1. INTRODUCTION

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The increasing exploitation of finfish resources, and the depletion of a number of major fish stocks that formerly supported industrial-scale fisheries, forces continued attention to the once-called 'unconventional marine resources', which include numerous species of cephalopods. Cephalopod catches have increased steadily in the last 40 years, from about 1 million metric tonnes in 1970 to more than 4 million metric tonnes in 2007 (FAO, 2009). This increase confirms a potential development of the fishery predicted by G.L. Voss in 1973, in his first general review of the world's cephalopod resources prepared for FAO. The rapid expansion of cephalopod fisheries in the decade or so following the publication of Voss's review, meant that a more comprehensive and updated compilation was required, particularly for cephalopod fishery biologists, zoologists and students. The FAO Species Catalogue, 'Cephalopods of the World' by C.F.E. Roper, M.J. Sweeney and C.E. Nauen was published in 1984 to meet this need.

The number of cephalopod species that enter commercial fisheries has continued to grow significantly since 1984, as a result of a still-growing market demand and the expansion of fisheries operations to new fishing areas and to deeper waters. It has been suggested that the cephalopod 'life-strategy' may guarantee survival against environmentally stressful conditions, including those caused by heavy fishing. However, as cephalopod fisheries experienced further extensive development, parallel concern developed regarding potential overexploitation. Thus, a broad consensus emerged among fishery biologists to apply the experience gained from errors made in finfish management to avoid possible failures in cephalopod exploitation. To help prevent potential failures, refined species identification capabilities are required, as well as a more detailed and accurate compilation of information on cephalopod species, distribution, biology, fisheries and catch statistics. Consequently, FAO recognized that a new edition of the 'Cephalopods of the World' catalogue was required. To achieve this expanded goal, several authors with particular areas of specialization were assembled to enhance the accuracy, coverage and utility of this revised catalogue.

In our attempt to make this document as comprehensive and as useful as possible, the taxonomic coverage of this edition of the catalogue is organized into 3 levels of interest:

Level 1: species of cephalopods currently exploited commercially and species utilized at the subsistence and artisanal levels;

Level 2: species of occasional and fortuitous interest to fisheries; this includes species considered to have a potential value to fisheries, based on criteria such as edibility, presumed abundance, accessibility, marketability, etc.; species of actual or potential interest to research museums also are considered under this level.

Level 3: species with no current interest to fisheries, which are listed only with the basic information available.

The inclusion of such a wide range of species is necessary to provide the most comprehensive inventory of species potentially useful to mankind, regardless of their current commercial status. For example, this work should be useful for the ever-expanding search for development and utilization of 'natural products', pharmaceuticals, etc.

The catalogue is based primarily on information available in published literature. However, yet-to-be-published reports and working documents also have been used when appropriate, especially from geographical areas where a large body of published information and data are lacking. We are particularly grateful to colleagues worldwide who have supplied us with fisheries information, as well as bibliographies of local cephalopod literature.

The fishery data reported herein are taken from the FAO official database, now available on the Worldwide web: FISHSTAT Plus 2009. This information is supplemented by field observations made by the authors in many parts of the world, both in preparation of the 1984 volume, as well as for the current edition. These field visits provided opportunities to examine fresh material at landing sites, markets and laboratories, as well as to obtain first-hand information about local cephalopod fisheries from regional fisheries workers. Additional examinations of preserved specimens occurred in museums.

During the 20-plus years separating the two editions, the rapid development of cephalopod fisheries worldwide and the simultaneous increase in the population of fisheries scientists, their research and publications, made available an enormous amount of new data and research results. Sometimes it is difficult to evaluate the reliability of published data, especially with regard to the identification of species in areas where the cephalopod fauna has not been sufficiently studied taxonomically. It is entirely understandable that field workers isolated from good library and museum/collection facilities find it difficult to correctly identify the species they encounter in the field. Moreover, the discovery of new species, the more accurate delimitation of known species, or even the introduction of nomenclatural changes, may cause confusion and lead to the use of scientific names that are incorrect by modern standards. Although great care was exercised to evaluate and correct such published information used in the preparation of this catalogue, some incorrect interpretations may have occurred. Another potential limitation, in the taxonomic literature especially, is that information on the economic importance of species is rather scarce or of a very general nature. Also, important information may have been overlooked if published only in local fisheries literature that is unavailable on an international scale. All of these potential limitations, however, have been significantly mitigated during the preparation of the new edition because of the availability of on-line fisheries databases and bibliographic search capabilities.

With regard to the limitations mentioned above, we heartily request that readers who detect any errors in the information presented, or who have additional information and data that will enhance the accuracy and utility of this book, please contact and inform one of the authors or the Species Identification and Data Programme (SIDP) of the Marine Resources Service, Fisheries Resources Division, Fisheries Department, FAO Rome.

For further reading and information on cephalopod biology, fisheries and resources, several references and websites are listed at the end of references.

1.1 Plan of the Catalogue

This catalogue is organized by families and their appropriate genera within major cephalopod groups. The type genus within each family is treated first, then all remaining genera are listed alphabetically. The type species within each genus is treated first, then all species are listed alphabetically.

Level 1 includes the most important species for fisheries utilization, and it consists of detailed information in all 12 categories listed below. **Level 2**, which comprises those species of occasional or potential interest to fisheries, consists of whatever information is available and appropriate for the 12 categories. **Level 3**, those species for which there is no current direct or indirect interest to fisheries, consists of basic information (i.e. scientific name, size, geographical distribution, literature). The format within the species sections includes the first two levels of treatment (Level 1 and Level 2) presented together. Species included in Level 3 are presented at the end of each family.

Consequently, each major group and family is introduced with general descriptive remarks, illustrations of diagnostic features, highlights of the biology and relevance to fisheries. The information that pertains to each species in Levels 1 and 2 is arranged by categories as follows: (1) scientific name; (2) synonymy; (3) misidentifications; (4) FAO names; (5) diagnostic features with illustrations; (6) maximum known size; (7) geographical distribution with map; (8) habitat and biology; (9) interest to fisheries; (10) local names; (11) remarks (12) literature.

(1) Scientific Name: Reference to author, date and publication citation is given for the original description of each species.

(2) Frequent Synonyms: Principal synonyms and name combinations are listed. Due to the complex situation/evolution of Myopsid and Oegopsid squid systematics in the last decades, this section is particularly detailed in this volume; even synonyms not “frequent” in a common language usage and/or different names used for species by different authors are reported, as an additional tool/information to the users.

(3) Misidentifications: Misidentifications as other species are reported here and discussed in detail when appropriate under section 11, Remarks, along with other nomenclatural points.

(4) FAO Names: English, French and Spanish names for each species, used primarily within FAO, are selected on the basis of the following criteria: (i) each name must apply to one species only, in a worldwide context; (ii) the name must conform to FAO nomenclatural spelling; (iii) the name should apply only to a cephalopod species, and should not lead to confusion with species names in other major animal groups. Wherever possible, these names are selected based on vernacular names (or parts of names) already in existence within the areas where the species is fished. FAO species names, of course, are not intended to replace local species names, but they are considered necessary to overcome the considerable confusion caused by the use of a single common name for many different species, or several names for the same species.

(5) Diagnostic Features: Distinctive characters for the species are given as an aid for identification, accompanied by pertinent illustrations. Species identifications should be attempted only after verification of the family through use of the illustrated key to families. Reference to FAO Species Identification Guides is given wherever relevant.

(6) Size: The known mantle length (or total length in some cases) of both males and females is provided where possible. Sizes or measurements might not be completely comparable because they were taken mostly from preserved or fixed specimens, but measurements of commercially important species often come from fresh material. Because of the elasticity of tentacles and arms, total length is not a very accurate measurement. Where both total length and mantle length are given, the respective figures do not necessarily pertain to the same specimen but may have been obtained from different sources. The available information on the size attained by some species often is very meagre, so the maximum reported size cited here might be considerably smaller than the actual maximum size. Maximum weight is given when available.

(7) Geographical Distribution: The entire known geographic range of the species, including areas of seasonal occurrence, is given in the text and shown on a map. In cases where only scattered records of occurrence are available, question marks have been used to indicate areas of suspected or unconfirmed distribution.

(8) Habitat and Biology: The known depth range of the species and information on salinity and temperature of its habitat are given where available. For the sake of exactness actual depth data are reported, as given in the referenced literature. Information on biological aspects, such as migration, spawning season and area, longevity, prey, and predators, also is included. Due to the dominant role of squids in the marine environment, this section is especially detailed in this volume.

(9) Interest to Fisheries: This paragraph gives an account of the areas where the species is fished and of the nature of the fishery; its importance either is qualitatively estimated (minor, moderate, major or potential) or actual figures of annual landings are provided. Data on utilization (fresh, dried, cooked, frozen, canned, etc.) also are given where available. Here, too, the quality and quantity of the available information varies considerably among the species, and it is reported in as much detail as possible in relation to the squid’s significance to the fisheries.

(10) Local Names: These are the names used locally for the topic species. The present compilation is necessarily incomplete, since only a fraction of the local names applied to specific entities actually is published. In many cases, local names are available only for species that support traditional fisheries. Apart from possible omissions due to limitations of literature available, some of the names included may be somewhat artificial, i.e. through transliteration of indigenous words into English. The local species name is preceded by the name of the country concerned in capital letters and, where necessary, by geographical specifications in lower case letters.

(11) Remarks: Important information concerning the species, but not specifically linked to any of the previous categories, is given here. For example, in some cases the taxonomic status of certain scientific names requires further discussion. Other nomenclatural problems are discussed in this section, such as the use of subspecies names.

(12) Literature: This includes references to the most important publications relevant to the species, particularly on biology and fisheries. Additional references are included in the bibliography. In the case of a few uncommon species, only systematic papers are available. The massive amount of literature relevant to fisheries for many species of squids required that appendices be compiled for this Volume. The appendix includes a list of publications useful to gain an understanding of the species biology, ecology and fisheries. Publications are listed by author's name, date of publication and key words for the publication's contents.

1.2 General Remarks on Cephalopods

The group known as cephalopods (class **Cephalopoda**) is the most complex in the phylum Mollusca, and indeed, in all of the invertebrate phyla. Cephalopods include exclusively marine animals that live in all oceans of the world with the exception of the Black Sea, from the Arctic Sea to the Antarctic Ocean and from the surface waters down into the deep sea.

Cephalopods first appeared as a separate molluscan taxonomic entity, the nautiloids, in the Upper Cambrian period (over 500 million years ago), but more than half of these ancestors were already extinct by the end of the Silurian, 400 million years ago, when only the nautiluses survived. Meanwhile, other forms arose in the late Palaeozoic (between 400 and 350 million years ago), including those of the Subclass Coleoidea, but most of them became extinct by the end of the Mesozoic, about 150 million years ago. The only members of the subclass Coleoidea that exist today are the forms that developed in the Upper Triassic and Lower Jurassic (between 200 and 150 million years ago).

Although there is a long fossil record of many different groups, all living cephalopods belong to two 'subclasses': the **Coleoidea**, which includes the major groups known as squids, cuttlefishes *sensu lato*, octopods and vampires, and the **Nautiloidea**, containing two genera, ***Nautilus*** and ***Allonautilus***, the only surviving cephalopods with an external shell.

At the present time the status and understanding of the **Systematics** and **Classification** of the Recent Cephalopoda is under considerable discussion. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa usually can be placed in well-defined families. The higher classification, however, still is not resolved. The classification above the family level is controversial and a broad consensus still needs to be achieved. This situation is not unexpected for a group of organisms that has undergone explosive research attention in recent decades.

Consequently, rather than accept and promote any particular scheme of classification, before consensus and stability are achieved, we will use an 'operational breakdown' that is satisfactory for the objectives of this Catalogue. For practical purposes we separate the cephalopods into several groups, without assigning or implying taxonomic relationships. **Figure 1** diagrams several of the classification schemes currently under discussion.

In this work the following groups are used, as illustrated in **Figure 2**[1/]:

Nautiluses
Cuttlefishes
Bobtail squids
Bottletail squids
Pygmy squids
Ram's horn squid
Myopsid squids
Oegopsid squids
Vampires
Cirrate octopods
Incirrate octopods

Unresolved taxa:

Spirula
Idiosepius
Bathyteuthis
Chtenopteryx
Sepiadariidae

Plural versus singular usage of cephalopod common group names is standardized as follows:

squid, cuttlefish, octopod, octopus, vampire, nautilus refer to one individual or one species;

squids, cuttlefishes, octopods, octopuses, vampires, nautiluses refer to two or more individuals and/or species. These terms are also used to indicate the major groups.

The term '**cuttlefishes**' also is used '*sensu lato*' to indicate the following groups: Cuttlefishes, Bobtail squids, Bottletail squids, Pygmy squids and the Ram's horn squid. Cuttlefishes, along with Nautiluses were treated in Volume 1 (Jereb and Roper, 2005).

We differentiate between the members of the family Octopodidae, which are called **octopus/octopuses**, and the members of the whole group (Incirrate and Cirrate or any combination of non-Octopodidae taxa), which are called **octopod/octopods**. Octopods will be treated in Volume 3.

This second volume of the Catalogue is focused on Squids.

1.3 General Remarks on Squids

Squids occur in almost all marine habitats of the world. Salinity is considered to be a limiting factor in squids distribution; they are generally restricted to salinity concentrations between 27 and 37‰. However, ***Lolliguncula brevis***, which lives and reproduces in waters of 17‰, demonstrates a capacity for a higher degree of salinity tolerance (Hendrix *et al*., 1981). Some species

[1/] The endings used in the group names do not imply any level of classification.

Roper *et al*. (1984)

Order	Suborder
Teuthoidea	Myopsida
Sepioidea	
Vampyromorpha	
Octopoda	Cirrata
	Incirrata

Engeser and Bandel (1988)

Superorder	Order	Suborder
Decapoda	Spirulida	
	"higher decapods" (name not given)	Teuthina
		Sepiina
Vampyromorphoidea	Vampyromorpha	
	Octopoda	Cirrata
		Incirrata

Clarke (1988b)

Order	Suborder
Sepioidea	
Sepiolioidea	
Teuthoidea	Myopsida
	Oegopsida
Vampyromorpha	
Octopoda	

Sweeney and Roper (1998)

Superorder	Order	Suborder
Decabrachia	Spirulida	
	Sepiida	
	Sepiolida	
	Teuthida	Myopsina
		Oegopsina
Octobrachia	Vampyromorphida	
	Octopodida	Cirrina
		Incirrina

Young *et al*. (1998a)

Division	Superorder	Order	Suborder
Neocoleoidea	Decapodiformes	Oegopsida	
		Myopsida	
		Sepioidea	Sepiida
			Sepiolida
			Spirulida
			Incertae sedis
	Octopodiformes	Vampyromorpha	
		Octopoda	Cirrata
			Incirrata

Boletzky (1999)

Grade	Superorder	Order
	Decabrachia	Spirulida
		Sepiida
		Sepiolida
		Idiosepiida
		Teuthida
Vampyropoda	Pseudooctobrachia	Vampyromorpha
	Octobrachia	Cirroctopoda
		Octopoda

Haas (2002)

1	2	3	4	5
Neocoleoidea	Decabrachiomorpha	Oegopsida		
		Uniductia	Spirulida	
			Myopsida	Loliginida
				Sepiida
	Octobrachiomorpha	Vampyromorpha		
		Octopoda	Cirrata	
			Incirrata	

Fig. 1 Some conflicting suprafamilial classifications of living coleoid cephalopods

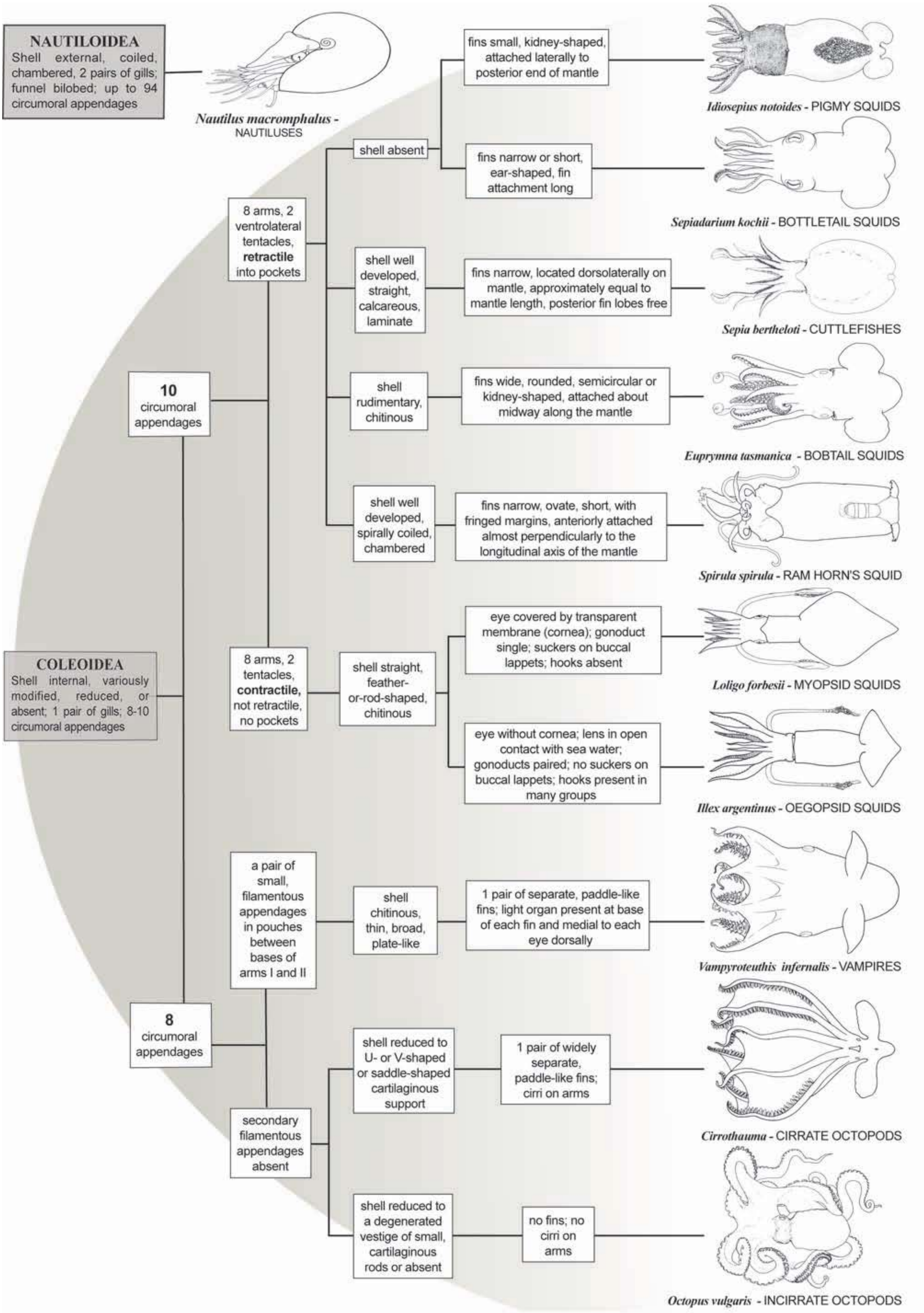


Fig. 2 Living cephalopods

inhabit the Red Sea and the southern coasts of the Iberian Peninsula (Guerra, 1992), where the salinity is higher than 37‰ and other species have been found in waters where salinity ranges between 25 and 18‰ (Sea of Marmara; Unsal *et al.*, 1999). The habitat depth range extends from the intertidal to over 5 000 m. Many species of oceanic squids undergo diel vertical migrations: they occur at depths of about 200 to 700 m during the day, then at the onset of twilight and increasing darkness, they ascend into the uppermost 200 m for the night. A deeper-living layer of diel migrators occurs from about 1 000 m to 600 m during the daytime. The abundance of squids varies, depending on genera, habitat and season, from isolated individuals, small schools with a few dozen individuals, to huge schools of neritic and oceanic species with millions of specimens.

