

CEPHALOPODS

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GENERAL REMARKS

The molluscan class Cephalopoda includes (1) decapodiforms, such as squids and cuttlefishes, (2) octopodiforms, including the vampire squid as well as a variety of octopods, and (3) their more distant relatives, the chambered nautilus (Young et al., 1998). The first 2 groups listed above comprise the Neocoleoidea. Cephalopods are characterized by a well-developed head with a circumoral (surrounding the mouth) arrangement of arms that bear suckers and/or hooks (except in *Nautilus*). The mouth has chitinous beak-like jaws; as in other molluscs a chitinous tongue-like radula (band of teeth) is present in most species. The shell is generally reduced, modified, or absent and is enclosed by the mantle in neocoleoids. An external shell occurs only in *Nautilus* (restricted to Indo-Pacific), although a shell-like egg case is found in female argonauts. The size of adult cephalopods ranges from about 2 cm to approximately 20 m in total length.

Cephalopods are soft-bodied animals; their primary skeletal features include a cartilaginous cranium and, in most forms, a rigid structure in the mantle composed of chitin (the gladius or "pen"), calcium carbonate (cuttlebone and ram's-horn shell), or cartilage (fin supports in finned octopods). One pair of gills is present except in *Nautilus*, which has two pairs. The central nervous system is highly developed, with a large brain modified from the molluscan circumesophageal nerve ring. The highly developed eyes of most neocoleoids have a lens to focus images on the retina, a visual system often compared with that of vertebrates.

Coloration is variable depending on group and habitat; most species have numerous chromatophores (pigment sacs controlled by neuromuscular action) and iridocytes (shiny, reflective platelets) in the skin. Rapid changes in colour patterns and skin texture are an integral part of their behaviour. While shallow-living cephalopods are able to conceal themselves by chromatophore-produced colour patterns and texture changes, many deep-sea forms camouflage themselves by producing bioluminescent light from photophores (light-producing organs) which eliminates their silhouettes against the downwelling light in the dimly-lit mid depths.

Water is taken into the mantle (body) cavity for respiration, through the opening between the mantle and head. Contraction of mantle muscles expels the water from the mantle cavity through the funnel (a small ventral tube, sometimes called a siphon) for propulsion and elimination of waste products, in addition to completion of the respiratory cycle. Most neocoleoids can produce ink, which is also expelled through the funnel. The ink may take the form of a mucoid "pseudomorph", to decoy predators, or a cloud, which has been compared with a smoke screen.

Locomotion is achieved by (1) drawing water into the mantle cavity followed by its jet-like expulsion through the funnel, and by (2) flapping or undulation of fins on the mantle, as well as by (3) crawling along the bottom on the arms (mostly octopods). Fins also provide balance and steering during jetting.

The sexes are separate, eggs are heavily yolked, and development is direct, without true metamorphic stages. Cephalopod eggs may vary in size from about 1.7 cm long in some *Octopus* species to 0.8 mm long in *Argonauta*, which are also octopods. Eggs have one or more layers of protective coatings and generally are laid as egg masses. Egg masses may be benthic or pelagic, varying among major taxonomic groups. Time of embryonic development also varies widely, from a few days to many months, depending on the species and temperature conditions. Hatching may occur synchronously from a single clutch or be extended over a period of 2 to 3 weeks. Hatchlings from benthic eggs may be either benthic, and morphologically similar to the older stages, or planktonic. Pelagic hatchlings are planktonic and, in some species, very different from more developed conspecifics. The term "paralarva" has been adopted for early stages of cephalopods which differ morphologically and ecologically from older stages.

Cephalopods occur in all marine habitats of the world, though none are found at salinities less than about 17.5 parts per thousand. The range of depths extends from intertidal to over 5 000 m. Many species of oceanic cephalopods undergo diel vertical migrations, wherein they occur at depths of about 400 to 1 000 m during the day, then ascend into the uppermost 200 m or so during the night. Abundance of cephalopods varies (depending on group, habitat, and season) from isolated territorial individuals (primarily benthic octopods and sepioids) through small schools with a few dozen individuals to huge schools with millions of oceanic squids.

The total number of living species of cephalopods currently recognized is fewer than 1 000; about 109 species in 31 families occur in the Western Central Atlantic Ocean and adjacent areas (Caribbean Sea and Gulf of Mexico). Both decapods and octopods are common in these waters. These major groups are easily distinguished by external characteristics. The squids have an elongate body with lateral fins, and eight arms with stalked suckers in two or more rows, plus two longer tentacles which have an organized cluster (tentacular club) of two to many rows of suckers (or hooks) at the distal end. Decapod suckers bear chitinous rings which are sometimes modified into hooks. The octopods have a short, sac-like body generally with no lateral fins (some deep-sea octopods have a pair of paddle-like fins), and eight arms only (no tentacles) which have unstalked suckers without chitinous rings along the length of the arms. Sepioid decapods (bobtail squids) also have a short, sac like body, but have fins and an arm crown similar to that of the squids, with two tentacles in addition to eight arms. The status of the systematics of cephalopods is rapidly changing, as research has in-

creased substantially in the past 25 years. However, phylogenetic relationships among families within the major groups remain uncertain.

Many, though not all, cephalopod species exhibit external sexual dimorphism, either in structural or size differences. Males of many forms possess a modified arm (hectocotylus) for mating. The hectocotylus may consist of modified suckers, papillae, membranes, ridges and grooves, flaps, etc., but in all cases it functions to transfer the spermatophores (sperm packets) from the male to an implantation site on the female. The spermatophores may be implanted inside the mantle cavity, around the mantle opening on the neck, in a pocket under the eye, around the mouth, etc. The males of some species also exhibit modifications to other arms, in addition to the hectocotylus. Females of some species also develop modified structures (e.g., arm-tip photophores) when mature. The mode of reproduction and egg-laying is unknown for many forms, especially oceanic and deep-sea species.

The life expectancy appears to be about 1 to 2 years in most neocoleoids, but larger species of squids and octopods (e.g., giant squid - *Architeuthis* spp. and the giant octopus *Enteroctopus dofleinii*) and those in cold habitats may live somewhat longer. Conversely, small oceanic species such as pyroteuthids may complete their life cycles in less than 6 months. Some species die after spawning, but this phenomenon is not universal.

Cephalopods are active predators that feed upon shrimps, crabs, fishes, other cephalopods, and, in the case of octopods, on other molluscs. In turn, cephalopods are major food items in the diets of toothed whales, seals, pelagic birds (penguins, petrels, albatrosses, etc.), and both benthic and pelagic fishes (e.g., sea basses, lancetfishes, tunas, and billfishes).

Cephalopods are extremely important as food for human consumption, and well over 3 million t are caught each year. Fishing pressure on cephalopods has increased as stocks of finfishes have been depleted worldwide. Cephalopod fisheries are especially intense in Japan, the Orient and in the Mediterranean/Eastern Atlantic waters. Fishing techniques include small traps (octopods), wiers, lures and jigs (some cuttlefishes and squids), lampara nets (nearshore squids), and midwater and otter trawls (squids and octopods). Certain species of squids are attracted to light, then jigged or seined. Occasionally cuttlefishes and octopods are caught in hand-nets or are speared. The total commercial catch of cephalopods in the Western Central Atlantic varied during 1993 to 1998 between 19 000 and 31 000 t, mostly landed in Mexico.

