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AN INTRODUCTION TO THE CEPHALOPODA

by

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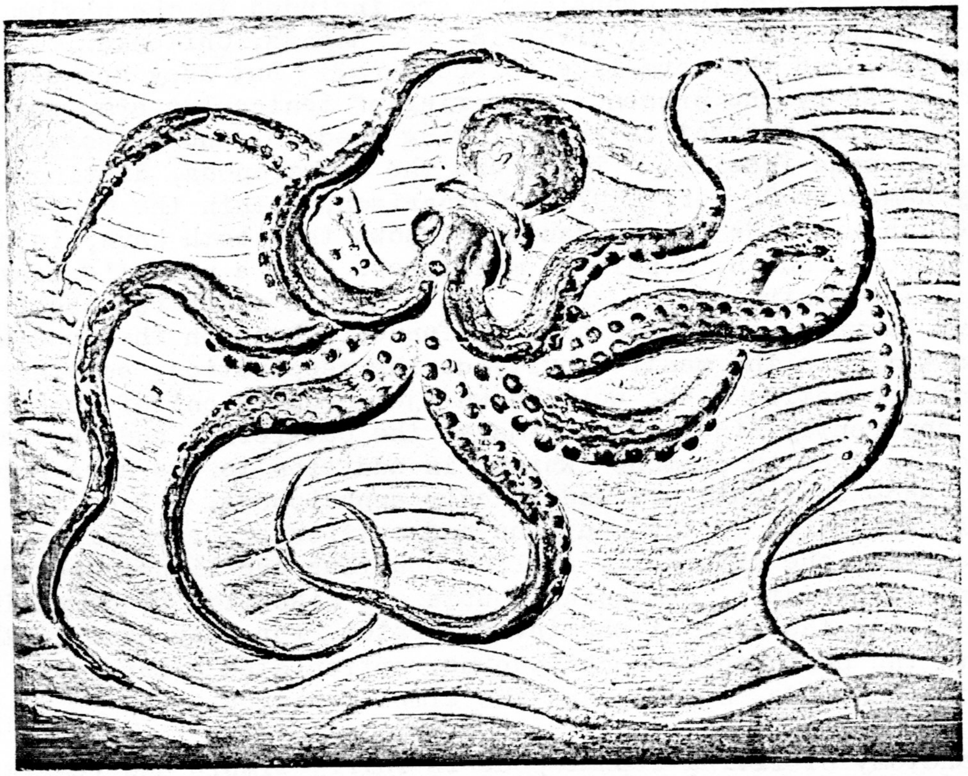

CONTENTS

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1. CEPHALOPODS AND THEIR RELATIVES

Despite obvious differences between a giant squid and a limpet, these animals are classified by zoologists together in the phylum Mollusca. The differences are only superficial for, like the whale and the mouse, squids and limpets are linked by a number of basic similarities. Both have an external skin-like covering, called the mantle, which is open at one end. This encloses the viscera, and secretes an external shell, of the limpet and the internal shell of the squid. Both have a symmetrical arrangement of horny rasping teeth, the radula, in the mouth, and both respire by means of feather-like gills, ctenidia, within the mantle cavity. In both animals, the respiratory pigment is haemocyanin.

For these reasons the Cephalopoda are included in the phylum Mollusca together with the Gastropoda, Bivalvia, Scaphopoda, Chitonida, Monoplacophora, and the worm-like Aplacophora. But they are separated as a distinct class by the presence of a ring of tentacular arms surrounding the mouth which is present in every living species, and preserved rarely as a trace in some fossils. These are the Cephalopoda, distinguished and informally named by Cuvier, 1797. Comparison, within the Cephalopoda, of the cuttlefish with the Pearly Nautilus shows that both have, in addition to the molluscan radula, a pair of mandibles, like a parrot's beak, situated in the centre of the arms. Both have a chambered shell for controlling buoyancy, and both have a 'funnel', beneath the head which circulates water in the mantle cavity during respiration, serving also as an organ of locomotion - the well-known 'jet-propulsion' of cephalopods. These two apparently dissimilar animals, the cuttlefish and the nautilus, have basic features in common; which, in addition to the arms surrounding the mouth, show that both are undoubtedly cephalopods. Once the zoological affinities of the nautilus and cuttles are recognised, it is easy to see that the externally shelled nautilus and limpet are, after all, not so very different. Remaining doubts are dispelled by comparing cephalopods with the rest of the invertebrates, for they have little in common with the pentaradiate echinoderms, articulated arthropods, brachiopods, annelids, corals, and the simple sponges.

The anatomy of living cephalopods is fairly simple and remarkably constant throughout the class. All living cephalopods have a 'circle' of arms surrounding the mouth, and we know that some extinct fossil forms were constructed on the same plan. The arms are not strictly arranged in a circle since none are situated on the median line, but are placed symmetrically on either side of it. The arms of living coleoid cephalopods are numbered 1-4, and designated 'left' and 'right', from the dorsal mid-line. The tentacles, one on either side, are situated between the third and fourth arms and are also designated 'left' and 'right'.

Today there are about 650 living species of cephalopod distributed from within the Arctic Circle to the Antarctic continent. All are carnivorous, and most are active predators feeding on fish and crustaceans at depths between a few metres and down to nearly 5,000 metres. All are exclusively marine, for none survive in fresh water.

Among the Cephalopoda are some of the largest invertebrates ever known: the giant squid Architeuthis measures up to 17 metres; the late Cretaceous ammonite Pachydiscus had a shell measuring almost 2 metres across its greatest diameter; but, in contrast, the minute Sepiola and Ideosepius are usually less than 5 centimetres in length.

Cephalopods are rated by zoologists as advanced molluscs. The elaborate behaviour of these animals, resulting from a highly developed nervous system and a centralised brain, their parental care and intelligent hunting techniques, and the undoubted intelligence exhibited under experiment by Octopus, confirms this assessment. But, if advancement is founded on general distribution or occupation of diverse habitats, then cephalopods fail to equal even the simple headless bivalve passively filtering particles suspended in the water. Both Scaphopods and cephalopods have remained conservatively in the sea, neither having penetrated even the littoral zone as a regular habitat. Chitons, bivalves and gastropods all vigorously occupy the littoral zone, but the chitons are left behind by the bivalves and gastropods when it comes to occupying fresh water habitats, and the gastropods entirely outstrip the bivalves when it comes to occupying terrestrial subaerial habitats. By this rating gastropods dominate all other molluscs, being carnivorous and herbivorous, marine and fresh water, terrestrial, arboreal, and even subterranean; occupying all the continents up to altitudes of 5486 metres, and all the seas down to 5200 metres. They have, like the cephalopods, abandoned the shell in adult marine nudibranchs and the terrestrial slugs, and they show no sign of a serious decline, even in the face of man's increasing pollution and destruction of habitats.

Nevertheless, the slow gait of the garden snail does not impress one in the same way as the flashing speed, the brilliant bioluminescence and the scintillating colour changes of marine squids. No gastropod equals the massive and menacing bulk of Architeuthis, nor the cunning ambush of the common cuttle when hunting crustaceans. Cephalopods are advanced animals that have thoroughly exploited one habitat - the sea. They have successfully challenged the vertebrates in their repeated returns to the sea; the reptiles in the Mesozoic and the mammals in the Cainozoic; and have retained a place in the hierarchy of marine animals second only to the cetaceans, and extending in time over 500 million years.

2. LIVING CEPHALOPODS - GENERAL ANATOMY

Three living species of Nautilus exist today in the S.W. Pacific. The genus has a planispiral shell coiled above the head of the animal, and is divided by septa into about 36 chambers pierced by a calcareous tube - the siphuncle. The animal occupies the last chamber which can be closed by means of a leathery operculum. Within a circle of about 90 retractile arms is the mouth with its horny beak which, in Nautilus, has a coating of calcium carbonate. As in all cephalopods, the upper mandible closes within the lower, and behind it is the radula formed of chitinous teeth. The arms are without suckers or hooks but have encircling raised annulations. The two simple eyes are without lens or cornea. Beneath the head two muscular flaps overlap ventrally to form a funnel which circulates water in the mantle cavity for both respiration and locomotion. There are four gills at the back of the mantle cavity, but no ink sac. Two adductor muscles are attached to the inside wall of the living chamber; the 'funnel', or hyponome, is attached to the underside of the head but is free ventrally and protrudes 3-4 cm beyond the edge of the shell. When the animal is swimming the hyponome can be delicately adjusted so that precisely controlled movements are possible.

The rest of the living cephalopods have only two gills in the mantle cavity, either eight or ten arms with suckers, and well-developed eyes with cornea and lens; the shell, if present, is internal.