General charcteristics

The size of adult squids ranges from less than 10 mm mantle length (e.g. some members of the family Pyroteuthidae) to the giant squid ***Architeuthis*** sp. and the colossal squid ***Mesonychoteuthis hamiltoni***, at well over 2 m mantle length. The largest specimens may weigh over 500 kg, but the average size of commercial species is 200 to 400 mm mantle length and about 0.1 to 2.0 kg total weight.

Squids are easily distinguished by external characteristics: they have an elongate, cylindrical body with posterolateral fins on the mantle (rarely, the fins extend for the length of the mantle); 10 circumoral appendages anteriorly on the head, not connected at bases with a web (except Histioteuthidae); 8 arms with 2 (occasionally 4 or more) series of stalked suckers with chitinous rings (and/or chitinous hooks in some groups) that extend along the entire arm length; 2 longer tentacles with an organized cluster of 2 or more series of stalked suckers (and/or hooks) at the distal section (tentacular club); the proximal tentacular stalks usually are devoid of suckers or hooks.

Squids are soft-bodied, bilaterally symmetrical animals with a well-developed head and a body that consists of the muscular mantle, the mantle cavity that houses the internal organs, and the external fins. The head bears an anterior circum-oral (surrounding the mouth) crown of mobile appendages (arms, tentacles). Arms and tentacles bear suckers and/or hooks, which are powerful tools to seize prey. The mouth, at the interior base of the arm crown, has a pair of chitinous jaws (the beaks) and, as in other molluscs, a chitinous tongue-like radula (band of teeth).

The ancestral mollusc shell is reduced to a rigid structure composed of chitin, the gladius or pen, sometimes quite thin and flexible.

The loss of the external shell allowed the development of a powerful muscular mantle that became the main locomotory organ for fast swimming, via water jettisoned from the funnel. The funnel (also known as siphon, an archaic term correctly applied to some other molluscs, but not to modern, extant cephalopods) is a unique, multifunctional, muscular structure that aids in respiration and expulsion of materials, in addition to locomotion. Oxygenated water is drawn through the mantle opening around the head (neck) into the mantle cavity, where it bathes the gills for respiration. Muscular mantle contraction expels the deoxygenated water from the mantle cavity through the ventrally located funnel. The discharge jet serves to eliminate nephridial and digestive wastes, as well as to complete the respiratory cycle and for locomotion. Female reproductive products (eggs, egg masses) also are discharged through the funnel. Squids produce ink, a dark, viscous fluid also expelled through the funnel. The ink may take the form of a mucoidal 'pseudomorph' (false body) to decoy potential predators, or of a cloud to obscure the escaping cephalopod.

One pair of gills (ctenidia) is present, for respiration, i.e. to extract the oxygen from the water. Squids may use anerobic muscle layers, and cutaneous respiration also occurs.

The circulatory system

The circulatory system is distinctive within the Mollusca. It is a closed system (blood contained within vessels), similar in many respects to that of vertebrates, that fulfills the demand for the more efficient circulation required by an active locomotory system. The system is composed of a principal, or systemic, heart, two branchial hearts and developed arterial, venous and capillary systems that supply blood to the muscles and organs. The oxygenated blood passes from the gills through the efferent branchial vessels to the systemic heart, where it is expelled from the ventricle through three aortas: the cephalic or dorsal aorta, which supplies the head and the anterior part of the gut; the posterior, minor or abdominal aorta that supplies the mantle and fins along with the posterior part of the gut and the funnel; and the gonadal aorta that develops gradually with sexual maturation of the animal. The blood is collected through sinuses and capillaries into the veins, through which it passes to the branchial hearts that pump it through the filaments of the gills. The circulating respiratory pigment used for oxygen transport is copper-containing haemocyanin, a system of rather lower efficiency than the iron-containing haemoglobin of vertebrates. Blood sinuses in living squids are much reduced and replaced functionally by muscles. The circulatory system therefore has to work against the peripheral muscle-induced pressure, which increases with increasing activity (maximum during jet-swimming). It also has to cope with the resistance of the small diameter of the final capillary blood vessels, and the low oxygen carrying capacity of the blood (less than 4.5% by volume). In spite of these limitations, the system has other functional modifications (see for example Wells and Smith, 1987; Martin and Voight, 1987) that achieve the capacity to deliver oxygen at a rate comparable to that of active fishes, enabling squids to accomplish extraordinary swimming, attack and escape performances.

The excretory system

The excretory system also differs markedly from that of other molluscs and, along with the closed circulatory system and the branchial circulation, enables unique relationships between blood and the final secretion, the urine. The excretory system consists basically of the renal sac with the renal appendages (organs comparable to vertebrate kidneys), the pericardial glands, the branchial hearts and the gills. Squids are ammoniotelic, whereby ammonium ions are continuously released by the gill epithelium and by renal appendages into the surrounding water. Ammonium ions are used by buoyant squids to replace denser chloride ions in fluids in the coelom and in the body tissues. Because this solution is less dense (and hence more buoyant) than seawater, it provides lift for neutral or positive buoyancy.

The nervous system

The nervous system is highly developed, with a large brain and peripheral connections, contrasting with the original molluscan circumesophageal nerve ring. Among its most remarkable features is the giant fibre system that connects the central nervous system with the mantle muscles. This system consists of three orders of cells and fibres and ensures the immediate and simultaneous contraction of mantle, fins and retractor muscles of both sides, rather than an anterior to posterior sequential contraction that would be counter-productive for water movement (expulsion). Also remarkable is the eye development of squids, for which vision plays a major role in life. Their eyes are large, have a design generally similar to that of fishes and other vertebrates (e.g. a lens focuses images on the retina), and all the available evidence suggests that the ocular/visual performance is comparable to that of vertebrates. Squids also have developed a system to keep the focused image stationary on the retina while the animal turns, by moving the eyes in coordination with the head/body movement. This is extremely important for hunters that rely on sight, and it is accomplished by connections of the eye muscles with the statocysts, a bilateral mechanism similar to the vestibulo-optic system of fishes. The statocyst system provides squids with information on their orientation, as well as changes in position and direction of movement. It is a highly developed system that consists of two separate cavities located bilaterally in the cartilaginous skull, posteroventral to the brain. The statocysts contain nervous cells and receptors differentiated to detect both linear acceleration, with the aid of calcareous stones called statoliths, and angular acceleration. Some squids also have extra-ocular photoreceptors (photosensitive vesicles) about which little is known; in mesopelagic squids they appear to monitor light intensity in order to enable the animals to match their counter-illumination with the ambient light with their own photophores (light-producing organs). Squids are provided with numerous mechano- and chemoreceptors and recent evidence indicates that in some species, e.g. ***Loligo vulgaris***, ciliate cells form lines in several parts of the body, a system analogous to the lateral-line system in fishes.

Squids are able to change colour by using a complex system of chromatophores under nervous control. The chromatophores are pigment-filled sacs present in the skin, and capable of remarkable expansion and contraction. This system responds virtually instantaneously to contemporary situations in the environment, and it is critical for survival. Squid species also have iridocytes (shiny, reflective platelets) in the skin. Squids' behaviour includes rapid changes in overall colour and colour pattern and many deep-sea forms camouflage themselves by producing bioluminescent light from photophores which eliminate their silhouettes against the down-welling sunlight in the dimly-lit mid-depths.

Locomotion

Locomotion is achieved by a combination of jet propulsion and flapping or undulating the fins on the mantle. The fins on the mantle also provide balance and steering during jet propulsion. Many families of midwater squids have evolved to 'low energy life styles' and achieve neutral buoyancy by producing and storing in tissues or in different organs substances/elements with specific properties, such as oils or solutions of ammonium ions. This capability enables squids to inhabit open water, even in the great depths in the ocean, the greatest volume of living space on earth.

Feeding

Squids are voracious, active predators that feed upon crustaceans, fishes and other cephalopods. The speed of squids, their high mobility and powerful visual systems, along with strongly-muscled arms and tentacles, both equipped with suckers and/or hooks, make them extremely efficient hunters. A common hunting technique involves extremely rapid shooting forward of the tentacles to capture the prey, while in some oegopsid squids the tentacles may be used like long, sucker-covered fishing lures. The captured prey is brought to the mouth and killed by bites of the strong, chitinous beaks, equipped with powerful muscles. Digestion is rapid and efficient and squid metabolism is essentially proteinic: there is little or no digestion/assimilation of carbohydrates and lipids. Food conversion is highly efficient but such active animals like squids can eat from 3 to 15% of their body weight each day.

Reproduction

Squids are dioecious (separate sexes) and many species, though not all, exhibit external sexual dimorphism, either in morphological or morphometric differences. Females frequently are larger than males and males of most species possess one, occasionally two, modified arm(s) (the hectocotylus) for transferring spermatophores to females during mating. The males of some species also exhibit modifications to other arms, in addition to the hectocotylus. The hectocotylus may be simple or complex and can consist of modified suckers, papillae, membranes, ridges and grooves, flaps. The one or two "nuptual" limbs function to transfer the spermatophores (tubular sperm packets) from the male's reproductive tract to an implantation site on the female. The spermatophores may be implanted inside the mantle cavity (where they may penetrate the ovary), into the oviducts themselves, around the mantle opening on the neck, on the head, in a pocket under the eye, around the mouth or in other locations. Females of a few species also develop gender-specific structures (e.g. arm-tip photophores) when mature.

Mating often is preceded or accompanied by courtship behaviour that involves striking chromatophore patterns and display.

Copulatory behaviour varies significantly among species, in colour and textural display, proximity of male and female, duration of display and spermatophore transfer, and the location of implantation of the spermatophores on the female.

The gonads form a single mass at the posterior end of the mantle cavity, and female gonoducts may be paired (in oegopsids) or single, as in other squids. The reproductive systems are highly complex structures with ducts, glands and storage organs. Female squids have nidamental glands and loliginids have accessory nidamental glands, as well. Spermatophores are produced in the multi-unit spermatophoric gland and stored in the Needham's sac, from which they are released through the terminal part of the duct, the "penis". This term is not strictly accurate, because the spermatophores are passed to, or taken by, the hectocotylized arm(s), which in turn transfer(s) the spermatophore(s) to the female. The number and size of spermatophores vary greatly, depending on the species and group (for reviews on spermatophore structures and function see Mann *et al*., 1966, 1970; Mann, 1984; Nigmatullin *et al*., 2003). Once in contact with seawater, the so called 'spermatophoric reaction' begins. The spermatophores evert, with the resultant extrusion of the sperm packet caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher. The resulting extruded sperm packet is named spermatangium (or sperm bulb or body). Sperm are able to survive several months once stored in the female, at least in some species, and fertilization of mature ova may take place either in the ovary, the mantle cavity or the arm cone formed by the outstretched arms while the eggs are laid. Fertilized eggs are embedded in one or more layers of protective coatings produced by the nidamental glands and generally are laid as egg masses. Egg masses may be benthic or pelagic.

Eggs of neritic, inshore squids, except in ***Sepioteuthis***, generally are very small (only a few millimetres in diameter) and frequently are laid in finger-like pods each containing from a few to several hundred eggs. Deposited in multi-finger masses (sometimes called 'sea mops'), these eggs are attached to rocks, shells or other hard substrates on the bottom in shallow waters. Many oceanic squids lay their eggs into large sausage-shaped or spherical gelatinous masses containing tens or even hundreds of thousands of eggs that drift submerged in the open sea.

Growth and life history

Development of squid embryos is direct, without true metamorphic stages. However, hatchlings undergo gradual changes in proportions during development and the young of some species differ from the adults. Thus, the term 'paralarva' has been introduced for these early stages of cephalopods that differ morphologically and ecologically from older stages. The paralarvae of many deep-sea species of squids occur in the upper 100 m of the open ocean; then they exhibit an ontogenetic descent, gradually descending to deeper depths with increasing size until the adult depth is attained. Time of embryonic development varies widely, from a few days to many months, depending on the species and the temperature conditions. Hatching may occur synchronously from a single clutch or be extended over a period of 2 or 3 weeks.

In spite of the large number of studies and research carried out on squids, especially in recent decades, the life history of many species still is unknown, and our knowledge of the life cycles of the members of this interesting group remains fragmentary. Information comes from studies in the field as well as from observations in the laboratory. However, little is known of life history for species that are not targets of regular fisheries, and only a few squid species have been reared successfully in the laboratory. Studies and monitoring of growth are complicated by the high variability in individual growth rates. This makes it difficult to apply conventional methods, e.g. length frequency analysis, used for more traditional resources such as fishes and crustaceans. Determination of age also is difficult, because squids have few hard structures that show daily marks (rings) that enable direct estimates of age. In the last 20 years, progress has been made on the study and analysis of squid statoliths that has resulted in an increased knowledge of age. This has led to changes in our conceptions about the physiology and ecology of many species, but more research is required before a full understanding is achieved (see Jereb *et al*., 1991; Okutani *et al*., 1993; Jackson, 1994a, Lipinski and Durholtz, 1994 for reviews and discussions). Principal results obtained from the research generally confirm a very high growth rate in squids, comparable to that of the fastest-growing fishes.

The life expectancy of most squids appears to range from a few months to one or two years, and many small oceanic squids, such as pyroteuthids may complete their life cycles in less than six months. Recent evidence, however, suggests that larger species of squids, for example the giant squid (***Architeuthis*** spp.), as well as those that live in coldest habitats, may live for several years.

A general consensus exists that spawning is a terminal event, in spite of the high variability in the duration of individual spawning periods (5 to 50% of ontogenesis; Nigmatullin, 2002b) as well as the type of spawning, e.g. from one-time, total spawning, to prolonged, intermittent, multiple batches (see Rocha *et al*., 2001 for a review). All squids die after their spawning period.

Systematics status

The total number of living species of squids that currently are recognized is more than 300; 295 are listed in the present volume. The status of the systematics of squids has changed in the last 30 years, as research and associated scientific discussions have increased substantially. However, phylogenetic relationships among many families remain uncertain, and new species are described fairly frequently as new habitats are explored and as families are gradually better-understood.

Conclusions

Squids are important experimental animals in biomedical research with direct applications to human physiology and neurology, for example. Because of their highly developed brains and sensory organs, they are valuable in behavioural and comparative neuro-anatomical studies. In addition, the extremely large single nerve axons of some squids, the largest in the animal kingdom, are used extensively in neuro-physiological research.

The bite of squid can be painful at the least to humans, or secondarily infected, or, rarely, lethal. A documented threat by squids to humans is from the large ommastrephid squid, ***Dosidicus gigas***, which forms large aggressive schools that are known to have attacked fishermen that have fallen in the water, causing several confirmed deaths. Scuba divers also have been attacked. Therefore, squids must be handled carefully.

1.4 Interest to Fishery and Role in the Ecosystem

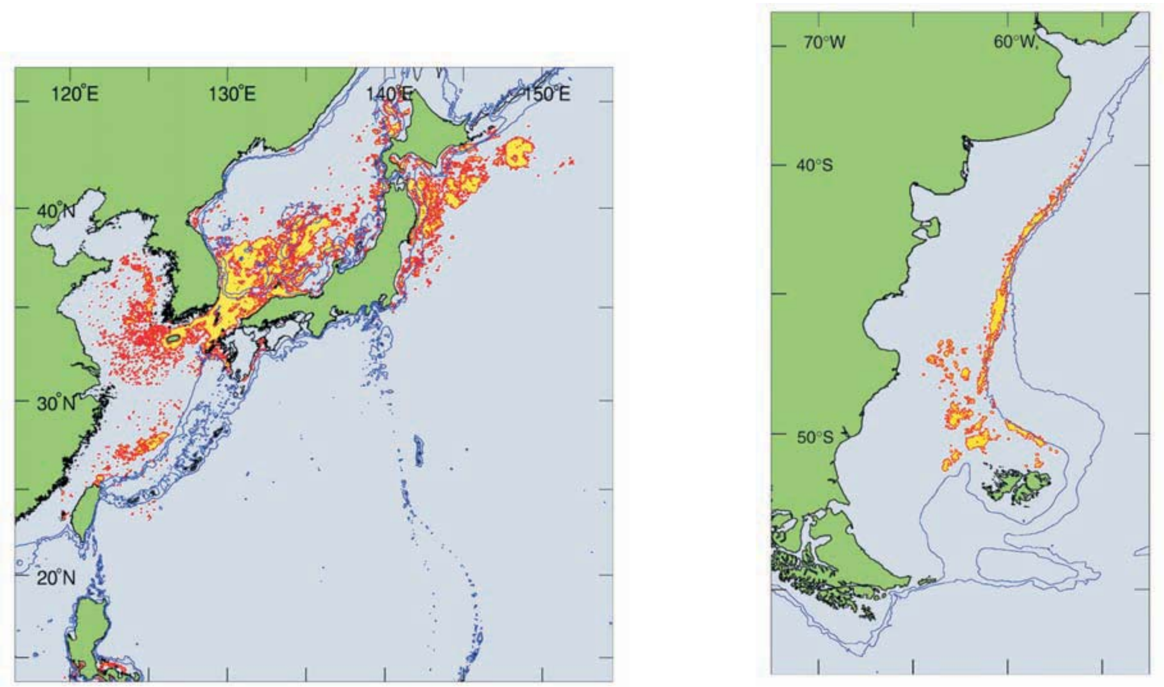
Squids are an important resource for human consumption. Of the total cephalopod catch of over 4 million tonnes reported for 2007 by FAO statistics (FAO, 2009), over 3 million tonnes were squids, i.e. about 74%. The impressive increase in squid production during the last 25 years is due mainly to the 'discovery' and increasing exploitation of squid resources in the southwest Atlantic, principally for ***Illex argentinus***, as well as an increase in the production of other major squid target species, mainly ***Todarodes pacificus*** in the northwest Pacific and ***Dosidicus gigas*** in the eastern Pacific. ***Illex argentinus*** catches exceeded 1 million tonnes in 1999, a record peak which placed this species at the eleventh position in value of the total world marine-species production for that year. Fluctuations in squid catches are responsible for the major fluctuations in total cephalopod landings, changes usually related to a combination of environmental, marketing and/or political causes.

About 30% of world squid catches is taken in the southwest Atlantic; followed by the eastern Pacific, with about 20%, then the Northwest Pacific (about 13%); however, smaller-scale fishing activities in other areas also developed consistently in the last decades (see, for example, the Indian Ocean fisheries).

Numerous fishing techniques and methods to capture squids have been developed over time. These were extensively reviewed, for example, by Rathjen (1984, 1992 [1991]) and Roper and Rathjen (1991). They include lures, jigs, lampara nets, midwater trawls and otter trawls.

Jigging is the most widely used method, which accounts for almost half of the world squid catch, primarily ommastrephids, but also a few loliginids. This technique is employed primarily at night, when many species of squids are attracted to the fishing vessel by lights. **Figure 3** shows the distribution of the world's light fishery for some of the most important squid species. Jigs, which feature numerous, variously-arranged, barbless hooks (Plate I, 6), are lowered and retrieved by jigging machines that simulate the constant swimming behaviour of natural prey, inducing the squids to attack them. While simple hand-jigging machines are still used in small-scale, artisanal fisheries, large modern vessels for industrial fishing activities are equipped with scores of automated, computer-controlled jigging machines, each capable of catching several tonnes per night (Plate I, 1 and 5).