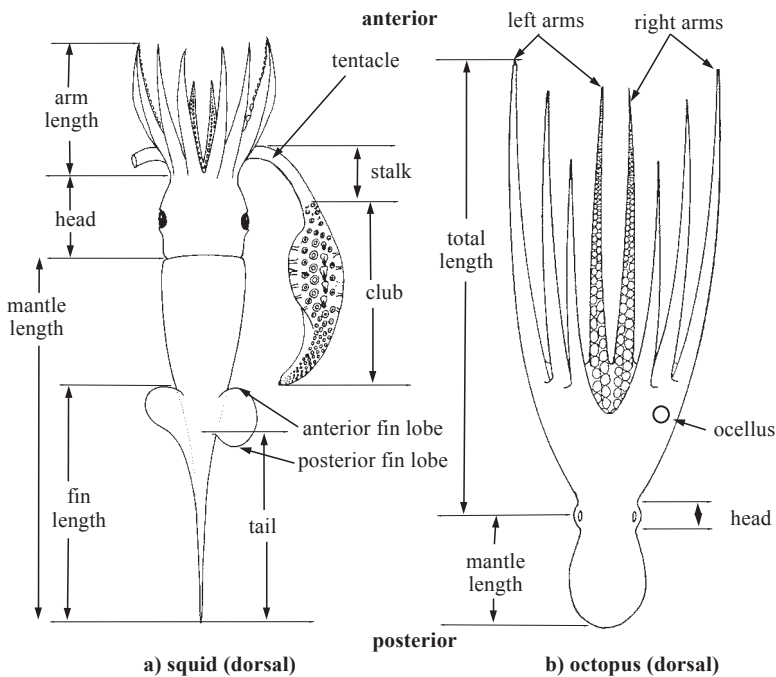
Cephalopods are also important experimental animals in biomedical research with direct application to man. Because of the highly developed brain and sensory organs, cephalopods are valuable in behavioural and comparative neuroanatomical studies. In addition, some cephalopods possess extremely large single nerve axons and these are used extensively in all aspects of neurophysiological research.

The bites of cephalopods, especially octopuses, can be painful at the least, poisonous or secondarily infected, or, rarely, lethal (several human deaths have been recorded in Australia due to blue-ringed octopus, *Hapalochlaena*). Cephalopods must therefore be handled carefully.

Preparation of the accounts that follow have relied heavily on the cephalopod pages of the Tree-of-Life project on the World Wide Web (Young, Vecchione, and Mangold, <http://tolweb.org/tree/eukaryotes/animals/mollusca/cephalopoda/cephalopoda.html>). Readers can find additional information about all extant cephalopod families at that URL web site. Comments by Michael J. Sweeney were very helpful in polishing a draft of this presentation.

In the presentation of family accounts, Decapodiformes are listed first, followed by Octopodiformes, which is divided into cirrate octopods, incirrate octopods, and vampire squids. Because phylogenetic relationships are unresolved among families of either decapods or incirrate octopods (Young and Vecchione, 1996), families are presented in alphabetical order within these groups. Keys are provided to local genera for all families. Details of species are included for the speciose and commercially important families Loliginidae, Ommastrephidae, and Octopodidae. Genera (in some cases subfamilies) are in alphabetical order within families and, for families of commercial interest, species alphabetical within genera.

TECHNICAL TERMS AND MEASUREMENTS



Abdominal septum - median septum traversing the posterior mantle cavity parallel to the body axis. It extends from the posterior visceral mass to the ventral mantle wall. The ventral mantle artery runs along the anterior end of this septum.

Aboral - away from or opposite the mouth.

Accessory nidamental glands - glands of unknown function consisting of tubules containing symbiotic bacteria. Found in sepioids and loliginid squids.

Adult - a female that has mature eggs (these are frequently stored in the oviducts), or a male that has produced spermatophores (these are stored in Needham's sac).

Afferent blood vessel - vein carrying blood toward an organ.

Anal flaps (= anal valves) - small flaps on the lateral sides of the anus (Fig. 1).

Anal pads - ovoid pads of unknown function, apparently glandular, located on both sides of the anus in some sepioids.

Anus - opening of the digestive tract, just inside the funnel, through which undigested remains of food, as well as ink, are expelled.

Anterior - toward the arm tips.

Antitragus - knob that projects inward from the posterior surface of the central depression in the funnel locking apparatus of some squids.

Arm - one of the circumoral appendages of cephalopods. In decapodiforms each member of the fourth pair of arms is modified to form a tentacle. The second pair of arms is modified in vampire squids and has been lost in octopods.

Armature - the grappling structures of the arms and tentacles, including both suckers and hooks.

Beak - one of the 2 chitinous jaws of cephalopods. The dorsal beak inserts within the lower beak to tear tissue with a scissors-like cutting action.

Brachial - pertaining to the arms.

Brachial crown - the combination of arms and tentacles that surround the mouth.

Brachial pillar - a very narrow and elongate anterior region of the head between the eyes and the base of the brachial crown. A brachial pillar is especially well developed in many young cranchiid squid.

Brain - medial portion of the central nervous system. It includes the subesophageal and supraesophageal masses but generally does not include the large optic lobes.

Branchial - pertaining to the gills.

Brooding - incubation of eggs by the parent. A characteristic feature of incirrate octopods but also found in some squid (e.g., Gonatidae).

Buccal - pertaining to the mouth.

Buccal connective - muscular membrane that runs from the buccal support to the base of the adjacent arm (Fig. 2).

Buccal crown - umbrella-like structure that surrounds the mouth and is surrounded by the brachial crown. It consists of buccal supports and the buccal membrane. The buccal crown is present in most decapodiforms but absent from all octopodiforms.

Buccal lappet - see buccal support.

Buccal mass - muscular bulb at the beginning of the digestive system that contains the mouth, beaks, radula and various glands.

Buccal membrane - the muscular membrane that connects the buccal supports and together with the supports, forms the buccal crown. The pigmentation of the buccal membrane often differs from that of the adjacent oral surfaces of the arms (Fig. 2).

Buccal suckers - small but normal suckers that are present on the oral surface of the buccal supports of some decapodiforms (bathyteuthid families, some loliginids and some sepiids) (Fig. 2).

Buccal support (= buccal lappet) - one of 6 to 8, large muscular flaps of the buccal crown that surround the mouth. The supports are connected by the buccal membrane. The buccal supports are thought to be homologous with the inner ring of tentacles that surround the mouth of nautilids.

Caecum - region of the digestive tract of all cephalopods between the stomach and intestine.

Calcareous - composed of calcium carbonate (CaCO_3).

Calimus - the conical papilla of the end-organ of the hectocotylus in many incirrate octopods. It is located at the distal termination of the sperm groove and usually lies adjacent to the last arm sucker (Fig. 3).

Carpal sucker - suckers in the locking apparatus at the base of the club.

Carpal knobs - muscular bumps that replace some suckers on the carpal region of the club.

Carpus - the proximal "wrist" area of the tentacular club (Fig. 4).

Chitin - a horny polysaccharide substance (fingernail-like) that forms the sucker rings, hooks and beaks of most cephalopods.

Cartilaginous tubercles - rigid cartilaginous spines, with one or several cusps, in the skin of certain squids and octopods (Fig. 5).

Chromatophore - in general: a pigment cell. In cephalopods the chromatophore is an organ composed of numerous cells including one containing pigment granules that is surrounded by many slender muscle cells. Under nervous control, the muscles rapidly expand and flatten the pigment cell which spreads the pigment over a relatively broad area.

Cirri - muscular, finger-like structures that arise laterally on the oral surfaces of the arms of some octopodiforms. Cirri are homologous with trabeculae of decapodiforms.

Club-fixing apparatus - arrangement of suckers and matching knobs on the carpal region of the tentacular club that permits the 2 clubs to be locked together.

Coelom - an internal body cavity of mesodermal origin that is lined by an epithelium. Cephalopods have two coeloms, the visceropericardial coelom and the nephridial coelom.

Chorion - a tough secreted membrane that surrounds the egg.

