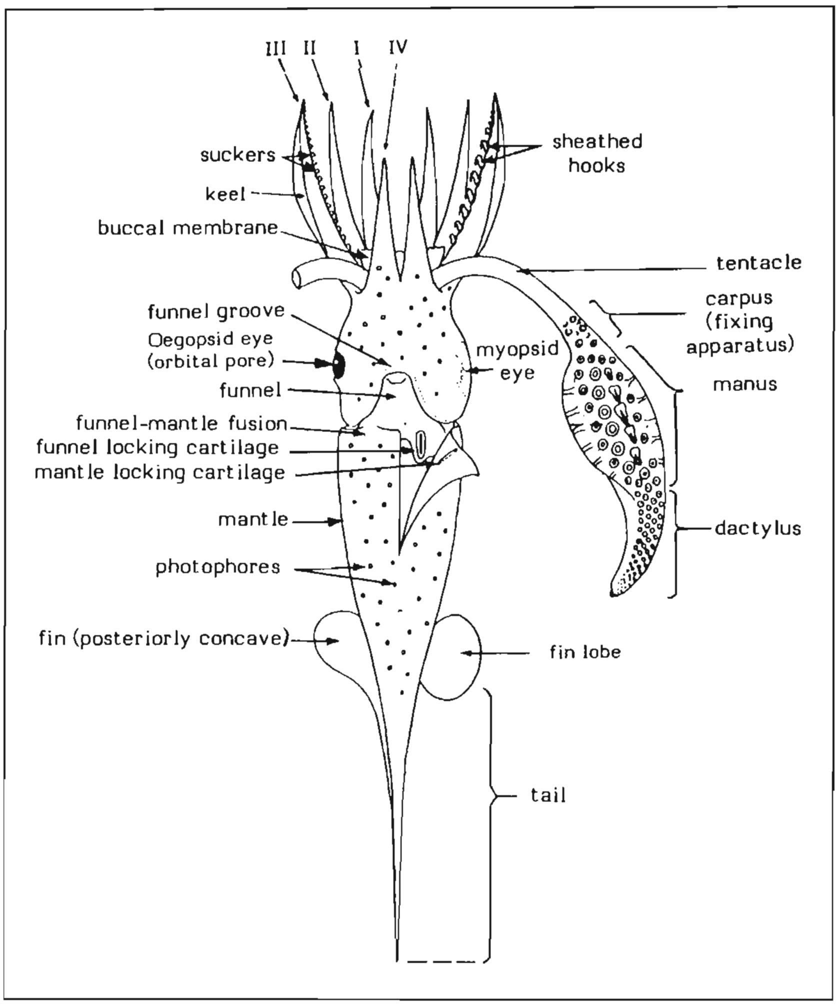

Figure 2
Composite diagram illustrating basic squid features, ventral aspect.

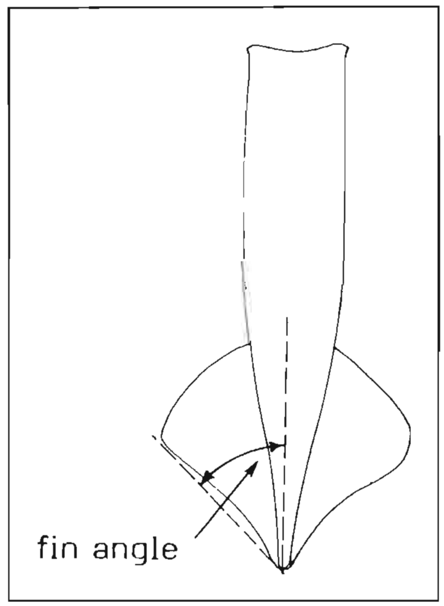

Figure 4
Measurement of fin angle.

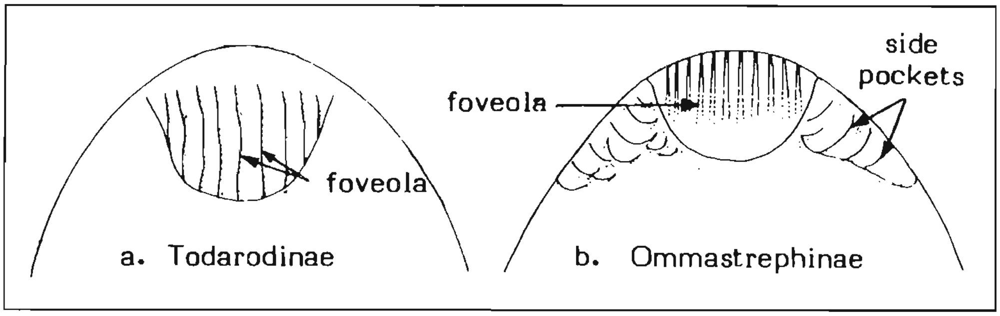

Figure 5
Funnel grooves of some Ommastrephidae.

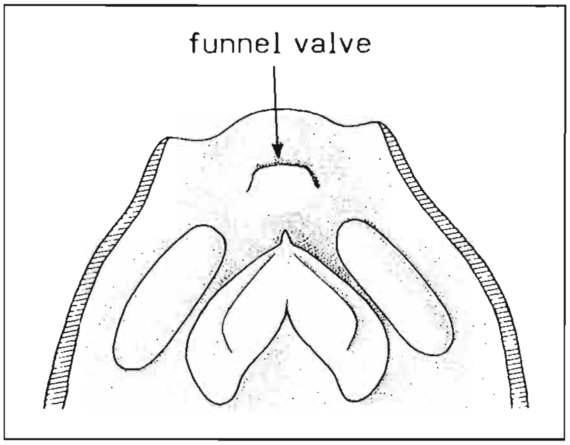

Figure 6
Interior of funnel, opened to show funnel organ.

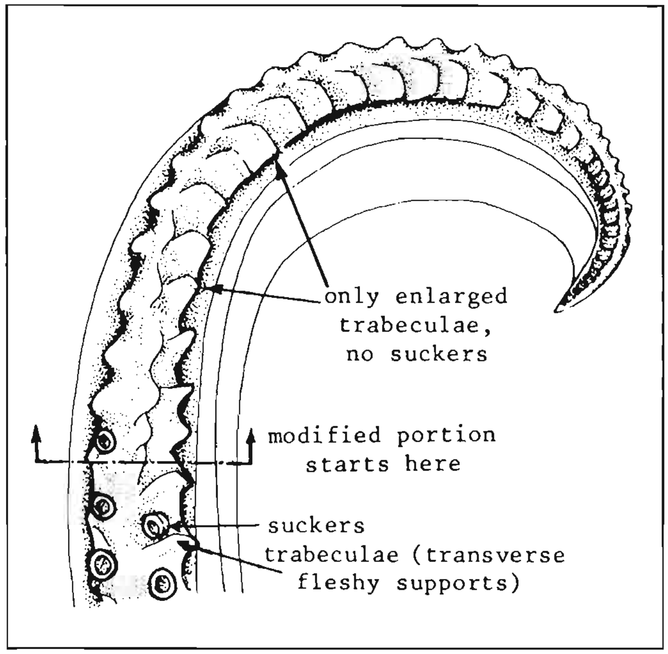

Figure 8
Hectocotylized arm of a squid.

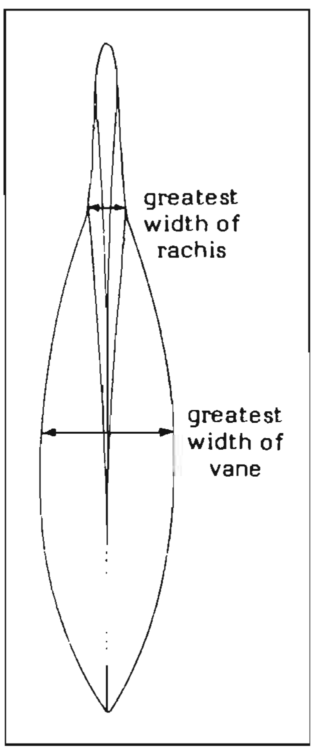

Figure 7
Gladius, showing measurement of rachis and vane.

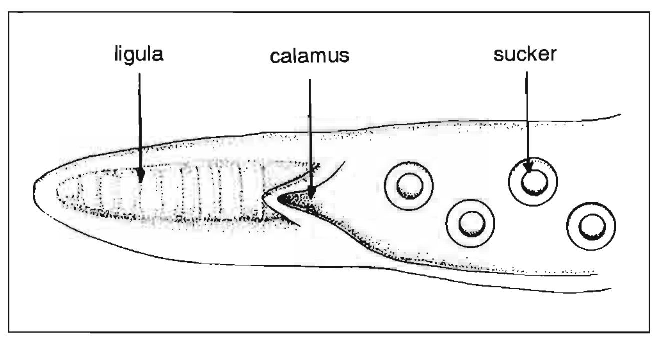

Figure 9
Hectocotylized arm of an octopod.