Trawling is the secondmost productive fishery method to catch squids (Plate I, 2). Formerly, almost all squids were caught as bycatch in trawl fisheries for finfishes and shrimps. However, the amount of squids taken as bycatch in bottom trawls for finfish fisheries drove increasing attention to the resource by the 1980s; this led to the development of the (principally) midwater trawl fisheries specifically targeting squids, particularly the South Atlantic/Sub-Antarctic fishery for ***Illex argentinus***. Trawling is a very efficient technique to catch species, but soft-bodied animals like cephalopods are often damaged by the other species in the catch, particularly in benthic and epibenthic otter trawls. Even in fisheries in which squid-specific trawling occurs, the huge catches of squids per tow often result in crushed and damaged product. Consequently, trawled squid product generally is less valuable than jig-caught squids. However, modern oceanic trawlers can process on board many metric tonnes of cephalopods per day, which helps insure a high-quality product. Bottom trawling can be very dangerous for benthic habitats because of the physical damage it causes to the seabed and associated fauna and because of its lack of selectivity. Consequently, less intense exploitation by this traditional fishing technique and an approach toward diversification of methods and redistribution of the fisheries through different areas were encouraged and still are highly recommended, especially in situations where small-scale fisheries still exist and new, more efficient methods can be implemented. Nearshore, neritic squids frequently are caught by purse seines, lift nets, beach seines, etc.



a) Kuroshio Current Province
(*Todarodes pacificus* and *Ommastrephes bartramii*)

b) Southwest Atlantic Province
(*Illex argentinus*)

Fig. 3 Distribution of the world's light fisheries for ommastrephids (illustrations based on night-time satellite imagery) (from Rodhouse *et al*., 2001)

The utilization of squids for human consumption is extensive and diverse. Products range from fresh food, eaten raw as 'sashimi' in Japan and, in recent years, worldwide, and fresh-cooked, as well as various types of processed product (dried, canned, frozen, reduced to meal, etc.). The high protein and low fat content of cephalopods make them an important and healthy element in the human diet. Considering the present level of exploitation of the commercially-fished squid populations, a further increase in such fishery production is likely to occur, first by expansion of the fisheries into the less-fished regions of the oceans, e.g. the Southern Ocean, probably the 'last frontier' in the field of marine fisheries. There, a standing stock of squid biomass as high as 100 million tonnes was estimated by scientists, based on an estimate of 30 million tonnes consumed by vertebrate predators (see Rodhouse *et al*., 1994 for details), even though squid captures are rarely highly successful. Therefore, a priority for the future research in the field of Antarctic cephalopod biology will be to assess the squid biomass there, quantitatively and qualitatively, with the objective of determining and developing a sustainable fishery production. However, polar squids probably are longer living and slower growing than species currently harvested. Therefore, caution must be exercised in assumptions and decisions for management of polar squid fisheries.

In the future, it is likely that attention will be focused on finding other species and families to replace fish stocks that become severely reduced by overfishing. Even though clear evidence reveals the existence of large cephalopod resources available for exploitation in the open oceans, based on the estimated consumption by predators (see Clarke, 1996b; Piatkowski *et al*., 2001a for reviews), many oceanic squids are distasteful for human consumption as their tissues have a high ammonium content. Research is being carried out on how to remove this factor on a commercial scale, but results will take time and catches will need to be processed before marketing and utilization. A number of ommastrephid squids that lack ammonium are considered to be underexploited. These include: ***Sthenoteuthis pteropus***, ***Ommastrephes bartramii***, ***Martialia hyadesi***, ***Todarodes sagittatus***, ***Sthenoteuthis oualaniensis***, ***Nototodarus philippinensis***, ***Dosidicus gigas***, and the circumpolar, sub-Antarctic ***Todarodes filippovae***. Exploitation of these species would provide large tonnages of high quality cephalopods and would require only minor development in catching techniques. However, it will be necessary to determine where these species congregate for feeding and spawning activities. An analysis of biomass, production and potential catch for the Ommastrephidae species is presented in Nigmatullin (2004).

Although a number of other oceanic squid families have large populations and high quality flesh, they are not currently exploited on a commercial scale except for a few seasonal fisheries. These include members of the families Thysanoteuthidae, Gonatidae and Pholidoteuthidae, for example. Increased exploitation of these groups, however, would also require some research and development of catching techniques. Commercial exploitation of the cosmopolitan family Histioteuthidae also could be considered, since at least one large commercial-level catch has been made in the North Atlantic (see Okutani, personal communication, *in* Clarke, 1996a). However, the increased exploitation of these oceanic squid species might have unpredictable, far-reaching negative effects on the mesopelagic ecosystem. Therefore, great caution must be exercised in developing this kind of fishery.

Almost all of our knowledge of the general biology of cephalopods, in fact, is limited to the shelf-living species, as well as to those ommastrephids that move onto the shelf at certain seasons. These represent only about 15% of all cephalopod species. Even so, many gaps still exist in our knowledge about their life cycles, especially as far as the relationships among species are concerned (e.g. prey-predator balances). Some populations of harvested species have shown sudden, occasionally catastrophic, declines before adequate biological data could be gathered and analysed. Squid stocks experienced true collapses at least in two well-known and documented cases. These were the northwest Pacific ***Todarodes pacificus*** fishery failure in the 1970s and the northwest Atlantic ***Illex illecebrosus*** fishery collapse in the 1980s. While the ***T. pacificus*** fishery has recovered, the ***I. illecebrosus*** fishery has remained insignificant. These collapses are thought to have occurred mainly as a consequence of temporarily unfavourable environmental conditions or actual long-term environmental changes, probably aggravated by heavy fishing pressure (Dawe and Warren, 1993).

A significant challenge thus exists to deepen our knowledge and learn the details of distribution, life history and biology of exploited species in order to allow rational utilization of the stocks. The necessity for research as a key factor towards attaining this goal has been stressed by many authors (e.g. Lipinski *et al*., 1998b) and it is especially important in the fields of life-cycle clarification, stock structure and genetics, role in the food web and interactions with the environment. The last topic seems of particular interest within the more general context of global climate/environmental changes, since the unusual biological characteristics and short life cycles of squids are strongly linked to immediate, temporal environmental circumstances. Therefore, squids are potentially very good 'indicator species' to predict or reflect changes in environmental conditions, both locally and on a broader scale (see Pierce *et al*., 2008b for a review).

Perhaps even more significant is the challenge that exists for future exploitation of new species or populations. The role of squids in the ecosystem, in fact, is more complex than it was thought to be only a few decades ago. Squids can be considered subdominant predators that tend to increase in biomass when other species, particularly their predators and competitors for food, become depleted, as a result of a combination of heavy or excessive fishing, other human impacts, oceanographic fluctuations and competition for food (see Caddy, 1983, and Caddy and Rodhouse, 1998 for a detailed analysis of the transition from finfish-targeted fisheries to cephalopod-targeted fisheries). In turn, squids are major food items in the diets of innumerable species of fishes, toothed whales (e.g. sperm whales, beaked whales, dolphins, porpoises), pinnipeds (seals, sea lions) and seabirds (penguins, petrels, albatrosses).

Muscular squids derive their energy from crustaceans, fishes and other cephalopods. At the same time, they are a very efficient food storage for the large, oceanic predators, by rapidly converting oceanic resources into high energy food. On the other hand, neutrally buoyant ammoniacal squids, which probably greatly outnumber the muscular squids in biomass, also provide food to many of the same predators, but not over the continental shelf and with consistently lower energy per unit body mass. We know virtually nothing about the details of feeding, growth, life cycles, periodicities, distribution and spawning in ammoniacal species.

In spite of our relatively incomplete knowledge, it is now clear that squids are a dominant component within marine ecosystems and that their abundance ultimately may influence the abundance of their predator and prey populations. Studies of the effects of consumption of important pelagic squids and fishes by predatory fishes on the northeastern shelf of the United States (Overholtz *et al*., 2000), concluded that changes in predator abundance may have important implications for the long-term fishery yields of pelagic species. Consistent with our present knowledge is the concept that removal of squids through fisheries would have a continuous impact on the environment: populations of small midwater fishes would increase, while top predators like cetaceans, seabirds, seals and even some fish populations, would decrease.

Taking into consideration these factors, increasing effort should be focused on improving scientific knowledge of this group. Squid catches need increased monitoring, especially in those areas of major environmental fluctuations and where fisheries management is complicated by multiple countries exploiting the same resource. Cooperation, collaboration and commitment are required to better understand these important and fascinating animals.

1. 5 Illustrated Glossary of Technical Terms and Measurements

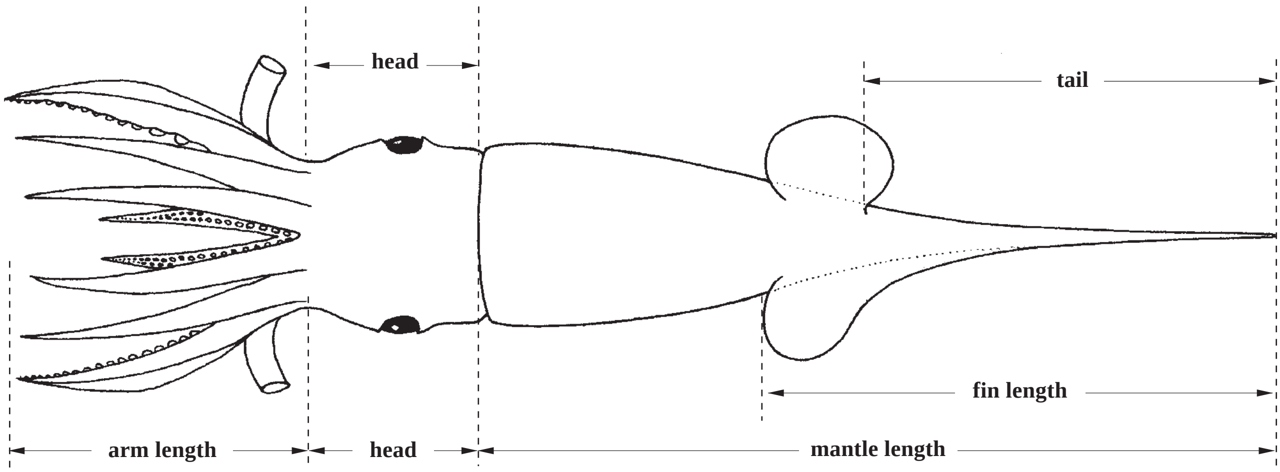


Fig. 4 Schematic illustration of a squid

Aboral – Away from or opposite to the mouth.

Abyssal – The great depths of the ocean: from 2 000 to 6 000 m.

Accessory nidamental glands – Glands of unknown function; consist of tubules containing symbiotic bacteria. Found in all **decapodiformes** except oegopsid squids.

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

Afferent blood vessel – Artery vessel carrying blood toward an organ.

Afferent nerve – Nerve carrying impulses toward the brain or specific ganglia.

Anal flaps – A pair of fleshy papillae involved in directing releases of ink, 1 flap situated at each side of the anus (Fig. 5).

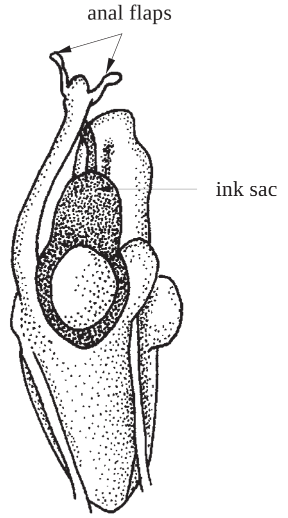


Fig. 5 Terminal portion of the digestive track

Anal pads – Ovoid pads of unknown function, apparently glandular, one located on each side of the anus in some squids (e.g. bobtail squids).

Anterior – Toward the head-end or toward the arm-tips of cephalopods.

Anterior salivary glands – Glands on or in the buccal mass that aid in preliminary digestion.

Anterior suboesophageal mass – See **Brachial lobe**.

Antitragus – Knob that projects inward from the posterior surface of the central depression in the funnel-locking apparatus of some squids (Fig. 6).

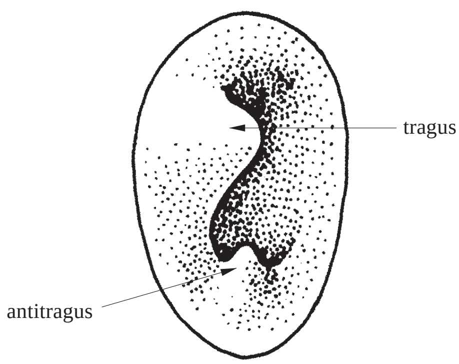


Fig. 6 Funnel-locking cartilage

Anus – Terminal opening of the digestive tract, in the anterior mantle cavity, sometimes extending to inside the funnel, through which digestive waste products, as well as ink, are expelled.

Apomorphic – Derived from a more ancestral condition. Loosely considered the 'advanced' condition.

Arm – One of the circumoral appendages of cephalopods. Arms are designated by the numbers I to IV, starting with I as the dorsal (or upper) pair. In squids each appendage of the fourth ancestral pair is modified to form a tentacle.

Arm formula – Comparative length of the 4 pairs of arms expressed numerically in decreasing order: the largest arm is indicated first and the shortest last, e.g. IV>III>II>I. If IV>III=II>I, then arm IV is the largest, followed by arm III which is the same size as arm II and both are larger than arm I.

Armature – The grappling structures of the arms and tentacular clubs, including suckers and/or hooks.

Bathypelagic – The deep midwater region of the ocean.

Beak – One of the 2 chitinous jaws of squids bound in powerful muscles. The dorsal beak is referred to as the 'upper' beak and it inserts within the 'lower' (ventral) beak to tear tissue with a scissors-like cutting action.

Belemnoidea – A fossil group of cephalopods that is thought to be the sister group of the Coleoidea. Belemnoids are distinguished by the presence of hook-like structures on the arms rather than suckers.

Benthopelagic – A free-swimming animal that lives just above the ocean floor but rarely rests on the ocean floor.

Bilateral symmetry – The symmetry exhibited by an organism or an organ if only one plane can divide the animal structure into 2 halves that are mirror images of each other.

Bioluminescence – The production of light by living organisms, sometimes called 'living light'. The light is produced through a chemical reaction that generally takes place in complex organs called photophores or light organs.

Brachial – Pertaining to the arms.

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

Brachial lobe (of the brain) – The anteriormost part of the brain located ventral to the oesophagus. The large axial nerve cords that run down the centres of the arms connect to this lobe. The proper name is 'anterior suboesophageal mass'.

Brachial photophore – Photophore located on the arms.

Brachial pillar – A narrow, elongate anterior region on the paralarval or juvenile head of some families, between the eyes and the base of the brachial crown; especially well developed in young cranchiid squids.

Brain – Medial portion of the central nervous system that includes the suboesophageal and supraoesophageal masses but generally does not include the large optic lobes.

Branchial – Pertaining to the gills.

Branchial canal – A large opening at the base of each gill lamella and between the primary afferent and efferent blood vessels of the gill.

Branchial gland – Elongate or spheroidal gland adjacent and parallel to the gill attachment to the mantle wall.

Branchial heart – A gland at the base of the gill through which afferent blood is pumped to the gill. It also is the site of hemocyanin (the blood respiratory pigment) synthesis.

Brooding – Incubation of eggs by the female. A characteristic feature of incirrate octopods, but also found in some squids (e.g. **Gonatidae**).

Buccal – Pertaining to the mouth.

Buccal connective – Thin muscular band that attaches the buccal support of the buccal membrane to the base of the adjacent arm. The position of attachment of the connective on the fourth arms was recognized in the early twentieth century as an important character for phylogenetic relationships among **decapodiformes** (Fig. 7).

Buccal crown – Umbrella-like structure that surrounds the mouth and in turn is enveloped by the brachial crown. It consists of buccal supports and the buccal membrane.

Buccal lappet – A small, subtriangular flap at the tip of each buccal support of the buccal membrane; thought to be homologous with the inner ring of tentacles that surrounds the mouth of nautiluses. May bear suckers (Fig. 7).

Buccal mass – Muscular bulb at the anteriormost part of the digestive system that consists of the mouth, beaks, radula, muscles and pairs of salivary glands.

Buccal membrane – The muscular membrane that encircles the mouth like an umbrella (Fig. 7). It connects the buccal supports to form the buccal crown. The pigmentation of the buccal membrane often differs from that of the adjacent oral surfaces of the arms.

Buccal membrane connectives – See **Buccal connective** (Fig. 7).

Buccal suckers – Small suckers on the buccal lappets/ membrane of some species (Fig. 7).

Buccal support – Muscular rod fused to buccal membrane as supporting rib; 6 to 8 in number (Fig. 7).

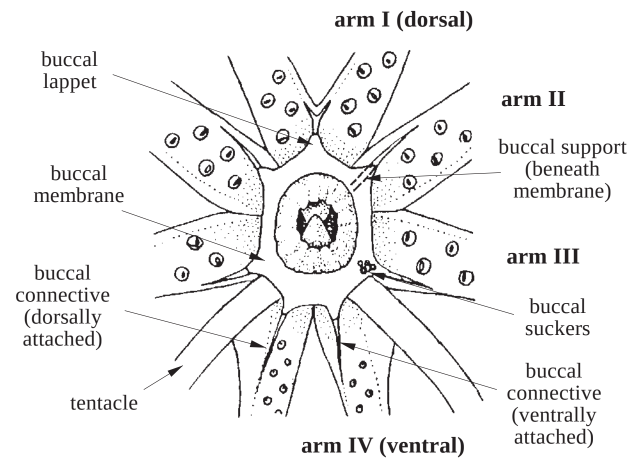


Fig. 7 Buccal anatomy of decapods

Buoyancy (neutral, positive, negative) – The tendency to float in seawater. A neutrally buoyant object does not rise or sink but maintains its position in the water; a positively buoyant object will rise and a negatively buoyant object will sink.

Caecal sac – The sac-like, thin-walled posterior portion of the caecum in the digestive tract that lacks the internal, ciliated leaflets characteristic of the anterior portion of the caecum.

Caecum – Region of the digestive tract of all cephalopods between the stomach and intestine. It is the primary site of food absorption.

Calcified – Chalky, calcareous material of calcium salts (calcium carbonate), formed by deposition.

Cambrian period – Oldest period of the modern geological timescale.

Carpal cluster (= Carpal pad) – An usually distinct group of suckers and knobs on the carpus of the tentacular club (Fig. 8).

Carpal knobs – Small, rounded, hemispherical, muscular protuberances on the carpus to which carpal suckers from the opposite club adhere during the locking of the clubs (Fig. 8).

Carpal-locking apparatus – Arrangement of suckers and matching knobs on the carpal region of the tentacular club that permits the 2 clubs to be locked together (Fig. 8).

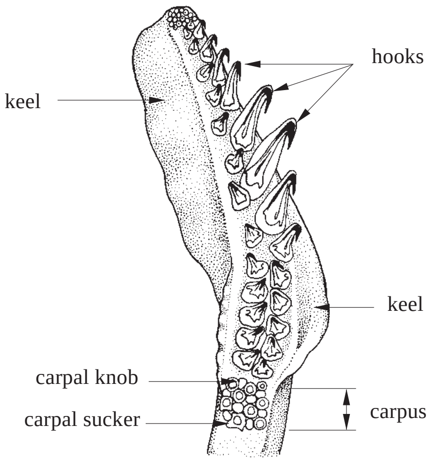


Fig. 8 Tentacular club of squid

Carpal suckers – Small suckers on the carpus of the club that adhere to the carpal knobs on the opposite carpus during the locking of the clubs (Fig. 8).

Carpus – The proximal zone of small suckers and knobs on the base of the tentacular club in some families (Fig. 8).

Cartilaginous structures or "scales" – Cartilage-like structures in the skin of certain squids; may be overlapping and scale-like, or multifaceted platelets, knobs or papillae (Fig. 9).

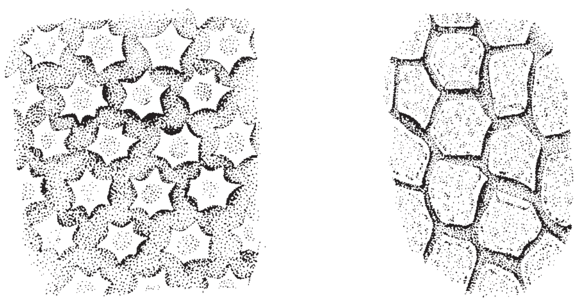


Fig. 9 Two types of cartilagineous structures or "scales"

Cement body – Structure in the spermatophore that allows adhesion of the discharged spermatophore to a female (Fig. 29).