Collar - muscular structure extending from the nuchal cartilage to the funnel that forms a one-way valve that lets water enter the mantle cavity but closes as the mantle contracts thereby forcing exhalent water out through the funnel.

Conus of gladius - cone-shaped structure at the posterior end of the gladius (Fig. 6).

Conus field - the sides of the conus that continue along the vanes of the gladius.

Cornea - smooth, thin, turgid, transparent skin without muscles that covers the eyes to protect the eye lenses of incirrate octopods and some decapodiforms.

Counterillumination - the production of bioluminescent light by an animal to conceal its silhouette against the downwelling light.

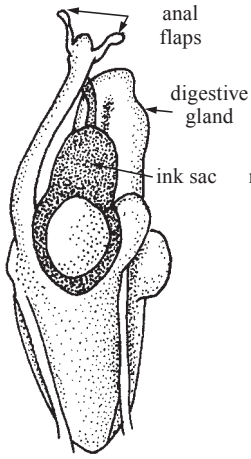


Fig. 1

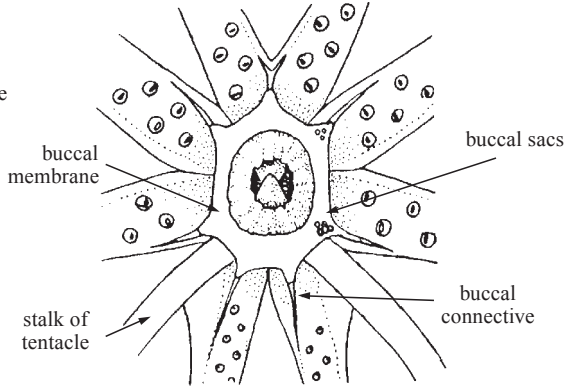


Fig. 2 diagram of oral surface of brachial crown and buccal membrane of a squid

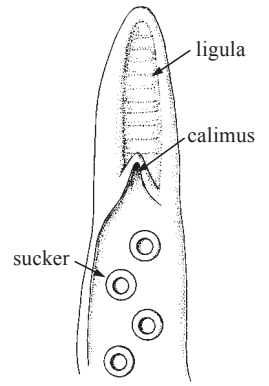


Fig. 3 hectocotylus of an octopus

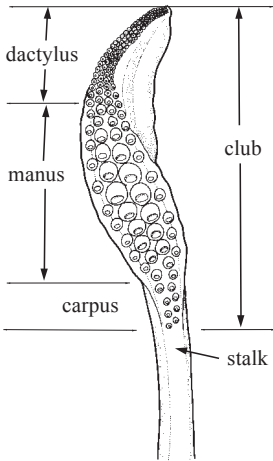


Fig. 4 distal end of tentacle of a squid

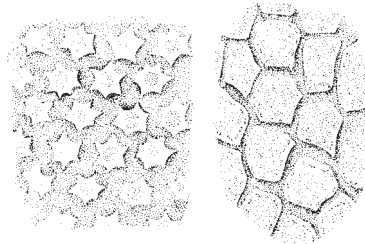


Fig. 5 cartilaginous scales

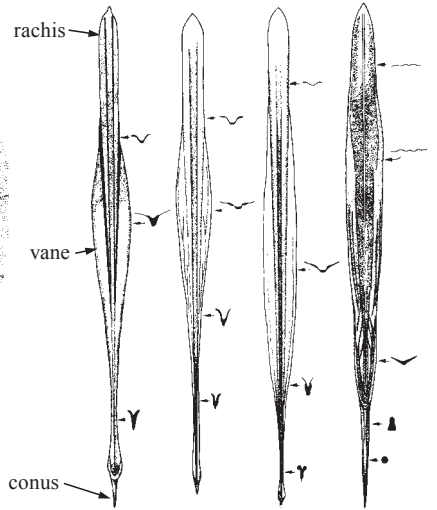


Fig. 6 gladiuses

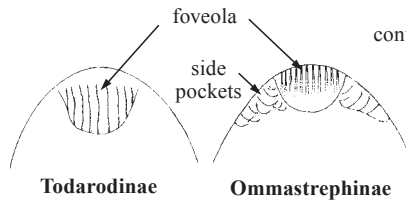


Fig. 7



Fig. 8 funnel locking cartilage

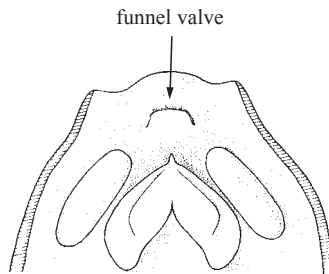


Fig. 9 funnel organ

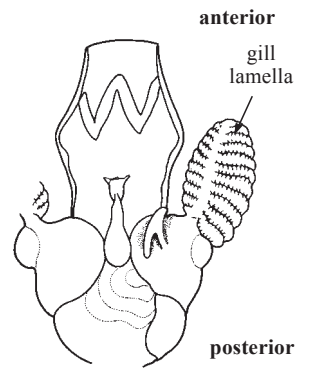


Fig. 10 gill

Crop - expansion (i.e. a broadening or a side pocket) of the esophagus for storing food.

Dactylus - the distal section of the tentacular club of squid, often characterized by suckers of reduced size.

Decapodiformes - higher-level taxon (superorder) including bobtail squid, ram's horn squid, and cuttlefish.

Diel vertical migration - vertical migration of animals in response to changes in downwelling light.

Digestive gland - primary organ in cephalopods that secretes digestive enzymes. It is also important in absorption and excretion (Fig. 1).

Distal - situated away from the point of origin or attachment. For example, the arm tip is the distal end of arm.

Dorsal - toward the uppermost surface of a cephalopod, opposite the ventral surface where the funnel is located.

Efferent vein - a vein carrying blood away from an organ.

Egg mass - a large number of eggs encapsulated in a gelatinous matrix or a large number of such structures that are attached together. The egg mass of an oceanic squid can be a large, fragile gelatinous ball or tube carrying many thousands of eggs. In contrast, the egg mass of a neritic squid (lolidinid) can be composed of very tough capsules each carrying several hundred eggs with many capsules attached together at their bases and to the substrate to form an egg mass.

Epithelial pigmentation - The pigmentation that is contained in epithelial cells which are unable to change their shape. Colour in most cephalopods, however, is due to pigment granules that are contained in specialized organs, the chromatophores, that can change shape rapidly under nervous control. See chromatophores.

Esophagus - the portion of the digestive tract between the buccal mass and the stomach. Often a portion of the esophagus is expanded to form a crop for food storage.

Fin angle - the angle between the longitudinal axis of the mantle and the posterior border of one fin.

Fins - the pair of muscular flaps used in swimming and located along the dorsolateral surface of the mantle, usually in its posterior half.

Fin lobe - the portion of a fin that extends anteriorly from the fin's anterior point of attachment and/or posteriorly from the fin's posterior point of attachment. This is often called the "free" lobe.

Foveola - transverse membranous fold of skin that forms a pocket in the funnel groove of ommastrephid squids (Fig. 7).

Funnel (= siphon) - the ventral, muscular tube through which water is expelled from the mantle cavity. The funnel is thought to have evolved from the molluscan foot.

Funnel groove - the depression in the ventral surface of the head into which the funnel fits.

Funnel locking apparatus - the funnel component (generally cartilagenous) of a structure that "locks" the ventrolateral mantle to the funnel. This lock, depending on its form, can either restrict all movement between the funnel and mantle or allow just anterior-posterior slipping. See Mantle locking apparatus (Fig. 8).

Funnel organ - the glandular structures on the internal dorsal and ventral surfaces of the funnel (Fig. 9).