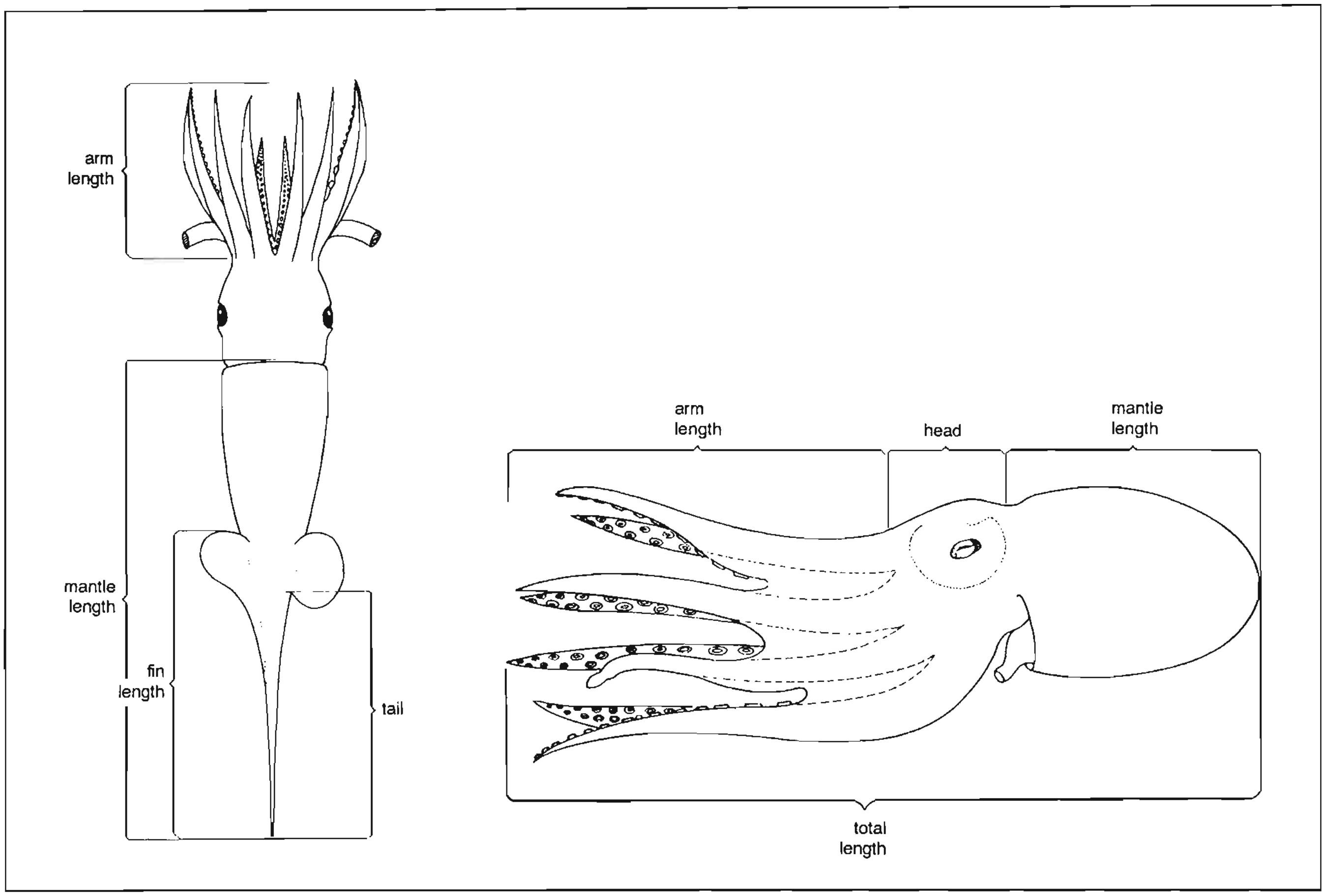

Figure 10
Some standard measurements on cephalopods. Squid (left); octopod (right).

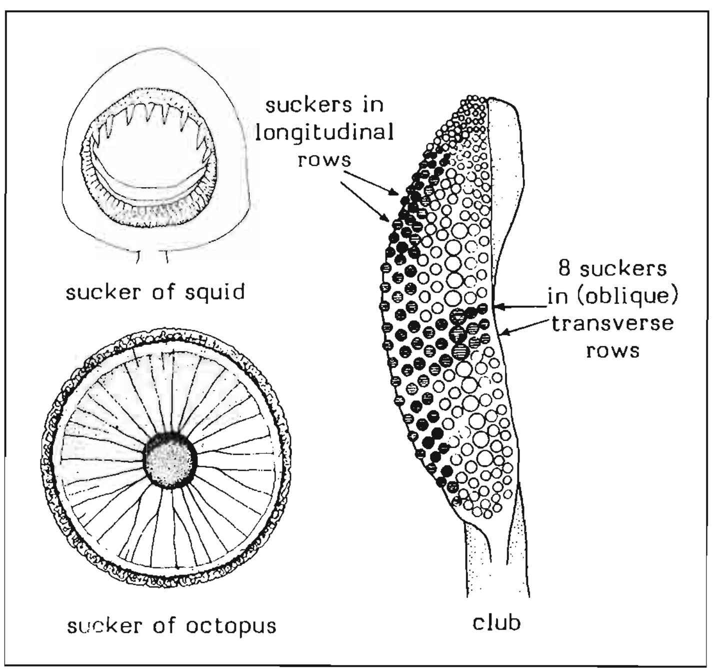

Figure 11
Suckers and configuration of suckers (schematic) on tentacular club.

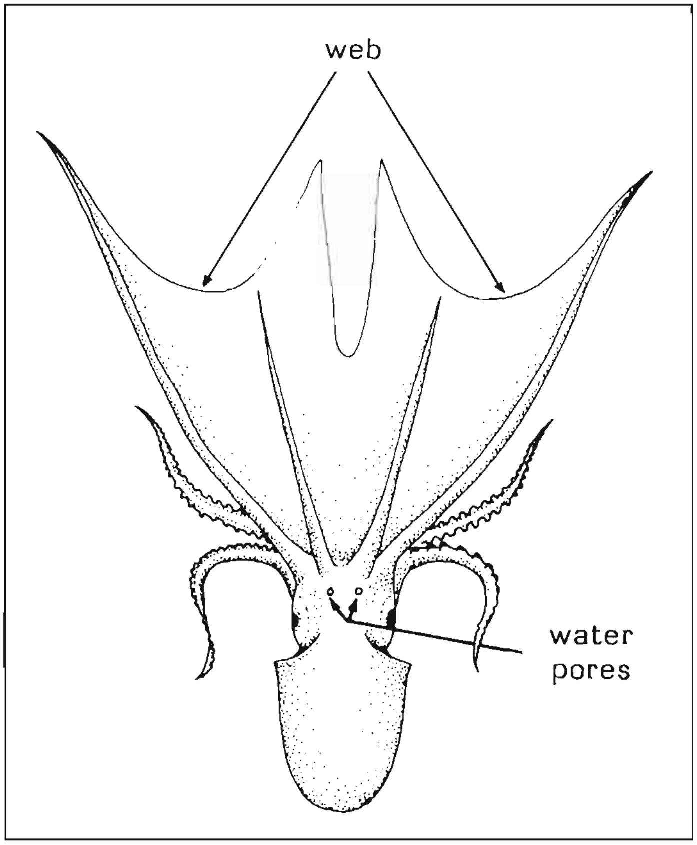

Figure 12
The pelagic octopod *Tremoctopus*.

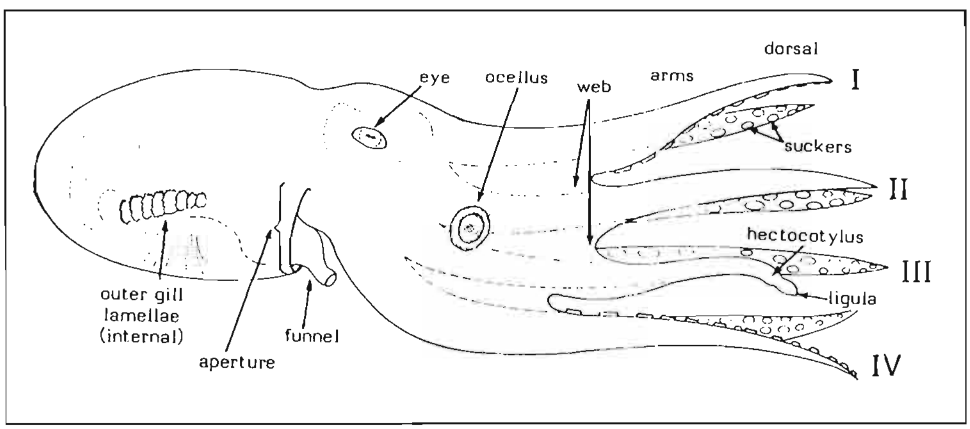

Figure 13
Schematic lateral aspect of octopod features.

Key to neritic cephalopods of the northeastern United States

1 Suckers with narrow stalks and with chitinous rings that might be modified into hooks; usually ten circumoral appendages comprised of eight arms and two tentacles (tentacles, however, can be lost during development)—squids and sepioids 4

1 Suckers without stalks and without chitinous rings or hooks; eight circumoral appendages (arms only)—octopods 2

2(1) Any of the following characters present: fins; body gelatinous; water pores located on ventral surface of head at base of arms; broad membranous flaps on dorsal arms; left third arm coiled in sac below eye . . . . **oceanic octopods**

2(1) None of the characters listed above 3

3(2) Ink sac absent in adults; arms short; suckers small; a large cirrus located dorsal to each eye; right arm III of males hectocotylized with huge, broad, spade-shaped ligula with prominent transverse ridges . . . . ***Bathypolypus arcticus*** **(Fig. 14)**