The Sepioida includes the ten-armed, shallow water and bottom-dwelling cuttlefish: Sepia officinalis, the common European cuttle, may be taken as a representative of this order. It has an internal, minutely-chambered phragmacone ('cuttle bone') for controlling buoyancy. The mantle cavity is muscular and the hyponome an entire rounded muscular tube. Eight grasping arms have suckers all along the inner surface, while two long tentacular arms, normally tucked into pouches between the third and fourth arms, have bunches of suckers only on their club-like tips. In both cuttles and squids each sucker is furnished with a serrated horny ring. The body is flattened dorso-ventrally, shield-shaped, and the mantle has numerous pigmented cells which can produce a brilliant array of colours and patterns for sexual display, fright, or camouflage. The ink sac is large and used readily by irritated or frightened cuttles. Swimming is powered either by the hyponome or by means of two lateral flange-fins which almost encircle the body up to the mantle opening.

The deep water Spirula is included with Sepioids in nearly all traditional classifications, but this arrangement is now thought to be unsatisfactory. Spirula is anomalous in having a squid-like body with an internal spirally-coiled shell divided, like Nautilus, into 25-37 gas-filled chambers. It is small, up to 3 inches long, with two terminal fins on a short dumpy body. Spirula lives in nearly all the tropical and sub-tropical seas at depths between 180 and 900 metres where the pressure on the shell must be in the region of half a ton.

Teuthoidea is represented by the ten-armed squids of shelf and open seas. The essential difference between a squid and a cuttle is that the squid has a reduced horny strip - the gladius - in place of the cuttle's broad, chambered internal shell. As a result the cuttle is broad, flat, and shield-shaped, while the squid is long, round, and torpedo-shaped. The fins of squids are usually confined to the posterior half or third of the body and tend to be spear- or arrow-shaped. In both squids and cuttles the suckers are pedunculate - raised on muscular stalks, while in some squids the serrated ring around the sucker is elongated and forms hooks.

Between the squids and the octopods a single species, Vampyroteuthis infernalis, constitutes the order Vampyromorpha. It lives between a third of a mile and two miles deep in tropical and sub-tropical waters. Its colour is a deep purplish-black and it has the consistency of a jelly-fish. The eight arms are joined by webs reaching almost to the tips of the arms. A pair of reduced worm-like arms can be completely withdrawn into two pockets lying between the first and second arms, but these cannot be homologous with the tentacles of cuttlefish and squids since they occupy a place between the third and fourth arms.

The fifth extant order of cephalopods is the Octopoda. Octopods have only eight arms - no tentacles - and no shell apart from small calcareous plates embedded in the mantle. Unlike the flattened cuttle and the cylindrical squids, the octopods resemble a rounded sack with eight legs and two prominent eyes at the opening. They live mostly in shallow waters feeding on crustaceans, mainly crabs, but some are found at great depths, Eledonella at 5278 m. and some Octopus at a maximum of 3412 m. In octopods the suckers are sessile and without a horny ring. The argonauts are octopods with the first pair of arms modified for secretion of the 'egg-nest' shell. The male is very reduced in size.

3. BUOYANCY

One of the basic requirements of any swimming animal is to achieve near neutral buoyancy so that little energy is wasted in keeping at a given depth.

Nautiloids and the extinct ammonoids achieved this by means of a chambered and gas-filled external shell. It was conical, coiled or straight, and divided, from the apex to near the aperture, by septa into a series of chambers where buoyancy can be controlled by varying the ratio of gas to liquid.

This chambered part of the shell is the phragmacone. The chambered shells of the nautiloids and ammonoids enabled the animals to rise and sink with the diurnal movements of the zooplankton, freeing them from the restrictions of bottom living. As early as the Mesozoic era the belemnoids and teuthoids freed themselves from the unwieldy shell. The belemnoids kept the phragmacone at the rear balancing it with a calcareous rostrum - the familiar fossil belemnite - and retained only the dorsal part of the body chamber the pro-ostracum. The squid-like teuthoids did even better and abandoned all but the pro-ostracum, and, in some, lightened the body tissues to achieve neutral buoyancy.

During the Mesozoic a group of cephalopods, the sepioids, shifted the phragmacone over the back, abandoned the counter-balancing rostrum, and placed the centre of buoyancy over the centre of gravity. The crucial result of all these innovations was that the mantle, freed from the enclosing shell, became muscular and evolved into a powerful means of jet-propulsion. Nevertheless, there still remained a place for the 'old-fashioned' external shell of Nautilus, whose long-term success is confirmed by the three living species found abundantly in the south-west Pacific. Spirula retains an internal spirally-coiled shell which, placed in an extreme posterior position, must result in a head-down position for the animal.

Squids, having abandoned pneumatic means of buoyancy, have developed other methods. Loligo swims constantly to avoid sinking. In the cranchiid squids the coelomic space between the viscera and the body wall is filled with a liquid in which a high proportion of ammonium salts replaces sodium chloride. As ammonium is lighter than sea water, its presence gives the animal neutral buoyancy.

Giant squids have an even more remarkable solution to the problem. A large stranded Architeuthis in New Zealand was towed, soon after it was dead, back into the water where it floated. Local fishermen claim that the flesh of Architeuthis, used as bait, causes the hooks to "rise to the surface". Numerous reports exist of dying giant squids floating at the surface of the sea, and during the decade 1870-80 many dead and dying giant squids were reported floating at the surface off Newfoundland. Architeuthis has no coelomic cavity filled with ammonia-rich liquid and no buoyant material is known from any other part of its anatomy; one can only conclude that the solid tissues themselves have lightened and become buoyant. This must be the ultimate step in the emancipation of the cephalopods from the buoyant calcareous shell.

4. LOCOMOTION AND RESPIRATION

The idea that cephalopods anticipated the human discovery of jet-propulsion by about 500 million years is well known; but these versatile animals have developed three types of propulsion: jet-swimming, fin-swimming and web-swimming.

Jet-swimming, is most highly developed in the squids, particularly in Loligo. The mechanism is extremely simple. Water, entering the mantle cavity through spaces between the sides of the head and the mantle, passes rearwards in two streams to the two feather-like gills at the back of the mantle cavity. There respiration takes place. The two streams of water then unite, change direction, and pass forward past the anus and ink sac to the funnel, to be forcibly ejected by muscular contractions of the mantle. A system of flap-valves in the funnel and on either side of the head ensures that water circulates only in one direction.

Respiration is the primary function of the circulation of water in the mantle cavity and it continues as long as the animal lives, whether it is active or at rest. The process is under the control of the pallial nerves which are a little over 1 mm. in diameter, about 50 times thicker than the nerves in other animals. A fear-inducing stimulus interrupts the normal respiratory cycle with a powerful impulse that travels swiftly down the 'giant' pallial nerve to activate the mantle muscles into rapid and violent motion. Water is expelled from the mantle cavity, together with a cloud of ink, and the squid darts backwards several feet. The very rapid darting movement of Loligo, controlled by its 'giant' nerves, has earned it the description 'a little squirt with a big nerve'.

Loligo is confined to the continental shelf; it is mainly pelagic, but it occasionally rests on the sea bottom. Since it lacks the buoyant phragmacone of Sepia, having only a thin but rigid horny strip, it is heavier than water and must therefore swim continuously. Captured squids cruise back and forth, day and night, from wall to wall of their tank, not by jet-swimming (although the respiratory cycle continues) but by means of the broad arrow-shaped fin extending from the posterior tip to about half-way down the body. At the end of each run the action of the fin is reversed and the squid changes direction without turning around: there seems to be no preference between backward and forward swimming. If an emergency arises and jet-swimming is resorted to the fin is wrapped close around the body, producing a streamlined shape. Escape movements are always backwards in squids and cuttles.

In Sepia two lateral fins almost encircle the body and undulations pass in either direction for, like squids, cuttles travel backwards or forwards with equal ease. All cuttlefish and squids use fin-swimming for general migratory movements; jet-swimming is reserved for serious occasions - towards prey or away from danger - but the gentle ejection of water from the funnel during respiration probably contributes to the overall movement during fin-swimming.

Web-swimming occurs in all the cirrate octopods and in two incirrate genera; also in Vampyroteuthis and in two squids, Histioteuthis and Cirroteuthis. The eight arms are interconnected by triangular webs which in some forms reach almost to the tips of the arms. This umbrella-like arrangement opens out slowly and closes a little faster, the movement resembling the pulsing contractions of the medusoid jellyfish. The funnel is usually weak and probably serves only the respiratory needs of all these sluggish web-swimmers. Near-neutral buoyancy is achieved by the presence of gelatinous tissue in the bodies of these strange cephalopods, which have a strong superficial resemblance to jellyfish.