Funnel valve - semicircular muscular flap extending from and continuous with the posterodorsal funnel wall. The funnel valve apparently acts as a one-way valve to prevent inspiration of water through the funnel when mantle expansion draws in water to pass over the gills for respiration.

Gill - paired organs for the exchange of respiratory gases with sea water.

Gill lamella - gill leaflet that extends perpendicular to the axis of the gill and contains the respiratory epithelium (Fig. 10).

Gladius - the chitinous remnant of the shell in many decapodiforms and *Vampyroteuthis*. It is generally feather-shaped and lies in the dorsal midline of the body along the full length of the mantle. The gladius lies within the shell sac which secretes it.

Hatchling - young cephalopod that has just hatched from the egg.

Hectocotylus - the modified arm in males used for transferring spermatophores to the female. In cirrillates the hectocotylus is one member of the ventrolateral arm pair while in decapodiforms frequently one or both members of the ventral arm pair are modified. Many species of coleoid cephalopods lack a hectocotylus (Figs 3, 11).

Hook - horny structure that looks like a single claw and is derived from the inner sucker ring in some decapodiforms. Hooks may be found on the arms and/or tentacular clubs of squid (Fig. 12).

Ink sac - organ composed of a gland that secretes ink, a sac that stores ink and a duct that connects it to the intestine. The ink sac generally appears black from the outside although it may be covered by silvery tissue in some species (Fig. 1).

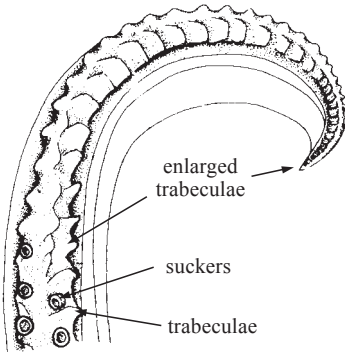


Fig. 11 hectocotylized arm of a squid

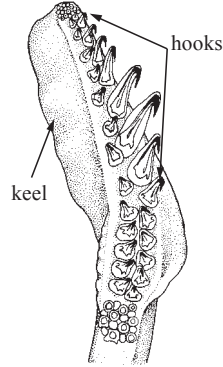


Fig. 12 tentacular club of an onychoteuthid squid

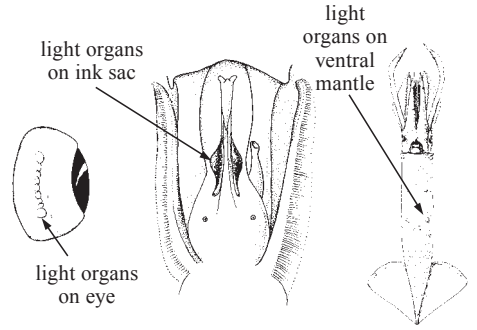


Fig. 13 examples of photophores

Integument - skin.

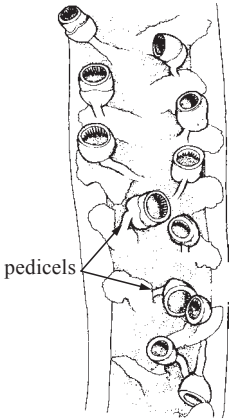


Fig. 14 detail of arm

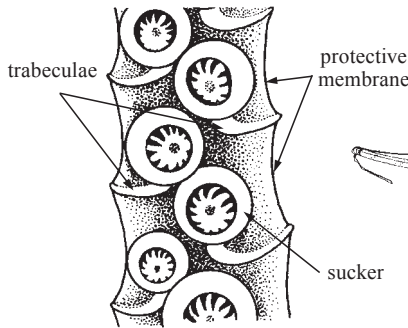


Fig. 15 detail of arm

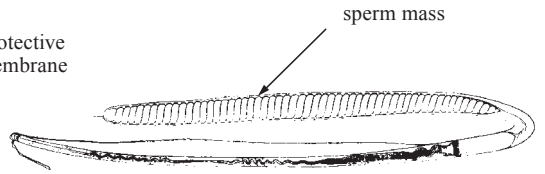


Fig. 16 spermatophore

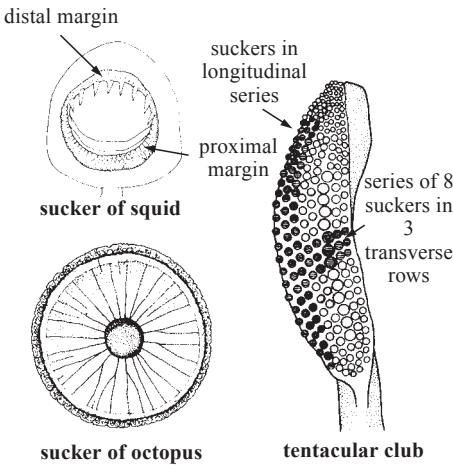


Fig. 17 suckers and how they are counted

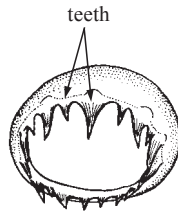


Fig. 18 sucker ring

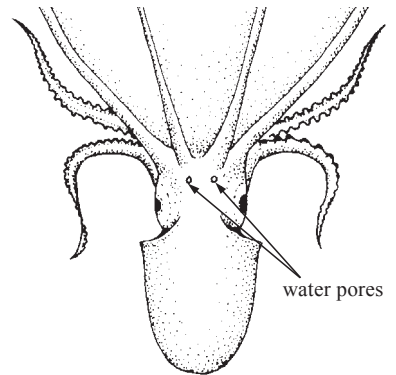


Fig. 19 dorsal view

- Intestine** - distal region of the alimentary canal between the stomach/caecum complex and the anus.
- Juvenile** - life history stage between the paralarval and subadult stages.
- Keel** - flap of tissue on the dorsal-aboral region of the arms and tentacular clubs in Decapodiformes (= swimming membrane).
- Lateral** - away from the midline.
- Lateral ridge** - muscular structure along the lateral region of the mantle of some octopods.
- Light organ** - see Photophore (Fig. 13).
- Ligula** - the portion of the sucker-free end-organ of the hectocotylus of many incirrate octopods that is generally elongate and grooved. The ligula in octopodids is often spatulate in shape with transverse ridges (Fig. 3).
- Mantle** - the fleshy, usually muscular, tube-like or sac-like body wall that covers the visceral region and encloses a space called the mantle cavity.
- Mantle cavity** - space enclosed by the mantle. In cephalopods the mantle cavity contains the visceral sac, gills, anus, openings of the gonoducts, nephridial pores and various muscles and septa.
- Mantle locking apparatus** - the mantle component (usually fibrous) of the structure that "locks" the mantle to the funnel. See Funnel locking apparatus.
- Mantle length (ML)** - the standard measure of length in coleoid cephalopods. In decapodiforms ML is measured along the dorsal midline from the mantle margin to the posterior tip of the body, excluding long tails. In octopodiforms ML is measured from a line joining the midpoint of the eyes (rather than the anterior mantle margin since the latter is obscured by the head/mantle fusion) to the posterior-most area of the mantle.
- Manus** - the central, usually expanded, region of the tentacular club.
- Mature** - in cephalopods this term refers to sexual maturity which is determined for females by the presence of ova (mature eggs) free in the coelom or oviducts, and for males by the presence of spermatophores in Needham's sac. See Adult.
- Medial** - toward the midline.
- ML** - abbreviation for Mantle Length, the standard length measurement for cephalopods.
- Neck** - the region separating the posterior end of the cephalic cartilage and the collar. Only those cephalopods with elongate heads (e.g., chiroteuthids) have distinct necks.
- Needham's sac** - the large storage sac for spermatophores that is an expanded region of the genital duct at the base of the penis in males.
- Nominal species** - a species that is based on a morphological type. A properly named species but not necessarily a valid species.
- Nidamental glands** - large glandular structures found in most decapodiforms and nautilids that lie in and open directly into the mantle cavity. The glands are composed of numerous lamellae that are involved in secretion of egg cases or the jelly of egg masses.
- Nuchal cartilage** - see Nuchal-locking apparatus.
- Nuchal crest** - prominent transverse ridge in most decapodiforms that extends across the dorsal and along the lateral surfaces of the head at its posterior end.
- Nuchal folds** - fixed folds of the head integument that adjoin the nuchal crest posteriorly and are perpendicular to it. The function of the folds is uncertain.
- Nuchal locking apparatus** - a cartilagenous locking structure in decapodiforms located mid dorsally just posterior to the head. It is composed of the nuchal cartilage, which also forms an attachment site for collar and head retractor muscles, and a cartilage on the mantle that underlies the gladius. The apparatus keeps the head and mantle aligned dorsally during mantle contractions.
- Nuchal region** - the posterodorsal region of the head and the area immediately posterior to it.
- Ocellus** - false eye spot found in pairs (ocelli) on some octopods between the eyes and the bases of the dorsolateral and ventrolateral arms. May enclose an iridescent ring.
- Ocular photophore** - photophore that lies on the eyeball.
- Oral** - toward or on the side of the mouth.
- Oviduct** - female gonoduct. The oviduct conducts eggs from the visceropericardial coelom, that holds the ovary, to the exterior and is often used to store eggs. In some argonautoid octopods eggs are fertilized and undergo either partial (*Argonauta*) or complete (*Ocythoe*) embryonic development within the oviduct.
- Oviducal gland** - gland surrounding the end of the primary oviduct and responsible for secreting some of the external coatings over spawned eggs.