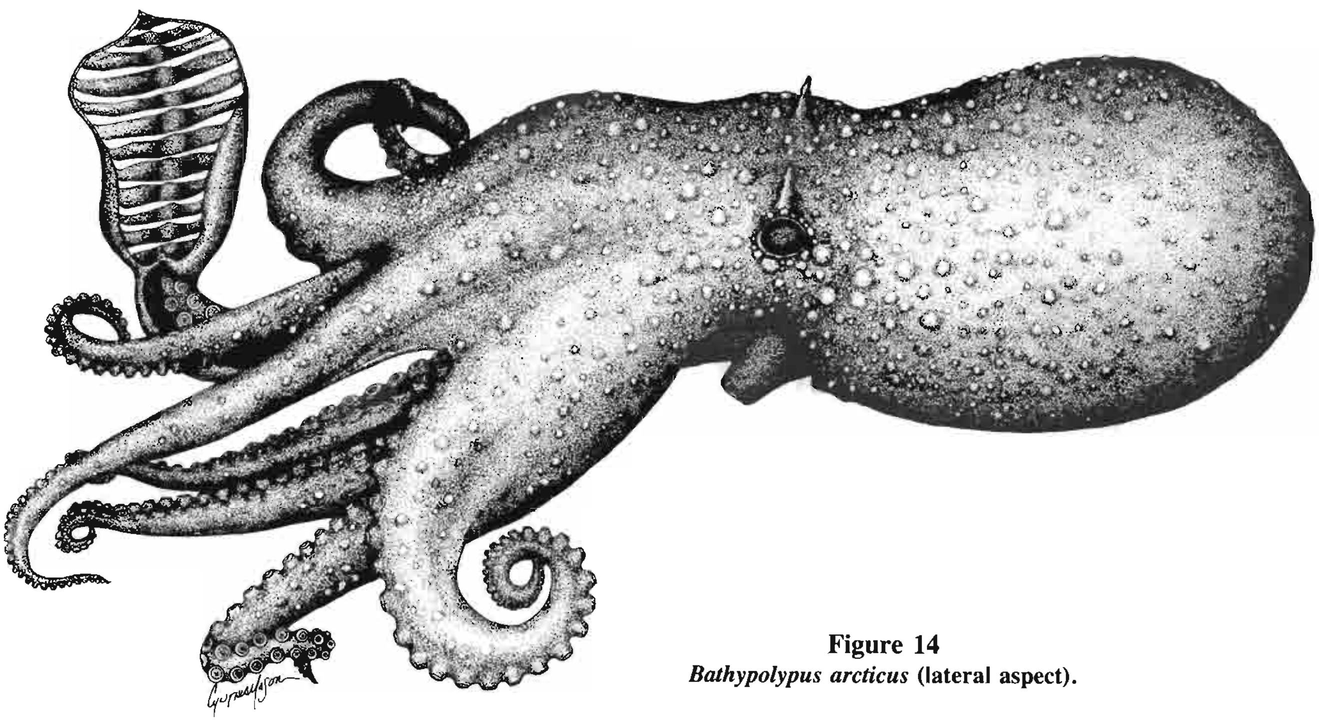

Figure 14
Bathypolypus arcticus **(lateral aspect).**

3(2) Ink sac present; arms moderately long; suckers large; cirri above eyes small or absent; ligula of hectocotylized right arm III of males very small . . . . ***Octopus vulgaris*** **(Fig. 15)**

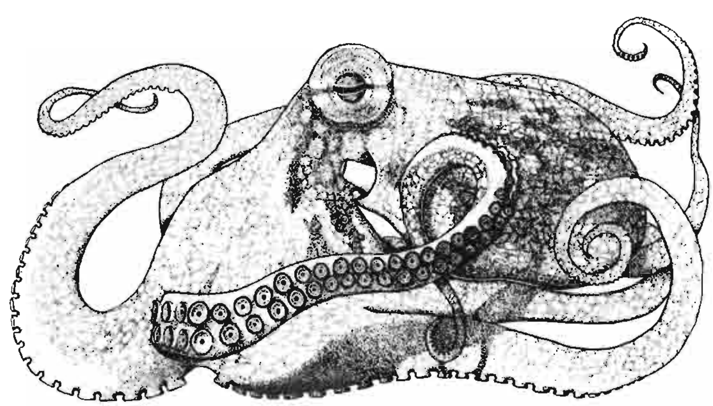

Figure 15
Octopus vulgaris **(lateral aspect).**

4(1) Any of the following characters present: suckers modified into hooks; numerous conspicuous light organs on surface of mantle, head, arms, or tentacles; tissues gelatinous; mantle surface with cartilaginous tubercles .... **oceanic squids**

4(1) None of the characters listed above **5**

5(4) Fins extend to posterior tip of mantle, joined or nearly joined posteriorly **9**

5(4) Fins do not extend to posterior tip of mantle, broadly separate posteriorly **6**

6(5) Mantle fused with head dorsally; all arms except ventral pair united by broad web; ventral mantle broadly flattened into dark shield-like structure .... ***Stoloteuthis leucoptera* (Fig. 16)**

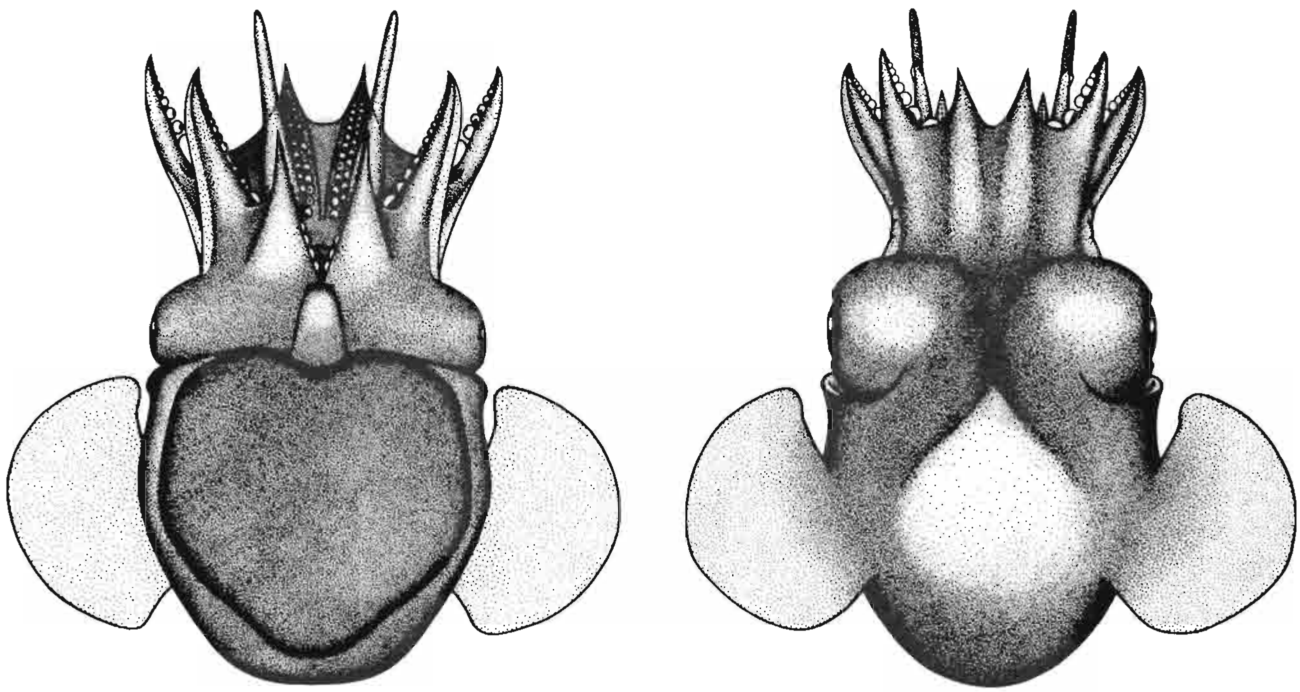

Figure 16
***Stoloteuthis leucoptera*. Ventral aspect (left); dorsal aspect (right).**

6(5) Mantle free from head dorsally; only arms III and IV united by a web; mantle rounded ventrally **7**

7(6) Light organs present on ink sac . . . . *Semirossia tenera* **(Fig. 17)**

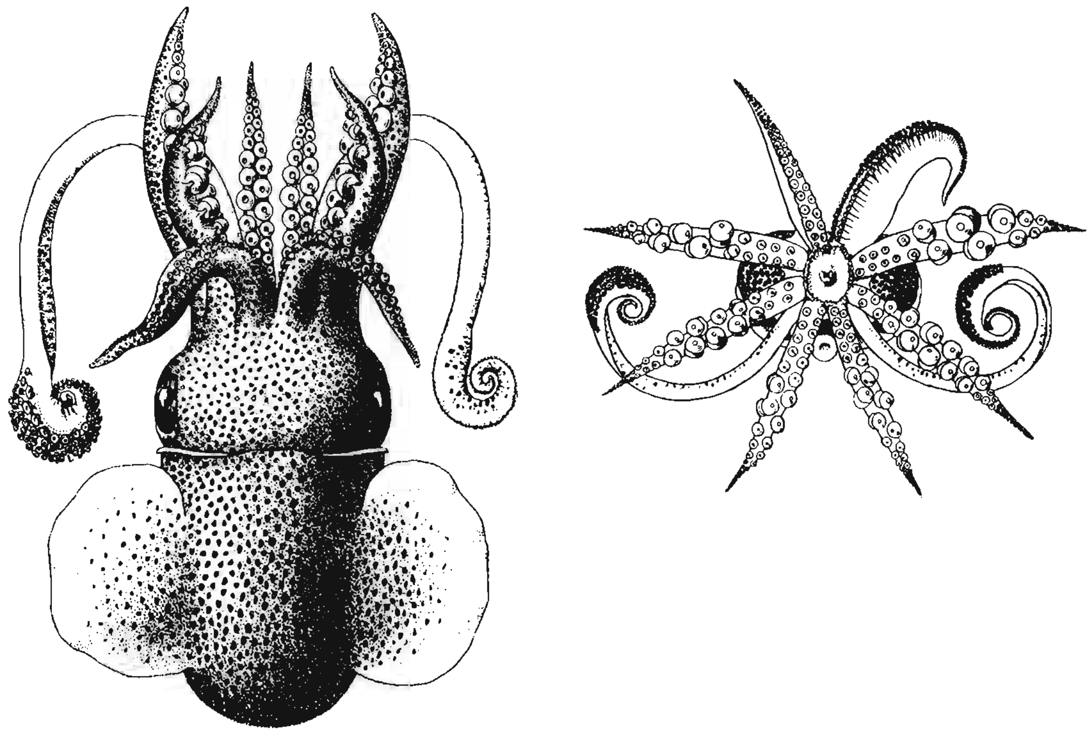

Figure 17
***Semirossia tenera*. Dorsal aspect (left); oral aspect of male (right).**

7(6) No light organs on ink sac **8**

8(7) Dorsal pad of funnel organ short, without posterior extensions; anal flaps large, with expanded blades **(Fig.18 left)** . . . . *Rossia palpebrosa* **(Fig. 19)**

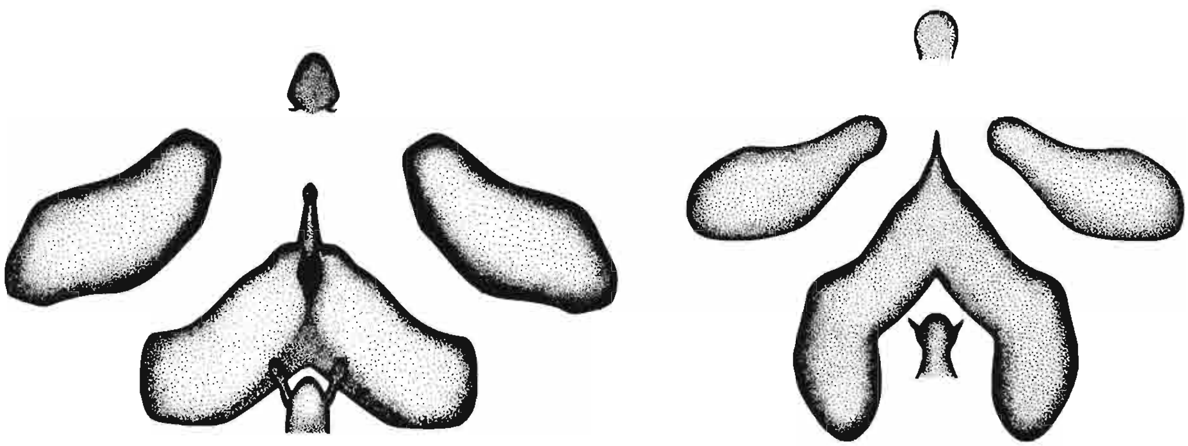

Figure 18
Anal palps, funnel organs, and funnel valves. *Rossia palpebrosa* (left); *Rossia megaptera* (right).

