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Physiology of Coleoids

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PART M, CHAPTER 4: PHYSIOLOGY OF COLEOIDS

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INTRODUCTION

In the last 30 years, it has been realized that all the living cephalopods that we know anything much about, with the single exception of *Nautilus*, grow fast and die young. Typical life histories last 1 to 2 years (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, p. 12–14 and Table 1), with very rapid growth (milligrams at hatching to hundreds of grams at death), often followed by a single spawning and subsequent rapid death.

It is only fair to say that all the cephalopods we know anything much about are shallow-water species living on the continental shelves and that nearly all of the physiological information available comes from a very few species, notably *Octopus vulgaris*, *Sepia officinalis*, *Loligo vulgaris*, *Illex illecebrosus*, *Sepioteuthis lessoniana*, and *Lolliguncula brevis*. Except where specified otherwise, reference to these genera means these species in the account that follows. *Octopus* and *Sepia* will live in confined spaces, so they make convenient experimental animals; most of the available information on coleoid physiology comes from these two genera.

To grow fast and die young implies high metabolic rates, and everything that we know of the physiology of coleoids appears to be geared to this. It sets the coleoids apart from nearly all other mollusks and, indeed, nearly all other invertebrates. It certainly separates them from the modern *Nautilus*. One could argue that the ammonoids and belemnites, like modern coleoids, grew fast and died young. We can never be quite sure. We must always remember that the physiological picture of the coleoids to be outlined below is based on a detailed knowledge of a few species of comparatively shallow-water animals. We like to think these are typical representatives

of the group, but since we know, for example, very little about the physiology of deep-water ammoniacal squid or Cirroctopoda—or *Spirula* or *Vampyroteuthis*—we can only guess at the workings of many extinct forms. Some living animals live in deep, poorly oxygenated water and have metabolic rates even lower than those of the fish and crustaceans that share this habitat (SEIBEL, CHILDRESS, & GORODEZKY, 1997).

Proceed with care; extrapolation is always dangerous.

GROWTH

Species that can readily be kept in laboratories grow very rapidly indeed if fed *ad lib*. Exponential followed by logarithmic or linear growth from milligrams at hatching to kilograms at spawning can occur within two years (Fig. 1–2). This alone implies massive intakes of prey. *Sepioteuthis*, at a mantle length of a few centimeters, can devour 35 percent of its body weight in crustaceans or fish, growing by 7 to 12 percent daily at 25° C (HANLON, 1990). All the evidence, from fisheries data to experiments in which specimens were marked, released, and recaptured, indicates that similar growth rates are common in the wild. Coleoids can grow explosively. The known lifespans of a number of species are given in *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, Table 1, p. 14. BOYLE (1983) has described the life histories and growth rates of a range of living species.

The rates at which coleoids can convert food into flesh are remarkable. In captivity, the weight of prey taken has been compared with the gain in weight of a number of species. Food conversion rates, prey to predator, expressed as wet weights, can top 50 percent in octopods and sepiids and 25 to 30 percent in the more active squids (WELLS & CLARKE, 1996).

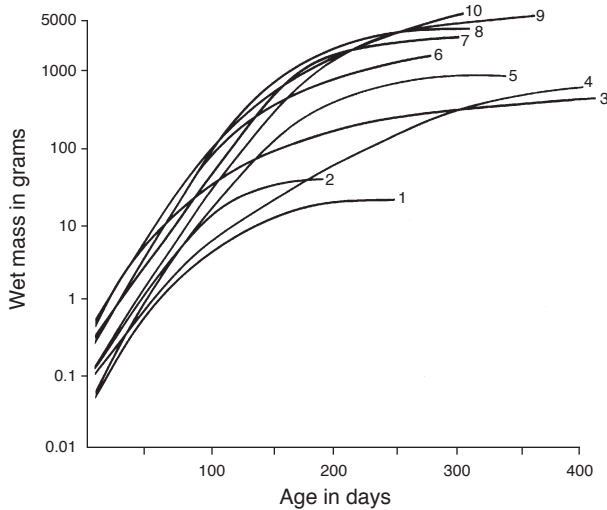


FIG. 1. Growth rates of octopuses in the laboratory. 1, *Octopus joubini* (at 25° C); 2, *O. digueti* (25° C); 3, *Eledone moschata* (12 to 20° C); 4, *O. bimaculoides* (18° C); 5, *O. briareus* (25° C); 6, *O. vulgaris*, Mediterranean (18 to 22° C); 7, *O. tetricus* (6 to 24° C); 8, *O. maya* (25° C); 9, *O. vulgaris*, South Africa (20 to 25° C); 10, *O. cyanea* (22 to 28° C) (Wells & Clarke, 1996, redrawn from Forsythe & Van Heukelem, 1987, where original sources are cited).

ESTIMATES OF AGE

Since spawning seasons often extend throughout much of the year, growth is so rapid, and conversion rates are so high, it is generally impossible to assess the age of a cephalopod at all reliably from its size. An individual may have been unlucky or unusually successful in its search for prey. It is known, moreover, that growth, particularly in the early stages, is sometimes critically dependent on temperature (FORSYTHE & VAN HEUKELEM, 1984). Fisheries-type data can thus be used at all reliably only to follow the growth of a cohort where the spawning season is limited. In general, such data are less useful than with fish because most cephalopod life cycles are so short. An example from *Sepioteuthis*, where both sorts of data are available, is given in Figure 3. The growth shown in laboratory-reared animals is faster than would be deduced from catches throughout the year, because hatchlings are added over a prolonged period; and the largest individuals tend to spawn, die, and disappear from the record (ALFORD & JACKSON, 1993).

Hard structures such as statoliths, beaks, and the gladii of squids all show striations that are assumed to indicate periodic variations in growth. The anatomy of these parts is described in the chapters on the gladius (*Treatise Online*, Part M, Chapter 10A–C) and statoliths (*Treatise Online*, Part M, Chapter 11). The critical question is what the striations represent. Two main lines of evidence are available. One, available for comparatively few species, compares the known age of aquarium-reared specimens with the number of increments shown on the hard parts. The second uses fisheries data, usually in the form of mantle lengths, giving more approximate aging and, again, compares these estimates with the rings or lines on the hard parts. One limiting factor is man-hours. Individual statoliths have to be ground to provide thin sections that are mounted for examination; the growth rings are 1.5 to 5 μm apart, so that magnifications of 400 to 600 are required. Gladii, being larger, have slightly wider striations but still have to be sectioned and examined with a microscope. Methods of preparing these structures for examination are discussed

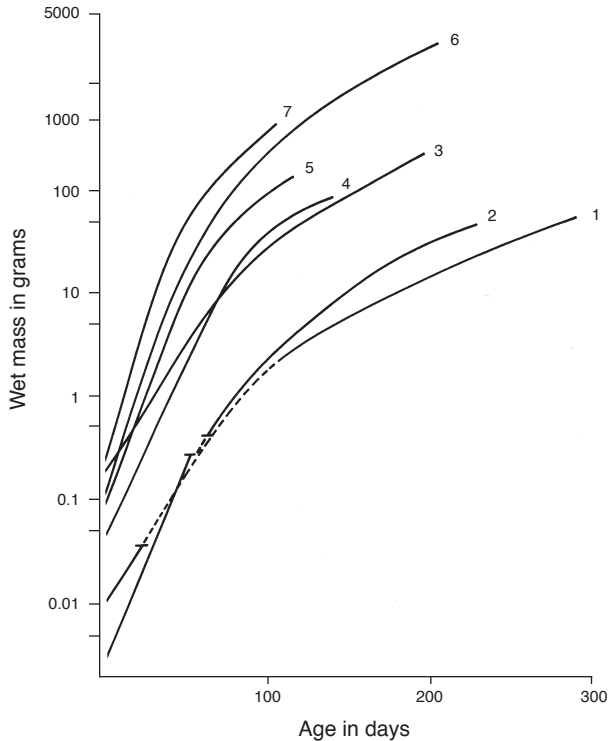


FIG. 2. Growth rates of decapods in the laboratory. 1, *Loligo forbesi* (at 15 to 18° C); 2, *L. opalescens* (15 to 18° C); 3, *Sepia officinalis* (21° C); 4, *Sepioteuthis sepioidea* (23 to 27° C); 5, *Sepia esculenta* (25 to 29° C); 6, *Sepioteuthis lessoniana* (25° C); 7, *Sepia subaculeata* (25 to 29° C) (Wells & Clarke, 1996, data from Forsythe & Van Heukelem, 1987, and Hanlon, 1990).

by JEREB, RAGONESE, and VON BOLETZKY, (1991). The number of striations found in the statoliths and gladii of a range of squids correlates well with the likely or known age, in days, of the animals concerned, so that there is a consensus that the periodicity is diurnal, caused, perhaps, by feeding at particular times of day.

A similar correlation has been found between the likely age in days and the number of chambers in the shell of *Sepia*. The possibility of being able to age a cephalopod simply by counting rings or chambers is so attractive that it is tempting to forget that the correlation is not always as perfect as one might wish. The papers cited by JEREB, RAGONESE, and VON BOLETZKY (1991) include examples where the ring or chamber per day hypothesis would yield wildly inaccurate estimates, as well as cases

where there is a good correlation. (A sample of laboratory reared *Sepia*, for example, added one chamber per 1.6 days at 25° C and one chamber per 6 days at 15° C.) Examples and critical appraisals of all the methods used to assess age from hard parts are discussed by JEREB, RAGONESE, and VON BOLETZKY (1991).