Paralarva - first free-living life history stage for those cephalopods found in the plankton that differ in both morphology and vertical distribution from older juveniles.

Pedicle - decapodiform sucker stalk. On some hectocotyls, suckers may be lost and the pedicels elongated into papillae or expanded into flaps or ridges (Fig. 14).

Penis - the long, muscular end of the male gonoduct that assists in transferring spermatophores to the female. Apparently, in species with a hectocotylus, the penis transfers spermatophores to the hectocotylus which in turn transfers them to the female. In species without a hectocotylus, the penis is often greatly elongate, capable of extending beyond the mantle cavity and can, apparently, transfer spermatophores directly to the female.

Photophore - organ that produces bioluminescence or 'living light' (Fig. 13).

Posterior - toward the closed end of the mantle and tail, away from the head and arms.

Primary conus - a conus on the gladius that is not formed by the infolding of the vanes.

Protective membranes - membranes, generally supported by trabeculae, that form lateral borders to the oral surfaces of the arms and tentacular clubs (Fig. 15).

Proximal - situated toward the point of origin or attachment. For example, the proximal end of the arm is the basal end of the arm.

Pseudomorph - a mass of ink and mucous that roughly has the dimensions of the cephalopod that secreted it.

Radula - a toothed ribbon that lies in the buccal mass and that aids in movement of food into the esophagus.

Rhachis - the central axis of the gladius which is usually thickened (Fig. 6).

Rostrum (gladius) - section of the gladius that extends posteriorly or posterodorsally from the conus. A rostrum on the gladius is found only in the Onychoteuthidae, Ancistrocheiridae, Lampadioteuthinae and Vampyroteuthidae.

Secondary conus - a conical region at the posterior end of the gladius that is formed by a inrolling and fusion of the vanes. The ventral line of fusion is usually apparent. The secondary conus may be rather short or over half the gladius length.

Secondary web - web that extends from each arm to the primary web in some cirrate octopods. Separation of the arm from the primary web seems to be associated with feeding and/or defense (bell and balloon postures) but the function is not well understood.

Sepioid gills - gills of some cirrate octopods that look superficially like gills of sepioids.

Shell sac - the sac that secretes the shell in the Coleoidea. The sac is composed of ectodermal epithelium that invaginates during embryonic development to form an internal sac.

Side pockets - pockets formed by small membranous folds of integument lateral to the foveola in the funnel groove in ommastrephid and thysanoteuthid squids (Fig. 7).

Siphuncle - the tube-like extension of the body wall, coelom and an external covering tube that penetrates the phragmocone and regulates gas exchange into the phragmocone chambers.

Sperm mass - the coiled rope of sperm that lies within the spermatophore (Fig. 16).

Spermatophore - a packet of sperm that is formed by the male and passed to the female during mating. In most coleoids, this packet is very complex and contains a "rope" of sperm (= sperm mass), an ejaculatory apparatus and a cement body. Except for the sperm, the entire structure is non-cellular and consists of a complex architecture of secreted material (Fig. 16).

Stalk of tentacle - region of the tentacle proximal to the club.

Stalked eyes - eyes that extend from the head on stalks. Two types exist: (1) stalked eyes in which the optic lobe is adjacent to the eye and separated from the brain by a long optic stalk and (2) stalked eyes in which the optic lobe remains adjacent to the brain and long optic nerves extend from the lobe to the eye. The former type is found exclusively in the Cranchiidae.

Stomach - a muscular organ of the digestive system where primary digestion occurs. The stomach is generally lined with cuticular ridges to aid in grinding food, and is supplied with digestive enzymes from the digestive gland. The stomach may be greatly expandable in size and serve as a storage area until food can be fully processed.

Subadult - stage at which all of the characters that typically define the species are present. The Subadult Stage follows the Juvenile Stage and precedes the Adult Stage. A Subadult Stage is defined in cephalopods because the adult phase often is temporally abbreviated.

Subequal - nearly equal. Generally refers to the length of the arms when these appear to be approximately the same length. Arm lengths cannot be measured very accurately due to variation in their states of contraction.

Sucker - muscular suction-cup on the arms and tentacles and occasionally on the buccal supports. Suckers of decapodiforms contain horny rings that often bear teeth or sometimes form hooks (Fig. 17).

Sucker rings - suckers of decapodiforms have 2 types of hard, horny rings. One, the inner ring, lies around the inner walls of the acetabulum and often bears teeth. The other, the outer ring, is composed of numerous platelets and lies on the surface of the infundibulum.

Sucker series - the longitudinal rows of suckers on the arms or tentacles. Series (= longitudinal rows) contrasts with rows (= transverse rows) in describing sucker arrangement (Fig. 17).

Sucker stalk - the structure between the sucker and the arm. In octopods it is a cylindrical structure about the same width as the sucker and in decapodiforms it is constricted into a conical pillar (= pedicel).

Sucker teeth - teeth on the inner, horny sucker rings of some decapodiforms (Fig. 18).

Tail - posterior narrow extension of the body posterior to the fins. The end of the fins and the beginning of the tail often overlap. An operational definition for point of demarcation for the purposes of measurement is: The point where a hypothetical line, continuous with the broad posterior edge of the fin, crosses the midline of the body.

Tentacles - modified fourth pair of arms in decapodiforms that are capable of considerable extension and contraction. Each tentacle consist of a proximal stalk usually devoid of suckers, and a distal club armed with suckers and occasionally hooks.

Tentacular club - the terminal, usually expanded part of the tentacle which bears suckers and/or hooks.

Tentacle pocket - an invagination of the anteroventral area of the head between the bases of the ventrolateral and ventral arms of sepoids and loliginids into which the tentacles can be (at least partially) withdrawn.

Terminal pad of tentacular club - a small, distinct pad or circlet of suckers at the tip of the club.

Terminal fins - fins with more than 50% of their length posterior to the muscular mantle. These fins, therefore, are at the "terminal" or posterior end of the body and are generally supported by an elongate secondary conus of the gladius.