Cephalic cartilage – Cartilage-like tissue that envelops the posterior part of the brain of cephalopods and encompasses the statocysts. Anteriorly the cartilage thins and entwines with muscular tissue, which makes a well-defined limit difficult to distinguish. The cartilage has a large central foramen through which the oesophagus passes and minor foramina for nerves and blood vessels.

Cephalic vein – Large vein that drains blood from the head region; it lies along the ventral surface of the visceral sac, beside or dorsal to the intestine. The cephalic vein terminates by dividing into the 2 vena cavae, each of which passes through the 'kidney' (nephridium), the branchial heart and into the gill.

Cephalopoda – The class within the Mollusca, characterized by bilateral symmetry, internal 'shell' or absence of shell (except nautiluses), anterior head, appendages and funnel, posterior mantle, mantle cavity with organs, and shell and fins when present.

Character state – A particular condition of a taxonomic character. For example, the character 'sucker' may include the 2 states: sucker with a horny ring or sucker without a horny ring.

Chemotactile – Refers to chemical and touch sensitivity.

Chitin(ous) – A horny polysaccharide substance (fingernail-like) that forms the sucker rings, hooks and beaks.

Chorion – A tough secreted membrane that encapsules the egg.

Chromatophores – Pigment-filled muscular sacs in the skin under individual nervous control that collectively provide the background colour, colour patterns and colour dynamics (play) of cephalopods.

Circumoral appendages – The 8 arms plus the 2 tentacles. All arise from the head and encircle the mouth (Fig. 7).

Clade – A monophyletic group. That is, a group whose members share a closer common ancestor with one another than with members of any other group.

Coelom – An internal body cavity of mesodermal orgin that is lined by an epithelium. Cephalopods have 2 coeloms, the viscero-pericardial coelom and the nephridial coelom.

Collar – Muscular, flange-like structure that extends from the nuchal cartilage to the funnel; it forms a one-way valve that allows water to enter the mantle cavity but closes as the mantle contracts, thereby forcing exhalent water out through the funnel.

Cone, conus – The spoon-like, cup-like, spiked or simple conical posterior terminus of the gladius; homologous to the phragmacone of fossil squids (Fig. 10).

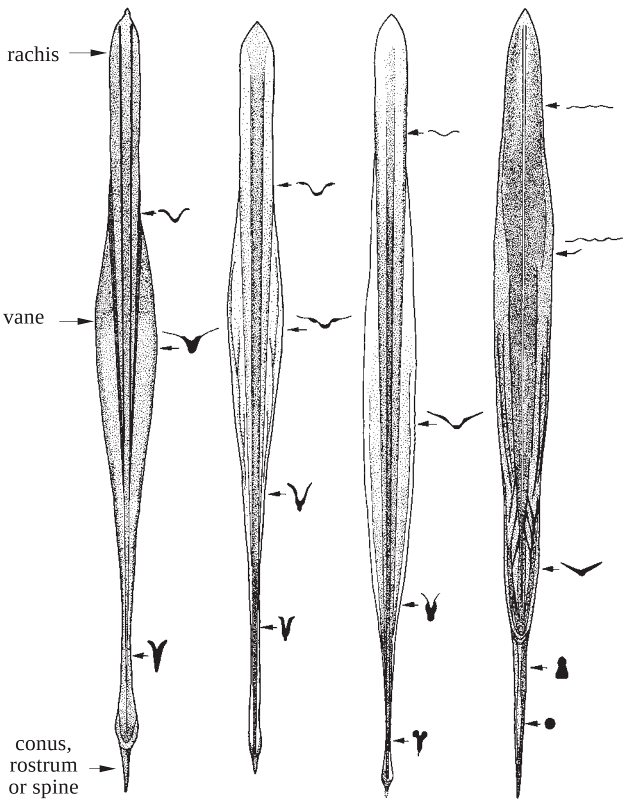


Fig. 10 Gladii of some squids

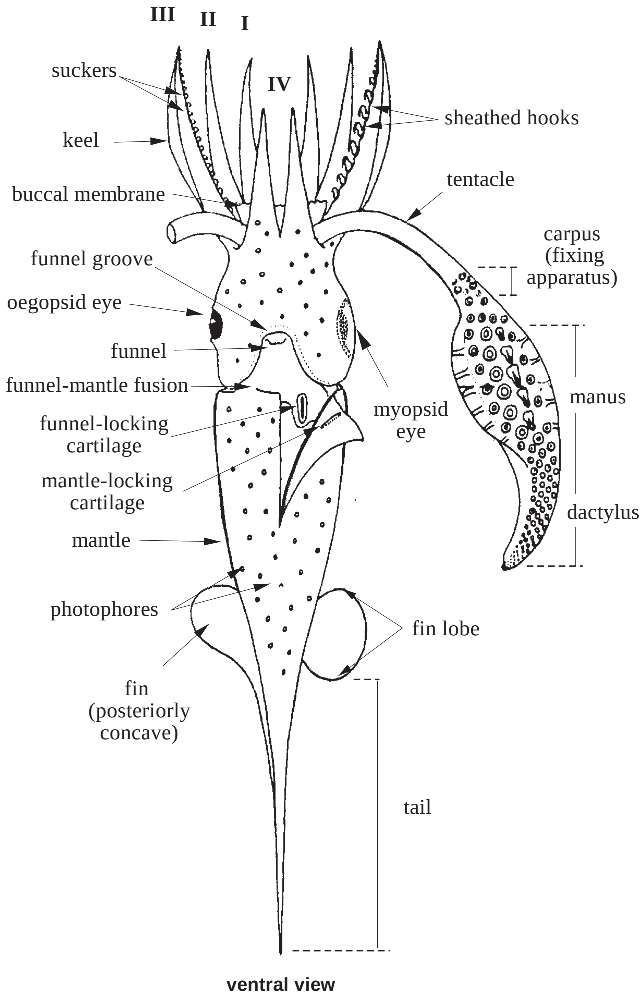


Fig. 11 A composite diagram illustrating basic squid features

Conus field – The sides of the conus that continue anteriorly along the vanes of the gladius.

Cornea – Smooth, thin, turgid, transparent skin without muscles that covers the eyes to protect the eye lenses of myopsid squids (Fig. 11).

Counter illumination – The production of bioluminescent light by an animal to conceal its silhouette against a lighted background. The process can allow an animal to become virtually invisible under dim directional light.

Cretaceous – The last period of the Mesozoic Era.

Cusp – A point or projection on a tooth of the radula or on a cartilagenous tubercule in the skin.

Dactylus – The distal, terminal section of the tentacular club, often characterized by suckers of reduced size (Fig. 11).

Decapodiformes – Higher-level taxon that includes all 10-limbed cephalopods (Fig. 2). Within the Decapodiformes, typically, two higher taxa are recognized: the Sepioidea, which includes the Sepiidae, Idiosepiidae, Sepiolidae, Spirulidae and Sepiadariidae and the Teuthoidea, which includes Myopsid and Oegopsid squids. Because of the long history of referring to these cephalopods by the common name **'decapods'**, the latter is maintained as the common name for the **Decapodiformes**.

Decapods – Common name for the **Decapodiformes**.

Demersal – Organisms that live close to the ocean floor.

Diel vertical migration – Vertical animal migration during twilight periods. Many mesopelagic animals migrate to shallow depths at sunset, where they spend the night feeding; then they descend at sunrise from near-surface waters to spend the day hiding at greater, darker depths. Some animals migrate vertically over 1 000 m, others migrate less than 100 m.

Digestive gland – Primary organ in cephalopods that secretes digestive enzymes. It is also important in absorption and excretion (Fig. 12).

Digestive gland duct appendages – Outpockets of the ducts leading from the digestive gland that are covered with glandular epithelium (Fig. 12).

Distal – Away from the central region of the body or point of origin; toward the peripheral parts (opposite of proximal).

Doratopsis – The peculiar paralarval stage that is characteristic of all members of the oegopsid squid family **Chiroteuthidae**.

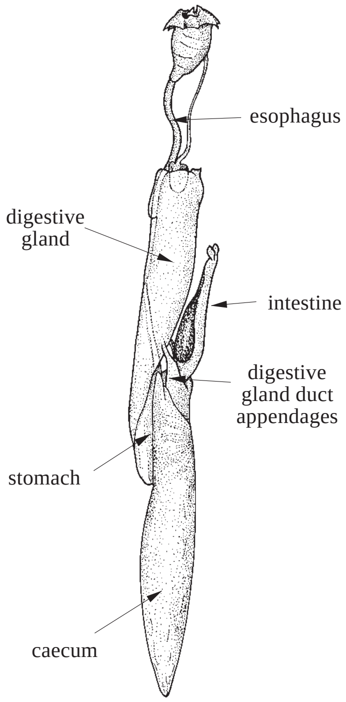


Fig. 12 Digestive system of squids
(after Bidder, 1966)

Dorsal – The uppermost or back surface of a cephalopod, opposite the ventral surface where the funnel is located (Fig. 13).

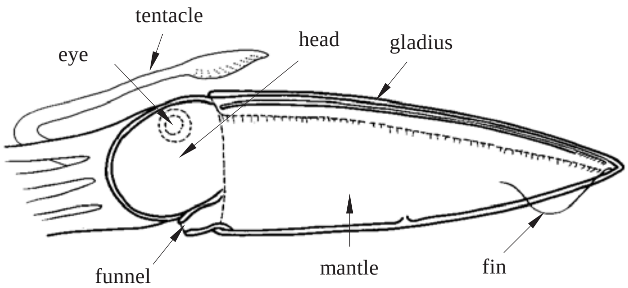


Fig. 13 Schematic lateral view of squid features

Efferent vein – Vein that carries blood away from the heart or an organ.

Efferent nerve – Nerve carrying impulses away from the brain or specific ganglia.

Egg mass – A large number of eggs encapsulated in a gelatinous matrix or a large number of such structures that are attached together. The pelagic egg mass of an oceanic squid can be a large, fragile, gelatinous ball that carries many thousands of eggs. In contrast, the egg mass of a neritic squid (loliginid) can be composed of hundreds of very tough, encapsulated eggs in strings, attached together at their bases and to the substrate.

Ejaculatory apparatus – Portion of the spermatophore involved in the vigorous extrusion of the sperm mass (Fig. 29).

Epipelagic zone – The uppermost pelagic zone of the ocean.

Epithelial pigmentation – The pigmentation contained in epithelial cells that are unable to change their shape in the absence of muscles and nerves. Colour in most cephalopods, however, is created by pigment granules that are contained in specialized organs, the chromatophores, that can change shape rapidly, by muscular action under nervous control (see **Chromatophores**).

Esophagus – See **Oesophagus**.

Exploitation rate (E) – When fishing mortality (F) and natural mortality (M) operate concurrently, the exploitation rate represents the fraction of dead animals due to the fishery (i.e. caught by the fishery), which is, F/Z where Z denotes the total (i.e. M+F) mortality rate.

Eye (position and size) – Eyes are the primary sensory organs of cephalopods; they usually are large and located one on each side of the head. However, some species have small eyes, eyes on stalks or telescopic eyes.

Eye pore (= orbital pore) – Small pore in the anterior edge of the corneal membrane which covers the eyes; present in most myopsid squids. The pore is the remnant of the large eye opening of oegopsids and allows fluid exchange between the lens and the exterior environment (Fig. 66).

Eyelid sinus (= optic sinus, = orbital sinus) – Indentation, often complex, of the anterior margin of the eyelid (Fig. 20).

Family – The taxon above the genus level, comprised of the most closely related genera.

Fin(s) – The pair of muscular flaps that arise along the dorsolateral surface of the mantle of squids; used for locomotion, steering and stabilization (Fig. 11).

Fin angle – The angle between the longitudinal axis of the mantle and the posterior border of one fin (Fig. 14).

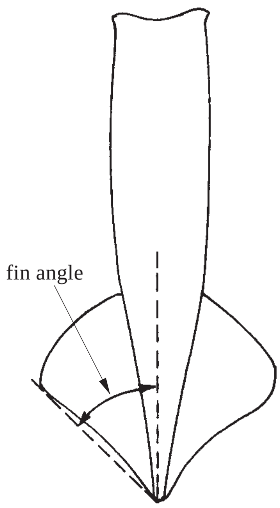


Fig. 14 Fin angle on squid

Fin attachment – A fin attaches to the mantle, to the opposite fin or some combination of these.

Fin cartilage – Cartilage associated with the fins of all fin-bearing cephalopods.

Fin length – Length from anterior lobe or anteriormost attachment of lobe to posteriormost attachment of fin to mantle or tail. Extremely long, spike-like tails usually do not include fin tissue.

Fin lobe – The portion of a fin that extends anteriorly from the fin's anterior point of attachment, or posteriorly from the fin's posterior point of attachment of the fin, to the mantle (Fig. 11). This often is called the 'free' lobe.

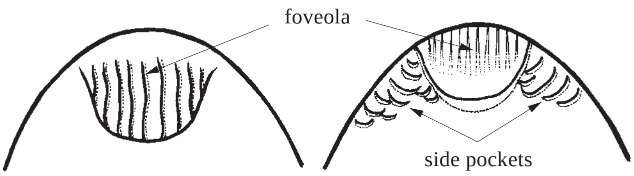
Fin position – Fins are located anterior to the termination of the muscular mantle (subterminal position) or mostly posterior to it (terminal position) or in an area of overlap between the two.

Fin shape – Fins are classified, somewhat arbitrarily, by their shape as sagittate, rhomboid, circular/elliptical, lanceolate, ear-shaped, ribbed, lobate or skirt-like.

Fixing apparatus – The mechanism of suckers and knobs on the carpal region of the tentacular club that permits the two clubs to be locked together during capture of prey (Figs 8 and 11) (see **Carpus**).

Foot – See **Molluscan foot**.

Foveola – Transverse, membranous fold of skin that forms a pocket in the anterior end of the funnel groove of some oegopsid squids (Fig. 15) (see **Side pockets**).



a) Todarodinae **b) Ommastrephinae**

Fig. 15 Funnel groove

Funnel – The ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration (reproductive and waste products and the ink also pass through the funnel) (Figs 11 and 13). Archaic term: **siphon**.

Funnel adductor muscles – Muscles that support the lateral attachment of the funnel to the head.

Funnel groove – The depression in the posteroventral surface of the head in which lies the anterior portion of the funnel (Fig. 11).

Funnel-locking cartilage – The cartilaginous groove, pit, pocket or depression on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together during locomotion and respiration, so that water is expelled only through the funnel and not around the mantle opening (Figs 11 and 16) (see **Mantle-locking cartilage**).

Funnel-mantle locking apparatus – The structure composed by the funnel-locking cartilage and the mantle-locking cartilage.

Funnel organ – The glandular structure fused to the internal surface of the funnel, generally a dorsal inverted

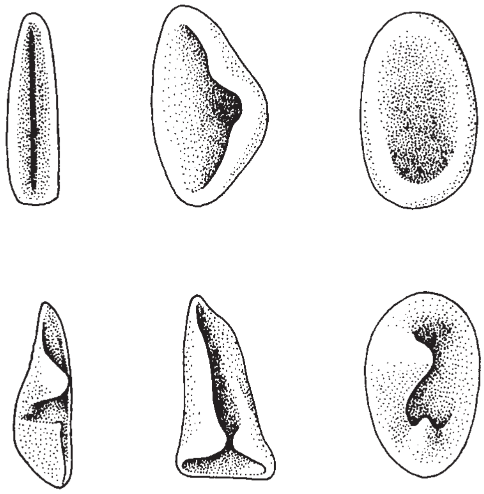


Fig. 16 Funnel-locking cartilage; examples of shapes and structures

V-shaped component with opposed ventral oblong components in squids (Fig. 17).

Funnel-retractor muscles – Large muscles that attach to the posterior corners of the funnel and extend posteriorly to attach to the sides of the shell sac (generally near the base of the gills) or, in some species, insert on the interior mantle wall.

Funnel valve – The semilunar muscular flap in the dorsal inner surface near the distal opening of the funnel in some species (Fig. 17).

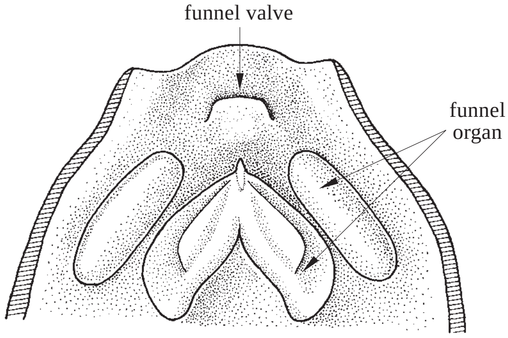


Fig. 17 Funnel organ and funnel valve components on inner surface of funnel of squids

Genus – The taxon below the family level and above the species level.

Gill – Primary organ for the exchange of respiratory gases with seawater (Fig. 22).

Gill lamella(e) – The leaf-like convoluted individual components of the gill through which gas exchange occurs (Figs 18 and 22).

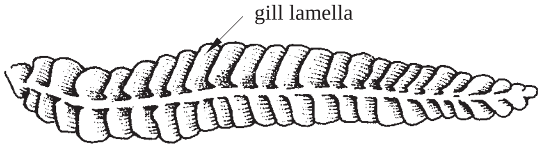


Fig. 18 Gill lamella, a single element from a complex structure

Gladius (= pen) – The feather or rod-shaped chitinous supporting structure in the dorsal midline of squids; the homologue of the shell of ancestral forms (Fig. 10).

Gladius length (GL) – Sometimes used as a measure of the body (= mantle) length when direct measurement of the mantle is unreliable (usually due to damage or deformation).

Gonoduct(s) – Tubular structure(s) of the reproductive system which serve(s) to transport reproductive products from the gonad into the mantle cavity, then to the exterior (see **Oviducts**).

Hatchling – Young cephalopod newly hatched from the egg.

Head length – A standard measurement within species growth stages and for species comparisons; measured from posterior limit to V-notch base of arms I (Fig. 4).

Head-mantle fusion – Zone of fusion of head and mantle; it varies among groups/families; of systematic and biological significance.

Hectocotylus – One (or more) modified arm in male squids used to transfer spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, trabeculae (Fig. 19).

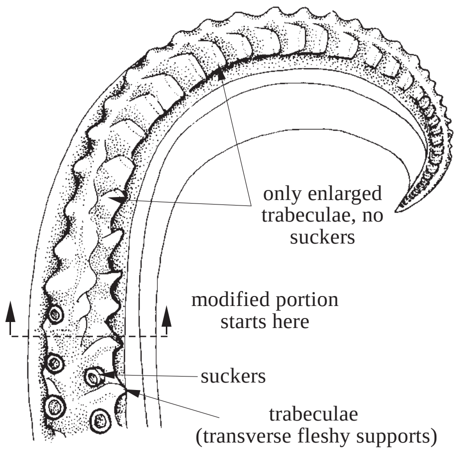


Fig. 19 Hectocotylized arm (*Illex oxygonius*)

Holotype – The single specimen designated by the original author of a species to represent the new species name. It is an international standard of reference that provides objectivity and stability for the species name.

Hooks – Chitinous, claw-like structures ontogenetically derived from the suckers on the arms and/or clubs of some oegopsid squids (Fig. 8).

Horny rings of suckers – Suckers of squids have 2 types of hard, horny rings. One, the inner ring, lies around the inner walls of the acetabulum (cup) and often bears teeth. The other, the outer ring, is composed of numerous minute platelets and lies on the surface of the infundibulum (outer rim) (Fig. 31).