Fisheries data, analyzed on the basis that cephalopods, like most fish, grow exponentially and then slow down to a maximum size (yielding an S-shaped growth curve for any individual), tend to yield estimates of age for the largest individuals well in excess of the ages estimated from statoliths (years rather than months). Which interpretation is correct can be settled only for species where both sorts of data are available together with independent evidence from laboratory-reared animals or from occasions

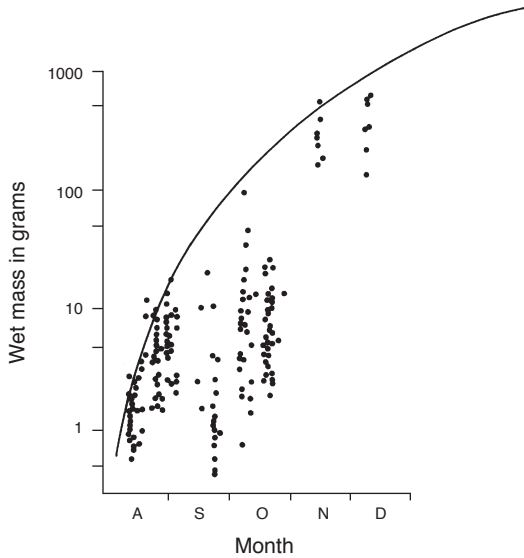


FIG. 3. A comparison of laboratory growth in *Sepioteuthis lessoniana* (solid line; adapted from Hanlon, 1990) with field data for wild squid of the same species, captured in the vicinity of Kominato Marine Biological Station, Japan, in 1977 (adapted from Segawa, 1987); A, August; S, September; O, October; N, November; D, December (adapted from Segawa, 1987; Hanlon, 1990).

where the growth of a cohort is clear and can be followed in detail. Where such information is available, the evidence suggests that statoliths give more realistic estimates than analyses in terms of formulae found appropriate for fish (JACKSON & others, 1997; JACKSON, ALFORD, & CHOAT, 2000). RODHOUSE (1998) has pointed out that the exponential growth of coleoids follows a pattern typical of the young stages of most other animals and that their life histories are best understood as examples of physiological progenesis, with accelerated maturation imposed upon an essentially juvenile physiology.

LOCOMOTION

The success of the earliest cephalopods is likely to have depended upon the simultaneous evolution of neutral buoyancy—the chambered shell—and jet propulsion. Withdrawal into the body chamber of the shell expelled water that would allow a near neutrally buoyant animal to escape from predators by a jump from the substrate, a performance that

natural selection would rapidly have improved into a directable jet and controllable buoyancy. Cephalopods became the dominant predators in early Paleozoic times, able to live in midwater and attack animals on the sea floor without fear of pursuit.

There is no need to suppose that at this stage in their evolution, a high metabolic rate was necessary or even desirable. The seas were generally less well-oxygenated than now (WILDE & BERRY, 1984), and there were no serious competitors for the niche of top, open-water predator.

Fish would have become a serious threat by Devonian times, and the situation steadily became worse as fish evolved jaws and neutral buoyancy. Fish locomotion is inherently more economical than jet propulsion. The problem is quite simple and quite simply insoluble. Thrust increases with the mass of fluid ejected by contraction of a mantle cavity or pushed backward by an undulating body or tail. Thrust also depends on the velocity of the fluid ejected or pushed back. Unfortunately, the energy required to accelerate and eject a

mass varies as mass times velocity squared ($e = 0.5mv^2$). The area that can be swept by a flat-sided body or tail is almost inevitably greater than the cross section of any cavity contained within a body or the cross section of a funnel used to direct a jet. In terms of fuel economy, fish were bound to win. The consequences are immediately detectable as soon as a jet-propelled cephalopod is run in a water tunnel: the oxygen cost of swimming is several times as great in a squid as in a salmon (Fig. 4).

The continued struggle to keep up with or away from fish has been a potent driving force in the evolution of cephalopods without shells. Ejectable mass can be increased only by enlarging the mantle cavity, and that is impossible while the animal is constrained by an external shell. JACOBS and LANDMAN (1993) argued that ammonites may have extended the mantle cavity outside the shell, but this seems unlikely, because the edge of the mantle has also to secrete the shell, a function that would effectively prevent its participation in locomotion (SAUNDERS & WARD, 1994).

The progressive abandonment of the external shell and the consequences of this is the history of the coleoids. To compete with fish, cephalopods had to become more fishlike, more streamlined, and with a higher ratio of locomotor muscle to body mass. If you cannot beat them, join them. PACKARD (1972) has argued forcibly that coleoid evolution can be understood only in the context of direct competition with fish.

There were, of course, advantages to a jet-propulsion system compared with undulant locomotion. Most fish cannot swim backward; cephalopods can direct the jet and accelerate rapidly forward or backward, an ability that must have increased their potency as predators and their unpredictability as prey. Moreover, it was, of course, always possible to move toward a fishlike locomotion by developing their control surfaces as undulant fins. Many modern cephalopods use their fins for slow cruising, reserving the less economical jet propulsion

for escape, for darts at prey, or for relatively rapid movement from place to place as might be required in migration or for swimming against a current. The illustrations in *Treatise Online*, Part M, Chapter 3 (Anatomy of Recent Forms, Fig. 1–4), and Chapter 5 (Reproduction and Lifespan, Fig. 9–14), show something of the range of fin shapes and sizes. Figure 5a–b shows the large sizes of the nerves running to the fins of Decabrachia.

Scrapping the shell meant abandoning neutral buoyancy. Some coleoids, the belemnites and sepiids being the most obvious examples, compromised by growing around and internalizing the shell. Further streamlining was possible only by reducing the shell to a stiffening gladius at the cost of losing any support from gas-filled chambers. This meant that the squid had to swim continuously or sink to the bottom. There were good reasons, outlined below, why this might sometimes have been an option with selective advantages.

The advantages did not always apply. Many families of living squid have redeveloped neutral buoyancy by changing the ionic composition of parts of their bodies, notably by retaining ammonium chloride in place of the heavier sodium chloride, a matter discussed in the section on buoyancy (p. 11 herein). The drawback to this solution is that the weight gain is slight per unit volume so that large volumes of ammonium chloride must be retained to balance the weight of guts and muscles. Ammoniacal squid are flabby animals, economical but slow, and restricted to deep waters in the open oceans. We know rather little about their physiology or behavior.

For the rest, the extravagance of jet propulsion and lack of neutral buoyancy has inevitably determined a high metabolic rate. And that in turn has arguably resulted in life histories that depend on a high, continuous input of high-energy food. There are no herbivorous coleoids and probably none that are able to survive long periods of starvation as readily as their fish rivals. Most

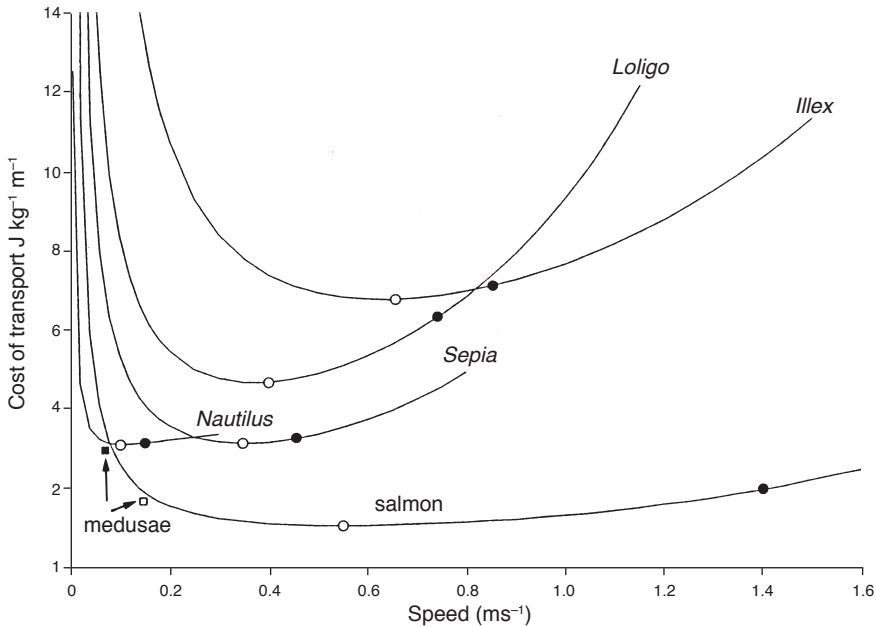


FIG. 4. The cost of transportation for a range of cephalopods compared with the cost for a salmon of comparable size (400 g). With the exception of *Nautilus*, driven at a few centimeters per second by its ventilatory stream, cephalopods are always less economical than fish. *Sepia*, largely fin propelled and neutrally buoyant, moves more economically but cannot achieve the same speeds as the jet-propelled squids. In each case, the open circles show the aerobically sustainable speed and the closed circles show the maximum speed observed. Cost of transportation figures for medusae (open and closed squares) are included, because cirriopods, which have never been run in respirometers, can move in a similar manner (adapted from O'Dor & Webber, 1991).

species must feed heavily and continuously, grow fast while the going is good, and breed before they are faced with lean months as large animals at unfavorable times of year. All aspects of the physiology of the species we know much about are biased by this necessity (O'DOR & WEBBER, 1986, 1991).

JET PROPULSION: THE ANCESTRAL MECHANISM

Nautilus ejects a jet in two distinct ways. The hood can be pulled down by powerful adductor muscles to block the entrance to the shell. This squeezes the fluid contents of the mantle cavity out under considerable pressure, producing a powerful jet. The jet can be directed forward, backward, or sideways by the flexible funnel. This is how *Nautilus* moves if it is in a hurry, when it can achieve speeds of about 0.25 m/sec (CHAMBERLAIN, 1987). Alternatively, a much

weaker jet can be produced by contraction of the large wings, the backward extensions of the hind parts of the funnel, which line the mantle cavity and extend as far back as the base of the gills. This is how the animal produces its respiratory stream, stroking water down from entrances close to the umbilicus on either side, down through the gills and out through the funnel (WELLS & WELLS, 1985; CHAMBERLAIN, 1987).