Trabeculae - muscular cones or flaps that support the protective membranes on the arms and tentacular clubs in decapodiforms. These are thought to be homologous with the cirri of the octopodiforms.

Tragus - particular inward projecting knob on the medial surface of the central depression in the funnel locking apparatus of some squids.

Truncate teeth - teeth on the inner horny of rings of decapodiform suckers that do not terminate in a point but rather a broad, flat tip.

Vane (= wing; lateral field) - broad, lateral portion of the gladius that arises from the rachis.

Ventral - toward the lower surface of the animal (i.e., the side on which the funnel is located).

Vesicular tissue - tissues found in some decapodiforms that contain numerous vesicles filled with water that usually contains ammonium chloride. The vesicles may be concentrated in certain structures (e.g., the ventral arms) or scattered throughout the animal. The light solution in the vesicles provide buoyant lift.

Water pores - one or 2 pairs of pores in the integument of the head that communicate with extensive spaces at the bases of arms on some pelagic argonautoid octopods (Fig. 19).

Web - muscular membrane that extends between the arms of many octopodiforms but is reduced or absent in most decapodiforms.

KEY TO FAMILIES OCCURRING IN THE AREA

- 1a. Suckers stalked with chitinous rings; usually 10 circumoral appendages (8 arms and 2 ventrolateral tentacles) although tentacles may be lost in some species **(Decapodiformes) → 2**
- 1b. Suckers without stalks (although bases sometimes constricted in finned octopods and *Vampyroteuthis*) and without chitinous rings; 8 arms but no ventrolateral tentacles
 **(Octopodiformes) → 26**
- 2a. Internal shell rudimentary or coiled and chambered; posterior mantle blunt **→ 3**
- 2b. Internal shell (gladius) extending the full length of the mantle and pen-shaped or feather-shaped; posterior mantle usually pointed (not in *Bathothauma*, *Bathyteuthis*, or *Pickfordiateuthis*) **→ 4**

- 3a. Shell calcified, coiled, chambered (Fig. 20) **Spirulidae**
- 3b. Shell chitinous and rudimentary or absent (Fig. 21) **Sepiolidae**

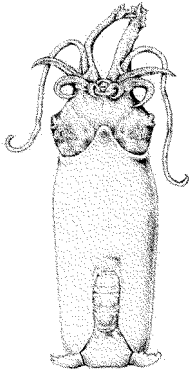


Fig. 20 Spirulidae

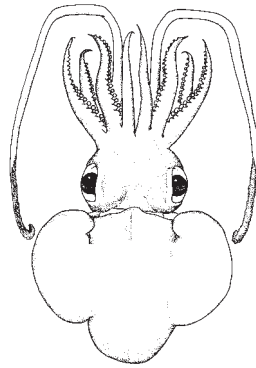


Fig. 21 Sepiolidae

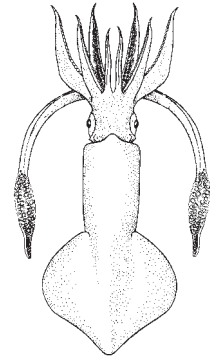


Fig. 22 Loliginidae

- 4a. Eye covered by a transparent membrane (cornea) (Fig. 22) **Loliginidae**
- 4b. Eye without cornea; lens in open contact with seawater → 5
- 5a. Funnel free from mantle; a funnel-mantle locking apparatus present → 6
- 5b. Funnel fused to mantle on each side; no funnel-mantle locking apparatus present → 25
- 6a. Funnel-mantle locking apparatus a simple, straight groove and ridge (the classification "simple and straight" includes some locking apparatuses that show considerable variation; for example, in the Octopoteuthidae and the Histiotteuthidae the central groove is fairly broad and may curve slightly; the homogeneity of this classification becomes apparent when this type of locking cartilage is contrasted with the more highly specialized types) → 7
- 6b. Funnel-mantle locking apparatus not a simple, straight groove and ridge → 20
- 7a. Arms with hooks. → 8
- 7b. Arms without hooks. → 11

- 8a. Tentacles and clubs absent in adults although present in paralarvae or occasionally juveniles (*Taningia*) but, when present, always with rudimentary clubs armed with few suckers (Fig. 23) **Octopoteuthidae**
- 8b. Tentacles present; fully developed clubs present → 9

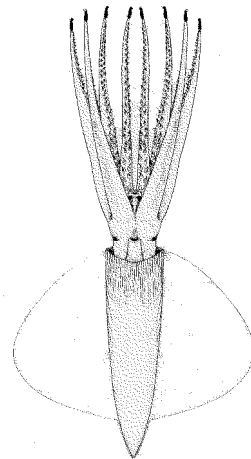


Fig. 23 Octopoteuthidae

- 9a. Photophores on viscera but not on mantle or surface of head or arms (Fig. 24) **Pyroteuthidae**
- 9b. Photophores on mantle and surface of head and arms but not on viscera. → **10**
- 10a. Photophores on tentacles but not on eyeballs (Fig. 25) **Ancistrocheiridae**
- 10b. Photophores on ventral eyeballs but not on tentacles (Fig. 26) **Enoploteuthidae**

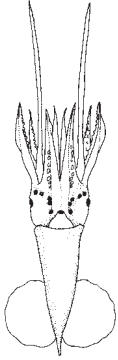


Fig. 24 Pyroteuthidae

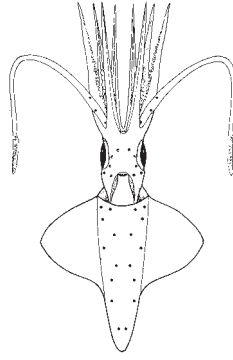


Fig. 25 Ancistrocheiridae

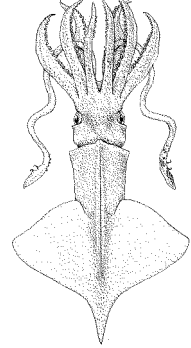


Fig. 26 Enoploteuthidae

- 11a. Buccal membrane connectives attach to the ventral sides of ventral arms. → **12**
- 11b. Buccal membrane connectives attach to the dorsal sides of ventral arms (this character is difficult to detect in some histioteuthids which have secondary modifications to the buccal membrane connectives) → **16**

- 12a. Hooks present on tentacular clubs (tentacles and clubs are lost in mature animals) (Fig. 27) **Onychoteuthidae**
- 12b. Hooks lacking on tentacular clubs → **13**

- 13a. Cartilaginous scales present on mantle (may be minute); tentacular clubs with 4 longitudinal series of suckers → **14**

- 13b. Cartilaginous scales lacking; tentacular clubs with more than 4 longitudinal series of suckers on some areas → **15**

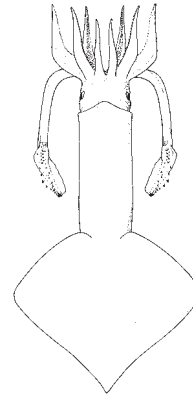


Fig. 27 Onychoteuthidae

- 14a. Tentacles present; with numerous, laterally compressed suckers (Fig. 28) **Pholidoteuthidae**
- 14b. Tentacles lost in adults; tentacles in juveniles small and weak, with few (about 6) poorly differentiated suckers (Fig. 29) **Lepidoteuthidae**

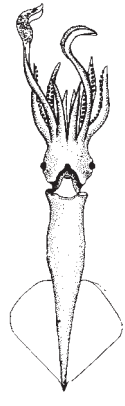
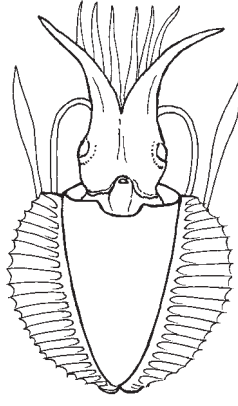
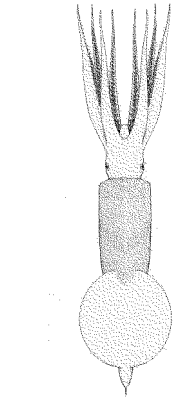
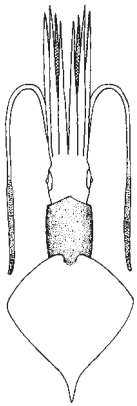