In the cranchiid squids jet-swimming is used for escape movements only; respiration takes place by means of peristaltic movement of the coelomic fluid. The mantle cavity is divided by a septum on each side of the body, producing four chambers. A hole in each septum allows water to pass from the anterior into the posterior chamber, while the gill itself acts as a valve ensuring one-way circulation. Contraction of the anterior coelomic sac increases the volume of the anterior mantle chamber, so that it fills with water drawn in through a restricted passage between the side of the head and the collar valve. Dilation of the anterior coelomic sac forces water through the opening in the septum, across the gill, and into the posterior mantle chamber, pushing the water already there out through the funnel. During this respiratory cycle the mantle cavity remains distended and the muscles play no part.

Swimming in octopods is a relatively sluggish activity compared with that of squids. It kicks off by means of its eight arms in an obvious swimming movement, but once 'water-borne' it closes the arms behind it and uses the funnel in a series of fairly rapid, but not powerful, jets, resulting in a jerky copepod-like motion. When coming to rest jet-swimming ceases and the arms spread out to make a balletic eight-point landing. There the octopus rearranges its arms and the funnel continues respiratory movements. The presence of a crab will stimulate different behaviour: the octopod then moves rapidly with a mixed swimming and scrambling motion over sand and rocks, no less graceful but more purposeful.

5. FEEDING AND HABITS

The feeding habits of Nautilus are less well known than those of other cephalopods, although the remains of bottom-living crustaceans are found in those caught. Nautilus inhabits depths down to 610 metres.

Octopods and cuttlefish, being easy to keep in marine tanks, have probably been studied more than any other cephalopods. Octopods hunt crabs, which they seem to relish as much as humans. The crab is captured and held by the sessile suckers lining the inside of the arms. Octopus vulgaris has about 240 suckers arranged in two rows on each arm, totalling nearly 2,000, so that a crab once caught stands no chance of escape but is turned over and bitten through the soft ventral side by the octopod's horny beak. Behind the beak a salivary gland secretes a poison which attacks the nervous system, so that a struggling crab is soon rendered helpless. The radula resembles that of the gastropods but it is probably used to assist in swallowing shelly pieces of crustacean.

The rest of the octopod's alimentary tract consists of oesophagus, stomach, caecum, pancreas, liver and intestine. In Octopus vulgaris digestion takes place in about 18 hours. The alimentary tract follows the usual folded cephalopod plan, like a U lying on its side; the mouth lies at the upper end of the U, the anus at the lower. An antarctic octopod, Grameledone setebos, was found to have pieces of seaweed in its stomach and the common American squid often bites off and swallows pieces of eel-grass which is found undigested in the intestine. Since the cephalopod digestive system seems unable to deal with vegetation, this would appear to be aberrant behaviour, unless the octopod swallowed an animal and the vegetation it was living on.

Most reports indicate that octopods hunt either at dusk or at night and, unless very hungry, are inactive during the day. Their favourite food is undoubtedly crustaceans, particularly crabs, but they will eat fish. Octopods certainly open bivalve shells in the same manner as starfish, and Octopus vulgaris is known to pull abalone (Haliotis tuberculata) from rocks in the Channel Islands.

In addition to the well known octopod cannibalism, they have been seen to eat some extraordinary food. Near Singapore an Octopus was observed eating a shore-living species of spider. Another Indo-Pacific species is locally believed to lie in wait at night for rats which come down to the shore to scavenge. And a captured octopod was kept alive in a tank on a diet of hard-boiled eggs, the shells perhaps resembling those of its normal crustacean diet.

The two tentacles and the funnel of the cuttlefish are its main hunting weapons. The long reach of the extensible tentacles, coupled with their lightning speed, allows the cuttle to strike at prey while it is still sufficiently far away for the predator's presence to be unsuspected. They seem to employ two hunting techniques, active hunting and lying in ambush. The first relies upon the buoyancy of the phragmacone, which allows the cuttle to hover a few inches above the sea floor. Undulations of the lateral fin propel it forward while jets of water are directed from the hyponome at the sandy bottom. Eventually a shrimp is uncovered and, apparently unaware that its sandy colour and nearly transparent body renders it virtually invisible, the shrimp begins to cover its head with sand. The movement betrays it to the cuttlefish which darts down and seizes it.

The ambush of a shrimp by a cuttlefish, has been reported in detail by J.B. Messenger; and observed by me in a remarkable film made at Plymouth. The cuttle reduces its buoyancy and sinks to the sea floor, covering its back with sand by means of the lateral fin and burrowing down a few centimetres. Only the top of the head, covered with sand, remains above the sea floor. At the first sight of a prawn, the cuttle turns to face it, marking its scuttling progress until it comes within the range of the tentacles which by now are almost out of their pouches and ready to strike. There is a sudden movement and a settling cloud of sand. Much too fast for the human eye to follow the tentacles have shot out, seized the prawn with the terminal suckers, and hauled it back to be held by the eight arms until it is eaten. It takes about 15 m sec. for the tentacles to reach the prawn and about 85 m sec. to retract them, so that the whole process takes about one tenth of a second. Digestion in cuttles is completed in about 12 hours, compared with 18 hours in octopods and 6 hours in squids.

Squids, except for the Loliginidae, live away from shore lines and at various depths. Some have been taken at depths of two miles.

They eat a variety of foods but the majority hunt and eat fish. Loligo, with its torpedo-shaped body, has a remarkable turn of speed and can catch fast-swimming mackerel which it kills by a swift bite in the neck. Sometimes they run riot among a school of fish, like foxes in a chicken coop, attacking more than they can possibly eat in a frenzy of killing. The ferociously aggressive Humboldt Current Squids, Ommastrophes gigas, weigh up to 350 pounds and measure up to 3.5 m. overall. They are known to attack tunny fish and eat everything except the head.

The pedunculate suckers of squids cover the inside of the eight arms and are for the most part confined to the club-like tips of the tentacles. Some species, Architeuthis for example, have suckers scattered along the length of the tentacles as well as at the tips; and some species of the Loliginidae have suckers on the membrane surrounding the mouth and beak. Three genera, Galiteuthis, Abralis and Onychoteuthis, show a remarkable modification of the serrated horny ring of the suckers, which is asymmetrically elongated to form a series of cat-like claws, which hold a struggling, slippery fish very efficiently. This is no recent innovation: some Mesozoic belemnoids had hooks on the tentacles.

Another extraordinary modification of the suckers is seen in Galiteuthis; the club-like tips of the two tentacles, furnished with fearsome-looking claws, are held together near the base of the tips by suckers alternating as sockets and studs. These operate exactly like press-fasteners in order that the clawed tips of the tentacles may be held close together.

In squids the radula seems only to assist in swallowing; the digestion of these energetic animals, with their high metabolic rate, is usually completed in 4-6 hours.

6. REPRODUCTION

In the cephalopod molluscs the sexes are always separate. Elaborate courtship rituals and parental care testify to the advanced nature of these animals. Sexual dimorphism is apparently common, the male being usually smaller than the female; this characteristic has been convincingly demonstrated in some Jurassic ammonites. All molluscs lay eggs while a few retain the eggs within the mantle cavity until they are hatched. The majority of marine bivalves and gastropods have a free-swimming larval (or veliger) stage before settling on the bottom where metamorphosis takes place and the juvenile begins growth and development. Cephalopods lay relatively large yolky eggs and omit the veliger stage; the young hatch out as miniature adults, ready to engage directly in an active predatory life. Young octopods and cuttlefish are remarkably precocious and begin jet-swimming and hunting small crustaceans almost as soon as they are hatched: some newly-hatched cuttlefish will even squirt their ink if sufficiently irritated.

The female oviduct or male duct opens into the mantle cavity beside the anus; the ducts may be either paired or single. Perhaps the most extraordinary element of cephalopod reproduction is the male sex organ. One of the arms is modified to serve the function of a penis. The male produces elongated cylindrical packets of sperm (spermatophores) which are pulled from the genital opening by the genital arm and deposited on various parts of the female or even introduced directly into the mantle cavity. The specialized male arm is called a hectocotylus. In the argonauts the hectocotylized arm is completely detached from the male and left in the mantle cavity of the female where it has a short independent existence. This organ was first described by Cuvier as a parasite and given the name Hectocotylus octopodis. Only after much bitter dispute was the real nature of the sucker-bearing 'parasite' understood, but the name hectocotylus has remained. In fact Aristotle had recognised the sexual nature of the hectocotylus more than 2,000 years ago.

Copulation in Loligo takes place after the male has swum alongside the female and made a sexual display by spreading the arms and turning dark red. They may then copulate head to head or parallel, with the ventral sides in contact, while the male grasps the female firmly by the head. Spermatophores are placed inside the mantle cavity by the hectocotylized fourth left arm.

In the octopods the modified male arm is the third on the right. The female is caressed by the male at arms' length, the tip of the hectocotylus inserted in the mantle cavity, and the sperm deposited near the opening of the oviduct. In cuttlefish the male places spermatophores in the region of the mouth of the female, and in Nautilus four arms on the right side are modified to form a sleeved projection called a spadix.