This second mode of jet propulsion is interesting in relation to the energetic cost of locomotion, because movement comes free of charge, being incidental to respiration. At very slow speeds, *Nautilus* is actually more economical than fish, despite the employment of jet rather than undulant propulsion (Fig. 4). Adductor muscles of fossils have left large scars marking attachments to the shell. The state of the funnel in extinct forms is more difficult to determine, since there is no direct attachment to the shell.

COLEOID JET PROPULSION

Living coleoids develop a jet quite differently. Here, the contents of the mantle cavity are typically expelled by the contraction of circular muscles in a greatly thickened mantle wall. The outgoing stream is trapped and directed through a flexible funnel. The essential structures of this system are described in *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 2–3.

The contracting mantle must not elongate as the water is squeezed out. This is achieved by tough connective-tissue tunics inside and outside the circular muscles. The collagenous fibers in these corsets are oriented predominantly longitudinally, with an angle of about 27° between the crisscrossing fibers and the long axis of the mantle. A second lattice, with an angle of about 30°, is at right angles to the inner and outer tunics in the plane of the radial muscles that lie in thin sheets between the circulars. The effect of this arrangement is that any tendency to elongate reduces the volume enclosed by the connective tissue fibers, so that the circular or radial muscles—whichever series is not contracting at the time—are extended (WARD & WAINWRIGHT, 1972).

It was long believed that both ventilation and jet propulsion were driven by alternating contraction of the radial muscles, expanding the mantle cavity and drawing water in at the sides of the mantle, followed by contraction of the circular muscles, forcing the water out through the funnel. Recordings of the electrical activity in the muscles of *Sepia* have shown, however, that the circular muscles are inactive during ventilation at rest. Water is indeed drawn in by contraction of the radial muscles in the classical manner, but it is then expelled by elastic recoil of the connective tissue framework (GOSLINE & SHADWICK, 1983), aided by contraction of the rearward extensions of the funnel, much as in *Nautilus*. Only when the animal begins to swim as well as to ventilate do the circular muscles start to contribute, becoming fully active only in escape jet propulsion. It seems

likely that only the thin outer and innermost layers of circular muscle are active in gentle cruising; these contain abundant mitochondria and blood vessels, suggesting that they are aerobic, with a sufficient oxygen supply to support continuous activity. The thicker anaerobic circular muscles become active only in emergency, running up an oxygen debt if active for more than a few seconds. There is an obvious parallel with the situation in fish (BONE, BROWN, & TRAVERS, 1994). In *Loligo opalescens*, a similar pattern is shown in ventilation, with the radial muscles or the circular muscles being active and squeezing the connective tissue lattices, so that recovery is again by elastic recoil. Escape jets start with hyperinflation by the radial muscles, followed by forceful contraction of the circular muscles (GOSLINE & others, 1983). Only in *Eledone* (the only octopus tested) did contraction of the radials and the circulars alternate in the classical manner during normal ventilation (BONE, BROWN, & TRAVERS, 1994).

Giant Fibers

The existence of giant nerve fibers running from the brain to the stellate ganglia (Fig. 5b) and thence to the muscles of the mantle of squids has been known since the 1930s; physiologists have used these huge nerve fibers to establish much of what is known about the working of nerve fibers in general, attracting people to work on squids who have otherwise had little interest in cephalopods, alive or extinct. There is a resulting massive literature (GILBERT, ADELMAN, & ARNOLD, 1990). Giant nerve fibers are needed if all parts of a long thin mantle are to contract simultaneously. The velocity of conduction in a nerve varies as the square root of its diameter, so the diameter of nerve fibers to the most distant parts of the mantle must be dramatically greater than to the nearest elements, a matter that has given great happiness to generations of physiologists.

Octobranchia, with their compact, almost spherical mantle cavities, do not have giant

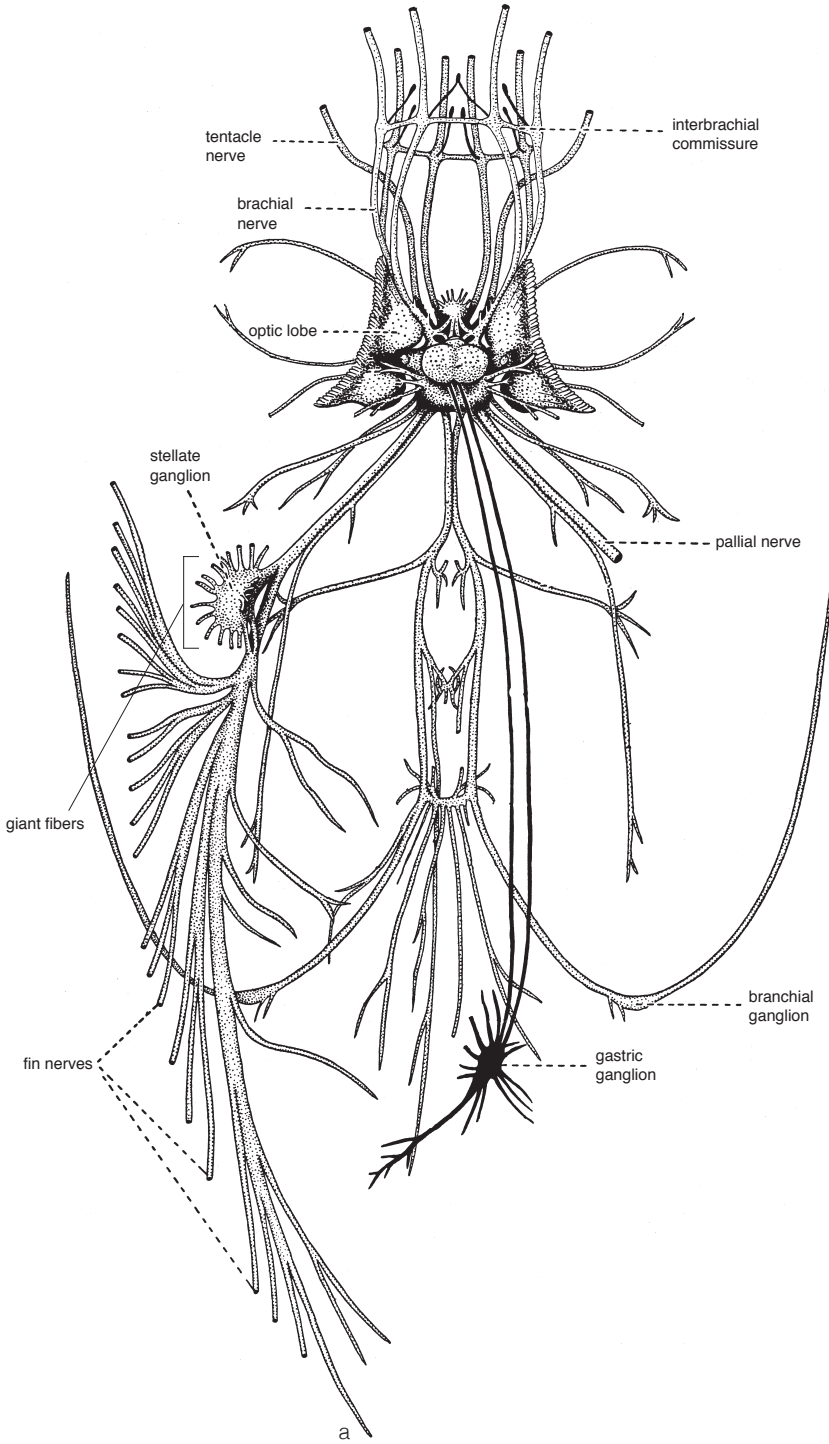


FIG. 5a. (For explanation, see facing page.)

fibers radiating from the stellate ganglia to the mantle.

In squids and sepiids, the giant nerve fibers are not involved in ventilation at rest, and the conventional wisdom has long accepted that these animals have, in effect, two gears: the giant fibers fire in escape jets and in rapid swimming. This, it seems, is as untrue as the story about alternate contraction of the circular and radials; squids in water tunnels can move smoothly from slow to maximum speeds, with no indication of a shifting of gears involving the giant fibers. Even in rapid escape responses the action of the two—small and giant—fiber systems is complex, typically starting with a small-fiber response that is joined, after about 0.1 sec, by a giant-fiber response; contractions caused by the two systems summate. The only situation so far found in which the giant fibers fire at once and dominate the response is the rather artificial one wherein a startle response has been produced in restrained animals by a flash of light or electric shock (GILLY, HOPKINS, & MACKIE, 1991).

CRANCHIID SQUID

One group of coleoids, the cranchiid squid, do not propel themselves by contracting the wall of the mantle. These animals, which achieve neutral buoyancy by retaining ammonium chloride in their coelomic cavity, move the respiratory stream and thus propel themselves by peristaltic movements of the walls of the coelom. A thin, horizontal partition divides the mantle into a prebranchial space on either side and a common postbranchial cavity (Fig. 6). The small gills hang below holes in the partition and probably act as valves, on the rare occasions when the mantle wall contracts to produce a more powerful jet (CLARKE, 1962).