Ink sac – The structure that manufactures and stores the ink of cephalopods; it lies parallel with the intestine and empties via a duct into the rectum (Figs 5 and 22).

Intestine – Distal region of the alimentary canal between the stomach/caecum complex and the anus (Fig. 12).

Juvenile – Life history stage between the hatchling and the nearly-mature subadult stages.

Keel – **(1)** A flattened, muscular extension along the aboral surface of some arms to render them more hydrodynamic (Fig. 11); **(2)** 1 or 2 expanded muscular membranes along the tentacular club of some groups (Fig. 8).

Lateral – Pertaining to the side(s) of an organism or structure, away from the centre or midline.

Lateral funnel-adductor muscles – See **Funnel-adductor muscles**.

Lateral membranes of arms IV – See **Tentacular sheath**.

Lateral-line analogue – Sensory structure analogous to the lateral-line of fishes. The lateral-line analogue, which senses vibrations transmitted by seawater, is located along a series of lines on the dorsal surface of the head, with some sensory cells extending onto the bases of the arms.

Length at 50% maturity – Mantle length at which 50% of specimens examined in a representative sample is sexually mature, according to the maturity scale and the statistical model used.

Lens (eye) – A spheroidal, transparent, polysaccharide structure through which light is transmitted to the retina.

Lens (in photophores) – Structure in a photophore that can focus or disperse bioluminescent light.

Light guides – Structures in photophores that specifically direct light via internal reflection.

Light organ (= photophore) – A simple or complex structure that produces bioluminescence (cool light) by intrinsic (self generated) or extrinsic (bacterial) means (Figs 11 and 20).

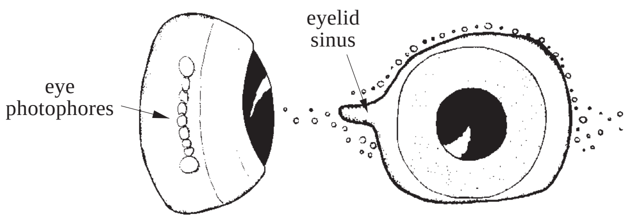


Fig. 20 Light organs (photophores) on ventral surface of squid eyeball, eyelid or orbital sinus

Lips – Two concentric, muscular, glandular rings of skin that surround the mouth and beaks.

Mantle – The fleshy (muscular) tubular or sac-like body of cephalopods; provides propulsion through jet-like expulsion of water; contains the viscera *sensu lato* (Figs 11 and 13).

Mantle cavity – Space enclosed by the mantle. In cephalopods the mantle cavity contains the visceral sac, gills, anus, ink sac, gonads, nephridial pores and various muscles and septa (Fig. 22).

Mantle length (ML) – The standard measure of length in coleoid cephalopods. In **squids** ML is measured along the dorsal midline from the anterior mantle margin to the posterior tip of the body (Fig. 4).

Mantle-locking cartilage – The cartilaginous ridge, knob or swelling on each side of the ventrolateral, internal surface of mantle that locks into the funnel component of the locking apparatus during locomotion (Figs 11 and 16) (see **Funnel-locking cartilage**).

Manus – Central or 'hand' portion of club between the dactylus distally and the carpus proximally (Fig. 11).

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 (Fig. 22) and for males by the presence of spermatophores in Needham's sac (see **Adult**).

Medial(n) – Pertaining to a structure located toward, on, or along the dorsal or ventral midline.

Mesopelagic zone – The middle-depth zone of the pelagic realm of the ocean.

Mollusca – One of the major invertebrate phyla. Some of the common molluscs are snails and clams. The **Cephalopoda** is a class within the Phylum Mollusca.

Molluscan foot – A major structure in molluscan morphology. In gastropods the foot is the muscular sole that the animal crawls with. In cephalopods the funnel, and possibly the arms and tentacles are derived from the molluscan foot.

Monophyletic group – A natural group (taxon) that shares a common ancestor.

Myopsida – A high-level taxon (order) within the **Decapodiformes**. In recent classification, the **Myopsida** (including the families Loliginidae and Australiteuthidae) have been considered the sister group of the **Oegopsida** and the 2 groups together compose the **Teuthoidea** (squids).

Neck – The region that separates the posterior end of the cephalic cartilage and head musculature. Only those cephalopods with elongate heads (e.g. the oegopsid squid family Chiroteuthidae) have distinct necks.

Needham's sac (=spermatophore/ spermatophoric sac) – The elongate, membraneous organ of males where completed, functional spermatophores are stored. It opens into the mantle cavity (or externally) through the penis (Fig. 21).

Nephridial coelom – The cavity of the renal (kidney) sac. It connects with the exterior via the renal pore and with the viscero-pericardial coelom via a pair of slender ducts from the latter.

Nephridial papillae – Small raised openings to the renal cavities.

Neritic – The region of the ocean that overlies the continental shelf.

Nidamental glands – Large glandular structures in females 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 (Fig. 22).

Nominal species – A species that has been formerly described and is based on a morphological type. It is an available name but not necessarily a valid species.

Nuchal cartilage – See **Nuchal-locking apparatus.**

Nuchal crest – Prominent transverse ridge that extends across the dorsal head and down the lateral head surfaces at its posterior end.

Nuchal folds – Fixed folds or pleats of the head integument that adjoin the nuchal crest posteriorly and are perpendicular to it. The function of the folds is uncertain (Fig. 23).

Nuchal-locking apparatus – An oblong, cartilaginous-locking structure 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 an interlocking, complementary cartilage on the mantle that underlies the gladius. The apparatus keeps the head and mantle aligned dorsally during mantle contractions (Fig. 23).

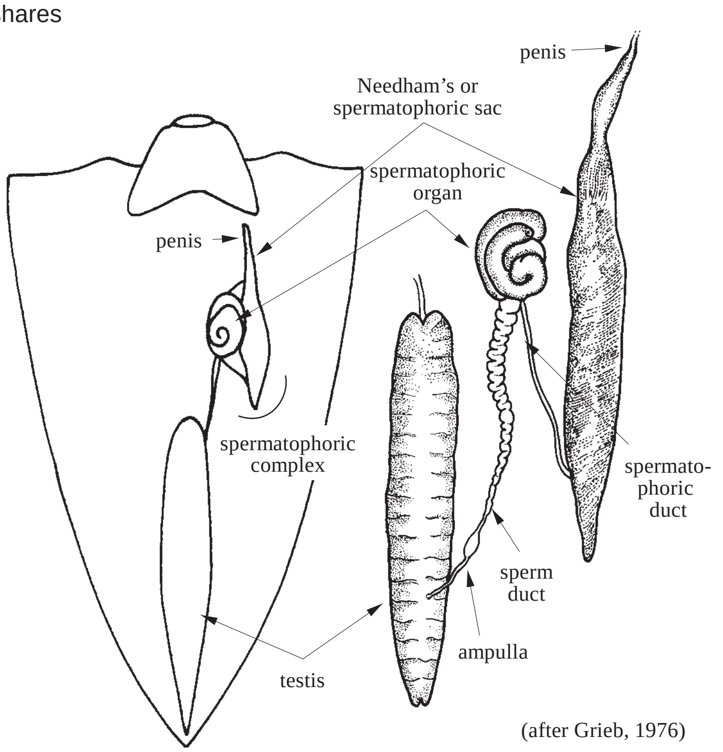
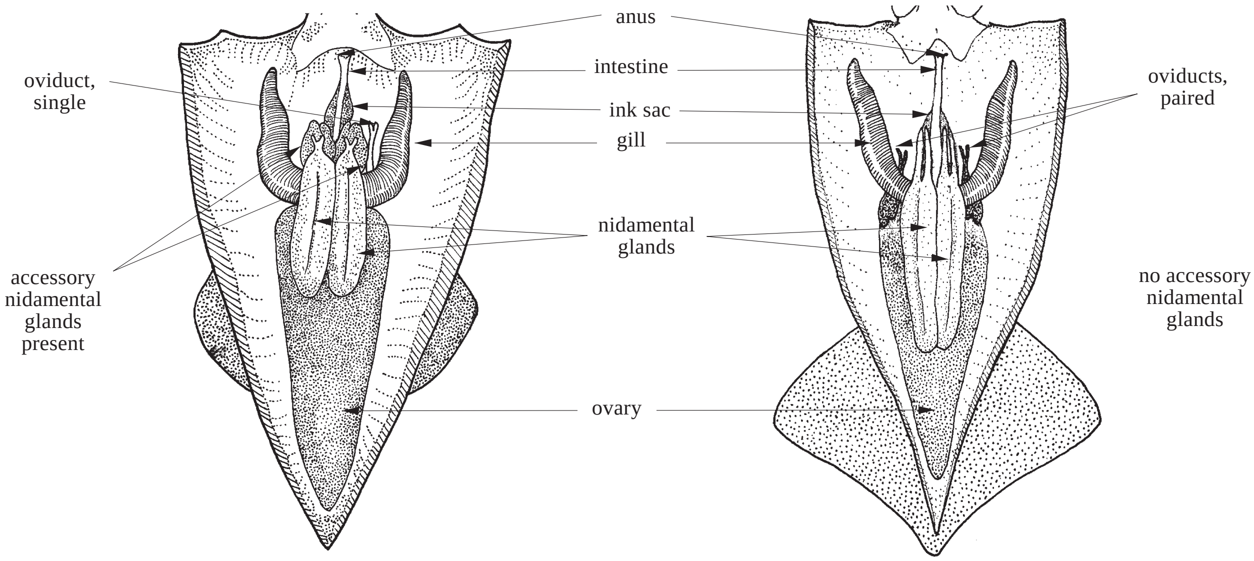


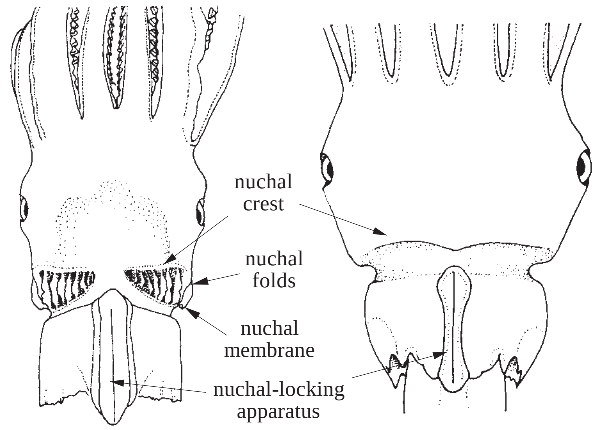
Fig. 21 Male squid reproductive apparatus



a) Loliginidae **b) Ommastrephidae**

Fig. 22 Internal organs of Decapodiformes

Nuchal membrane (= occipital membrane) – A thin membrane that connects the main nuchal folds at their posterior ends (Fig. 23).



a) *Onychoteuthis* **b) *Onykia***

Fig. 23 Nuchal folds and nuchal crest

Nuchal organ – Small sensory organ with photoreceptor-like sensory cells that is located in the nuchal region of apparently all coleoid cephalopods.

Nuchal region – The dorsolateral area around posterior part of the head and the area immediately posterior to it, normally covered by the anterior mantle wall.

Occipital crest – See **Nuchal crest**.

Occipital folds – See **Nuchal folds**.

Occipital membrane – See **Nuchal membrane**.

Ocular photophore – Photophore that lies on the eyeball (Fig. 20).

Oegopsida – A high-level taxon within the **Decapodiformes**. In recent classification, the **Oegopsida** (oceanic or open-eyed squids) has been considered the sister group of the **Myopsida** (inshore or covered eyed squids) and the 2 groups together compose the **Teuthoidea** (squids). At present the the composition and affinities of the **Oegopsida** are unresolved.

Oesophagus (esophagus) – The portion of the digestive tract between the buccal mass and the stomach (Fig. 12).

Olfactory organ – A chemosensory organ present in all coleoid cephalopods.

Olfactory papilla – A pit, or bump-like to finger-like protuberance on the posterolateral surface of each side of the head; of olfactory function.

Ontogenetic descent – The progressive descent into a deeper-water habitat as a mesopelagic cephalopod grows older and larger. This distribution pattern is particularly common in many pelagic chiroteuthid and cranchiid squids.

Opening/closing trawl – A trawl whose mouth is open during fishing at a known depth but is closed during descent and retrieval.

Optic lobes of brain – Large lobes of the brain associated with the eyes. In some squids the optic lobes may be separated from the rest of the brain by an optic stalk of varying length.

Optic sinus – See **Eyelid sinus**.

Oral – Toward or pertaining to the mouth.

Orbital pore (= eye pore) – Minute pore in the anterior part of the transparent tissue (cornea) that covers the eyes of most myopsid squids; remnant of the primary eyelids (Fig. 66).

Orbital sinus – See **Eyelid sinus**.

Order – The taxonomic catageory above the family level.

Oviduct(s) – Female gonoduct(s). The oviduct conducts eggs from the visceropericardial coelom, that encompasses the ovary, to the mantle cavity and often is used to store eggs (Fig. 22).

Oviducal gland – Glandular structure that surrounds the anterior end of the primary oviduct and secrets some of the external coatings around spawned eggs.

Paralarva – The term that indicates the first free-living life history stage (typically planktonic) for those cephalopods that differ in morphology and ecology from older juveniles.

Pedicel (= sucker stalk) – A short, tubular stalk that supports a sucker in sepioids and teuthoids (Fig. 24).

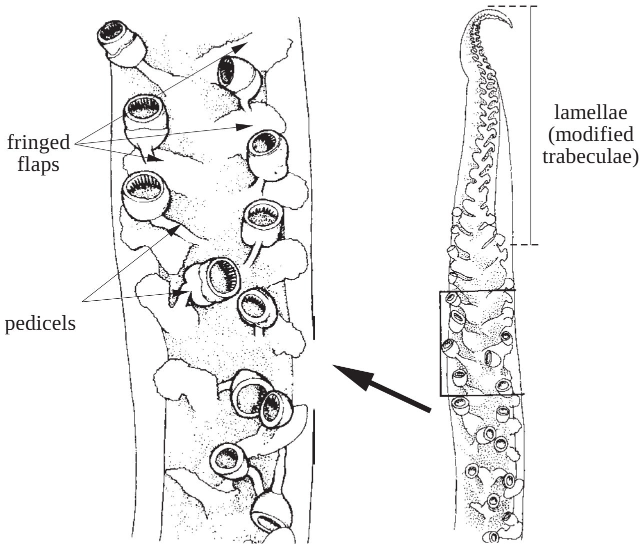


Fig. 24 Hectocotylized arm of males

Pelagic – **(1)** Free swimming in open ocean; **(2)** The region of the ocean away from the ocean floor.

Pen – See **Gladius**.

Penis – The long, muscular terminal section of the male gonoduct that serves to transfer spermatophores to the female (Fig. 21). 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 often is greatly elongate, capable of extending beyond the mantle opening and apparently can transfer spermatophores directly to the female.

Photocytes – Cells that produce bioluminescence in photophores.

Photophore – An organ that produces and distributes bioluminescence or 'living light', either intrinsically through biochemical reaction or extrinsically through luminescent bacteria (Figs 11 and 20) (see **Light organ**).

Phylum – The major, formative, principal taxonomic level, above Class.

Polarity (Evolutionary) – The direction of evolution. That is, one state is 'primitive' (plesiomorphic) and another is 'derived' (apomorphic).

Polarize (Evolutionary) – To determine the direction of evolution. That is, to determine which state is 'primitive' (plesiomorphic) and which is 'derived' (apomorphic).

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

Primary conus – A solid conus on the gladius that is not formed by the in-folding of the lateral vanes.

Protective membrane – Thin web-like integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers, supported by muscular rods called trabeculae (Fig. 25) (see **Trabeculae**).

Proximal – Situated nearest or next to the centre of the body or nearest the point of origin or attachment of a muscle, appendage, etc. (opposite of distal).

Pseudomorph – An ejected mass of ink and mucous that approximates the size and shape of the cephalopod that released it; i.e. a false body that fixes the attention of a predator while the cephalopod escapes.

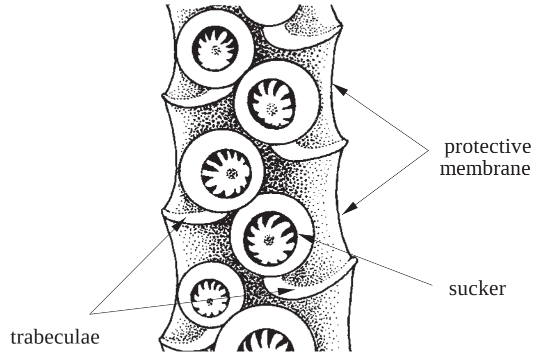


Fig. 25 Trabeculae, protective membranes and suckers on arm of squid

Rachis – The thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support vanes (Fig. 10) (see **Gladius, Vane**).

Radula – The chitinous, ribbon-like band in the mouth of cephalopods that contains up to 7 transverse rows of teeth that aid in transport of food into the oesophagus (Fig. 26); is a significant higher taxonomic value.

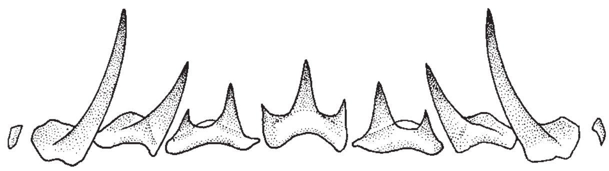


Fig. 26 Radula

Recent – Geological term referring to an organism or species that is living or has lived within the past 10 000 years, or to an object formed or events that have occurred within the past 10 000 years.

Renal appendages – Structures that form the nephridium (= kidney). The renal appendages are out-pockets of the veins within the renal sac (primarily the venae cavae) that are covered with renal epithelium. The renal sac empties into the mantle cavity via the nephridial (or renal) pores.

Renal pore – The opening(s) of the renal cavities into the mantle cavity, through which urine is discharged.

Rhynchoteuthion – Paralarval stage of the Ommastrephidae characterized by the fusion of the tentacles into a trunk-like proboscis (Plate VIII, 49).

Rostrum (= spine) – A spike-like posterior projection of the gladius, exterior to the conus (Fig. 10).

Secondary conus – A conical region at the posterior end of the gladius that is formed by an in-rolling and fusion of the vanes. The ventral line of fusion usually is apparent. The secondary conus may be rather short or exceed half the gladius length (Fig. 27).

Secondary fin – A non-muscular fin-shaped structure found in some oegopsid squids, located posterior to the true or primary fin (Fig. 28) The secondary fin may act as a buoyancy organ.

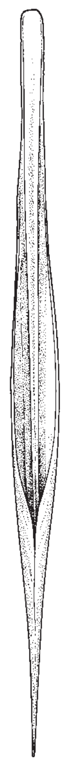
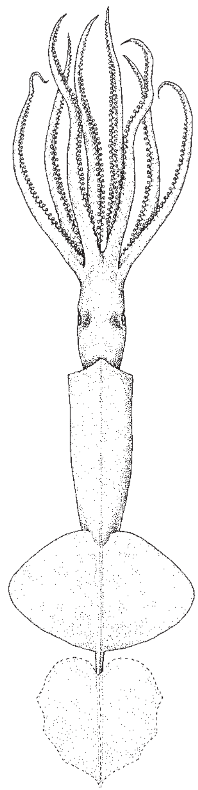


Fig. 27 Secondary conus



Grimalditeuthis bonplandii

Fig. 28 Secondary fin

Semelparous – A reproductive strategy in which females spawn once then die. Sometimes called terminal or 'big-bang' spawners. Many squids are semelparous but in some species reproduction is prolonged.

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

Side pockets – Small membranous folds of the integument that form small, shallow pockets lateral to the foveola in the funnel groove (Fig. 15) (see **Foveola**).