Fig. 28 Pholidoteuthidae Fig. 29 Lepidoteuthidae Fig. 30 Ctenopterygidae Fig. 31 Brachioteuthidae

- 15a. Fins nearly as long as the mantle, supported by strong, transverse, muscular ribs; minute suckers present on oral surface of buccal membrane (Fig. 30) **Ctenopterygidae**
- 15b. Fins less than half the mantle length and without supporting ribs; no suckers on buccal lappets (Fig. 31) **Brachioteuthidae**

- 16a. Row of photophores on ventral surface of eye; buccal membrane with 8 separate lappets (Fig. 32) **Lycoteuthidae**
- 16b. No photophores on eyes; buccal membrane with 7 lappets or less → 17

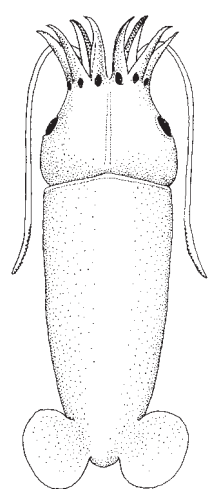
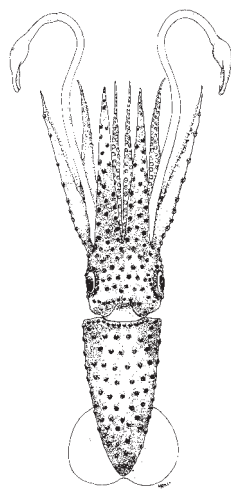
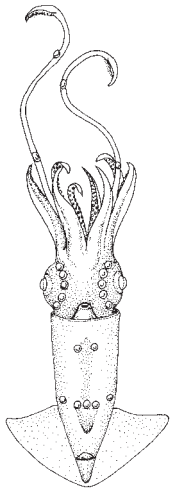


Fig. 32 Lycoteuthidae Fig. 33 Histioteuthidae Fig. 34 Bathyteuthidae

- 17a. Surface of mantle, head and arms covered with numerous photophores, usually large and distinct (Fig. 33) **Histioteuthidae**
- 17b. Surface of mantle and head without photophores (arms may have a few photophores) → 18

- 18a. Minute suckers present on oral surface of buccal membrane (Fig. 34) **Bathyteuthidae**
- 18b. No suckers on oral surface of buccal membrane → 19

- 19a. Posterior borders of fins convex; carpal knobs in a single dorsal row or absent; adults not gigantic (Fig. 35) **Neoteuthidae**
- 19b. Posterior borders of fins concave; carpal knobs in a cluster alternating with carpal suckers; attains gigantic size (Fig. 36) **Architeuthidae**

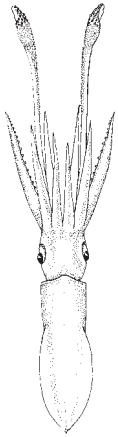


Fig. 35 Neoteuthidae

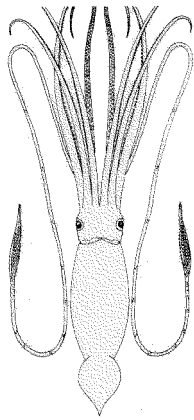


Fig. 36 Architeuthidae

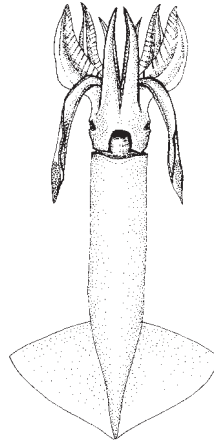


Fig. 37 Ommastrephidae

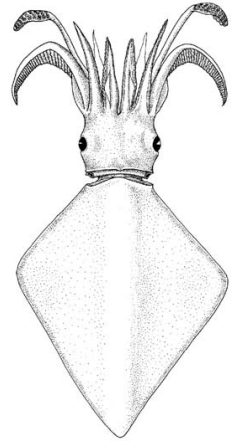


Fig. 38 Thysanoteuthidae

- 20a. Funnel locking apparatus with a longitudinal and a transverse groove → 21
- 20b. Funnel locking apparatus oval, triangular or oval with inward projecting knobs → 22

- 21a. Funnel locking cartilage T-shaped, with a longitudinal groove crossed by a transverse groove at its posterior end; fins less than 60% of mantle length (Fig. 37) **Ommastrephidae**
- 21b. Funnel locking cartilage shaped like a sidewise T, with a longitudinal groove from which a shorter groove branches medially; fins more than 80% of mantle length (Fig. 38) **Thysanoteuthidae**

- 22a. Funnel locking cartilage oval with posterior shelf or 1 or 2 knobs directed toward the centre of the concavity → 23
- 22b. Funnel locking cartilage oval or subtriangular, without shelf or knobs. → 24

- 23a. Club with suckers in 4 series (Fig. 39) **Chiroteuthidae**
- 23b. Club with many (more than 15) series of minute suckers (Fig. 40) **Mastigoteuthidae**

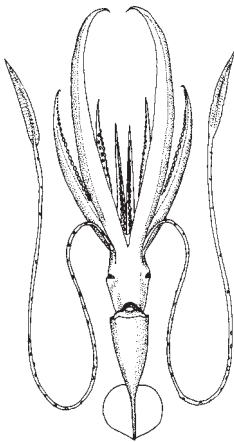


Fig. 39 Chiroteuthidae

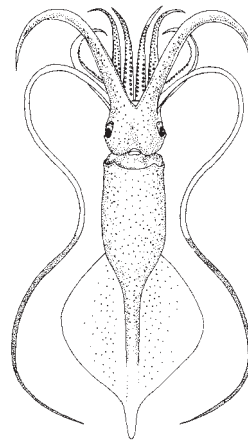


Fig. 40 Mastigoteuthidae

24a. Suckers on arms in 4 to 6 series; tail extremely long, greater than the mantle length (Fig. 41). **Joubiniteuthidae**

24b. Suckers on arms in 2 series; tail short (less than half the mantle length) or absent (Fig. 42) **Cycloteuthidae**

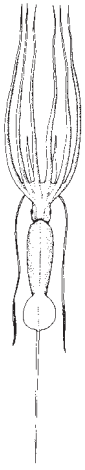


Fig. 41 Joubiniteuthidae

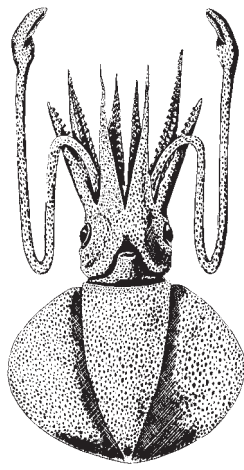


Fig. 42 Cycloteuthidae

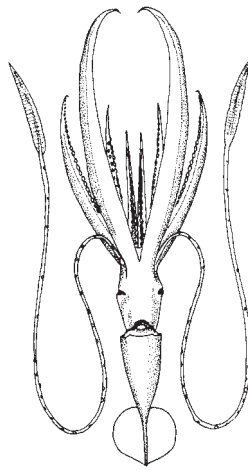


Fig. 43 Chiroteuthidae



Fig. 44 Cranchiidae

25a. Mantle free from head dorsally, articulates with head by ridge and groove *Grimalditeuthis* (Fig. 43) **Chiroteuthidae**