FINS

Most coleoids additionally or principally use fins. Information on fin structure is included in the chapter on anatomy (see *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 3). There is a huge range

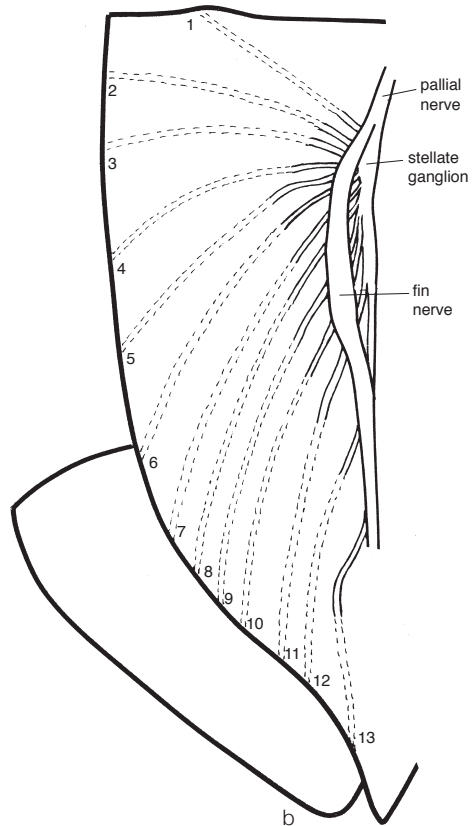
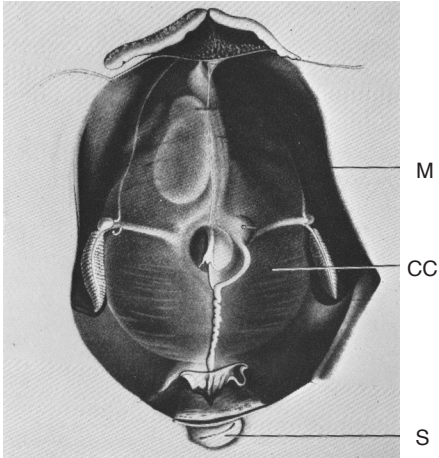


FIG. 5a-b. *a*, Nervous system of *Sepia*, seen from above, showing brain with stellate ganglion and fin nerves on left side (Tompsett, 1939); *b*, stellate ganglion and giant nerve fibers on left side of *Ommastrephes bartrami* (J. Z. Young, new).

of variation in fin form and in the extent to which the fins are important in locomotion. Squid such as *Loligo* and *Illex* fold the fins against the sides of the body during high-speed jet propulsion, using the fins only for gentle cruising. *Sepia*, when hovering or cruising slowly over the seafloor in search of food, hardly uses the jet other than for respiration. Many species substitute undulant fin movement for jet propulsion in routine movement. Fins can be used for gliding in upwelling currents (see below) or even as airfoils for gliding in air. Oceanic squid such as *Onychoteuthis* have been observed to fly in this manner. The planes formed by the wide fins are assisted, in this instance, by



1



2

Fig. 6. Cranchiid squid. 1, *Heliocranchia pfefferi* live but not actively swimming; it hangs vertically in the water with the arms and tentacles downward, $\times 2$; 2, *Cranchia scabra*, again head down, with the mantle cut along the midventral line and folded aside to expose the huge coelom, filled largely with ammonium chloride; M, mantle cavity wall; CC, coelomic cavity; S, siphon, $\times 2$ (Denton, Gilpin-Brown, & Shaw, 1969).

the third pair of arms, which are held out to form additional, flat, lift-generating surfaces. Following a fast, jet-propelled escape from the water, flying squid can glide for considerable distances.

Fins are also used in displays and in fights between rival males, which sometimes take the form of fin-beating contests (HANLON & MESSENGER, 1996).

CIRROCTOPODS

Cirroctopods hang close to the sea floor with a large interbranchial web forming an umbrella that can be contracted, umbrella-like, to propel the animal by closing the arms (VECCHIONE & ROPER, 1991). Because the mass of water being accelerated rather slowly is large, locomotor costs may be very low, comparable with those of medusae, which move in a similar manner (Fig. 4).

COST OF TRANSPORTATION

Jet propulsion is expensive. Squids that swim mainly by jet propulsion consume four or five times as much oxygen per kilogram-kilometer as streamlined fish of similar size (Fig. 4). The relative costs of finned and jet propulsion are not accurately known, but measures of the cost of transportation derived from runs in a water tunnel with a small range of species show quite clearly that those that use fins can move more economically, at least in the lower part of their speed range, than species relying mainly on jet propulsion (Fig. 4). Telemetered *Loligo forbesi* in the sea around the Azores, in fact, spend much of their time in upcurrents, planing downward on the wings formed by their large fins at very low metabolic cost (O'DOR & others, 1991, 1994). The existence of such species as *Illex*, which apparently depends almost entirely on the relatively uneconomical jet propulsion, is, arguably, a result of competition for scattered patchy resources in oceans that have a low density of food overall. In this situation, what matters overwhelmingly is the capacity to search large volumes of water in minimal time; this favors high-powered, fast-moving

animals. Once again, cephalopods have paralleled the evolution of fish, tuna in this instance being the most obvious example (O'DOR & WEBBER, 1991).

Migration

The size and appearance of hatchling cephalopods varies enormously (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, Fig. 8, p. 8). Some (*Sepia*, and many octopods) emerge as miniature adults and at once adopt a benthic or benthopelagic existence, like the adults. Others, *Octopus vulgaris* for example, and most squids, give rise to pelagic larvae, sometimes plainly adapted to feed quite differently from their parents. Oegopsids such as *Illex* lay great gelatinous masses of eggs in midwater. It is important in these cases that the young hatch in waters where there is appropriate food upcurrent of the regions where they will settle and feed as adults. The adults must return to spawn where they themselves were laid. The North Atlantic population of *Illex*, for example, feeds off Nova Scotia but spawns near Florida, upstream in the Gulf Stream (see *Treatise Online*, Part M, Chapter 7, Ecology and Mode of Life, Fig. 4, p. 14).

Migrations present great energetic problems. Most cephalopods cannot store fats to fuel their long journeys as fish do. They must migrate as quite large animals to achieve the absolute speeds necessary to make the journey, and they must, for the same reason, swim by uneconomical jet propulsion. The energy requirements are well in excess of any possible reserves, so they must feed en route. It seems entirely probable that migrating shoals are cannibalistic, the smaller individuals falling victim to the larger as the journey continues (O'DOR & COELHO, 1993; O'DOR, 1998).

SIZE AND LOCOMOTION

The economic advantage enjoyed by fish is reduced as size decreases. The cost of transportation for a large (50 cm) squid can be five times that of a corresponding fish. At very small sizes (milligram, low Reynolds number)

jet propulsion can actually be more economical than undulant locomotion; skin friction costs rise relative to the cost of pushing aside or accelerating masses of water. Hatchlings of many coleoid species are small, as, indeed, are most species of adult cephalopods; the impression that the typical living cephalopod is a large animal probably arises because it is the relatively large species that are fished commercially. The modal size of 33 deepwater squid sampled by SEIBEL, CHILDRESS, and GORODEZKY (1997) was 10 g. Because cephalopods grow exponentially, even large species spend a great part of their life history as relatively small individuals. The disadvantages of jet propulsion are much reduced when the whole life history is considered (O'DOR & WEBBER, 1986).

BUOYANCY

GAS-FILLED CHAMBERS

Coleoids and nautiloids share a common mechanism for producing gas-filled buoyancy chambers. This was first established for *Sepia* by DENTON and GILPIN-BROWN (1961), later extended to *Nautilus* (DENTON & GILPIN-BROWN, 1966) and *Spirula* (DENTON, GILPIN-BROWN, & HOWARTH, 1967; DENTON & GILPIN-BROWN, 1971) and is probably universal for all living and extinct cephalopods. It is a mechanism fundamentally different from that found in fish.

As each chamber of the shell is formed (see *Treatise Online*, Part M, Chapter 8, Shell Morphology, for a description of the hard parts), it is full of a fluid close to seawater in composition. The contents remain in contact with the rest of the animal through the siphuncle, a thread or flat plate of tissue that includes arteries and veins, linking all the chambers to the circulation of the rest of the animal. The wall of the siphuncle removes sodium ions from the water in the now-isolated chamber by active transport, acting as a sodium pump. Chloride ions follow the sodium, maintaining electrical balance. The osmotic pressure of the fluid in the chamber is thus reduced, and water tends to follow the ions outward into the

bloodstream. Pressure drops within the chamber, so that gases dissolved in the blood of the vessels in the siphuncle come out of solution to replace the fluid removed. Pressure in the chambers rises slowly, reaching about 0.8 atm in the oldest chambers of the *Sepia* cuttlebone; in *Nautilus* it is a little higher, at 0.9 atm (Fig. 7). The oxygen content is initially slightly higher than the atmosphere, because most of the gas in solution in the blood is carried in the hemocyanin blood pigment, but this is progressively reduced until the contents of the older chambers is almost entirely nitrogen (Fig. 8).

The beauty of this system is that the gas will always be at atmospheric pressure or slightly less; the partial pressures of gases dissolved in seawater and therefore in the blood of the cephalopod vary with the local oxygen content but not with the hydrostatic pressure. Animals like *Sepia*, *Spirula*, and *Nautilus* can be hauled up from great depths without damage, unlike fish, which can be killed by the expansion of nonrigid swimbladders that must contain gas at pressures able to balance the hydrostatic pressure of their habitat (1 atmosphere for each 10 m depth, plus 1 at the surface). The bad news for cephalopods is that they must have chambers capable of resisting the considerable hydrostatic pressures at depth, so that each species has an ultimate depth limit at which the chambers will implode. The implosion-imposed depth limit is perhaps rarely reached because of the increasing difficulty of pumping out the cameral fluid as depth increases. Osmotic pressure is the force sucking out the cameral fluid into the blood. In principle, it cannot be greater than the difference between that of distilled water (all salts removed) and seawater (or blood with the same osmotic pressure as seawater). This gives a theoretical depth limit of 240 m (DENTON, GILPIN-BROWN, & HOWARTH, 1961, 1967; DENTON & GILPIN-BROWN, 1971). In practice, *Nautilus*, *Spirula*, and some species of *Sepia* live below this limit. *Sepia elegans* and *S. orbignyana* are regularly found down to about 500 m

(see *Treatise Online*, Part M, Chapter 7, Ecology and Mode of Life, Table 4). The surface of the tissue lining the siphuncular tube or the equivalent along the flat lower surface of the cuttlebone in *Sepia* includes narrow channels visible with an electron microscope that almost certainly allow local concentrations of salts well in excess of those of the ambient seawater, so that water can continue to be sucked out osmotically well below the originally postulated depth limit (DENTON, 1971).