Species – Populations of animals that interbreed or are potentially capable of interbreeding in nature. Considerable debate exists over the general definition of a species and how the theoretical definition should be applied in practice. With regard to the latter problem, cephalopod species generally are defined by distinct morphological traits not exhibited by any other species. This practice is valid if interbreeding does not occur. However, the amount of interbreeding (i.e. hybridization) that actually occurs in nature and contributes to or diminishes speciation is virtually unknown in cephalopods.

Sperm cord – The coiled rope of sperm that lies within the spermatophore (Fig. 29).

Sperm duct (= seminal duct) – The duct of male reproductive system that joins the testis with the spermatophoric organ (Fig. 21).

Sperm groove – Sulcus along the ventral side of the hectocotylus used to transfer the spermatophores.

Sperm mass – The mass of sperm held within the spermatangia of everted spermatophores.

Sperm receptacle – A bulbous structure in the buccal region or at the openings of the oviducts in females of certain squids for deposition of spermatangia.

Spermatangium (pl. spermatangia) – Extruded, exploded, evaginated spermatophores, often in the form of a round bulb.

Spermatheca(e) – Specialized sperm-storage structure(s) found in the skin of some female squids.

Spermatophore – A tubular structure manufactured by male cephalopods for packaging sperm; capable of holding millions of sperm, it is transferred and attached to the female until fertilization occurs (Fig. 29). It forms a spermatangium after the spermatophoric reaction occurs and the spermatophore has everted.

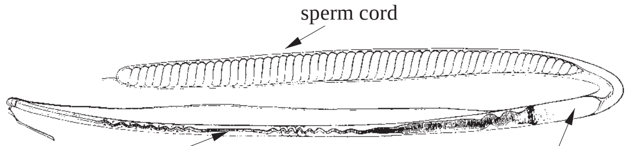


Fig. 29 Spermatophore

Spermatophore pad – A fleshy patch of tissue, usually in the mantle cavity of some female squids (e.g. loliginids), to which spermatangia adhere after mating and remain until fertilization occurs.

Spermatophoric complex – The unit formed by the sperm duct, the spermatophoric organ, the spermatophoric sac, the spermatophoric duct and the penis (Fig. 21).

Spermatophoric duct – The duct of male reproductive system through which the spermatophores, once formed, pass from the spermatophoric organ to the spermatophoric sac (Fig. 21).

Spermatophoric organ – Male organ where the spermatophores are formed (Fig. 21).

Spermatophoric reaction – The evagination of a spermatophore with the extrusion of the sperm mass, caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher.

Spermatophoric sac – See **Needham's sac** (Fig. 21).

Spine – See **Rostrum**.

Squid – Common name given to members of the Teuthoidea and some members of the Sepiolidae.

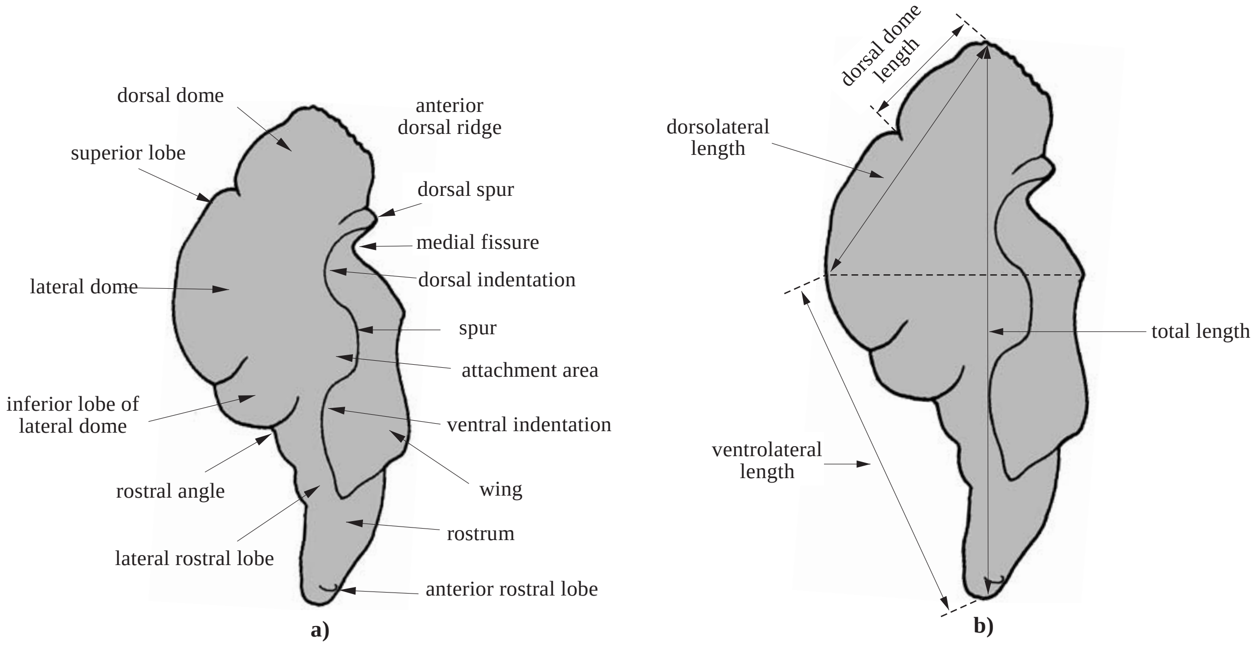


Fig. 30 Diagrams of a generalized teuthoid statolith (anterior view) with a) basic terms and b) basic dimensions labelled
(after Clarke, 1978)

Squid, general terminology – Diagramatic drawing with external features labeled, ventral view (Fig. 11).

Stalk of tentacle – See **Tentacle stalk**.

Stalked eyes – See **Eye, position and size**.

Statocyst – A paired sense-organ that detects gravity, angular acceleration and low-frequency sound. The statocysts are embedded within the cephalic cartilage and contain the statoliths.

Statolith – A calcareous stone in the statocyst that detects linear acceleration, angular acceleration and orientation (Fig. 30). Concentric rings in complex statoliths of many species can be used to estimate age.

Stellate ganglion – Major ganglion of the peripherial nervous system of neocoleoid cephalopods that controls nerves to the mantle muscles.

Stomach – The muscular organ of the digestive system where primary digestion occurs (Fig. 12). The stomach generally is 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, but the reproductive system is not mature and functional. It follows the juvenile stage and precedes the adult stage. A subadult stage is defined in cephalopods since the adult phase frequently is 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/s – Muscular, suction-cup structure/s on the arms and tentacles (occasionally on the buccal membrane) of squids; they are stalked, placed on muscular rods that contract (Fig. 31a). They usually are counted either in longitudinal or in transverse (oblique) rows (Fig. 31 b).

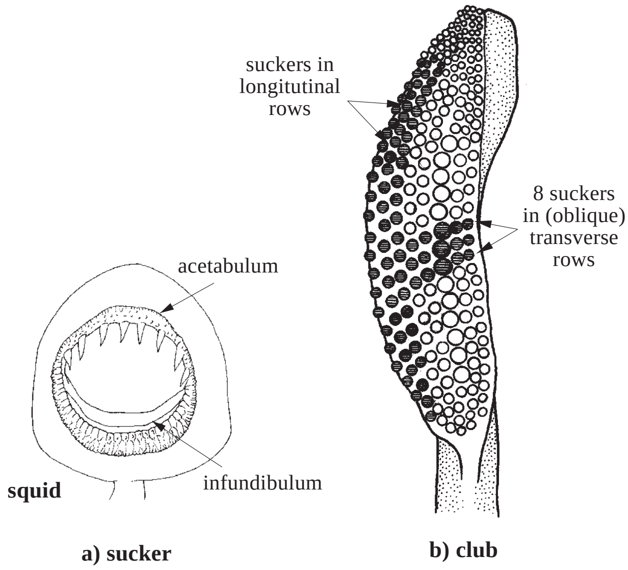


Fig. 31 Squid sucker and squid suckers orientation

Sucker ring – Chitinous, often serrated or toothed, ring that encircles the opening of suckers of squids (Fig. 32).

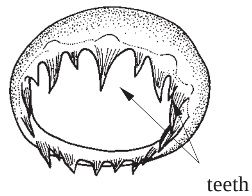


Fig. 32 Sucker ring

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

Sucker stalk – The muscular support and connective structure between the sucker and the arm. It is constricted into a conical pillar.

Sucker teeth – Sharp, blunt or rounded teeth on the inner horny sucker rings of some squids.

Superior buccal lobes – Lobes of the central nervous system that occur dorsal to the oesophagus where the latter enters the buccal mass.

Swimming membrane (= keel) – An elongate, flat muscular vane along the aboral surface of arms of squids that functions to streamline and support the arms during swimming (Fig. 8).

Synonym – One of 2 or more names applied to the same taxon/species.

Systematics – The classification of organisms into hierarchial groups based on phylogenetic relationships.

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 (Fig. 11).

Taxa, taxon – A taxonomic group of any rank. A taxonomic unit.

Tentacles – Modified fourth pair of appendages in squids, used for prey capture. The distal ends contain clubs with suckers and/or hooks; stalks frequently devoid of suckers (Fig. 11). Tentacles are capable of considerable extension and contraction, but they are not retractile into tentacular pockets in squids. Although the tentacles are derived evolutionarily from the fourth pair of appendages, the term ‘arms IV’ is reserved for the ventralmost pair of appendages, the ventral arms, which are evolutionarily the fifth pair of arms.

Tentacle absence – Tentacles can be absent because the species lacks tentacles, they are accidentally lost during capture, or they are naturally lost at a particular stage of development.

Tentacle pads – Poorly understood and complex pad-like photophores that are found on the tentacular stalks of some squids of the family **Chiroteuthidae**.

Tentacle stalk – Region of the tentacle proximal to the club.

Tentacle terminology – See Fig. 11.

Tentacular club – The distal, terminal, usually expanded, part of the tentacle that bears suckers and/or hooks. Used for capturing prey (Figs 8 and 11).

Tentacular pocket – A pocket that encompasses the base of each tentacle at its fusion with the head and provides space for complete retraction of the tentacle into the pocket (as in members of the Sepioidea and “sepioid squids”), or contraction of the tentacular stalk without retraction into the pocket (as in the true squids). It is present in members of the families Australiteuthidae and Loliginidae (Myopsida), Bathyteuthidae and Chtenopterygidae (Oegopsida).

Tentacular retractor muscles – Muscles that serve to coil the tentacle when retracted, in contrast with those muscles that serve to shorten (contract) the tentacle.

Tentacular sheath –The keels of arms IV are off-set laterally and often enlarged to fully or partially conceal, protect or encase the adjacent tentacles. The latter function is most fully developed in the chiroteuthids and mastigoteuthids.

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 generally are supported by an elongate secondary conus of the gladius.

Terminal organ – Alternative name for penis, as true definition of a penis is ‘organ of insertion’. In most cephalopods, the hectocotylized arm is used for spermatophore insertion, or placement, in the females.

Terminal pad (of tentacular club) – A small, distinct pad or circlet of small terminate suckers at the tip of the club.

Teuthoidea – The higher taxon that includes all squid-like **decapods**; now archaic. The monophyly of this taxon is questionable.

Total Length (TL) – Length measured from the posterior tip of the mantle to the anterior tip of the outstretched appendages (Fig. 4)

Trabeculae – Muscular rods that support the protective membranes on the arms and clubs of squids (Fig. 25). Occasionally membranes are reduced and/or trabeculae are elongated, so they extend beyond the edge of the membrane, papilla-like.

Tragus – Particular inward-projecting knob in the funnel-locking apparatus of some squids. It is the knob found on the medial surface of the central depression.

Truncate teeth – Teeth on the inner chitinous rings of decapod suckers that do not terminate in a point but rather a broad, flat tip.

Vane – Thin, lateral expansion of the gladius that arises from the rachis (Fig. 10) (see **Rachis**).

Ventral – The lowermost or belly surface of a cephalopod, the surface on which the funnel is located. Opposite the dorsal surface (Figs 11 and 13).

Visceral sac – The body region posterior to the head surrounded by the mantle. The body wall in this region that encases the viscera usually is rather thin-walled, hence the name ‘visceral sac’. The visceral sac also is called the ‘visceral dome’.

Visceropericardial coelom – The largest coelom in squids. It encloses the gonads, and partially encapsulates the stomach, caecum and ventricle, among other structures. The viscero-percardial coelom also communicates with the other squid coelom, the nephridial coelom, and the mantle cavity via a pair of ducts that open at the base of the nephridial papillae.

Web – A membranous sheet of greater or lesser extent that extends between the arms of many **octopods**, giving an umbrella-like appearance when the arms are spread out, e.g. on cirroteuthids. It is reduced or absent in most **decapods**.

1.6 Key to Recent Myopsid and Oegopsid Squids

1. Eight or 10 circumoral appendages; suckers (and/or hooks) present; no external shell . . . . . . **Coleoidea → 2**

2. Suckers stalked with chitinous rings; 10 circumoral appendages, 8 arms and 2 ventrolateral tentacles (tentacles may be lost in some species); mantle cavity communicates with the exterior via 3 openings . . . . **Cuttlefishes, Bobtail squids, Bottletail squids, Pigmy squids, Ram's Horn squid, Myopsid squids, Oegopsid squids → 3**

3. Internal shell straight, feather- or rod-shaped, chitinous; tentacles contractile, not retractile, into tentacular pockets; fins usually joined posteriorly; mantle edge near mantle cartilages with small projections or 'angles' . . . . **Myopsid Squids, Oegopsid Squids → 4**

4a. Eye covered by transparent membrane (cornea) (Fig. 33a) . . . . . . **Myopsid squids → 5**

4b. Eye without cornea and len in open contact with seawater (Fig. 33b) . . . . **Oegopsids squids → 6**

5a. Four longitudinal rows (series) of suckers on manus of tentacular clubs; fins united at posterior end of mantle; medial posterior border of fins concave (Fig. 34) . . . . . . **Family Loliginidae**

5b. Two longitudinal rows (series) of suckers on manus of tentacular clubs; fins not united at posterior end of mantle; medial posterior borders of fins convex (Fig. 35) . . . . . **Pickfordiateuthis**[1/]

5c. Fins not united at posterior end of mantle; a sepiolid-like, dumb-bell shaped photophore on the ventral surface of ink sac. . . **Family Australiteuthidae**[2/]

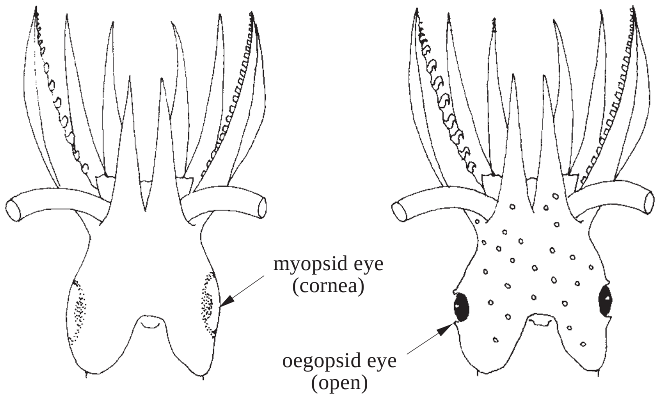


Fig. 33

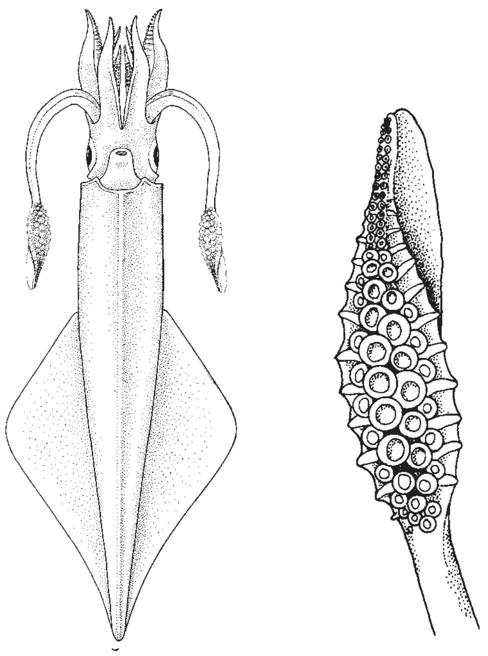


Fig. 34 Loliginidae (*Loligo*)

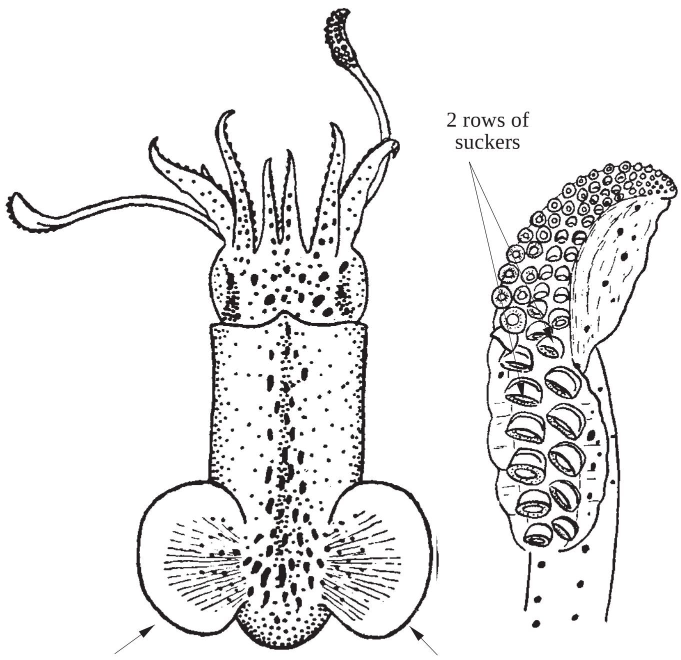


Fig. 35 Loliginidae (*Pickfordiateuthis*)

1/ *Pickfordiateuthis*, the sole genus in a formerly recognized family, recently has been placed in the family Loliginidae; it is included in the Key to indicate its unique characters within the loliginids.

2/ This new family of myopsid squid has been described from Australian waters by C.C. Lu, 2005.