The number and appearance of eggs laid by cephalopod females is variable. *Octopus* lays about a hundred; *Eledone* nearer sixty. *Loligo* produces sausage-shaped egg-masses attached at one end and forming radiating clusters. The eggs of *Sepia* are black, like bundles of small grapes, after being given a coating of ink as they are laid.

Female *Octopus* exhibit a great deal of parental care, brooding over her eggs, cleaning them with the tips of her arms, and jetting water from the funnel at them. However, the prize for parental care goes to the female argonaut. She produces a beautiful, paper-thin, often elaborately ornamental shell in which she lives brooding over the thousands of small eggs which are arranged on branching egg-strings, like strings of beads. the female is not attached to the shell, but if she is forcibly deprived of it she dies. This remarkable shell is without partitions and, though partly coiled, is open at the apex. It is secreted by the two dorsal topmost arms which are large and flattened, embracing the sides of the shell and secreting new material as it grows; it is therefore in no way homologous with the mantle-secreted shell of the nautiloids and the ammonoids. There nevertheless remains a disturbing similarity between the shells of argonauts and those of some Cretaceous ammonites. The argonaut shell is literally an egg-nest to house both mother and eggs; or, as one zoologist described it "not a house but a perambulator".

7. FUNCTION OF CEPHALOPOD INK

The author's careless dissection of a squid, *Loligo forbesi*, resulted in the puncture of the ink-sac. The flood of black ink over the mantle cavity was accompanied by a sharp increase in the general fishy smell and initiated a train of thought leading to an alternative interpretation of the function of cephalopod ink. This hypothesis removes the emphasis from the visual qualities of the black ink and places it on its olfactory properties.

The ink cloud, discharged by a threatened cephalopod, has traditionally been interpreted as functioning in the manner of a smoke-screen behind which the animal is supposed to make its escape. The analogy with naval fighting ships reflects our own human reliance on visual perception, a process depending upon complex mental interpretations of visual images. Lane (1957, p. 41) has already suggested that this may be an over simplification of the matter.

Many accounts exist of threatened cephalopods retreating rapidly and leaving a prominent black cloud between it and its pursuer. But the size of the ink-cloud alone is seldom enough to conceal the cephalopod or to baffle a serious predator since the velocity of pursuit would carry the predator right through the ink-cloud and bring the retreating cephalopod once again into view. Nevertheless, the ink cloud does serve as a check to predators and millions of years of selection have maintained a functioning ink-sac in coleoid cephalopods - confirming its utility.

Cousteau (1953, p. 166) suggested that the ink-cloud simulates the outline of the retreating cephalopod and thereby acts as a visual decoy. But this reflects our own habits of primary visual perception. I suggest that the true function of the ink is not a screen to cover retreat but a chemical decoy to delay, or prevent, pursuit. This hypothesis is supported by the following evidence.

MacGinitie (1949, p. 393) records how he prodded a moray eel in a tank with a long pipette and then sucked up some of the water from alongside its body. Squirting the water into the tank of an octopus resulted in rapid colour changes, temporary protuberances on the mantle, and other signs of alarm; but only when he simulated, with his arm, the undulating motion of an eel did the octopus discharge its ink. A combination of stimulae to both smell and sight being necessary to induce the full response. Lane (1957, p. 41) remarked that "A trace of octopus ink in water is sufficient to excite an eel. If a few drops are introduced into a moray's tank the eel dashes wildly about seeking its ancient prey". The American biologist, Denis L. Fox, tells me that he once offered to a moray eel a mussel (Mytilus californianus) which had been removed from its shell. The eel refused it. Fox then dipped the morsel in some octopus ink and offered it to the eel again. This time it was devoured avidly.

Lane (loc. cit., p. 42) continues by quoting Gilbert Klingel who disturbed an octopus while skin-diving off Great Inagua, off the Bahamas, and was enveloped in a cloud of ink. "From beneath the helmet there arose a faint odour quite unlike anything else. Fishy musk is the nearest description I can think of".

Again the MacGinities (Lane, 1957, p. 42) showed that the concentrated ink discharge from a mud-flat octopus could actually confuse a moray eel so that it was unable to recognise the scent of the octopus even when very close to it; though small concentrations of ink are enough to excite an eel. Lane (p. 43) goes on to suggest that the ink, in strong concentrations, actually paralyses the olfactory senses of the moray eel.

These accounts serve to emphasise the strong olfactory properties of cephalopod ink and its function may be demonstrated in the following hypothetical situation.

We may imagine how the predator of a cephalopod might catch its scent and move in pursuit. The cephalopod emits a cloud of ink and jets away leaving the ink-cloud hanging, an apparently tangible object, in the water. When the predator reaches the ink-cloud it receives the strongest possible olfactory indication of the apparent immediate presence of the cephalopod which, by now, is many yards away. Any visual indication of the retreating cephalopod would be completely overruled by the powerful olfactory indication of the cephalopod's presence in the ink-cloud. The cephalopod, even if sighted, would by now have changed its colour and pattern and, most probably, have turned whitish-grey in dimantic display.

Since visual perception has not been ruled out as insignificant the black colour of the ink-cloud probably serves as a focus of visual attention, in that it provides something to be seen, while the scent holds the predator as surely as the scent of rotting meat holds flies, ants, and whelks. The black colour thus serves as an ancillary to the primary olfactory function of a decoy.

This interpretation is offered as an alternative to the long-held view that cephalopod ink serves as a visual screen to cover retreat. Such a view, with its emphasis on the optical properties of the black ink-cloud, ignores its chemical ones and may well be wrong.

8. FOSSIL CEPHALOPODS

Cephalopods have a long geological history beginning in the Upper Cambrian. The principle evolutionary trend seems to have been a process whereby the mantle progressively envelope the shell so that the external chambered shell of the straight nautiloids became the internal shell of the belemnoids, cuttles and squids. Then, it seemed, the shell underwent a process of simplification, by loss of the buoyancy chambers, leaving only a dorsal plate or gladius. Thus the squids, and the living Vampyromorpha and the fossil Palaeoctopus became differentiated. Finally, the gladius was reduced to a few residual calcareous plates within the mantle of the octopods.

The loss of mechanical means of achieving buoyancy has gone parallel with the development of other means, anatomical and chemical, of maintaining neutral buoyancy. This reaches the ultimate development in Architeuthis in which the body tissues themselves have become buoyant.

Nautiloids, ranging in time from the Upper Cambrian to the present day, are the only possible candidates for ancestor of the ammonoids and of all the coleoid cephalopods. Their Palaeozoic history is complex, and it is beyond the scope of this introductory text to do more than hint at it. They produced straight and coiled forms all through the Palaeozoic, but, after giving rise to the ammonoids in the Devonian and the belemnoids in the Carboniferous, they finally settled down to a planispiral shell by the beginning of the Mesozoic and remained that way to the present day. Despite their decline in numbers of species, nautiloids may be regarded as a highly successful group in which conservative tendencies have allowed them to survive major periods of extinction.

Ammonoids first became distinct from nautiloids during Devonian times. Four distinguishing features are apparent: the simple sutural trace of the edge of the septum received an angular inflection (hence the name Goniatite); the nautiloid hyponomic sinus in the anterior edge of the body chamber was suppressed, except for the earliest Anarcestacae which retained a sinus until the end of the Devonian; the siphuncular tube moved away from its central position in the nautiloid septum; the protoconch became a calcareous bulb instead of the chitinous one of the nautiloids. From then onwards the goniatites evolved, by increasing complication of the sutural trace into ceratites with minutely divided lobes, and ammonites with minutely divided lobes and saddles. In addition, the ammonites enlarged the second lateral lobe so that it became a dominant feature in the ammonitic suture.

Ammonoid shells showed an incredible variety of forms which, upon analysis, resolve into a number of variations on a few basic themes. The rounded cadicone and the thin sharp-edged oxycone shell appeared repeatedly; rib and tubercle combinations produced patterns which are repeated all through the range of the ammonoids; uncoiled forms appeared in the Triassic ceratites, in the Jurassic ammonites, and were particularly abundant in the early Cretaceous, and continued into the late Cretaceous. But uncoiled heteromorphs never replaced normally coiled forms, but always occurred alongside them, even to the end of the Cretaceous.

The origin of the ammonoids is still a problem, but the standard argument is as follows: the only possible candidates for ancestor to the ammonoids are the nautiloids; but the majority of nautiloids have more differences than similarities except for a small group called the bactritids; these have a longish range in the Palaeozoic and have some shell characters in common with the ammonoids including an important character, the calcareous protoconch. A difficulty lies in the fact that bactritids are all straight while the earliest ammonoids are coiled.