25b. Mantle fused dorsally with head (Fig. 44) **Cranchiidae**

26a. Fins present; cirri on arms → 27

26b. Fins and cirri absent → 30

27a. Filamentous appendages present in pouches between bases of dorsal and dorsolateral arms; light organ present at base of each fin; colour dark maroon to black (Fig. 45). **Vampyroteuthidae**

27b. Both filaments and fin light organs at bases of fins absent; colour variable to dark maroon, never black → 28

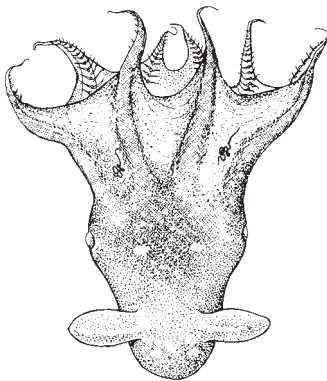


Fig. 45 Vampyroteuthidae

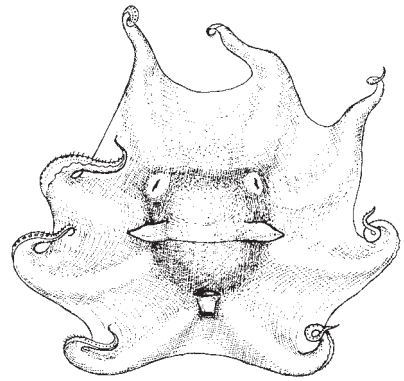


Fig. 46 Opisthoteuthidae

28a. Web attaches directly to arms (Fig. 46) **Opisthoteuthidae**

28b. Contractile intermediate membrane (secondary web) present between each arm and the primary web → 29

- 29a. Shell (cartilaginous fin support) simple, U-shaped (Fig. 47) **Stauroteuthidae**
- 29b. Shell more complex, with expanded fin-attachment areas (Fig. 48) **Cirroteuthidae**

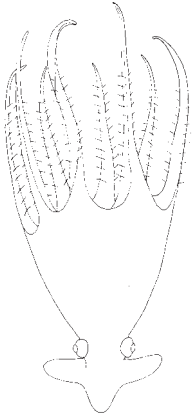


Fig. 47 Stauroteuthidae

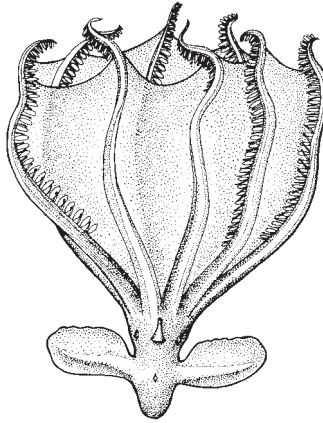


Fig. 48 Cirroteuthidae

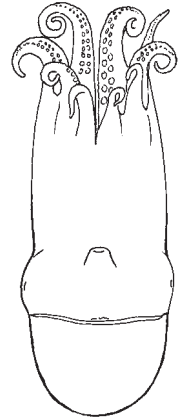


Fig. 49 Alloposidae

- 30a. Muscle tissue of body gelatinous → 31
- 30b. Muscle tissue of body firm (may be covered by gelatinous subdermal layer). → 34

- 31a. Suckers biserial distal to edge of web (Fig. 49) **Alloposidae**
- 31b. Suckers uniserial along entire length of arms → 32

- 32a. Digestive gland very elongate, spindle-shaped, pointed at one end (Fig. 50) **Vitreledonellidae**
- 32b. Digestive gland oblong, not pointed at end → 33

- 33a. Eyes tubular (Fig. 51). **Amphitretidae**
- 33b. Eyes, though not necessarily round, not tubular **Bolitaenidae**

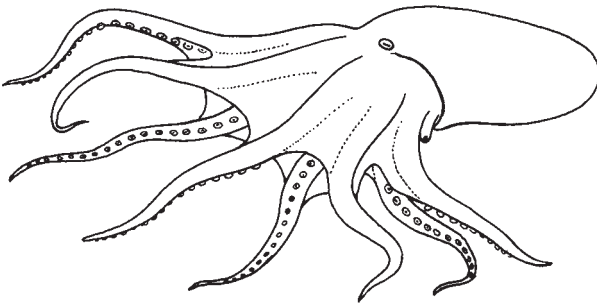


Fig. 50 Vitreledonellidae

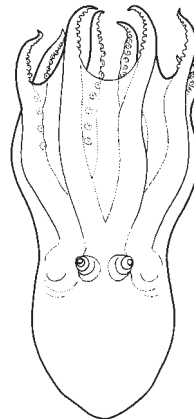


Fig. 51 Amphitretidae

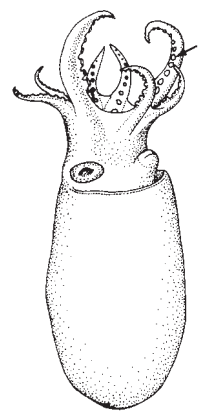


Fig. 52 Bolitaenidae

34a. Funnel locking apparatus absent; water pores on head absent; males not very much smaller than females, with left or right ventrolateral arm hectocotylized (never in pocket), with spoon-shaped, non-filamentous tip; females without dorsal arm flaps or permanent reticulate sculpturing of ventral mantle (Fig. 53) **Octopodidae**

34b. Funnel locking apparatus present; dwarf males very much smaller than females, hectocotylus (left ventrolateral arm) temporarily coiled in sac below eye, with extremely long filamentous tip → **35**

35a. Water pores present on head at bases of both dorsal and ventral arms; dorsal and dorsolateral arms of female joined by very deep, thin web (Fig. 54) **Tremoctopodidae**

35b. Dorsal water pores absent; web, when present, not as above → **36**

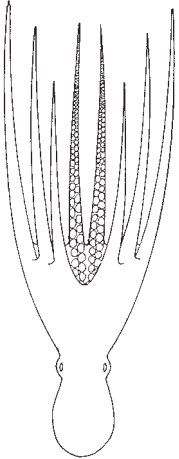


Fig. 53 Octopodidae

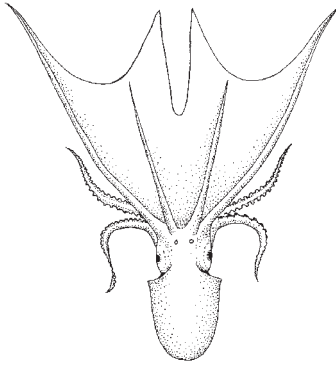


Fig. 54 Tremoctopodidae

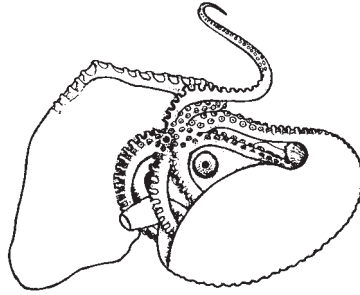


Fig. 55 Argonautidae

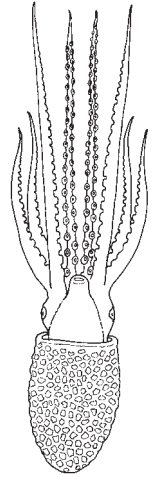


Fig. 56 Ocythoidae

36a. Dorsal arms of females with broad, membraneous flap that secretes and holds a thin, shell-like egg case; males with hectocotylus in non-stalked sac beneath eye (Fig. 55) . **Argonautidae**

36b. Females with permanent reticulate sculpturing of ventral mantle; dorsal arms of females lacking broad, membraneous flap; no shell-like egg case; males with hectocotylus in stalked sac beneath eye (Fig. 56) **Ocythoidae**