6a. Funnel free from mantle; funnel-mantle locking apparatus present . . . . → **7**
6b. Funnel fused to mantle on each side[3/]; no funnel-mantle locking apparatus present. . . . . → **32**

7a. Funnel-locking cartilage a simple, straight groove and ridge[4/] (Fig. 36a) . . . . → **8**
7b. Funnel-locking cartilage not a simple, straight groove and ridge (Fig. 36b, c, d, e, f) . . . . → **25**

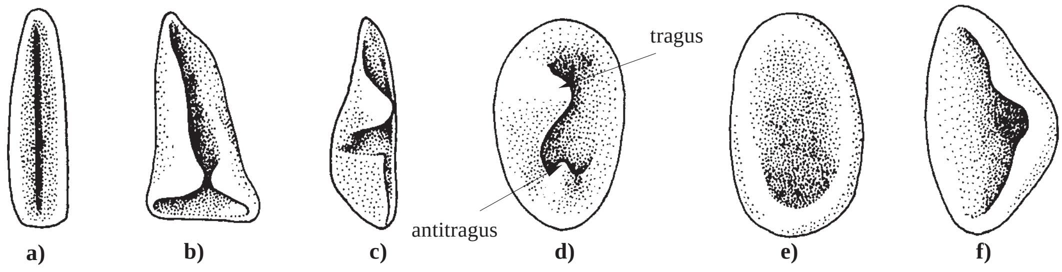


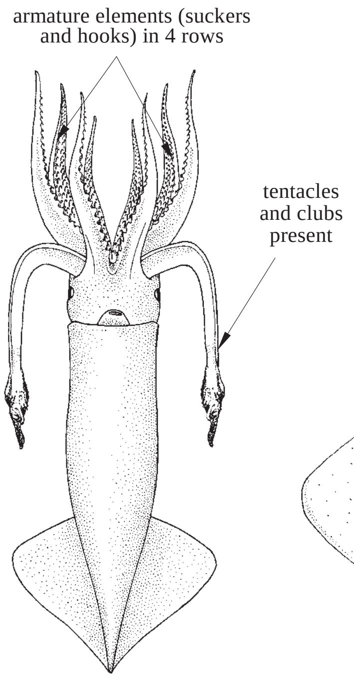
Fig. 36 Funnel-locking cartilage

8a. Arms with hooks or with suckers in 4 longitudinal rows on proximal half of ventral arms . . . . → **9**
8b. Arms without hooks and with suckers in 2 longitudinal rows on proximal half of ventral arms . . . . → **13**

9a. Armature (suckers, hooks) of arms in 2 rows . . . . → **10**
9b. Armature (suckers, hooks) of arms in 4 rows (Fig. 37). . . . . **Family Gonatidae**

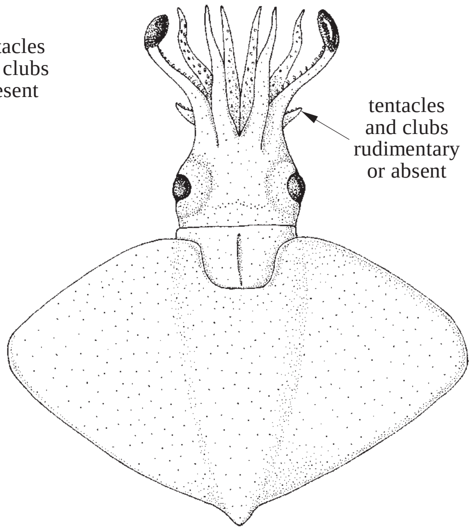
10a. Tentacles and clubs absent in adults although present in larvae or occasionally in juveniles (***Taningia***) but, when present, always with rudimentary clubs armed with few suckers (Fig. 38) . . . . . **Family Octopoteuthidae**
10b. Tentacles present; fully developed clubs present (Fig. 39) . . . . → **11**

11a. Photophores on viscera but not on mantle or surface of head and/or arms . . . . **Family Pyroteuthidae** (Fig. 39)
11b. Photophores on mantle and surface of head and arms but not on viscera . . . .→ **12**



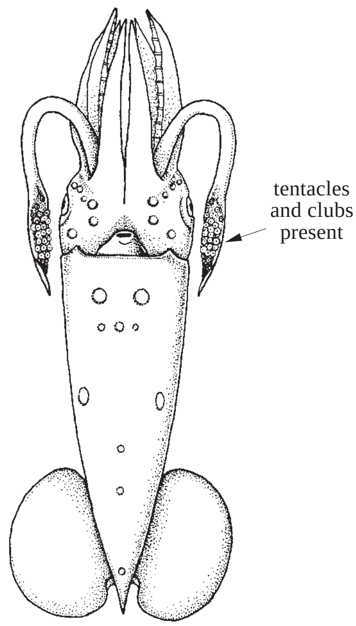
ventral view

Fig. 37 Gonatidae (*Gonatus*)



dorsal view

Fig. 38 Octopoteuthidae (*Taningia*)



ventral view

Fig. 39 Pyroteuthidae (*Pterygioteuthis*)

[3/] Fusion of the mantle component of locking apparatus to the funnel component also occurs in adults of one ommastrephid genus, *Sthenoteuthis*. However, the ommastrephid inverted T-shape (⊥) is retained.

[4/] The classification "simple and straight" includes some locking apparatuses that show considerable variation. For example, in the Octopoteuthidae and the Histioteuthidae 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 in the more highly specialized types, e.g. oval, ⊥-shaped.

12a. Photophores on tentacles but not on eyeballs . . . . **Family Ancistrocheiridae** (Fig. 40)
12b. Photophores on ventral eyeballs but not on tentacles . . . . **Family Enoploteuthidae** (Fig. 41)

13a. Buccal membrane connectives attach to ventral sides of arms IV (Fig. 42b) . . . . → **14**
13b. Buccal membrane connectives attach to dorsal sides of arms IV[5/] (Fig. 42a) . . . . → **20**

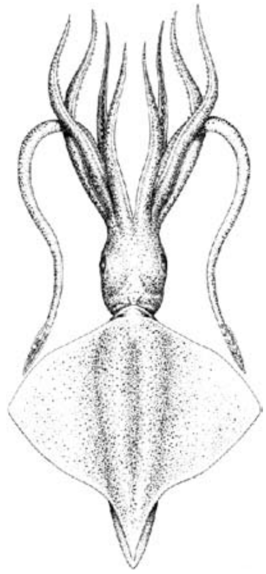


Fig. 40 Ancistrocheiridae (*Ancistrocheirus*)

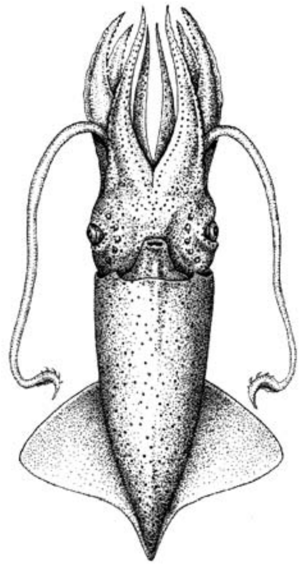


Fig. 41 Enoploteuthidae (*Abralia*)

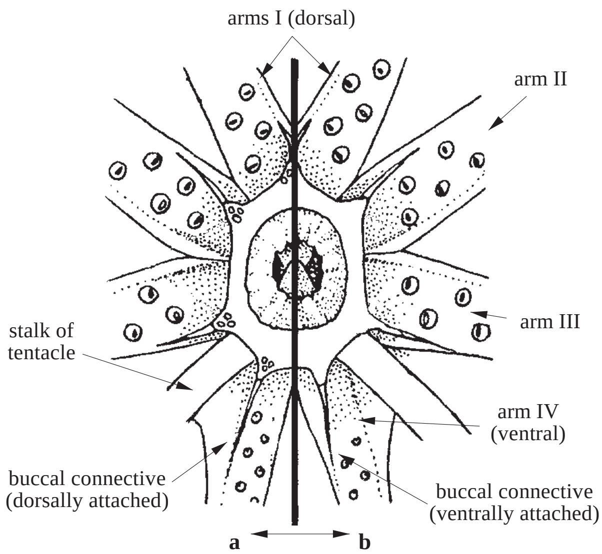


Fig. 42 Oral view

14a. Hooks present on tentacular clubs (Fig. 43a and b); tentacles and clubs are lost in mature animals (Fig. 43c) . . . . **Family Onychoteuthidae**
14b. Hooks lacking on tentacular clubs . . . . → **15**

15a. Cartilaginous scales present on mantle (may be minute); tentacular clubs with 4 longitudinal rows (series) of suckers . . . . → **16**
15b. Cartilaginous scales lacking; tentacular clubs with more than 4 longitudinal rows (series) of suckers on some areas . . . . → **17**

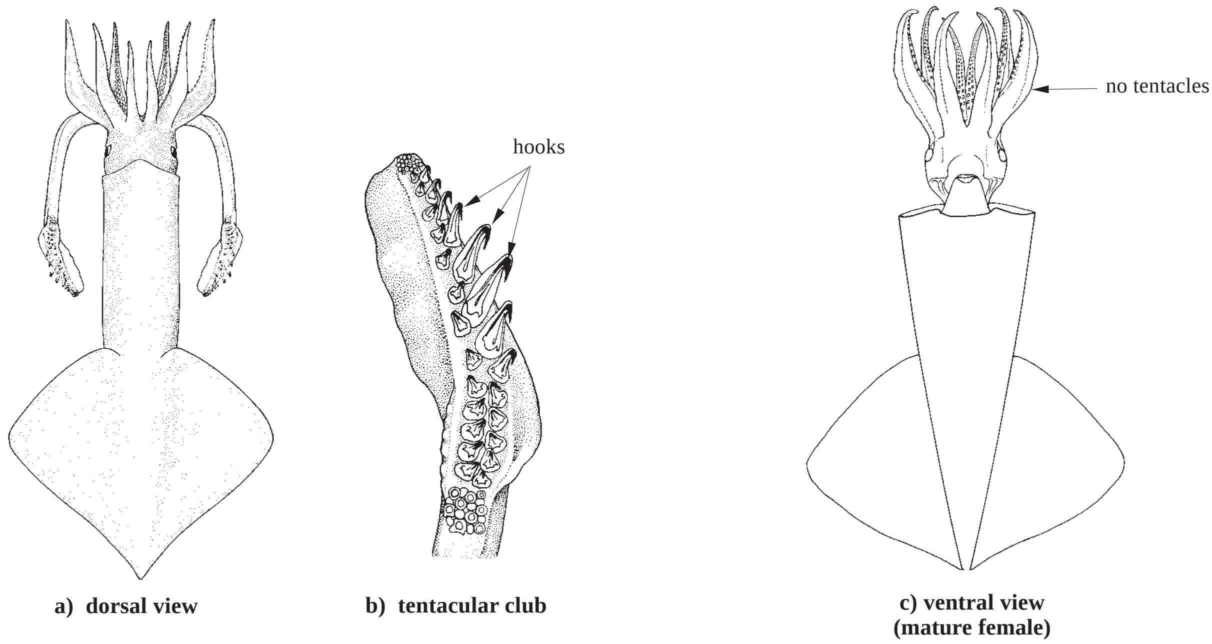


Fig. 43 Onychoteuthidae (*Onychoteuthis*)

[5/] This character is difficult to detect in some histioteuthids that have secondary modifications to the buccal membrane connectives.

16a. Tentacles present with numerous, laterally compressed club suckers . . . . . **Family Pholidoteuthidae** (Fig. 44)

16b. Tentacles lost in adults; tentacles in juveniles small and weak, with a few (about 6) poorly differentiated suckers . . . . **Family Lepidoteuthidae** (Fig. 45)

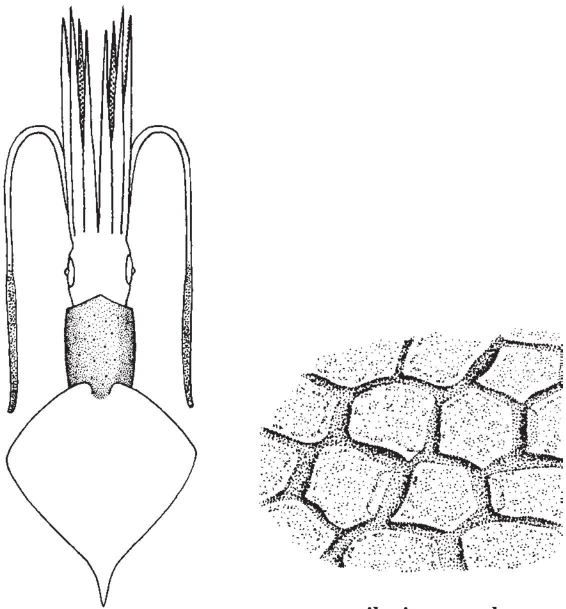


Fig. 44 Pholidoteuthidae (*Pholidoteuthis*)

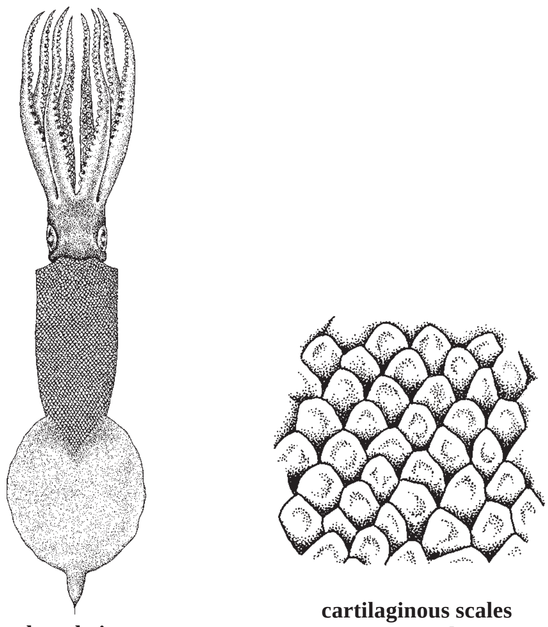


Fig. 45 Lepidoteuthidae (*Lepidoteuthis*)

17a. Fins nearly as long as mantle, supported by strong, transverse, muscular ribs; minute suckers present on oral surface of buccal lappets (Fig. 46) . . . . **Family Chtenopterygidae**

17b. Fins less than half the body length and without supporting ribs; no suckers on buccal lappets . . . . → **18**

18a. Tentacular clubs with 6 uniform longitudinal rows (series) of suckers; a long, spike-like tail present, greater than fin length (Fig. 47) . . . . **Family Batoteuthidae**

18b. Tentacular clubs with 2 or 4 longitudinal rows (series) of suckers . . . . → **19**

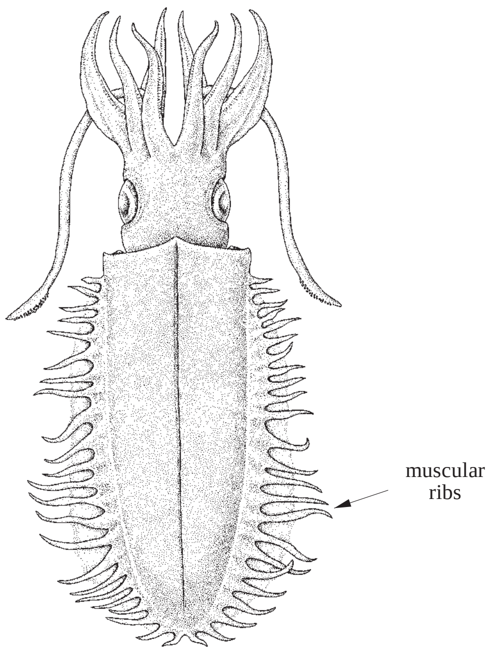


Fig. 46 Chtenopterygidae (*Chtenopteryx*)

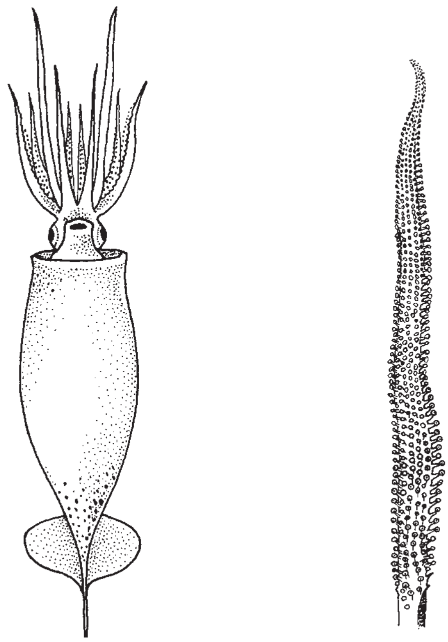
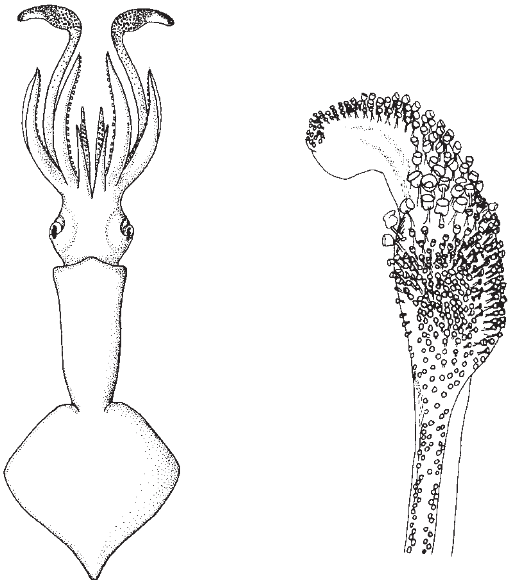


Fig. 47 Batoteuthidae (*Batoteuthis*)

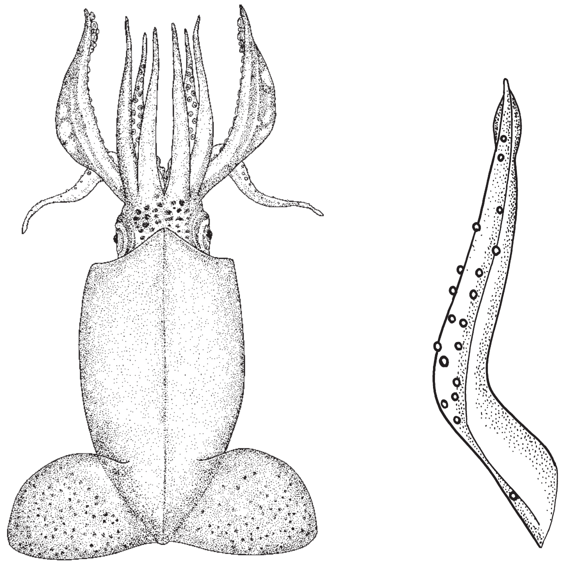
19a. Tentacular clubs with 4 longitudinal rows (series) of suckers on distal portion, numerous rows on proximal portion; no long, spike-like tail (Fig. 48) . . . . **Family Brachioteuthidae**

19b. Tentacular clubs with 2 longitudinal rows (series) of very widely spaced, tiny suckers; mantle broad, bluntly rounded posteriorly; fin short, wide, transversely oval (Fig. 49). . . . . ***Walvisteuthids***[6/]



dorsal view tentacular club

Fig. 48 Brachioteuthidae (*Brachioteuthis*)



dorsal view tentacular club

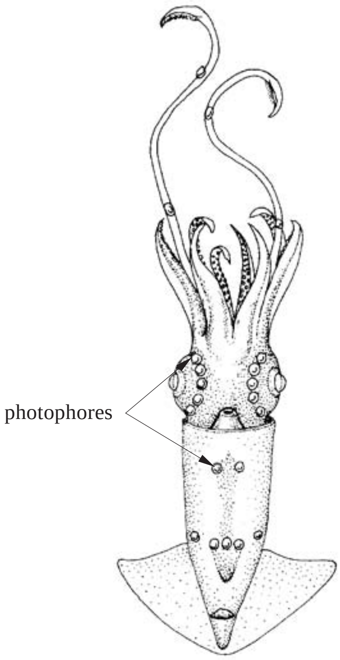
Fig. 49 Onychoteuthidae (*Walvisteuthis)*

20a. Ventral surface of eye with a single row of photophores; buccal membrane with 8 separate lappets (Fig. 50) . . . . **Family Lycoteuthidae**

20b. No photophores on eyes; buccal membrane with 7 lappets or less . . . . **→ 21**

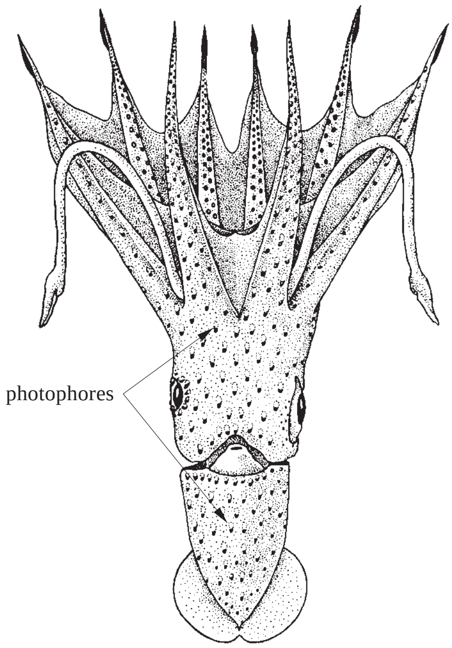
21a. Surface of mantle, head and arms covered with numerous photophores (usually large and distinct) (Fig. 51) . . . . **Family Histioteuthidae**

21b. Surface of mantle and head without photophores (base of arms may have a few photophores) . . . . **→ 22**



ventral view

Fig. 50 Lycoteuthidae (*Lycoteuthis*)



ventral view

Fig. 51 Histioteuthidae (*Histioteuthis*)

[6/] *Walvisteuthis*, the sole genus in a formerly recognized family, Walvisteuthidae, now considered to belong to the family Onychoteuthidae by an authoritative fraction of the scientific community (i.e. Young *et al.*, 2003). It is placed in the Key to indicate its unique characters within Onychoteuthidae.