AMMONIACAL SQUID

The loss of the chambered shell left cephalopods heavier than seawater. Proteins have a density of around 1.330, seawater 1.026. Fats and oils are considerably less dense and are the means by which many planktonic animals achieve neutral buoyancy, balancing the weight of protein and other heavy materials. Only one species of squid, *Gonatus fabricii*, has so far been found to do this, concentrating lipids in the digestive gland (KRISTENSEN, 1984). The more common mechanism, found in 13 of 26 families of squid examined (CLARKE, DENTON, & GILPIN-BROWN, 1979), is to replace sodium chloride with the lighter ammonium chloride. The gain per unit volume is not great: the density of a typical deep oceanic seawater is in the region of 1.026 g/cm³, while fluids from tissues concentrating ammonium chloride have a density of around 1.010, so that considerable volumes of body fluid have to be replaced to achieve neutral buoyancy. A further problem is that ammonium chloride is toxic, so that pools of the lighter fluid must be isolated from delicate tissue, notably the nerves. Cranchiid squid achieve this by the most obvious means, retaining large volumes of ammonium chloride, which is produced anyway as the predominant end product of protein metabolism, in greatly enlarged coelomic sacs (DENTON, GILPIN-BROWN, & SHAW, 1969). Other squid concentrate ammonia in special cells forming spongy tissues in the arms and mantle (Fig. 9). The greatest gain is achieved, of course, if these

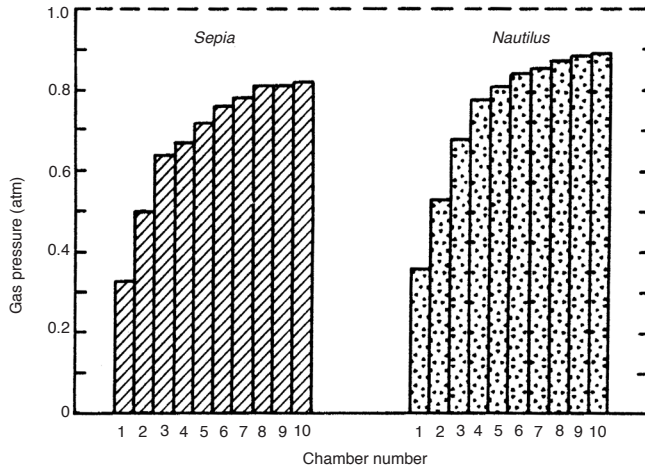


Fig. 7. Gas pressures in successive chambers of the shells of *Sepia* and *Nautilus*, counting backward from the last-formed chamber (1). During growth, *Sepia* lay down a new chamber every day or so; *Nautilus* one every few weeks and increasing to months as the animal grows to maturity (Denton, 1974).

cells actually replace the relatively heavy muscle tissue, rather than lying between the muscles. The result is rather flabby animals that, incidentally, for us are largely inedible, although not for whales and some other predators (VOIGHT, PÖRTNER, & O'DOR, 1994).

VENTILATION AND OXYGEN UPTAKE CUTANEOUS RESPIRATION

The skins of coleoids are thin but complex structures, generally including chromatophores and sometimes photophores (see *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 12–13), under direct control of the nervous system. In octobranchiates and sepiids, there are muscles that can alter skin texture, and there are blood vessels (blood vessels, perhaps surprisingly, are absent from the thinner skins of squids). So the skin is itself metabolically a very active tissue.

In *Octopus vulgaris*, the only instance so far where cutaneous uptake has been studied by means of direct measurements, up to 40 percent of the total oxygen uptake of the animal at rest occurs through the skin,

much of it consumed within the skin itself (MADAN & WELLS, 1996). Estimates based on the metabolites collected from blood vessels leaving the mantle of *Illex* and *Loligo* suggest even higher cutaneous uptakes, with up to 73 percent of the oxygen consumed by the mantle musculature of a swimming squid arriving in this way (PÖRTNER, 1994).

We know nothing about the situation in less active species. A very high proportion of the total oxygen requirement of many deepwater forms may be met through the skin, with a corresponding reduction in the size of the gills.

GILLS

Gills vary greatly in size and detailed structure. Other things being equal, large gills imply high metabolic rates, but other factors are also relevant. In such shallow-water or bottom-living species as *Octopus* and *Sepia*, the gills must be comparatively robust, thick-walled structures because of the grit and other debris brought in with the respiratory stream. Squid, living clear of the bottom, can risk thinner gill membranes. In oceanic forms living in deep clear waters, the gill membranes can be very thin and

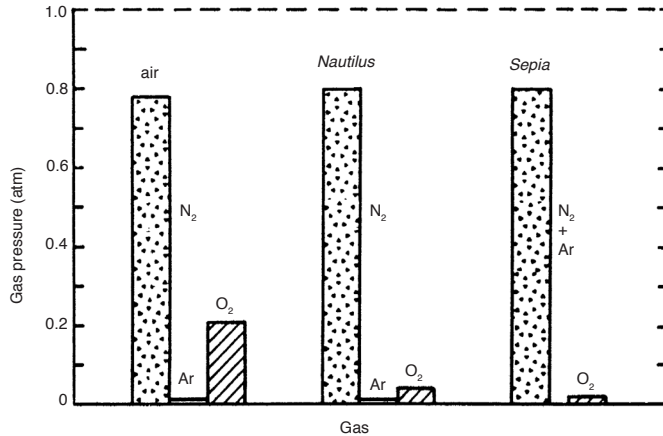


FIG. 8. The partial pressures of individual gases in air and in the older chambers (10, in Figure 7) of *Nautilus* and *Sepia*. The total pressure is always a little less than one atmosphere, whatever the ambient hydrostatic pressure (Denton, 1974).

delicate indeed. Oxygen uptake is thus easier per unit area, but deepwater squid are typically living in relatively hypoxic water and require a greater gill area for a given rate of uptake because of this (Fig. 10). Scale effects are relevant, because surface area rises as the square, and body volume as the cube of the linear dimensions of any animal. One would expect the contribution from cutaneous uptake to be most important in small cephalopods.

Circulation of Water and Blood Through the Gills

Each gill is attached at the base and along a membrane attaching the middle ridge of the gill to the dorsolateral wall of the mantle. The arrangements in *Octopus* and *Sepia* (as usual, it is these two genera that have been described in greatest detail) are somewhat different (Fig. 11–12).

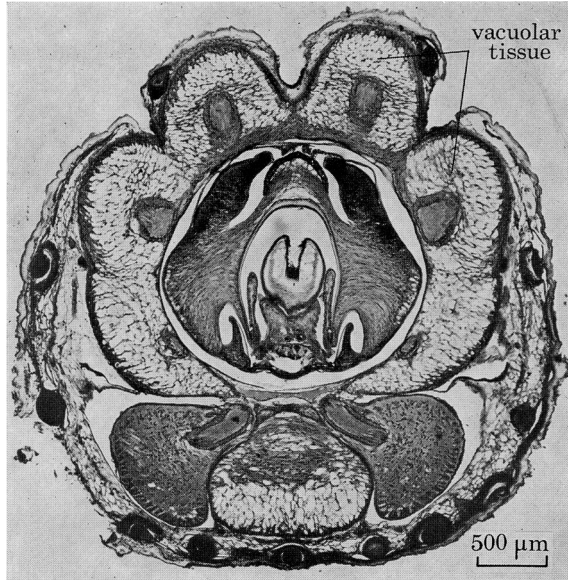
Each *Octopus* gill is asymmetrical, with the leading edges of the lamellae on the central side forming a series of bars facing the incoming respiratory stream. In life,

the inner side of each gill rests against one of the paired funnel retractor muscles (see *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, Fig. 6, p. 9). The ventilatory stream passes through the bars into the middle of each gill, out through the much folded respiratory surfaces, into a common postbranchial chamber (Fig. 11).

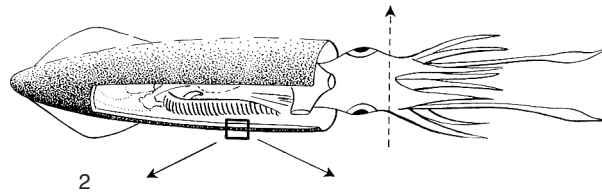
In *Sepia*, both sides of each gill face the respiratory stream. The leading edges again form a series of bars, here stiffened by cartilage and again devoid of exchange surfaces. Unlike the *Octopus* gill, where the water is free to flow along the length of the inside of each gill, the lamellae are separated by a series of membranes at right angles to a central membrane dividing the gill in two. The inner edge of the gill is braced against the funnel retractor muscle, as in *Octopus*, and the outer edge against the lateral wall of the mantle cavity (Fig. 12).