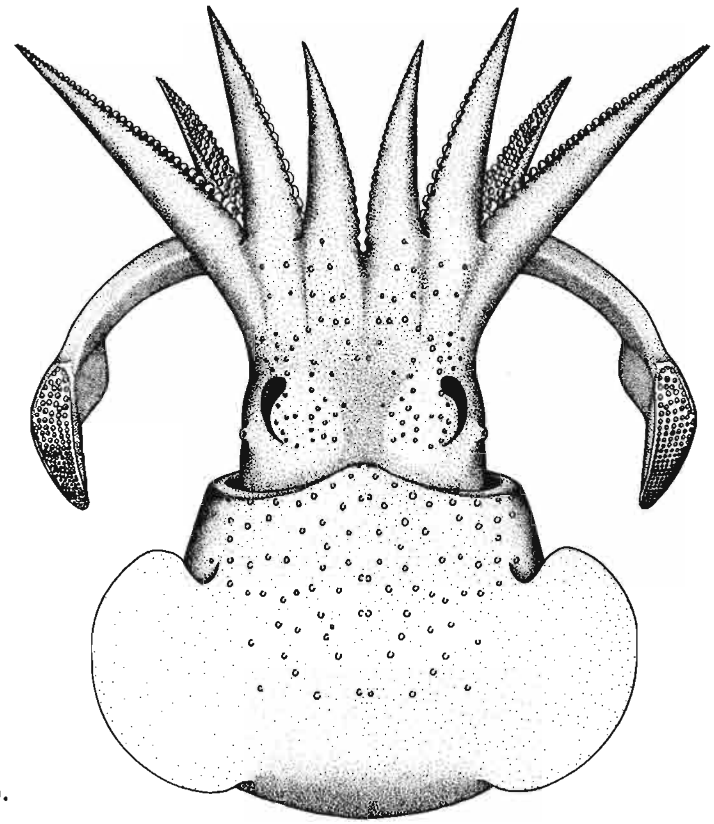

Figure 19
Rossia palpebrosa **(dorsal aspect).**

8(7) Dorsal pad of funnel organ long, with angles and posterior extensions on both sides; anal flaps small, without expanded blades **(Fig. 18 right)** . . . . ***Rossia megaptera*** **(Fig. 20)**

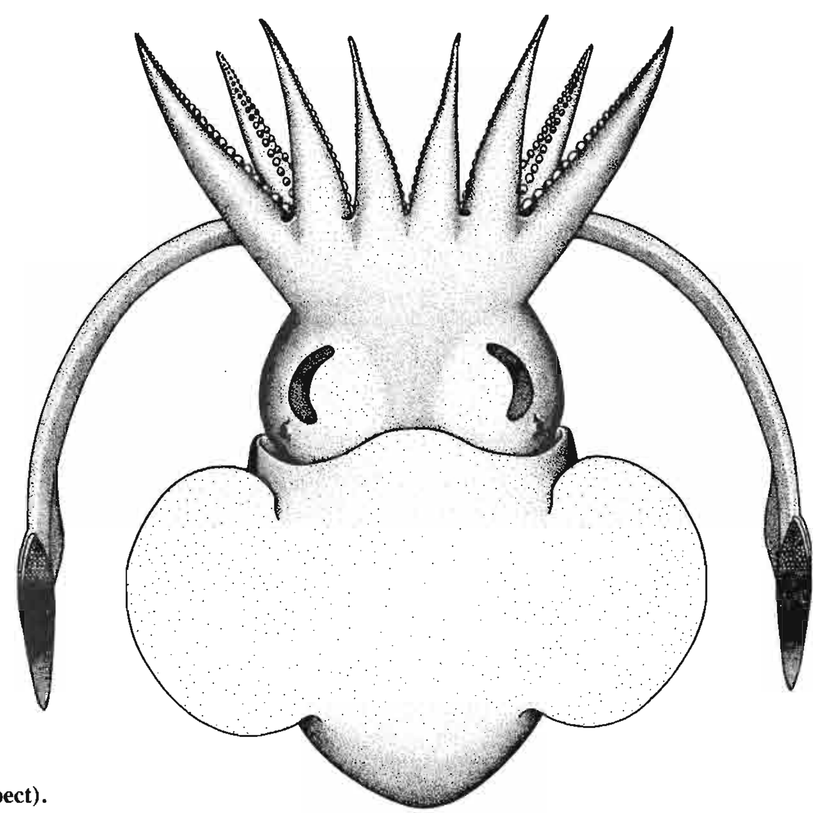

Figure 20
Rossia megaptera **(dorsal aspect).**

9(5) Eye covered by a cornea **10**

9(5) Eye without a cornea **12**

10(9) Fins in adults wider than long .... ***Lolliguncula brevis* (Fig. 21)**

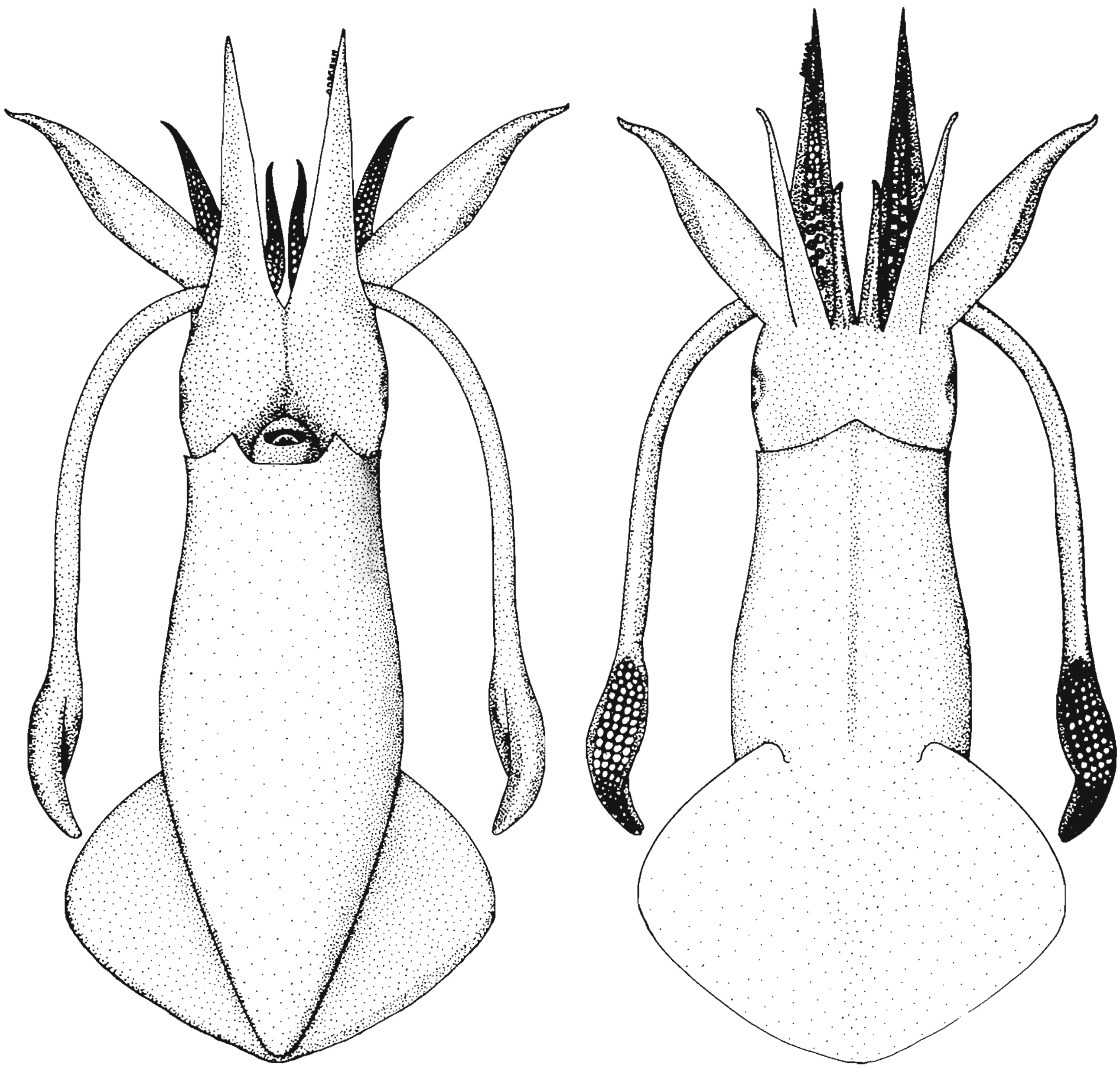

Figure 21
***Lolliguncula brevis*. Ventral aspect (left); dorsal aspect (right).**

10(9) Fins in adults as long as or longer than wide **11**

11(10) Ratio of greatest width of gladius vane to greatest width of free rachis is 2.4-3.7 **(Fig. 22)**; lateral margin of gladius vane usually thin although sometimes slightly darkened in preserved specimens; modified suckers in hectocotylized left ventral arm of males do not extend to arm tip . . . . ***Loligo pealei* (Fig. 23)**

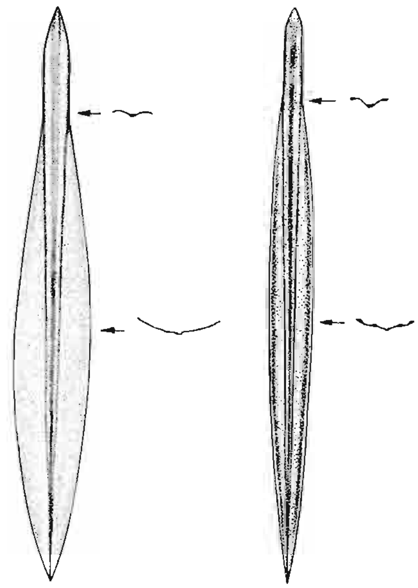

Figure 22
Gladii. *Loligo pealei* (left); *Loligo plei* (right).