Belemnoids, generally regarded as typically Mesozoic fossils, have recently been traced back to Lower Carboniferous rocks in N. America. Which group of nautiloids gave rise to them is not known but it is likely to have been a straight orthocone. Again, a comparison of nautiloid and belemnoid characters shows that the bactritids are the best candidates for ancestor to belemnoids, but, in this case the straight shell is not a handicap but an advantage.

The guard, or rostrum, of the belemnites is now widely believed to have functioned as a counter balance to the body, with the phragmacone acting as fulcrum; so that the centres of gravity and of buoyancy should come together in the centrally placed phragmacone. Thus the belemnite could change its buoyancy without changing its orientation. The persistence of this feature from Carboniferous to Lower Cainozoic times testifies to its functional importance.

The character which unites ammonoids and belemnoids with bactritids, but not nautiloids, lies in the nature of the protoconch which, in Nautilus is horny or chitinous, flexible, and never preserved in the adult shell; while the protoconch of bactritids, ammonoids and belemnoids is a round, inflated calcareous bulb and always preserved (unless damaged). Throughout Permo-Triassic and Lower Jurassic times, another group, clearly allied to belemnoids, evolved alongside. These were the phragmoteuthids, differing from belemnoids in lacking their bullet-like calcareous rostrum, but still retaining the phragmacone. These little-known, since rarely preserved and, until recently, under-studied animals, are important since they qualify as the best candidate as ancestor to squids and cuttles.

Cuttles first appear, with surprisingly modern-looking shells, in the Upper Jurassic Kimmeridge Clay of Britain and in the equivalent Lithographic Limestone of Solenhofen in Germany. These fossil phragmacones of Trachyteuthis are very obviously cuttles, even down to the strongly pustulated dorsal surface, the general outline, the posterior 'skirt'. There is no doubt that these gave rise to subsequent Cainozoic and living cuttles; but, like many fossil first-occurrences, (bats, bivalves and octopods for example) there is nothing leading up to them. Quite 'suddenly', in the Upper Jurassic, there are fully formed cuttles. Phragmoteuthids are the only reasonable candidates for ancestor of cuttles but there are no known intermediates.

Squids, surprisingly, occur earlier than cuttles in the Lower Jurassic, although, from an evolutionary point of view, they could be regarded as being more advanced than cuttles since they have reduced the phragmacone so that only the dorsal plate, the pro-ostracum, of the belemnites, survives as a gladius. Nevertheless, squid-like gladii were recorded as early as 1836 by William Buckland from the Lower Lias of the Dorset coast; while Upper Liassic shales at Holzmaden in Germany, have since yielded equally squid-like fossils.

Since nearly all squid-like gladii occur later that phragmoteuthids, it seems reasonable to hold that the latter gave rise to the former by loss of the phragmacone.

Octopods are a puzzle. In the fine lithographic limestone of Upper Cretaceous age in Lebanon, the impression of an undoubted eight-armed octopod was found. It is preserved with an outline of the body visible, and this shows a pair of postero-lateral fins together with a squid-like gladius within the body itself. This is Palaeoctopus, resembling very closely the living Vampyroteuthis infernalis, which also has fins and a gladius, and a change of shape from fusiform to sack-like.

This survey of cephalopod evolution, though the merest sketch, serves to support the theory that the main trend in cephalopod evolution has been the progressive loss of mechanical means of achieving neutral buoyancy in favour of anatomical and chemical means. Architeuthis and the cranchiid squids exemplify this achievement.

9. CLASSIFICATION OF CEPHALOPODS

There are probably as many classifications of the cephalopods as there are classifiers, but the classification which follows is not intended as yet another contribution to an already complicated field. It is a simplification: major groups have been reduced, or elevated, to ordinal rank and these distributed among three subclasses. The whole vexed question of the systematic position of Spirula and the Spirularostridae has been avoided, though I would like to see the former included in the latter. This classification merely simplifies a complicated field for the student, who, having grasped the temporal range and morphological diversity of the cephalopods, may abandon it and plunge into more advanced and controversial systematic questions.

Class: CEPHALOPODA Leach, 1817

Subclass: NAUTILOIDEA Agassiz, 1847*

Order: VOLBORTHELLIDA Koboyashi, 1937; Lr. to Mid. Cambrian. (Small orthoconic, septate shells, controversial and only tentatively included in the Cephalopoda.)

" ELLESMEROCERATIDA Flower, in Flower & Kummel, 1950; Up. Cambrian to Ordovician, Ashgill Ser. (Closely septate cyrtocones, marginal siphuncle with short septal neck.)

" DISCOCERIDA Flower, etc., 1950; Ordovician, Llanvirn to Devonian, Givetian. (Large brevicones; siphuncle ventral to central with expanded segments.)

" ENDOCERATIDA Flower, etc., 1950; Ordovician, Arenig to Silurian, Wenlock. (Up to 30 ft., endocones present, siphuncle ventral to subcentral.)

" ACTINOCERATIDA Flower, etc., 1950; Ordovician, Llanvirn to Carboniferous, Namurian. (Straight to weakly cyrtoconic, ventral siphuncle, inflated between septa.)

" MICHELINOCERATIDA Flower, etc., 1950; Ordovician, Arenig to Triassic, Norian. (Straight or cyrtoconic ribbed shells with siphuncle central or subcentral.)

" ASCOCERATIDA Flower, etc., 1950; Ordovician, Llandeilo to Silurian, Ludlow. (Deciduous longiconic stage, followed by inflated breviconic ascoceratid stage.)

" TARPHYCERATIDA Flower, etc., 1950; Ordovician, Arenig to Silurian, Ludlow. (Coiled or partly coiled and ribbed like ammonoids with hyponomic sinus; siphuncle ventral, central or dorsal, thick-walled, septa with orthochoanitic necks.)

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* Ecdyceratida Flower, 1962 omitted; see Teichert et al., 1964.

Order: ONCOCERATIDA Flower, etc., 1950; Ordovician, Llanvirn to Carboniferous, Tournasian. (Brevicones with constricted apertures and ventral siphuncle.)

" NAUTILOIDA Agassiz, 1847; Devonian to Recent. (Dorsally coiled, siphuncle central.)

" BACTRITIDA Shimansky, 1951; Ordovician to Permian. (Calcareous protoconch, simple sutures with shallow ventral V-shaped lobe, advanced forms with dorsal saddle and lateral lobes, siphuncle ventral, septal neck orthochoanitic.)

Subclass: AMMONOIDEA

Order: ANARCESTIDA Miller & Furnish, 1954; Lr. to Up. Devonian. (Some with basic 4 lobes; siphuncle ventral, neck retrochoanitic.)

" CLYMENIIDA Hyat, 1884; Upper Devonian. (Siphuncle dorsal, neck retrochoanitic.)

" PROLECANITIDA Miller & Furnish, 1954; Up. Devonian to Triassic. (Lenticular shells with goniatitic and ceratitic sutures; siphuncle with retrochoanitic necks.)

" GONIATITIDA Hyat, 1884; Mid. Devonian to Up. Permian. (Suture of 8 lobes; ventral prochoanitic siphuncular tube.)

" CERATITIDA Hyat, 1884; Permian to Triassic. (As for Goniatitida, but lobes subdivided.)

" PHYLLOCERATIDA Arkell, 1950; Triassic to Cretaceous. (Lobes and saddles subdivided, saddles with characteristic phyloid endings.)

" LYTOCERATIDA Hyatt, 1889; Jurassic to Cretaceous. (Mostly evolute, tending to uncoil; moss-like saddle endings with lobes bifid.)

" AMMONITIDA Hyatt, 1889; Jurassic to Cretaceous. (Lappets and ventral keel in some; lobes not bifid, sutures generally simpler.)

Subclass: COLEOIDEA

Order: AULACOCERIDA Bernard, 1895; Up. Carboniferous, Namurian to Lr. Jurassic, Toarcian. (Internal rostrum, phragmacone and pro-ostracum; ribbed rostrum almost embracing phragmacone.)

" BELEMNITIDA Steinmann, 1907; Lr. Jurassic, Sinemurian to Up. Eocene. (As for previous but without heavy long ribbing and shorter alveolus.)

" PHRAGMOTEUTHIDA Jeletzky, 1964; Permian to Lr. Jurassic, Sinemurian. (Internal phragmacone and pro-ostracum but no rostrum.)

" SEPIOIDA Leach, 1817; Up. Jurassic, Kimmeridgian to Recent. (Internal, dorsal, shield-shaped phragmacone; animal with 8 arms and 2 tentacles, suckers pedunculate.)

" TEUTHOIDA Naef, 1916; Lr. Jurassic, Sinemurian to Recent. (Internal dorsal gladius; animal with 8 arms and 2 tentacles, suckers pedunculate.)