At first glance, all cephalopod gills appear to be built wrong-way round, with the afferent blood vessels bearing deoxygenated blood upstream of the efferent vessels,

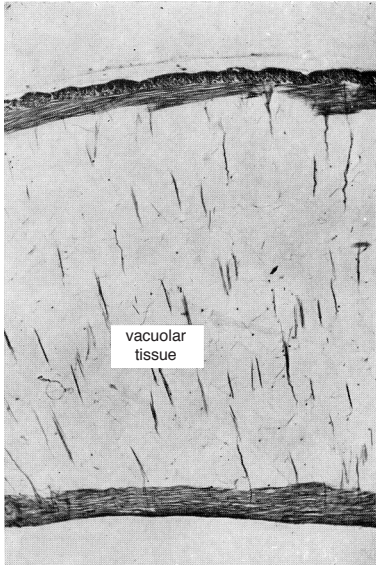
FIG. 9. The appearance of tissues containing ammonium chloride, 1, in the buccal region of *Histioteuthis*, and 3, in the mantle of *Octopoteuthis*, compared with 4, the muscular mantle of *Sepia*; view 2 shows the location of the photos shown in views 3 and 4. In the arms and mantle of ammoniacal squid, the muscle is often restricted to thin sheets surrounding the bulky vacuolar tissues (Denton, 1974).



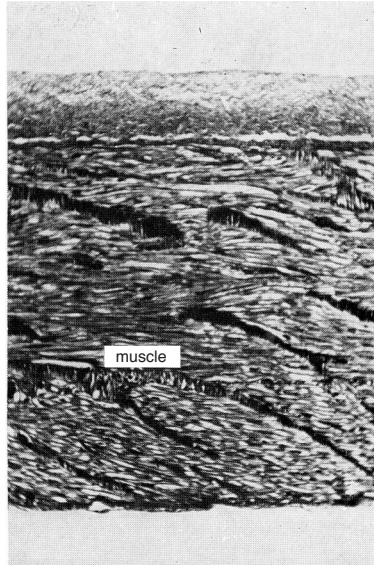
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FIG. 9. (For explanation, see facing page.)

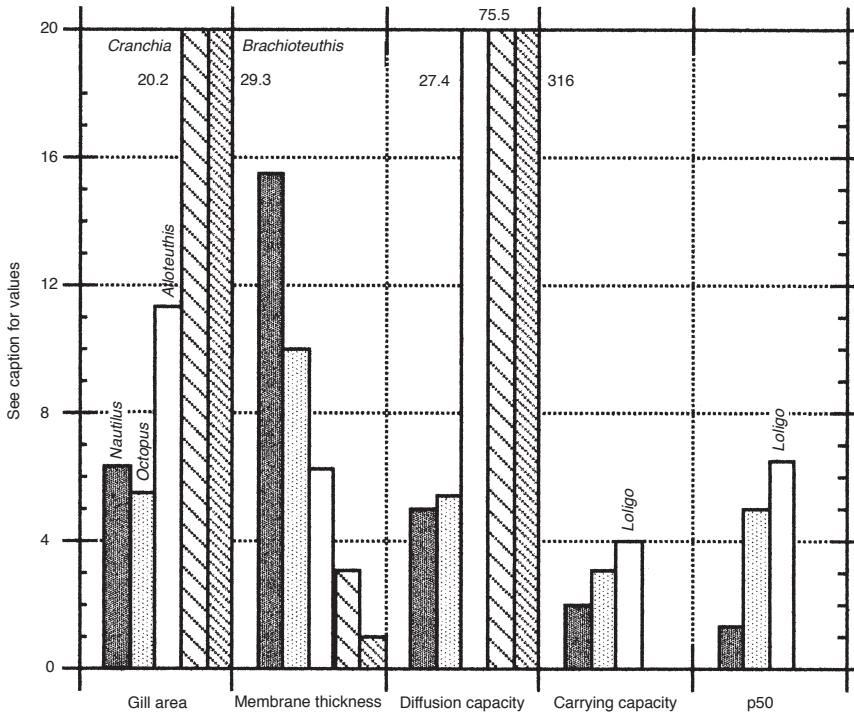


FIG. 10. Figures on vertical scale show gill areas (cm²g⁻¹), gill membrane thickness (μm), and diffusion capacities (O₂ ml min⁻¹ kg⁻¹) of *Nautilus*, *Octopus*, and three squids. *Alloteuthis* and *Brachioteuthis* are nonbuoyant; the former lives in shallow, well-aerated but sediment-rich tidal waters, the latter in deep, clear, and relatively hypoxic oceanic waters. *Cranchia* is a neutrally buoyant ammoniacal squid from the same habitat as *Brachioteuthis*. Blood oxygen carrying capacity (vols %) and p50 (mm Hg /10) are given for *Nautilus*, *Octopus*, and a fourth, shallow-water squid, *Loligo* (data from Eno, 1994, and Madan, 1996).

draining the gill of oxygenated blood. This is illusory, because the afferent vessels run along the outside (downstream side) of the gill lamellae and in through the complexly folded exchange surfaces to the efferents (Fig. 9–12). The exchange surfaces of octobranchiate lamellae are very much folded, compared with the simpler gills of Decabrachia.

OXYGEN UPTAKE AND METABOLIC RATE

The oxygen requirement of any cold-blooded animal depends not only on temperature but also on movement and digestion, either of which can greatly increase the resting metabolic rate. It can also vary diurnally. Unlike warm-blooded animals, ecto-

therms have no basal metabolic rate, their minimal resting rates depending upon their recent history. An *Octopus* that has been fed regularly will have two or three times the resting oxygen consumption of a starved animal under otherwise similar conditions (WELLS & others, 1983a, 1983b, 1983c).

The extent to which an active cephalopod can increase its oxygen uptake (its metabolic scope) can thus be stated only in terms of recent history. A regularly fed but active squid can treble its resting rate when swimming at its maximum sustainable speed. This is not a very impressive performance; a trout can increase its oxygen delivery by about eight times. Since the capacity to run up an oxygen debt also appears to be less than for most fish (Fig. 13–14), bursts

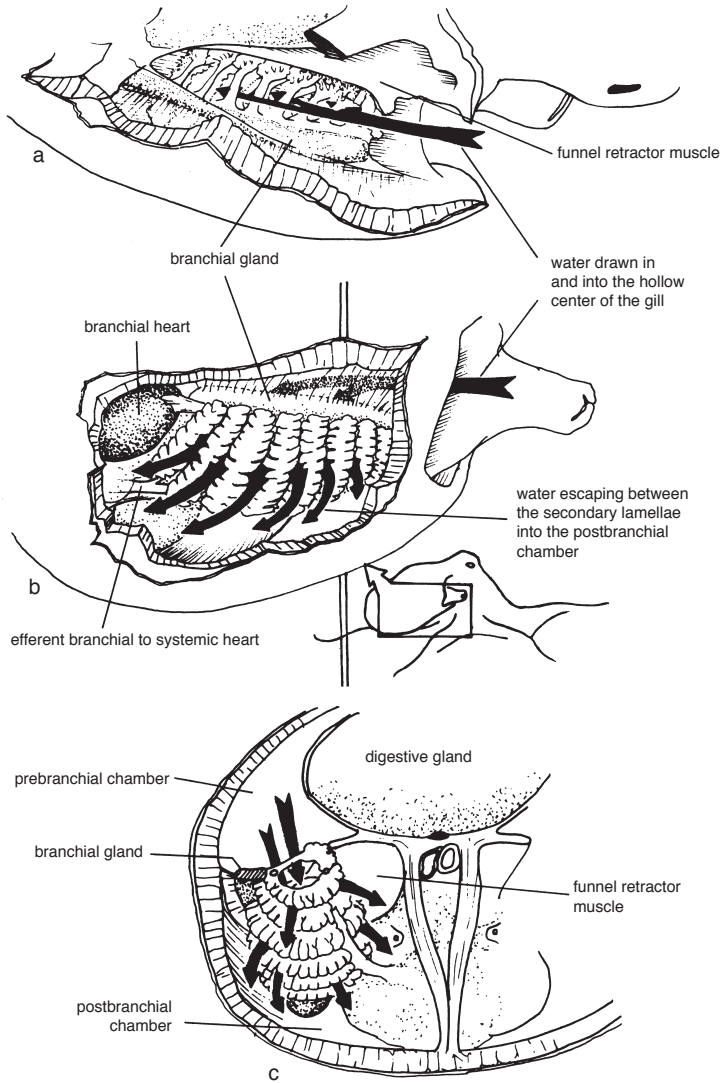


FIG. 11. Gill structure and water flow through the gills of *Octopus*. Black arrows show direction of water flow; *a*, right-hand side gill exposed by cutting away part of the dorsolateral wall of mantle cavity; *b*, lateral view; *c*, vertical section through mantle cavity at the level shown on view *b*, looking toward hind end of mantle; gill is attached to wall of mantle by a membrane and lodges against funnel retractor muscle centrally; water is drawn in through a grid formed by framework of lamellae on upper side of gill, passes into a space running length of gill, and flows out across much folded respiratory surfaces (Wells & Wells, 1982).

of maximum, nonsustainable speed can last only for seconds rather than minutes (O'DOR & WEBBER, 1986; O'DOR, 1988; FARRELL, 1991).