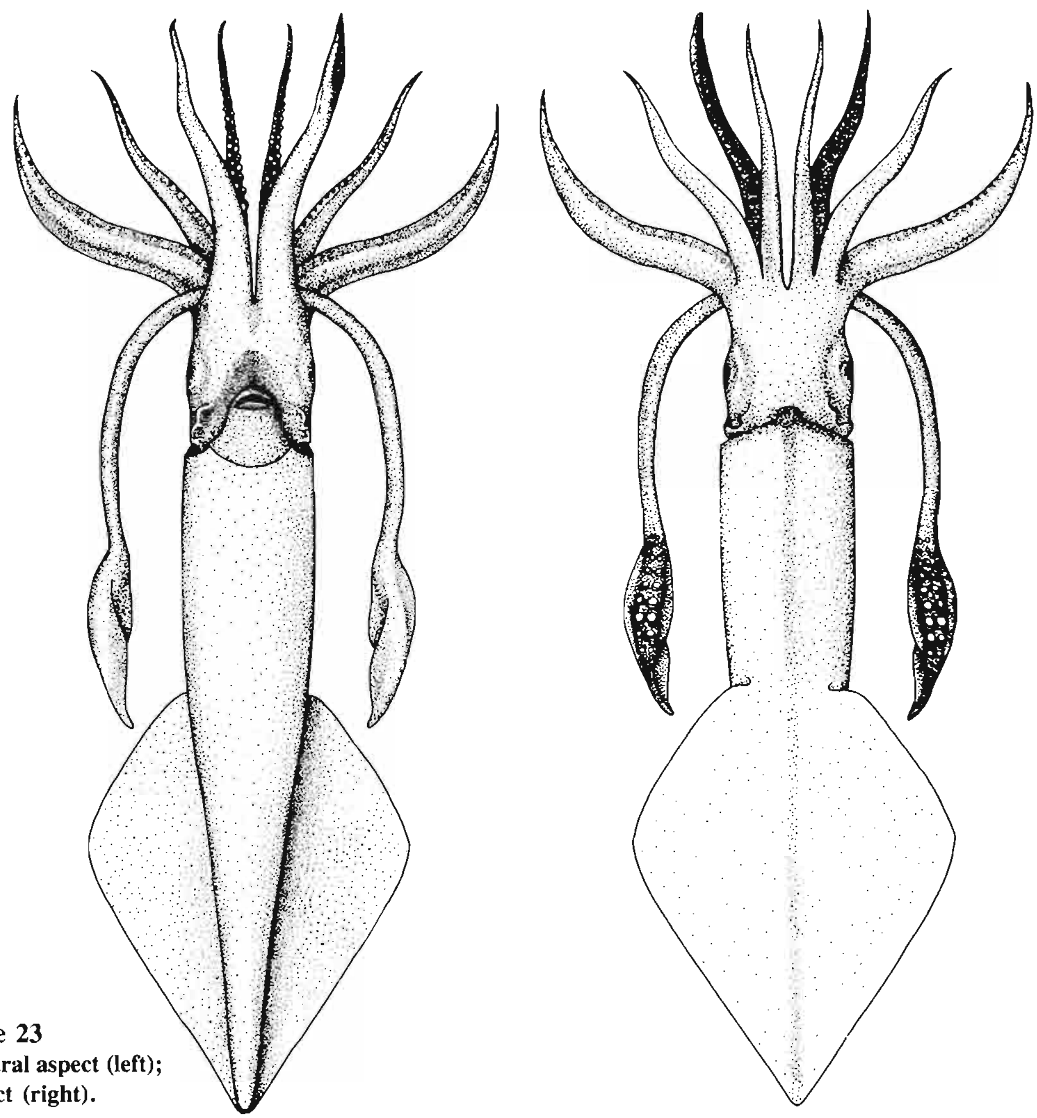

Figure 23
***Loligo pealei*. Ventral aspect (left); dorsal aspect (right).**

11(10) Ratio of greatest width of gladius vane to greatest width of gladius free rachis is 1.5-2.4; lateral margin of gladius vane usually thickened; modified suckers in hectocotylized left ventral arm of males extend to arm tip . . . . . . ***Loligo plei*** **(Fig. 24)**

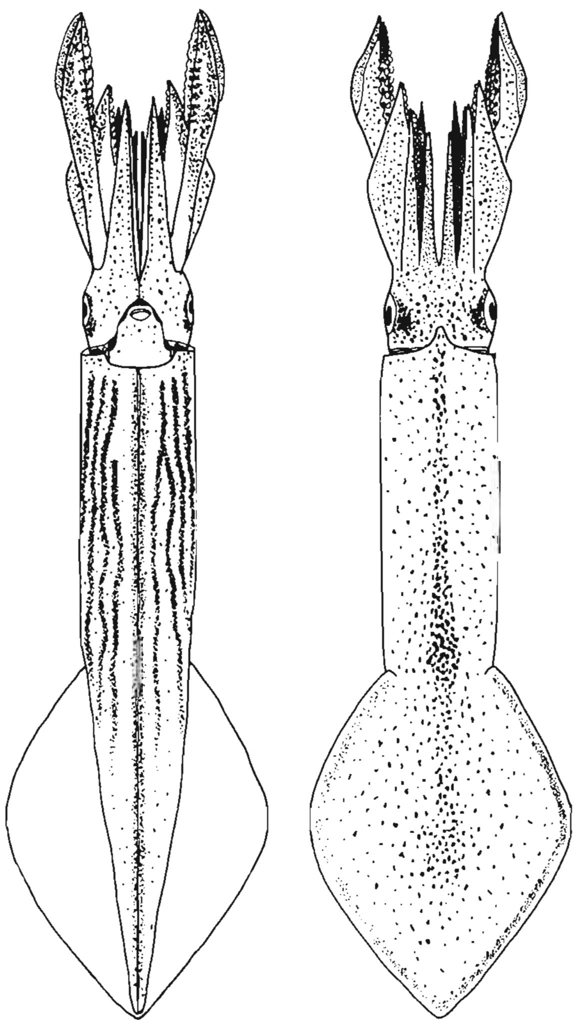

Figure 24
***Loligo plei*. Ventral aspect (left); dorsal aspect (right).**

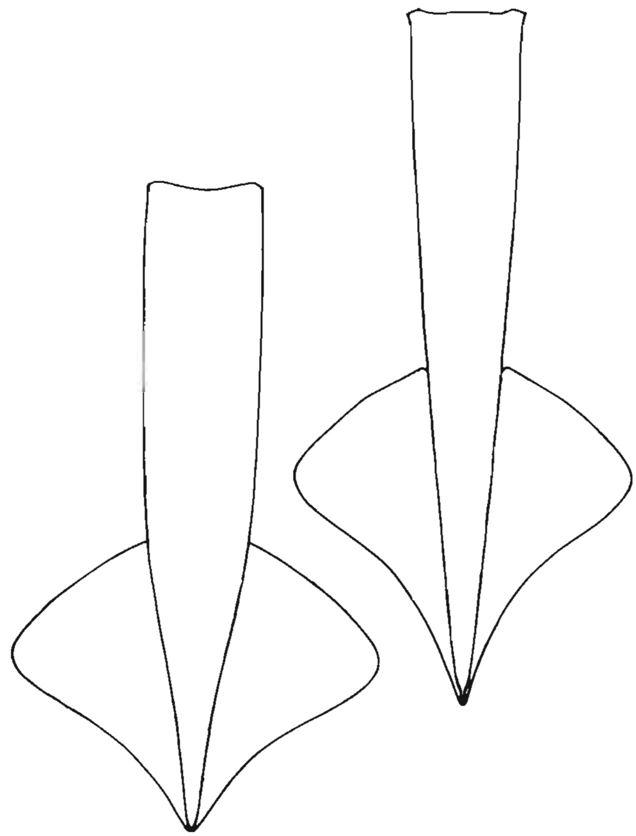

Figure 25
Comparison of ventral aspects of mantle and fin outline.
***Illex illecebrosus* (left); *I. oxygonius* (right).**

12(9) Dactylus of tentacular club with eight longitudinal rows of small suckers; funnel groove smooth, without foveola or side pockets **13**

12(9) Dactylus of tentacular club with four longitudinal rows of small suckers; funnel groove with foveola and side pockets **14**

13(12) Fin angle 40-50° **(Fig. 25 left)**; modified portion of hectocotylized ventral arm in mature males occupies about 15-25% of hectocotylized-arm length; head not noticably wider than mantle opening; suckers on lateral arms of males not enlarged .... ***Illex illecebrosus* (Fig. 26)**

13(12) Fin angle 25-40° **(Fig. 25 right)**; modified portion of hectocotylized ventral arm in mature males occupies about 30-35% of hectocotylized-arm length; head wider than mantle opening; suckers on lateral arms of males enlarged .... ***Illex oxygonius* (Fig. 27)**