22a. Minute suckers present on oral surface of buccal membrane/lappets (Fig. 52) . . . . . . **Family Bathyteuthidae**
22b. No suckers on oral surface of buccal membrane/lappets . . . . **→ 23**

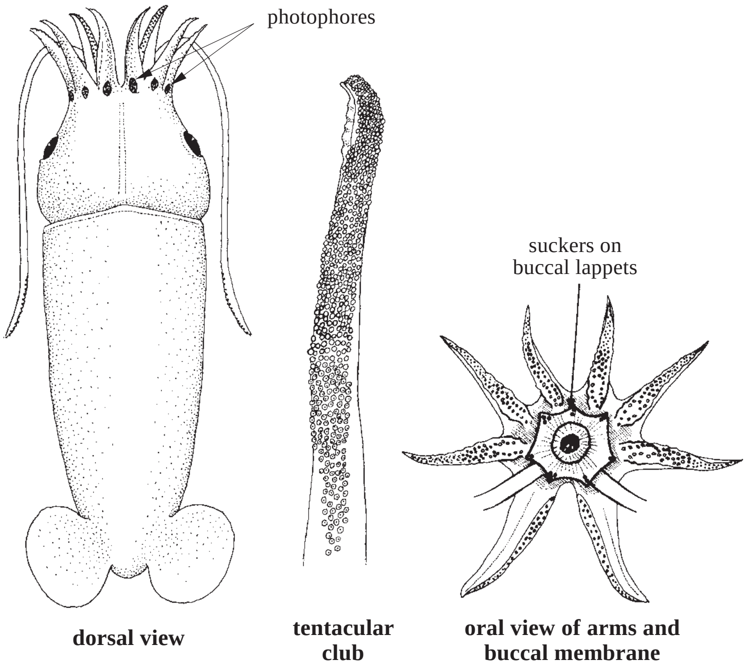


Fig. 52 Bathyteuthidae (*Bathyteuthis*)

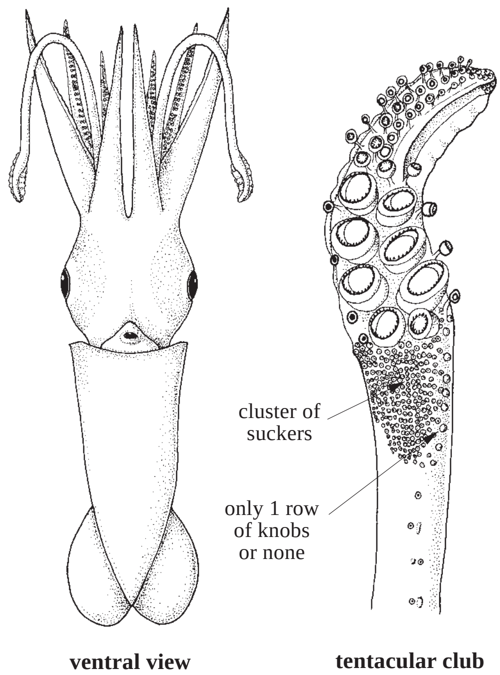


Fig. 53 Neoteuthidae (*Alluroteuthis*)

23a. Many small to minute suckers (or suckers and knobs) at proximal (carpal) end of manus (Figs 53 and 54) . . . . . . **→ 24**
23b. No cluster of small suckers at proximal (carpal) end of manus (Fig. 55) . . . . **Family Psychroteuthidae**

24a. Posterior borders of fins slightly convex; carpal knobs in a single dorsal row or absent; adults attain small size (Fig. 53) . . . . **Family Neoteuthidae**
24b. Posterior borders of fins concave; carpal knobs in a cluster alternating with carpal suckers; adults attain gigantic size (Fig. 54) . . . . **Family Architeuthidae**

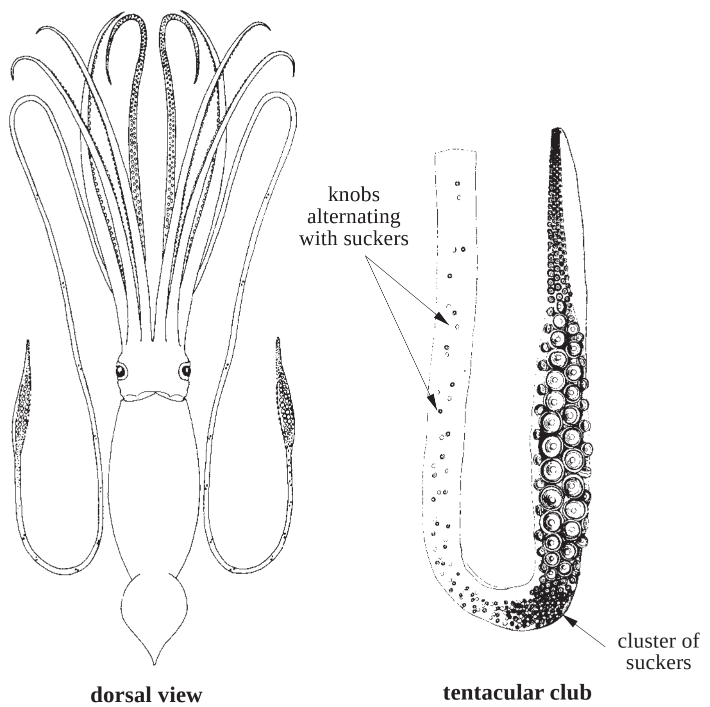


Fig. 54 Architeuthidae (*Architeuthis*)

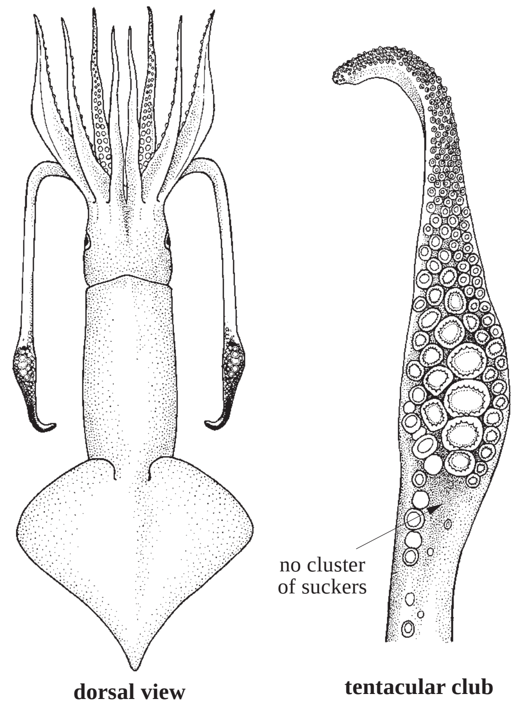


Fig. 55 Psychroteuthidae (*Psychroteuthis*)

25a. Funnel-locking cartilage with a longitudinal and a transverse groove: ⊥-shaped or ⊣-shaped (Fig. 36b and c) . . . . → **26**

25b. Funnel-locking cartilage (sub)triangular or oval with or without inward projecting knobs (Fig. 36d, e and f) . . . . → **27**

26a. Funnel-locking cartilage with a longitudinal groove crossed by a transverse groove at its posterior end, ⊥-shaped (Fig. 36b); fins less than 60% of mantle length (Fig. 56) . . . . **Family Ommastrephidae**

26b. Funnel-locking cartilage with a longitudinal groove from which a shorter groove branches medially, ⊣-shaped (Fig. 36c); fins more than 80% of mantle length (Fig. 57) . . . . **Family Thysanoteuthidae**

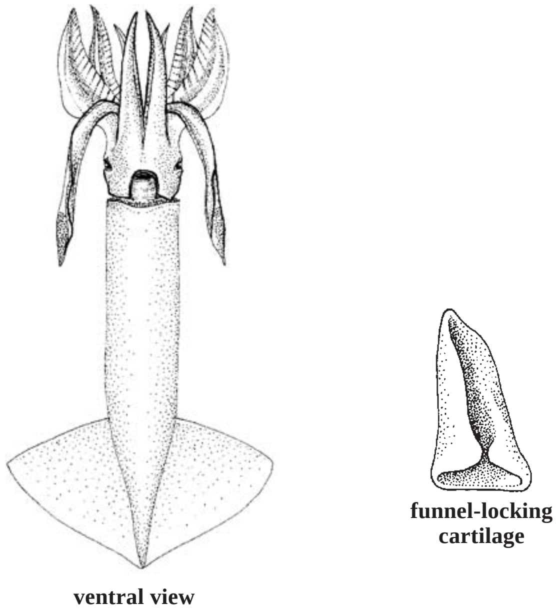


Fig. 56 Ommastrephidae (*Ommastrephes*)

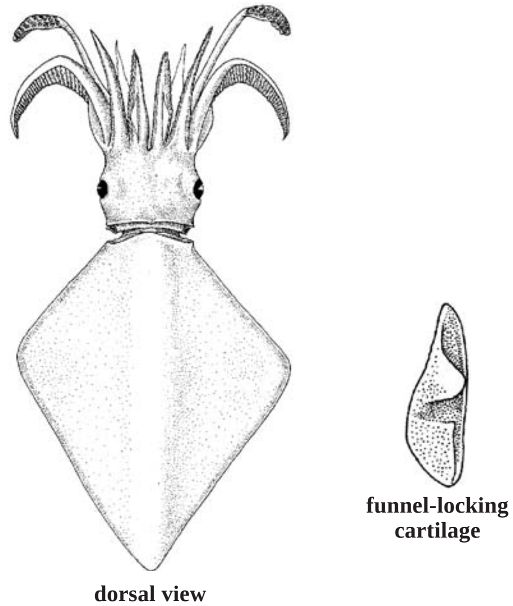


Fig. 57 Thysanoteuthidae (*Thysanoteuthis*)

27a. Funnel-locking cartilage oval with 1 or 2 knobs directed toward the centre of the concavity (Fig. 36d) . . . . . . → **28**

27b. Funnel-locking cartilage oval or subtriangular, without knobs (Fig. 36e and f) . . . . → **29**

28a. Club with only 4 longitudinal rows (series) of suckers (Fig. 58) . . . . **Family Chiroteuthidae**

28b. Club with many (more than 15) longitudinal rows (series) of minute suckers (Fig. 59) . . . **Family Mastigoteuthidae**

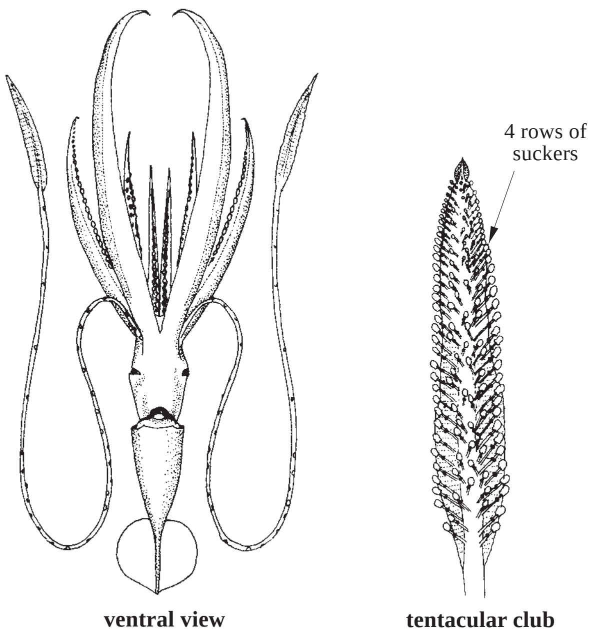


Fig. 58 Chiroteuthidae (*Chiroteuthis*)

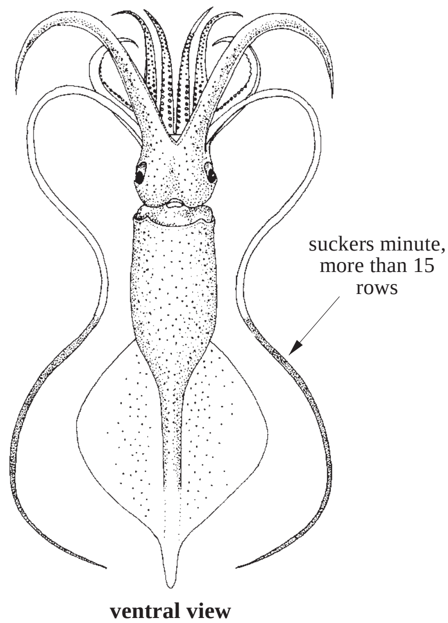


Fig. 59 Mastigoteuthidae (*Mastigoteuthis*)

29a. Suckers on arms in 4 to 6 longitudinal rows (series) . . . . → **30**

29b. Suckers on arms in 2 longitudinal rows (series); tail short (less than half of mantle length) or absent . . . . → **31**

30a. Six longitudinal rows (series) of suckers on arms I to III, 4 longitudinal rows of suckers on arms IV; tail extremely long (greater than mantle length), as a spike-like extension of the gladius; no fins on tail (Fig. 60) . . . . **Family Joubiniteuthidae**

30b. Three or 4 longitudinal rows (series) of suckers proximally on all arms; fins terminal, extremely long and broad, extend far posterior to mantle; gladius incorporated in fins to posterior tip (Fig. 61) . . . . **Family Magnapinnidae**

31a. Suckers on tentacular club in 4 longitudinal rows (series); mantle free dorsally (Fig. 62) . . . . **Family Cycloteuthidae**

31b. Suckers on tentacular club in 8 or more longitudinal rows (series); mantle fused dorsally to head (Fig. 63) . . . . **Family Promachoteuthidae**

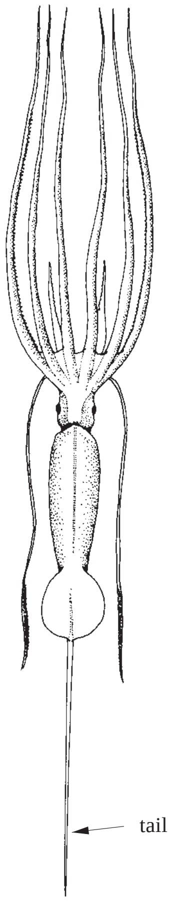


Fig. 60 Joubiniteuthidae (*Joubiniteuthis*)

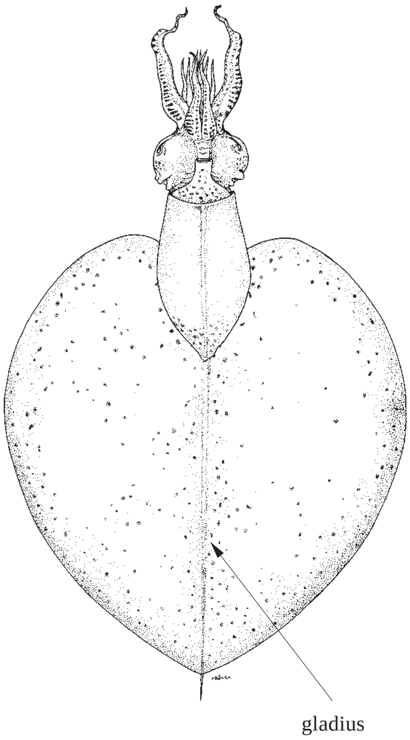


Fig. 61 Magnapinnidae (*Magnapinna*)

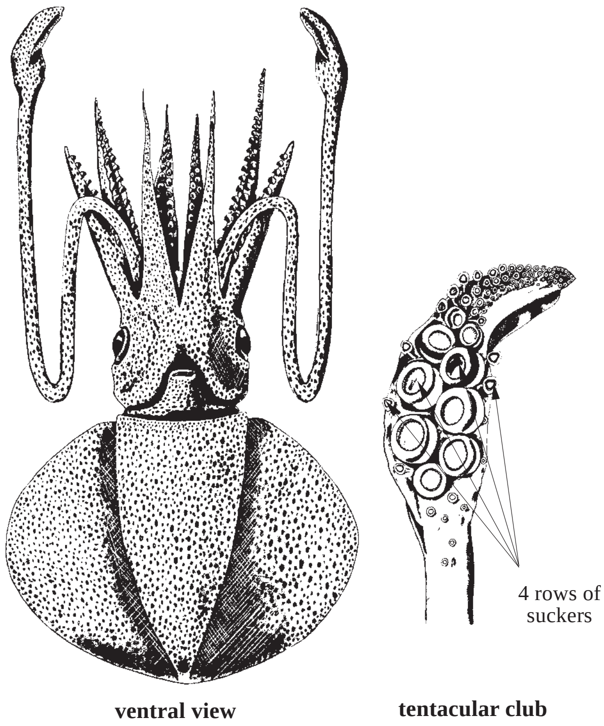


Fig. 62 Cycloteuthidae (*Discoteuthis*)

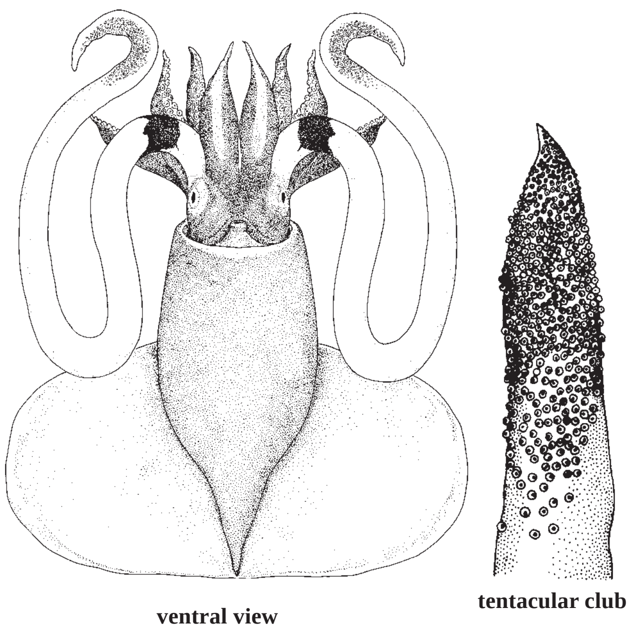


Fig. 63 Promachoteuthidae (*Promachoteuthis*)

32a. Mantle free dorsally, articulates with head by ridge and groove (Fig. 64) . . . . . **Family Grimalditeuthidae**

32b. Mantle fused dorsally with head (Fig. 65) . . . . **Family Cranchiidae**

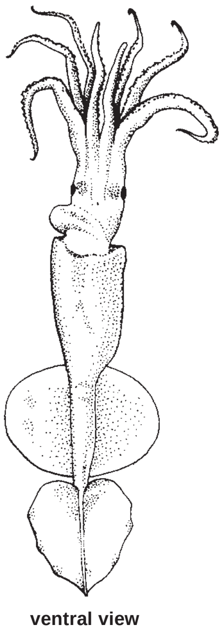


Fig. 64 Grimalditeuthidae (*Grimalditeuthis*)

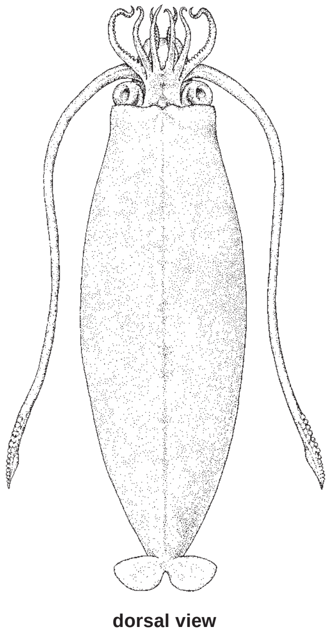


Fig. 65 Cranchiidae (*Helicocranchia*)