Order: VAMPYROMORPHA Rickford, 1940; Recent only. (Octopod-like with internal gladius and 2 reduced arm-like structures between 2nd and 3rd arms.)

" OCTOPODA Leach, 1817; Up. Cretaceous to Recent. (Sack-like cephalopods with 8 arms and sessile suckers.)

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EXPLANATION OF FIGURES 1-40

1. Order Ellesmerocerida, *Clarkoceras*, Lr. Ordovician (Treatise K138).
2. Order Endocerida, *Cameroceras*, Mid.-Up. Ordovician (Treatise K175).
3. Order Actinocerida, *Gonioceras*, Mid. Ordovician (Treatise K209).
4. Order Orthocerida, *Michelinoceras*, Lr. Ordovician-Up. Trias (lower fig.) *Orthoceras*, Mid. Ordovician (upper fig.) (Treatise K225, K227).
5. Order Ascocerida, *Parascoceras*, Up. Silurian (Treatise K272).
6. Order Oncocerida, *Octamerella*, Mid. Silurian (Treatise K296).

7. Order Discocerida, Phragmoceras, Mid. Silurian (Treatise K339).
8. Order Tarphycerida, Lituites, Mid. Ordovician, two views of aperture and a complete shell (Treatise K363).
9. Order Nautilida, Nautilus, Oligocene-Recent, wax internal mould for comparison with fossil nautiloids (Treatise K449).
10. Order Bactritida, Pseudobactrites, Lr.-Mid. Devonian (Treatise K502).
11. Order Anarcestida, Manticoceras, Up. Devonian (Treatise L13).
12. Order Clymeniida, Kosmoclymenia, Up. Devonian (Treatise L43).
13. Order Goniatitida, Goniatites, Lr. Carboniferous (Treatise L57).
14. Order Prolecanitida, Protocanites, Lr. Carboniferous (Treatise L70).
15. Order Ceratitida, Ceratites, Mid. Trias (Treatise L151).
16. Order Phylloceratida, Phylloceras, Lr. Jur.-Lr. Cret. (BMF, p. 107).
17. Order Lytoceratida, Lytoceras, Lr. Jur.-Lr. Cret. (BMF, p. 105).
18. Order Ammonitida, Eucoroniceras, Lr. Jurassic (Treatise L237).
19. Order Aulacocerida, Aulacoceras, Permian-Triassic (author's sketch).
20. Order Belemnitida, Cylindroteuthis, Mid.-Up. Jurassic (BMF, p. 127).
21. Order Phragmoteuthida, Geoteuthis, Lr. Jurassic (left); a reconstruction of a Lr. Jurassic phragmoteuthid (Donovan, p.20).
22. Order Sepioida, Sepia, dorsal view, Recent (F+H1, pl. 000).
23. Order Teuthoida, Ommastrephes, ventral view, Recent (Tryon 1, pl. 81).
24. Order Vampyromorpha, Vampyroteuthis, Recent (author's sketch, gladius Donovan).
25. Order Octopoda, Octopus, Recent (author's sketch).
26. Beak (lr.) and radula (up.) of Nautilus (Treatise K62, S.&T., p. 438).
27. Sessile sucker of an octopod (Tryon 1, pl. 36).
28. Pedunculate sucker of squid showing horny serrated ring (Tryon 1,pl.51).
29. Hectocotylus arm of a male argonaut (Tryon 1, pl. 17).
30. Hooked tentacles of squid Galiteuthis (Lane, pl. 9).
31. Phragmacone of cuttle Sepia (Tryon 1, pl. 86).
32. Gladius of squid (Tryon 1, pl. 58).
33. Shell and animal of Spirula (author's sketch based on Lane, p. 15).
34. Eggs of Sepia (Tryon 1, pl. 19).
35. Eggs of Loligo (loc. sit.).
36. Eggs of Octopus (loc. sit.).
37. Section through Nautilus (S. & T., p. 438).
38. Section through Sepia (Lane, p. 212).
39. Section through Loligo (Lane, p. 211).
40. Section through Octopus (Lane, p. 210).

Frontispiece: Detail from ceramic cladding to pillars, W. Wing, B.M.(N.H.).

Sources of illustrations: "Treatise on Invertebrate Paleontology", K-prefix indicates the Nautiloid volume, L-prefix the Ammonoid volume; "British Mesozoic Fossils", publ. Brit. Mus. (Nat. Hist.); "British Mollusca", Forbes & Hanley; "Manual of Conchology", Vol. 1, Tryon; D.T. Donovan, see bibliography; "Principles of Invertebrate Paleontology", Shrock & Twenhofel; "Kingdom of the Octopus", Frank Lane.

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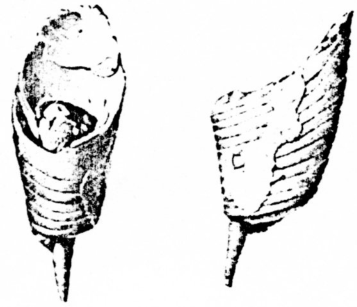

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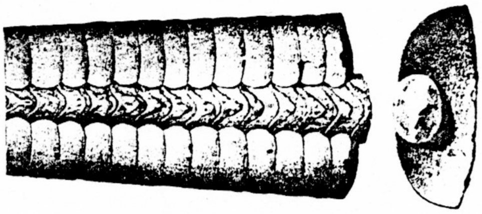

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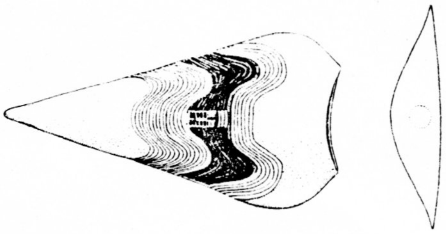

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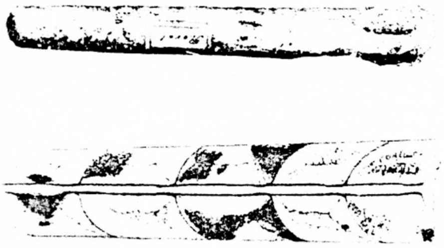

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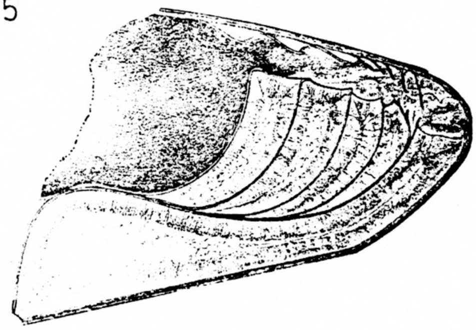

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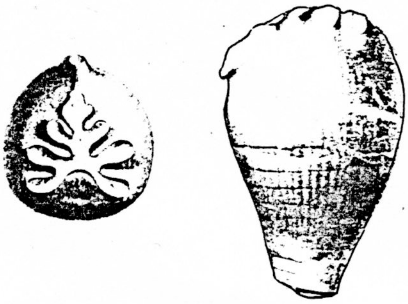

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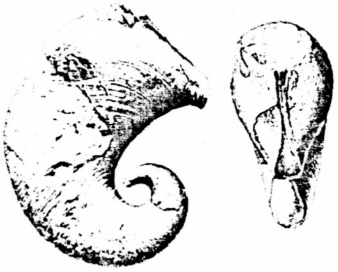

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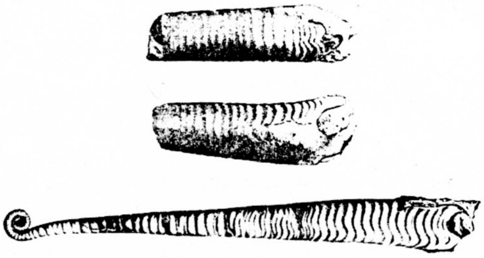

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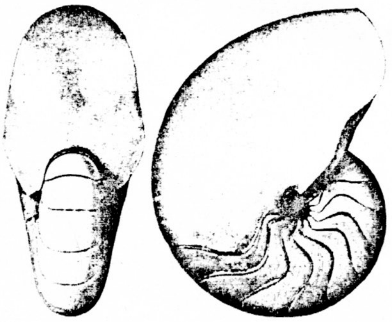

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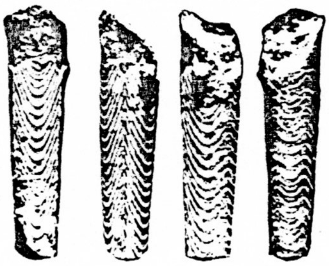