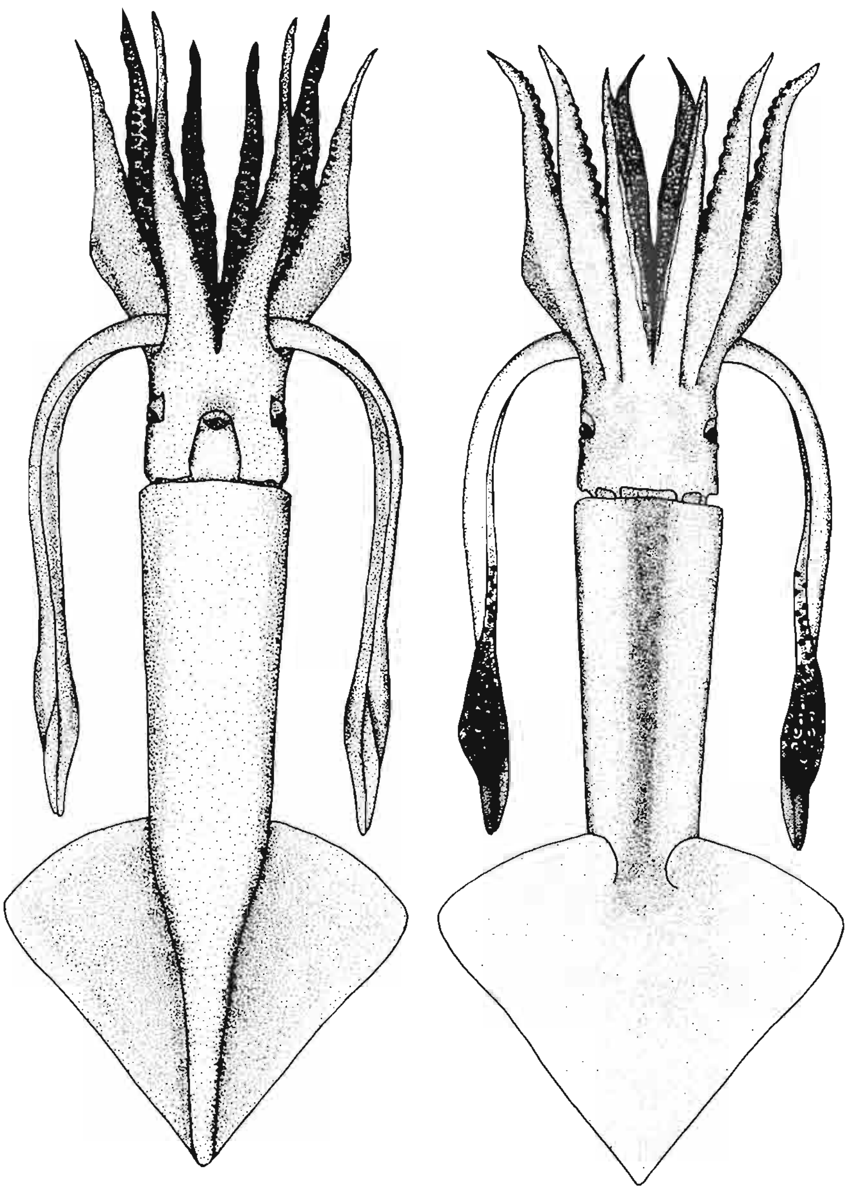

Figure 26
***Illex illecebrosus*. Ventral aspect (left); dorsal aspect (right).**

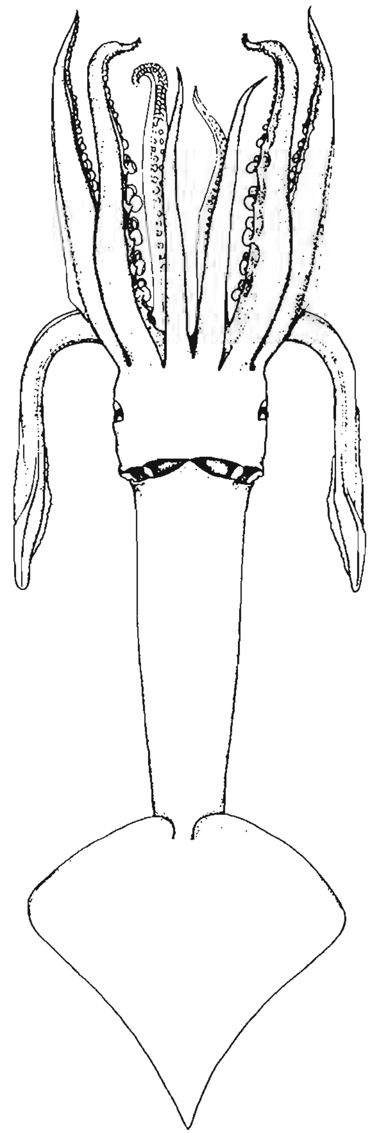

Figure 27
***Illex oxygonius* (dorsal aspect).**

14(12) Large, diffuse, compound light organ beneath integument on anterodorsal surface of mantle; not more than two suckers occur proximal to knobs on carpus of tentacular club; no reflective stripe on midline of ventral mantle .... ***Ommastrephes pteropus* (Fig. 28)**

14(12) No large dorsal light organ; longitudinal reflective stripe present along ventral midline of mantle surface; four to seven suckers occur proximal to first knob on carpal part of tentacular club .... ***Ommastrephes bartrami* (Fig. 29)**

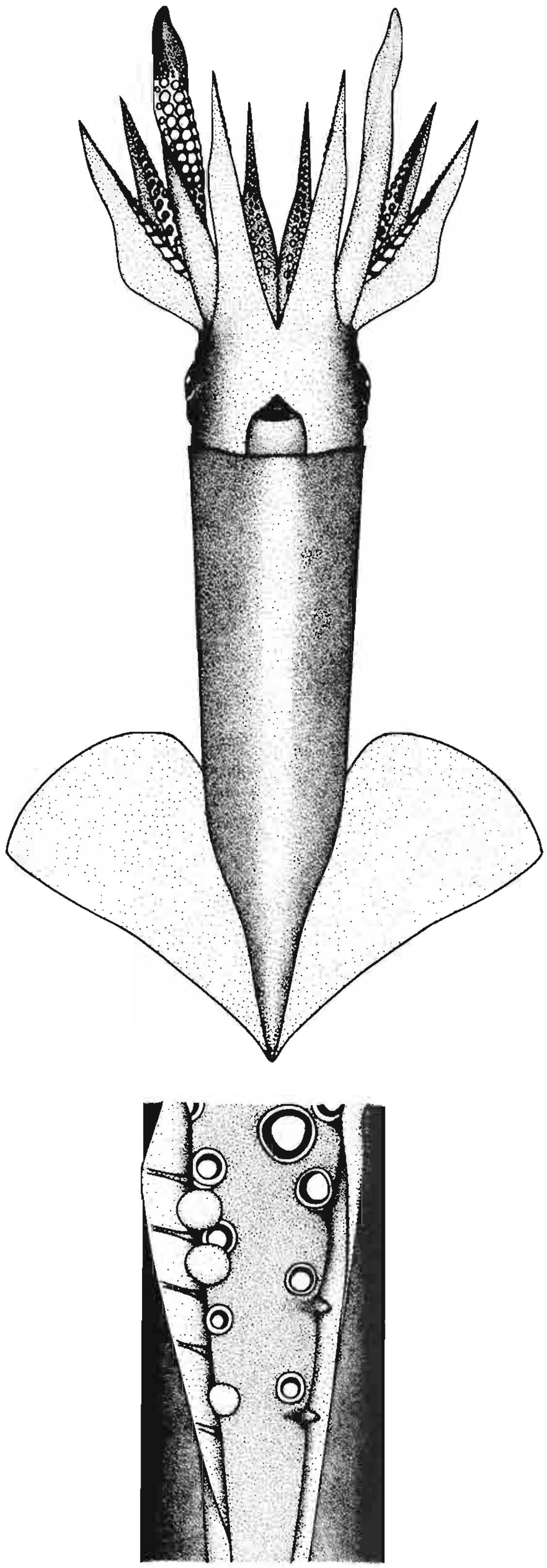

Figure 28
Ommastrephes pteropus. **Ventral aspect (top); carpal region of tentacular club (bottom).**

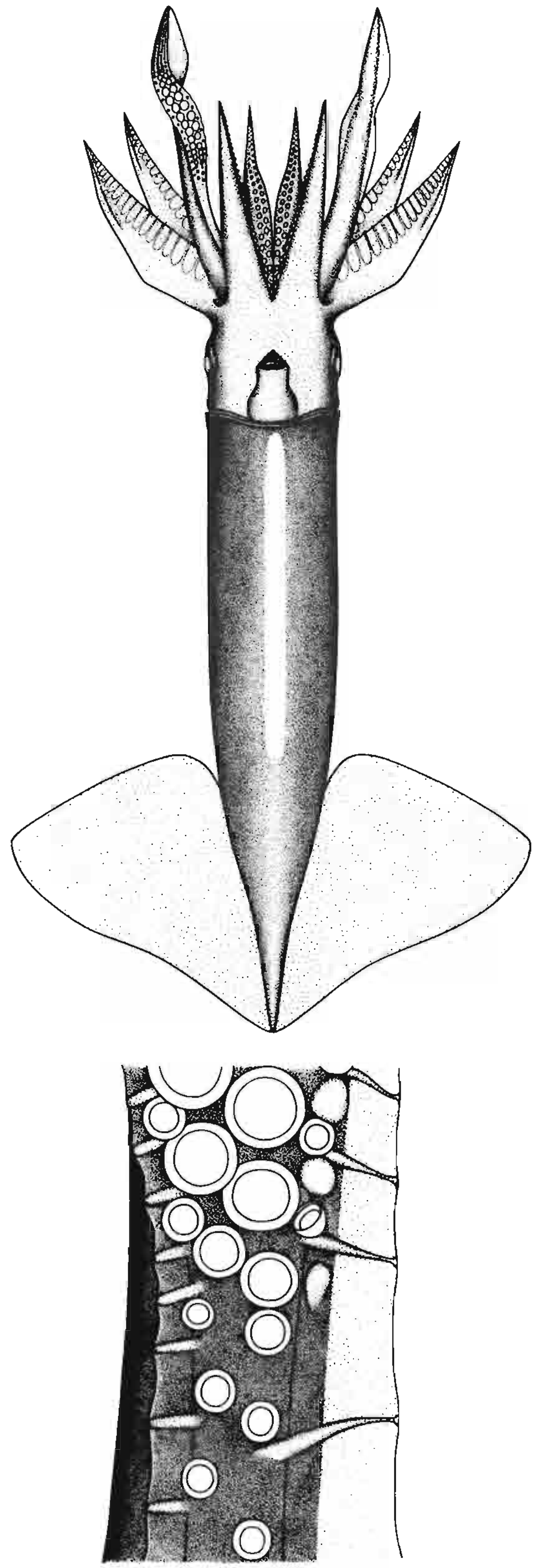

Figure 29
Ommastrephes bartrami. **Ventral aspect (top); carpal region of tentacular club (bottom).**

Annotated systematic list
Class Cephalopoda

The generic status of at least some species in each family of cephalopods discussed here is currently unsettled. Species-level systematics also might change in the Octopodidae, Sepiolidae, and Ommastrephidae from this area when thorough revisions have been completed. A review of the published literature and an examination of the collections of the National Museum of Natural History reveal that, in addition to the eleven species of neritic cephalopods we list from the northeastern United States, 91 oceanic species might occasionally be transported into these waters, and 18 other neritic species that generally are confined to Carolinian or subtropical waters might stray north of Cape Hatteras under unusual oceanographic circumstances.