Any increase in oxygen consumption, whether to pay for ongoing activities or

to pay off an oxygen debt, must involve increasing blood or water flow through the gills or increasing the rate of extraction. There is a dichotomy here. Active squid such as *Lolliguncula* remove only about 5 percent of the oxygen passing through

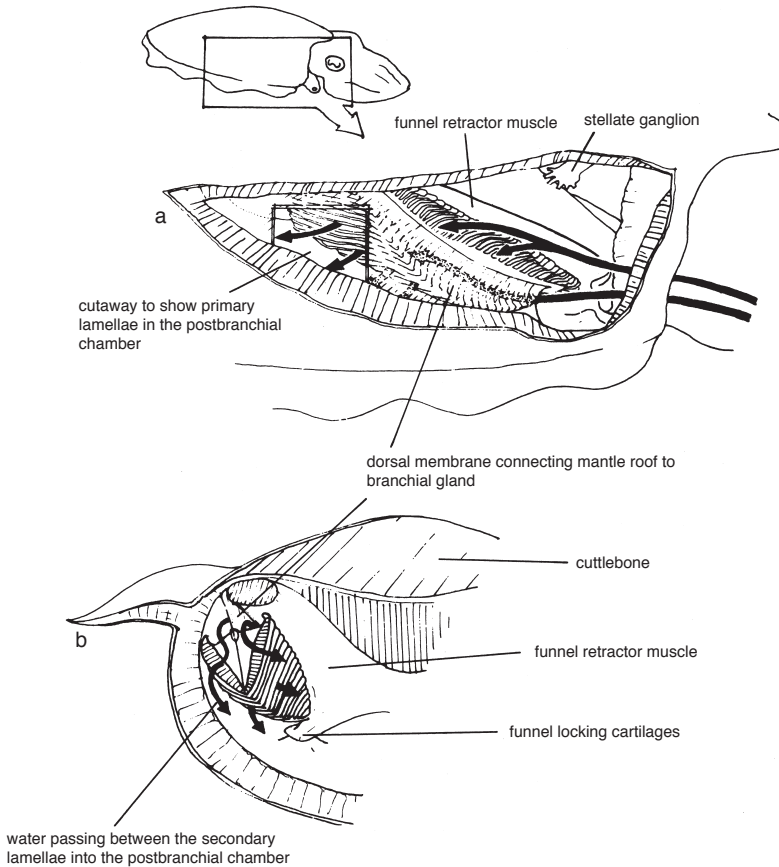


FIG. 12. Gill structure and water flow in *Sepia*. *a*, Cutaway view of mantle cavity, right side; *b*, transverse section of the same. Each gill is suspended from a membrane attached to the dorsolateral wall of mantle cavity. Water flows (black arrows) in on both sides of gill, down between cartilagenous framework of lamellae; each lamella forms a vertical sheet (so water cannot flow along the gill, as in *Octopus*) with the exchange surfaces ventrally. In life, outer edge of gill rests against wall of mantle and inner against funnel retractor muscle (Wells & Wells, 1982).

the gills; the volume of water required for jet propulsion exceeds the volume needed for respiration. If swum to exhaustion in a water tunnel or placed in hypoxic water, *Lolliguncula* will rest on the bottom; its extraction rate can then rise to 15 to 20 percent (Wells & others, 1988). *Octopus* uses jet propulsion relatively little. We have no figures for oxygen extraction while swimming but know that extraction at rest is regularly greater than 50 percent. Additional demand is met by increasing the ventilation rate and stroke volume. There is an obvious correlation with gill structure; *Octopus* has high-resistance, much-folded

gills that are specialized for extracting most of the oxygen from a small ventilatory stroke volume, about 3 percent of the body volume at rest; it can live in water that is only about 15 percent oxygen saturated. *Lolliguncula* has simpler gills, presenting relatively little resistance to a much greater through-flow of water (20 to 30 percent of the body volume per stroke); it soon dies in water that is less than 30 percent saturated. *Sepia*, which spends much of its life buried in the substrate, where large ventilatory movements would render it conspicuous, resembles *Octopus*; it extracts around 35 percent of the oxygen in the ventilatory

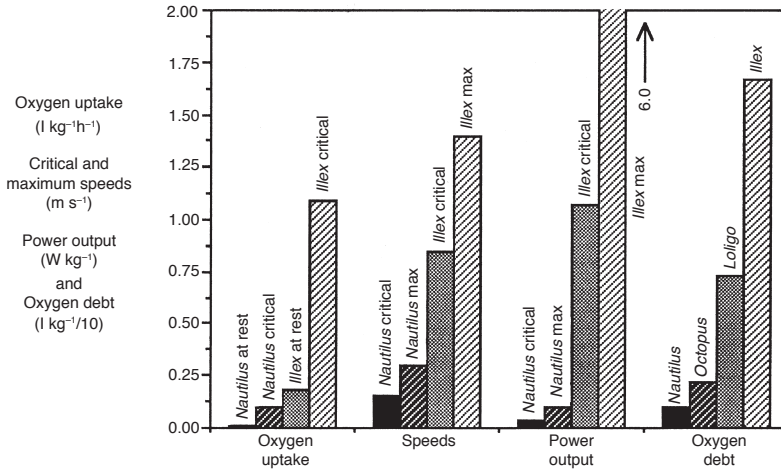


FIG. 13. Comparing performance of *Nautilus*, the squids *Illex* and *Loligo*, and *Octopus*. Oxygen uptake is given for the animals at rest and travelling at their critical, maximum aerobically sustainable speeds; coleoid has to produce 30 to 60 times the power per gram of the nautiloid to achieve 5-fold increases in critical and maximum speeds. Maximum speeds must be fuelled anaerobically. The capacity to carry an oxygen debt, here shown for *Nautilus*, *Octopus*, and two squids, the coastal *Loligo* and the oceanic *Illex*, has increased with fast-moving lifestyles (Wells, 1994).

stream at rest, passes a very small (1.5 percent) ventilation stroke volume, and can survive in water that is only 30 percent saturated (WELLS & WELLS, 1991).

There is an enormous range in metabolic rate to be found among coleoids. At one end of the scale, a squid such as *Illex* can consume as much as $33 \mu\text{mol O}_2 \text{ g}^{-1}\text{h}^{-1}$ (more than twice the uptake of a salmon of similar size) when swimming at its maximum sustainable speed and $6 \mu\text{mol}$ at rest on the bottom of its tank (WEBBER & O'DOR, 1985). At the other end of the scale, *Vampyroteuthis*, from the oxygen-minimal layer off California, consumes only $0.02 \mu\text{mol g}^{-1}\text{h}^{-1}$. Metabolic rate decreases with depth, it being argued that the need for rapid movement disappears progressively as the light fades so that predators and prey can no longer see each other at a distance (SEIBEL, CHILDRESS, & GORODEZKY, 1997).

Blood Gas Transport

The blood pigment is always the copper-based hemocyanin. Cephalopods have no equivalent of vertebrate red blood cells, so the concentration and consequent oxygen-

carrying capacity of the blood is limited by viscosity. It ranges from 2 vols percent in *Nautilus* to almost 5 vols percent in squids. The properties of the pigment are related to the ecology of the species concerned. Active, open-water squids that never have to face oxygen-deficient conditions have hemocyanins with low oxygen affinities that will unload oxygen to the tissues at high tensions. The p50 (half-saturated condition) of *Loligo vulgaris* blood is 70 mm Hg; that of *Octopus* is 50; and the hypoxia-tolerant, low metabolic rate of *Nautilus* is as low as 12 (Fig. 10). The low oxygen-carrying capacity is associated with very high oxygen utilization; the blood has unloaded nearly all of the oxygen carried by the time it is returned to the gills, even at rest. Inability to expand the arteriovenous difference is the principal reason for the low metabolic scope of cephalopods (JOHANSEN, BRIX, & LYKKEBOE, 1982).

There is a powerful systemic heart with arterial branches to all tissues, and, in coleoids, additional branchial hearts, one at the base of each gill, to push the blood through a second set of capillary beds in the gills (see *Treatise Online*, Part M, Chapter 3,

Anatomy of Recent Forms, p. 18, Fig. 20). In addition, most of the blood vessels, veins as well as arteries, are themselves contractile. Blood flow, where this has been studied, is always high pressure and high volume, a consequence of the need to fuel a high metabolic rate by a delivery system based on a blood pigment with a relatively low oxygen-carrying capacity (fish bloods carry 10 to 15 vols percent oxygen, compared with a maximum of 5 percent in cephalopods). When the low carrying capacity is added to the high cost of jet propulsion, it can be calculated that the heart of a 500 g *Illex* has to pump about eight times as much blood to fuel half the maximum sustainable speed of a fish of similar size (Fig. 14). The capacity of the circulation to deliver enough oxygen to the muscles is almost certainly the limiting factor in the evolution of yet swifter cephalopods (O'DOR & WEBBER, 1986; O'DOR, 1988; WELLS, 1994).

FEEDING AND DIGESTION

The anatomy of the digestive system is outlined in *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms and Figure 19.

Coleoids are all predators. The combination of suckered or hooked arms and a sharp beak means that they can catch and eat prey as large as or larger than themselves. The prey is sometimes killed by toxic saliva, and flesh is always bitten off and taken in relatively small pieces. The fact that the esophagus passes through the ring of ganglia forming the brain sets a limit to the dimensions of the fragments ingested. Squids and sepiids bite off and swallow fish scales and lengths of backbone, crustacean bristles, and pieces of cuticle. Octopuses adopt a different technique, injecting saliva into the carapaces of the crabs that they eat; the saliva includes proteases that attack muscle attachments, so that the octopus is able to extract and swallow fragments of muscle with few if any hard parts; the crab legs and carapaces are discarded as cleaned-out skeletons (NIXON, 1984). In addition, octopuses feed widely

on bivalves and gastropods, and here use the radula to bore a small hole in the shell (NIXON & MACONNACHIE, 1988), through which the octopus can inject a poison that blocks neuromuscular transmission, allowing it to pull out the prey; molluscan flesh, of course, includes no hard parts.

Octopuses have a large crop; Decabrachia pass the food directly into the stomach. Digestion in both instances is by installments, food passing in turn to the spiral caecum and thence to the intestine. In *Octopus* and *Sepia*, fluid can pass up a pair of ducts opening at the junction between stomach and caecum to the digestive gland, where fine particles are taken up directly into the cells. In *Loligo*, the gland produces digestive enzymes that pass down the ducts to the stomach and caecum with no return flow; absorption by squids is mainly through the walls of the caecum and intestine. In all instances, the digestive gland is an excretory organ, with wastes discarded from the cells in the form of brown bodies that pass down the digestive gland ducts to the intestine. In the intestine, these wastes from the digestive gland are compacted into strings, together with fish scales, fragments of crustacean cuticle, and so on and discharged periodically. Digestion is in general more rapid than in fish living in similar habitats (BOUCAUD-CAMOU & BOUCHER-RODONI, 1983).