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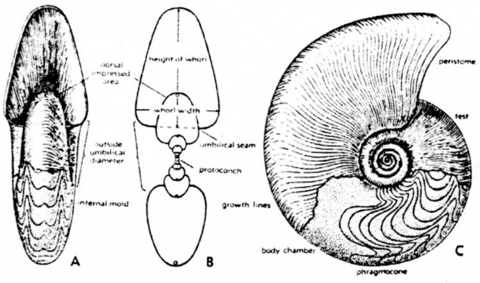

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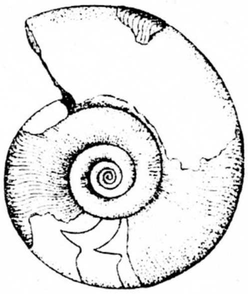

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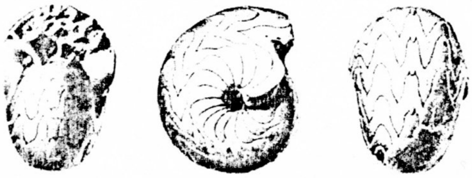

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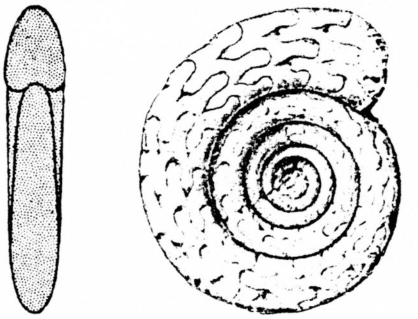

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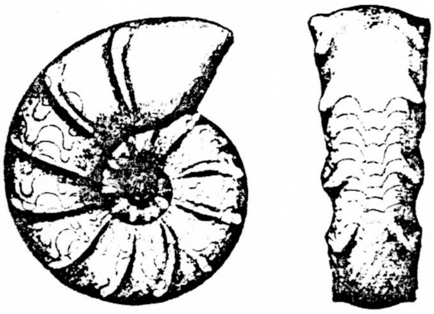

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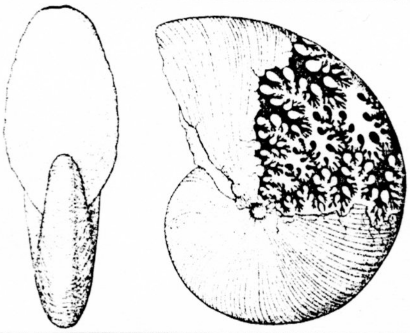

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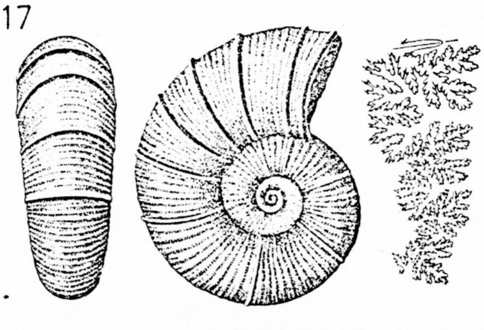

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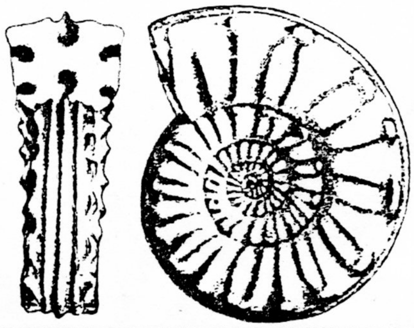

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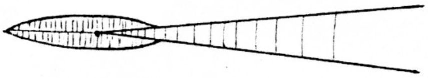

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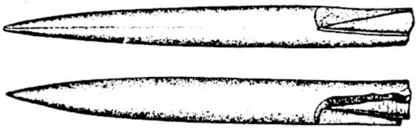

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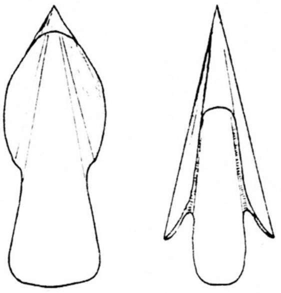

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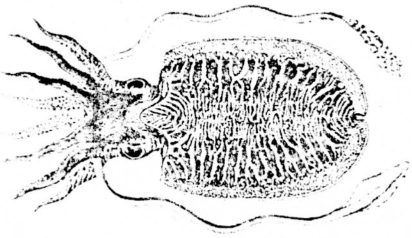

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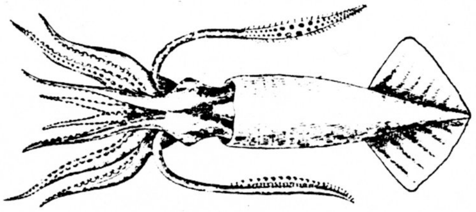

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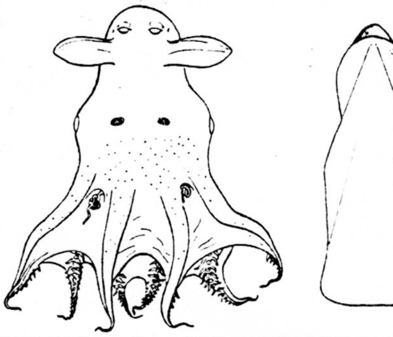

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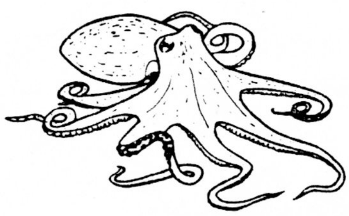

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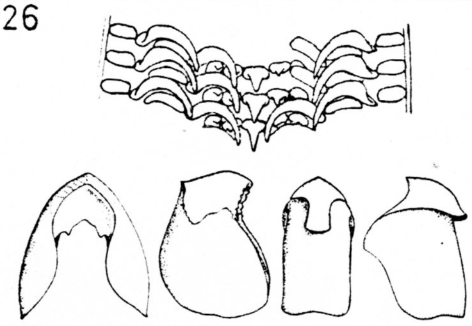

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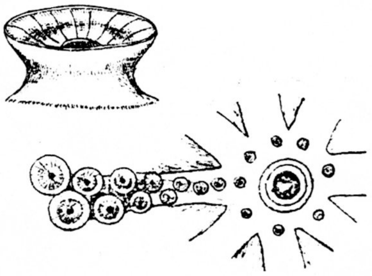

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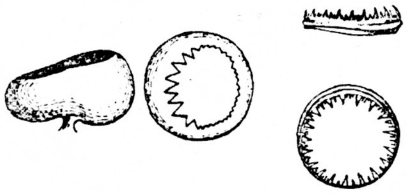

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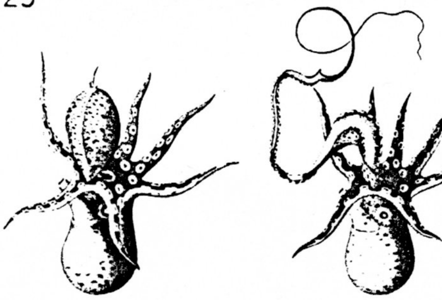

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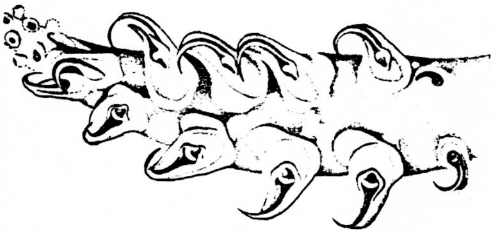

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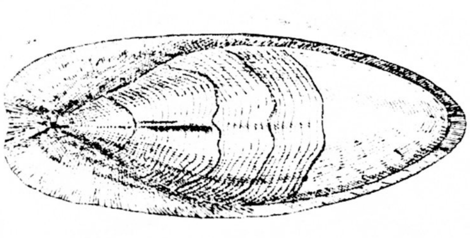

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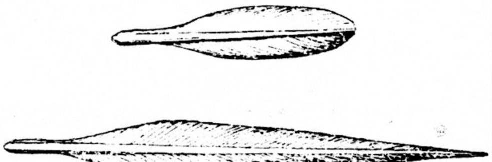

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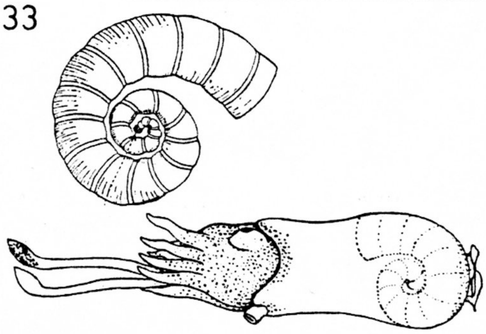