1 Neritic species

Order Sepioidea

FAMILY SEPIOLIDAE

Bobtailed squids are small benthic animals more closely related to the cuttlefishes than to the true teuthoid squids. Species-level systematics are confused, and the entire family, with many species around the world, is in need of revision.

***Rossia megaptera* Verrill 1881, Fig. 20.** This little-known species occurs from New York to Greenland on the outer shelf and slope at depths of 125-1500 m, with a maximum size of about 40 mm ML.

***Rossia palpebrosa* Owen 1834, Fig. 19.** An Arctic-Boreal species known from Greenland and the Canadian Arctic to South Carolina in the western Atlantic and from Spitzbergen to the North Sea in the eastern Atlantic. In the NMFS Groundfish-Survey collections, it is scattered along the outer shelf at depths of 88-175 m. Grows to about 45 mm ML. *Rossia glauposis* Loven 1846 and *R. sublaevis* Verrill 1878 probably are junior synomyms (Nesis 1987).

***Semirossia tenera* (Verrill 1880), Fig. 17.** Common on sand and mud bottoms on the central shelf at depths of 85-135 m, *S. tenera* is known to occur from the Gulf of Maine to the Gulf of Mexico and Caribbean Sea. Also reported from Surinam and French Guiana (Okutani 1983). Attains a size of about 50 mm ML. This is the only species of *Semirossia* from the northeastern United States, but its relationships with several other nominal species in the southern part of its range are confusing.

***Stoloteuthis leucoptera* (Verrill 1878), Fig. 16.** This beautiful little cephalopod has seldom been reported since Verrill's description. Apparently, however, it is not rare, as several hundred specimens are included in the NMFS Groundfish-Survey collections. *Stoloteuthis leucoptera* seems to be relatively common on the outer shelf and slope of the Gulf of Maine at depths of 175-340 m, and is found as far south as the Straits of Florida. This species, which reaches 25 mm ML, can be distinguished easily from all other neritic sepiolids in the Atlantic by the ventral shield-like structure of the mantle.

Order Teuthoidea

FAMILY LOLIGINIDAE

The systematics of the Loliginidae currently are in turmoil. In a little more than a decade, at least four different generic-level classifications have been proposed for species that include those we refer to as *Loligo* (Cohen 1976; Natsukari 1984; G.L. Voss, Univ. Miami, pers. commun., 1984; Brakoniecki 1986). We retain this generic designation for both species as a matter of continuity until such problems are resolved.

Although *L. pealei* and *L. plei* are distinct species, they are very similar and often are difficult to separate. Cohen (1976) examined 50 taxonomic characters and concluded that *L. pealei* and *L. plei* overlap in all but two: the structure of the hectocotylus and the ratio of vane width to rachis width in the gladius. Five other characters were found that, although overlapping, differed significantly between the two species. Furthermore, the two species are most similar in geographical areas where they are sympatric.

***Loligo pealei* Lesueur 1821, Fig. 23.** A very abundant species in the waters off the northeastern United States, *L. pealei* is the target of important commercial fisheries. Also the primary source of giant axons for neurological research in this region.

Loligo pealei occurs over the continental shelf and upper slope from the surface to about 400 m depth. It is found throughout the western North Atlantic from Newfoundland to Brazil, but apparently not around the islands of the Caribbean Sea (Cohen 1976). Vecchione (1981) described the early life history of *L. pealei*, and Summers (1983) reviewed the many published studies of its biology and ecology. Attains a maximum size of 500 mm ML.

***Loligo plei* Blainville 1823, Fig. 24.** *Loligo plei* tends to be limited to warmer waters than *L. pealei*. Where the two species are sympatric, *L. pealei* is usually found in deeper water than *L. plei*, although considerable overlap occurs. The maximum depth reported for *L. plei* is 370 m. *Loligo plei* is rare north of Cape Hatteras but has been collected as far north as the New York Bight. Its range extends south at least to southern Brazil and includes the islands of Bermuda, the Bahamas, and the Caribbean Sea, where it is sympatric with two other species currently assigned to the genus *Loligo*. Reported to reach a size of at least 350 mm ML.

***Lolliguncula brevis* (Blainville 1823), Fig. 21.** A species that is noteworthy for its euryhalinity, *L. brevis* is common in coastal waters from Delaware Bay south to Brazil and is the only species of cephalopod frequently caught in estuaries. Throughout its range, it is found in waters less than 20 m deep. Haefner (1964) compared the morphometrics of *L. brevis*, which attains a relatively small size of 120 mm ML, with the larger-growing *L. pealei* from the Middle Atlantic Bight; Vecchione (1982) described the development of *L. brevis*.

Order Teuthoidea (continued)

FAMILY OMMASTREPHIDAE

The family Ommastrephidae is currently under revision by several authors; numerous questions need to be resolved on a worldwide basis at both the generic and the species levels. Most members of the family are oceanic, but a few genera, including *Illex*, are strongly associated with the continental shelf and slope (although occasionally they are found far offshore). This is the only family included in the key whose species spawn pelagically.

Illex illecebrosus **(Lesueur 1821), Fig. 26.** This very abundant species is important in commercial fisheries. Its depth range extends from the surface to probably about 1000 m. A seasonal migration transports *I. illecebrosus* from the Gulf Stream right up to the shoreline. Geographical range includes the western Atlantic from the Straits of Florida to Greenland and Iceland and extends eastward to the British Isles; however, the eastern Atlantic populations may represent a separate species, *I. coindetii*, or subspecies. *Illex illecebrosus* grows to 350 mm ML. O'Dor (1983) reviewed the life history of *I. illecebrosus*, and its larval development and ecology have been discussed by Roper and Lu (1979), Vecchione (1979), and Vecchione and Roper (1986).

Illex oxygonius **Roper, Lu, and Mangold 1969, Fig. 27.** Except for mature adult males, *I. oxygonius* is very difficult to distinguish from *I. illecebrosus*, especially where the two species are sympatric. *Illex oxygonius*, however, has been found only as far north as Delaware and appears to be rare north of Cape Hatteras. It has been reported only as far south as Key West, Florida, although this could simply be an artifact of the difficulty in distinguishing *I. oxygonius* from *I. illecebrosus* and *I. coindetii*. *Illex oxygonius* has been reported from waters with bottom depths of 50-550 m and attains a size of 230 mm ML. Its distribution was summarized by Roper et al. (1984).

Order Octopoda

FAMILY OCTOPODIDAE

Octopod morphology is quite variable, making the taxonomy difficult. Morphometric indices, such as relative lengths of the arms, are often used in describing species but can be very misleading in any particular specimen because of the octopod's ability to extend or contract arms independently. Furthermore, artifacts of preservation can exacerbate this problem. Similarly, skin texture and color patterns can be of use in distinguishing among species, but, because these characters are related to different behavioral patterns and also can change dramatically during fixation and preservation, they also can be misleading. The generic-level systematics of the family are currently under revision.

We recommend that a series of specimens be obtained, including (if possible) mature adults of both sexes. For example, adult males of *Octopus vulgaris* and *Bathypolypus arcticus* are easily distinguished based on the hectocotylus. Once the adult males of these species have been compared, it will be easier to identify the less easily distinguished juveniles without having to dissect them to determine if the internal ink sac is present. Differences in ovarian egg size are consistent and useful for identification of adult females. The eggs of *O. vulgaris* are 3 mm or less in length whereas those of *B. arcticus* are about 13 mm long.

Octopus vulgaris **Cuvier 1797, Fig. 15.** Although this species occurs primarily south of Cape Hatteras, it is distributed as far north as Connecticut. The NMFS Groundfish-Survey collections from the Middle Atlantic Bight include several large specimens. As currently defined, this species has been reported from shallow (intertidal to 200-m depth) temperate and tropical waters of both the eastern and western North and South Atlantic Oceans, the Mediterranean Sea, Red Sea, Indian Ocean, and western Pacific Ocean. Possibly, though, this broad range might actually represent a complex of several similar, though currently unrecognized, species (Roper 1985). *Octopus vulgaris* has been reported to reach a size of 400 mm ML. The life cycle was reviewed by Mangold (1983).

Bathypolypus arcticus **(Prosch 1849), Fig. 14.** The most abundant neritic octopod in the waters of the northeastern United States. It is a cold-water species that also is found in the deep water of the continental slope as far south as the Straits of Florida. A species with considerable morphological variation, it has been reported from eastern Canada, Greenland, Iceland, the North Sea, and Spitzbergen. It is usually caught in trawls on mud bottoms at depths of 14 to 1000 m, and attains a maximum size of about 100 mm ML. O'Dor and Macalaster (1983) reviewed the life history of *B. arcticus*.

2 Oceanic species

Both of these species are common in epipelagic and mesopelagic waters of the Gulf Stream. They are transported onto the continental shelf of the northeastern United States by Gulf-Stream eddies.

Order Teuthoidea

FAMILY OMMASTREPHIDAE

Ommastrephes bartrami **(Lesueur 1821), Fig. 29.** Found in mid-latitude waters of the North and South Atlantic, Pacific, and Indian Oceans. It is absent from equatorial waters as well as from waters with temperatures of less than 10°C. In oceanic waters, *O. bartrami* occurs at the surface at night to about 1500 m depth.

Ommastrephes pteropus **(Steenstrup 1855), Fig. 28.** A Pan-Atlantic species of tropical and warm-temperate waters, *O. pteropus* is found where surface waters are warmer than 22°C. It is known to migrate vertically between the surface and deep waters and has been reported at depths down to 1500 m. Nesis (1987) has proposed that this species be assigned to the genus *Sthenoteuthis*.

3 Other oceanic species

Species that might be found in the waters off northeastern United States and that have been recorded in oceanic waters north of 26°N and west of 60°W.

Order Sepioidea

FAMILY SPIRULIDAE

Spirula spirula (Linnaeus 1758)

FAMILY SEPIOLIDAE

Heteroteuthis dispar (Ruppell 1844)
Nectoteuthis pourtalesi Verrill 1883

Order Teuthoidea

FAMILY LYCOTEUTHIDAE

Lycoteuthis diadema (Chun 1900)
Selenoteuthis scintillans Voss 1958
Lampadioteuthis megaleia Berry 1916

FAMILY ENOPLOTEUTHIDAE

Abralia veranyi (Ruppell 1844)
Abralia redfieldi Voss 1955
Abralia grimpei Voss 1958
Abraliopsis hoylei (Pfeffer 1884)
Abraliopsis pfefferi Joubin 1896
Pyroteuthis margaritifera (Ruppell 1844)
Pterygioteuthis giardi Fischer 1895
Pterygioteuthis gemmata Chun 1908
Enoploteuthis anapsis Roper 1964
Enoploteuthis leptura (Leach 1817)
Ancistrocheirus lesueuri (d'Orbigny 1839)
Thelidioteuthis alessandrini (Verany 1851)
(probably = *A. lesueuri*)

FAMILY OCTOPOTEUTHIDAE

Octopoteuthis megaptera (Verrill 1885)
Octopoteuthis danae Joubin 1931
Taningia danae Joubin 1931

FAMILY ONYCHOTEUTHIDAE

Onychoteuthis banksii (Leach 1817)
Onykia carribaea Lesueur 1821
Ancistroteuthis lichtensteini (d'Orbigny 1839)

FAMILY CYCLOTEUTHIDAE

Cycloteuthis sirventi Joubin 1919
Discoteuthis discus Young and Roper 1969
Discoteuthis laciniosa Young and Roper 1969

FAMILY GONATIDAE

Gonatus fabricii (Lichtenstein 1818)
Gonatus steenstrupi Kristensen 1981

FAMILY LEPIDOTEUTHIDAE

Lepidoteuthis grimaldi Joubin 1895
Pholidoteuthis adami Voss 1956
Tetronychoteuthis dussumieri (d'Orbigny 1839)
Tetronychoteuthis massyae Pfeffer 1912

FAMILY HISTIOTEUTHIDAE

Histioteuthis bonnelli (Ferussac 1835)
Histioteuthis celetaria (Voss 1960)
Histioteuthis corona (Voss and Voss 1962)
Histioteuthis dofleini (Pfeffer 1912)
Histioteuthis elongata (Voss and Voss 1962)
Histioteuthis meleagroteuthis (Chun 1910)
Histioteuthis reversa (Verrill 1880)

FAMILY NEOTEUTHIDAE

Neoteuthis thielei Naef 1921

FAMILY BATHYTEUTHIDAE

Bathyteuthis abyssicola Hoyle 1885

FAMILY CTENOPTERYGIDAE

Ctenopteryx sicula (Verany 1851)

FAMILY BRACHIOTEUTHIDAE

Brachioteuthis beanii Verrill 1881
Brachioteuthis riisei (Steenstrup 1882)

FAMILY ARCHITEUTHIDAE

Architeuthis princeps Verrill 1875
(as well as other poorly defined species of *Architeuthis*)

FAMILY OMMASTREPHIDAE

Illex coindetii (Verany 1837)
Todarodes sagittatus (Lamarck 1799)
Ommastrephes caroli Furtado 1887 (may = *O. bartrami*)
Ornithoteuthis antillarum Adam 1957
Hyaloteuthis pelagica (Bosc 1802)

Order Teuthoidea (continued)

FAMILY THYSANOTEUTHIDAE

Thysanoteuthis rhombus Troschel 1857

FAMILY CHIROTEUTHIDAE

Chiroteuthis veranyi (Ferussac 1835)

FAMILY MASTIGOTEUTHIDAE

Mastigoteuthis grimaldii (Joubin 1895)
Mastigoteuthis hjorti Chun 1913
Mastigoteuthis magna Joubin 1913

FAMILY GRIMALDITEUTHIDAE

Grimalditeuthis bomplandii (Veranyi 1837)

FAMILY JOUBINITEUTHIDAE

Joubiniteuthis portieri (Joubin 1916)

FAMILY CRANCHIIDAE

Cranchia scabra Leach 1817
Liocranchia reinhardti (Steenstrup 1856)
Leachia cyclura Lesueur 1821
Leachia atlantica (Degner 1925)
Egea inermis Joubin 1933
Helicocranchia pfefferi Massy 1907
Galiteuthis armata Joubin 1898
Bathothauma lyromma Chun 1906
Sandalops melancholicus Chun 1906
Taonius pavo (Lesueur 1821)
Megalocranchia abyssicola (Goodrich 1896)
Megalocranchia oceanica (Voss 1960)
Megalocranchia speculator Chun 1906
Teuthowenia megalops (Prosch 1849)

Order Vampyromorpha

FAMILY VAMPYROTEUTHIDAE

Vampyroteuthis infernalis Chun 1903

Order Octopoda

FAMILY CIRROTEUTHIDAE

Cirroteuthis muelleri Eschricht 1838
Cirrothauma murrayi Chun 1911

FAMILY STAUROTEUTHIDAE

Stauroteuthis syrtensis Verrill 1879
Grimpoteuthis grimaldii (Joubin 1903)
Grimpoteuthis megaptera (Verrill 1885)
Grimpoteuthis umbellata (Fischer 1883)

FAMILY OPISTHOTEUTHIDAE

Opisthoteuthis agassizii Verrill 1883

FAMILY BOLITAENIDAE

Eledonella pygmaea Verrill 1884
Japetella diaphana Hoyle 1885

FAMILY VITRELEDONELLIDAE

Vitreledonella richardi Joubin 1918

FAMILY OCTOPODIDAE

Benthoctopus piscatorum (Verrill 1879)

FAMILY TREMOCTOPODIDAE

Tremoctopus violaceus Delle Chiaje 1830

FAMILY OCYTHOIDAE

Ocythoe tuberculata Rafinesque 1814

FAMILY ARGONAUTIDAE

Argonauta argo Linnaeus 1758
Argonauta hians Lightfoot 1786

FAMILY ALLOPOSIDAE

Alloposis mollis Verrill 1880

4 Carolinian and subtropical neritic species

These might occasionally occur north of Cape Hatteras.

Order Sepioidea

FAMILY SEPIOLIDAE

***Semirossia equalis* (Voss 1950)**
***Rossia bullisi* Voss 1956**
***Rossia antillensis* Voss 1955**
***Rossia tortugaensis* Voss 1956**

Order Teuthoidea

FAMILY PICKFORDIATEUTHIDAE

***Pickfordiateuthis pulchella* Voss 1953**

FAMILY LOLIGINIDAE

***Loligo ocula* Cohen 1976**
***Loligo roperi* Cohen 1976**
***Sepioteuthis sepioidea* (Blainville 1823)**

Order Octopoda

FAMILY OCTOPODIDAE

***Octopus hummelincki* Adam 1936**
***Octopus joubini* Robson 1929**
***Octopus briareus* Robson 1929**
***Octopus burryi* Voss 1950**
***Octopus macropus* Risso 1826**
***Octopus defilippi* Verany 1851**
***Danoctopus schmidti* Joubin 1933**
***Scaeurgus unicirrhus* (d'Orbigny 1840)**
***Pteroctopus tetracirrhus* (Delle Chiaje 1830)**
***Tetracheledone spinicirrhus* Voss 1955**

Some recently published comprehensive works on cephalopods

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Systematic index

Note This is an index to the species included in the key and discussed in the text, but does not include the extralimital species listed on p. 18-20.

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Coordinating Editor's comments

Publication of the "Marine Flora and Fauna of the Eastern United States" is most timely in view of the growing universal emphasis on work in the marine environment and the critical need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

Michael Vecchione went to sea as a cabin boy on a three-masted schooner in Maine at the age of 16. He completed undergraduate studies in biology at the University of Miami in 1972, and then spent four and a half years in the United States Army. He has been working on cephalopods since his graduate studies on planktonic molluscs during 1976-79 at the Virginia Institute of Marine Science, School of Marine Science, College of William and Mary. After receiving the Ph.D. degree, he worked briefly for the U.S. Fish and Wildlife Service before accepting a faculty position at McNeese State University. There he studied cephalopods, zooplankton, and ichthyoplankton in addition to teaching during 1981-86. In 1986 he moved to his present position as Cephalopod Biologist at the National Marine Fisheries Service Systematics Laboratory at the National Museum of Natural History.

Clyde F.E. Roper's interest in marine biology developed while he was a commercial lobster fisherman in New Hampshire during summers through high school and undergraduate school at Transylvania College, Lexington, Kentucky. Lured to work as a research assistant in the summer following his first year of graduate school at the University of Miami's Institute of Marine Sciences (now Rosenstiel School of Marine and Atmospheric Science), Roper was captivated by cephalopods. He completed the M.S. and Ph.D. degrees at Miami, working primarily on oceanic and deep-sea squids. Roper has continued research on the systematics, biology, and behavior of cephalopods of the world at the Smithsonian Institution's National Museum of Natural History where he has been a Curator of Molluscs since 1966.

Michael J. Sweeney has worked at the National Museum of Natural History since 1968. His research interests are oceanic cephalopods and collections management. Restoration of antique automobiles occupies his spare time.

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