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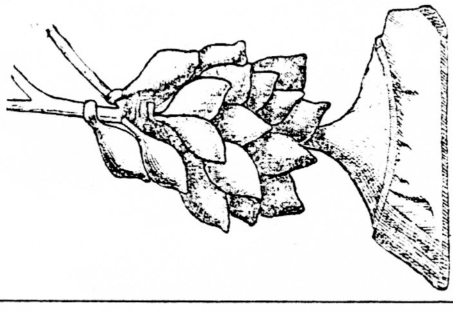

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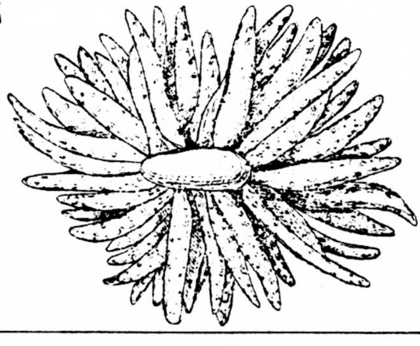

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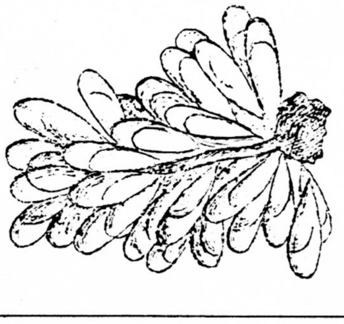

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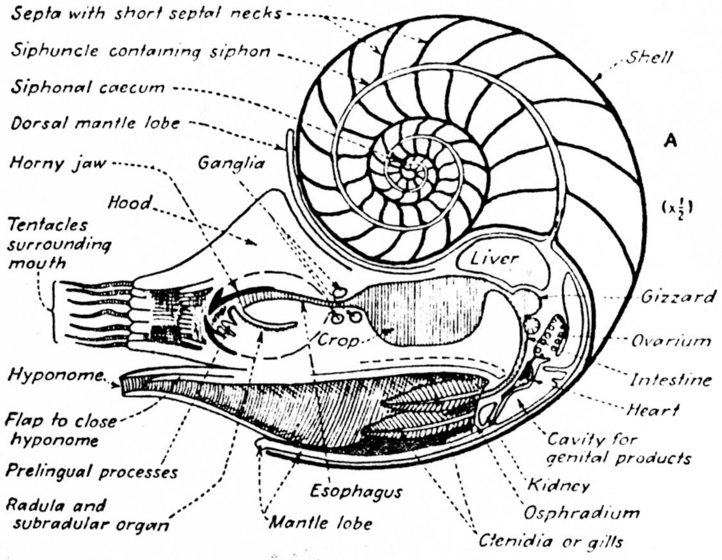
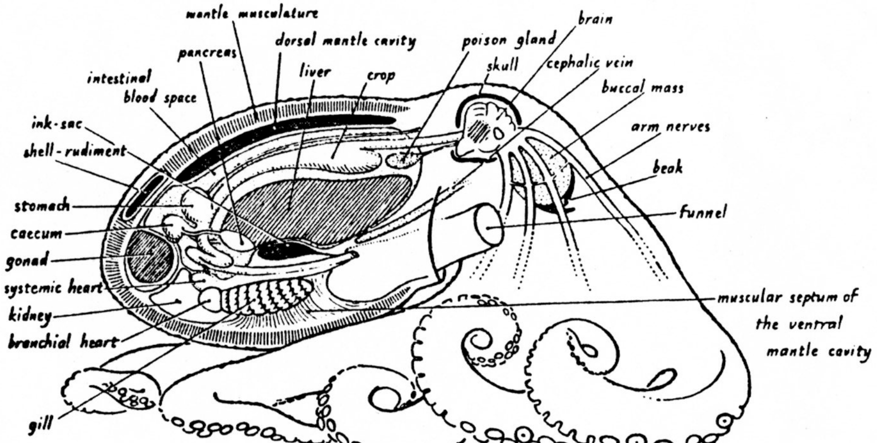
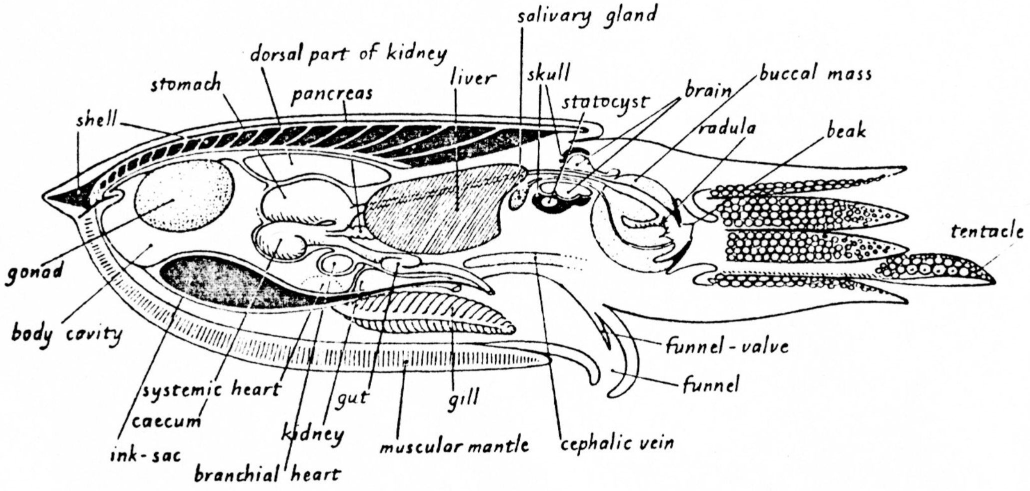

Septa with short septal necks
Siphuncle containing siphon
Siphonal caecum
Dorsal mantle lobe
Horny jaw
Ganglia
Hood
Tentacles surrounding mouth
Hyponome
Flap to close hyponome
Prelingual processes
Radula and subradular organ
Esophagus
Mantle lobe
Shell
A
(x½)
Liver
Crop
Gizzard
Ovarium
Intestine
Heart
Cavity for genital products
Kidney
Osphradium
Ctenidia or gills

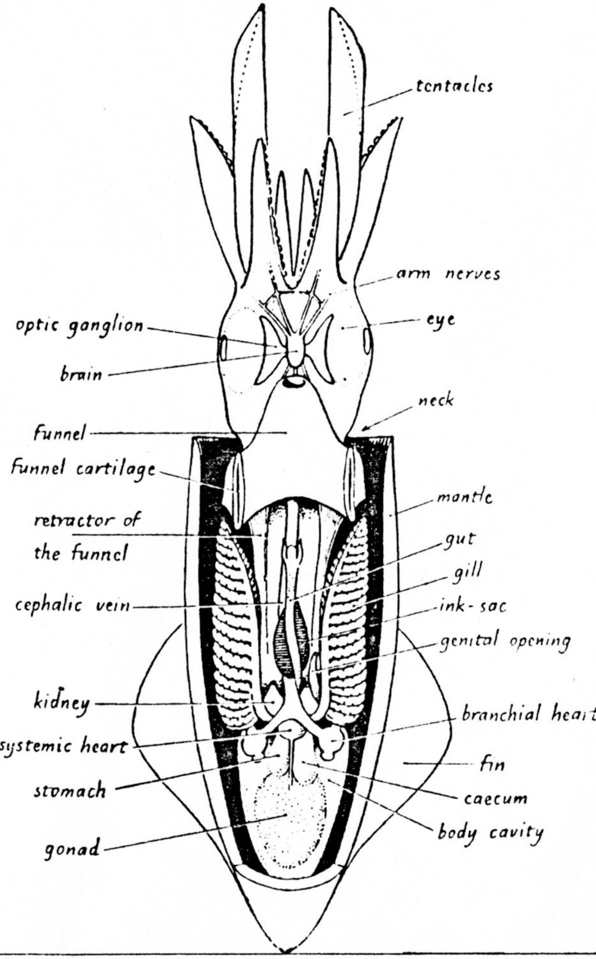
38


mantle musculature
pancreas
dorsal mantle cavity
intestinal blood space
liver
crop
poison gland
brain
skull
cephalic vein
buccal mass
ink-sac
shell-rudiment
stomach
caecum
gonad
systemic heart
kidney
branchial heart
gill
arm nerves
beak
funnel
muscular septum of the ventral mantle cavity

39


salivary gland
dorsal part of kidney
stomach
pancreas
liver
skull
statocyst
brain
buccal mass
shell
radula
beak
tentacle
gonad
body cavity
funnel-valve
funnel
systemic heart
caecum
gut
gill
kidney
ink-sac
muscular mantle
cephalic vein
branchial heart

40


tentacles
arm nerves
optic ganglion
eye
brain
neck
funnel
funnel cartilage
mantle
retractor of the funnel
gut
gill
cephalic vein
ink-sac
genital opening
kidney
branchial heart
systemic heart
fin
stomach
caecum
body cavity
gonad