In common with other mollusks, the capacity to store lipids is limited, and much of the lipid content of foods is discarded. Proteins are taken up readily, and proteins, generally in the form of muscle tissue, form the major energy reserves. Carbohydrates, which are anyway less common in prey, contribute comparatively little to coleoid metabolism (for a review, see O'DOR & WEBBER, 1986).

ELIMINATION AND RETENTION OF WASTES NOT VOIDED WITH THE FECES

The principal end product of protein metabolism in coleoids is ammonia, readily lost through the gills and general body

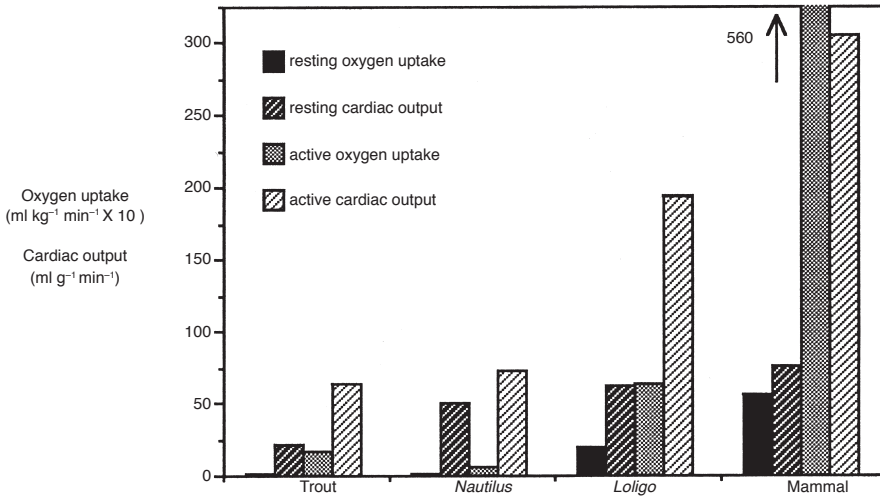


FIG. 14. Oxygen uptakes and cardiac outputs of *Nautilus* and a squid compared with those of a trout and a mammal, scaled for animals of 400 g flesh weight; systemic heart of a cephalopod is equivalent of ventricle only in a fish and left ventricle only in a mammal, so figures for cardiac output per gram of heart have been doubled in vertebrates (Wells, 1994).

surface. Smaller quantities of a range of nitrogenous wastes from urea to purines, together with amino acids, pass as an ultrafiltrate through the pericardial appendages driven by the pressure of the contracting branchial hearts. In Decabrachia, the pericardial coelom is widely connected with a system of coelomic spaces surrounding the guts; claw back of amino acids and carbohydrates that have passed through the pericardial appendages is widespread. From the pericardial coelom, fluid runs through the renopericardial canal into kidney sacs that surround outgrowths of the lateral venae cavae and which are themselves presumably concerned with adding or subtracting materials from the urine. Analysis is made difficult by the universal presence of mesozoan parasites in the benthic octopods and sepiids that can be kept easily in the laboratory (HOCHBERG, 1989). Urine is finally discharged through the renal pores into the mantle cavity. Octopods have a modified version of this system, with the renopericardial ducts linking the pericardial coelom around the

branchial heart appendages, directly to the kidney sacs. In this variant, reabsorption of useful carbohydrates and amino acids is through the walls of the pericardial ducts (MARTIN, 1983).

Some substances, it appears, are never excreted. These include heavy metals that are apparently accumulated in a detoxified form, particularly in the digestive gland. Copper, which is abundant in the hemocyanin of crustacean prey, seems, for example, to accumulate throughout the lifetime of the individual concerned (GHIRETTI & VIOLANTE, 1964). Since many cephalopods are cannibalistic, the survivors can have very large concentrations of heavy metals in their digestive glands. Figures for *Octopus* range up to 2000 to 4000 mg kg⁻¹ dry weight for copper, originating from the hemocyanin of its largely crustacean prey, 1500 for zinc, 700 for iron, and 50 for cadmium, with smaller concentrations of manganese and vanadium (MIRAMAND & GAURY, 1980). Comparable concentrations occur in *Alloteuthis* (BRYAN, 1976), *Eledone*, and *Sepia* (MIRAMAND & BENTLEY, 1992).

BRAINS, SENSE ORGANS, AND LEARNING

Figure 15 outlines the structure of the brain of *Octopus*. The brains of coleoids are large, even by vertebrate standards, with brain to body-weight ratios regularly exceeding those of fish (PACKARD, 1972). This is remarkable anyway, the more remarkable since in octopods, at least, the number of additional nerve cells in the arms greatly exceeds the number in the central nervous system (see *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 14). A large number of experiments have been made with *Octopus* to find out which bits of the brain do what. J. Z. YOUNG (1971) has reported details of the anatomy; WELLS (1978) has summarized the results of the many brain lesion and behavior experiments done by YOUNG and others. Particular attention has been paid to parts concerned in sensory analysis, learning, and memory. Local electrical stimulation of parts of the brain shows that the subesophageal lobes are concerned with the organization of local reflex activities, while such more complex motor responses as walking and swimming depend upon the basal lobes of the supraesophageal brain. Stimulation of the parts overlying the basal lobes has no effect, but brain lesion experiments show that these parts are concerned with learning and memory. In *Octopus*, visual and tactile learning appear to be regulated by the optic; vertical and superior frontal; and the inferior frontal, subfrontal and posterior buccal lobes, respectively. In terms of sheer numbers, the optic lobes, with 92 million neurons, dominate the supraesophageal part of the brain (42 million neurons in the rest). Among decabrachiates, the optic lobes typically form an even larger proportion of the brain, reflecting the overwhelming importance of vision in the lives of these animals. One result of all the anatomical and behavioral work that has been done is that the habits of a coleoid can be inferred from the relative sizes of the lobes of its brain (Fig. 16).

Coleoids have no recourse to the traditional retire-into-the-shell defense of their ancestors. They are soft bodied and good to eat. They survive by early detection of potential predators and prey and by reacting swiftly and efficiently (HANLON & MESSENGER, 1996).

EYES

Coleoid eyes closely resemble the eyes of vertebrates, with lenses to focus and irises to adapt to changing light conditions (Fig. 17). The retina carries very large numbers of closely packed sensory elements. Experiments with octopuses show that their visual acuity (the ability to separate vertical stripes) is better than 9.7 minutes of arc. The angle separating the retinal elements is considerably less than this, 1.2' to 1.3', indicating considerable oversampling so that neighboring elements must be joined together to increase sensitivity at the expense of acuity (MUNTZ & GWYTHYR, 1988). Squid generally have larger eyes than octopuses and probably have vision comparable with our own. Since retinal elements are added to the eyes as they grow, visual acuity should increase with size, if neighboring elements are not progressively connected together to further increase sensitivity.

Laboratory experiments with *Octopus* and *Sepia* show that these animals are color blind (MESSENGER, 1977; MARSHALL & MESSENGER, 1996), a finding consistent with the anatomy and biochemistry of their eyes. Only one sort of retinal element and one sort of retinal pigment are found. The spectral sensitivity of the pigment is similar to that of our own rods. There is one known exception, *Watasenia scintillans*, a bioluminescent species that has two further pigments and therefore seems likely to have color vision (MICHINOMAE & others, 1994).

The arrangement of the photoreceptors in two series at right angles makes the animals potentially sensitive to the plane of polarization of light, and there is behavioral evidence that the animals are able to detect this (MOODY & PARRISS, 1961).

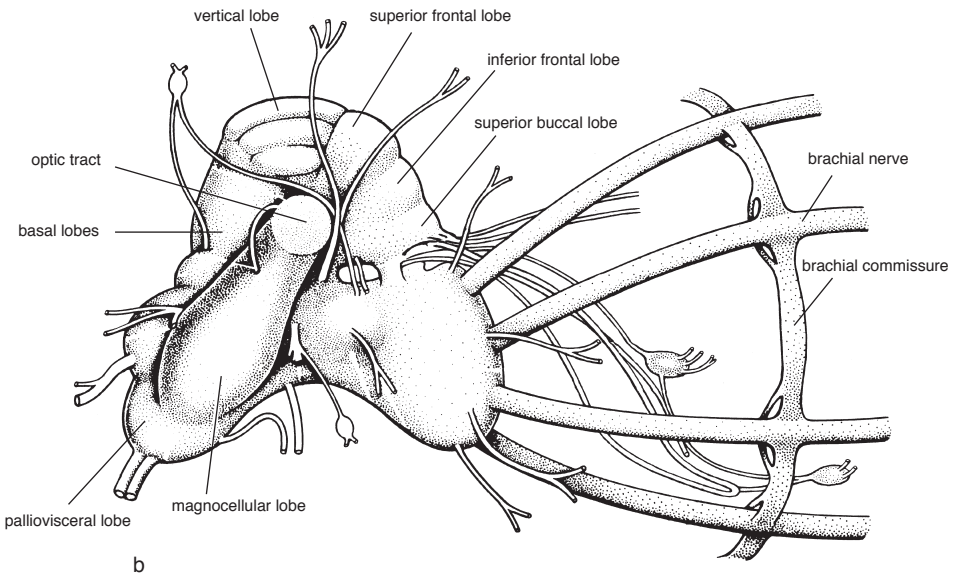
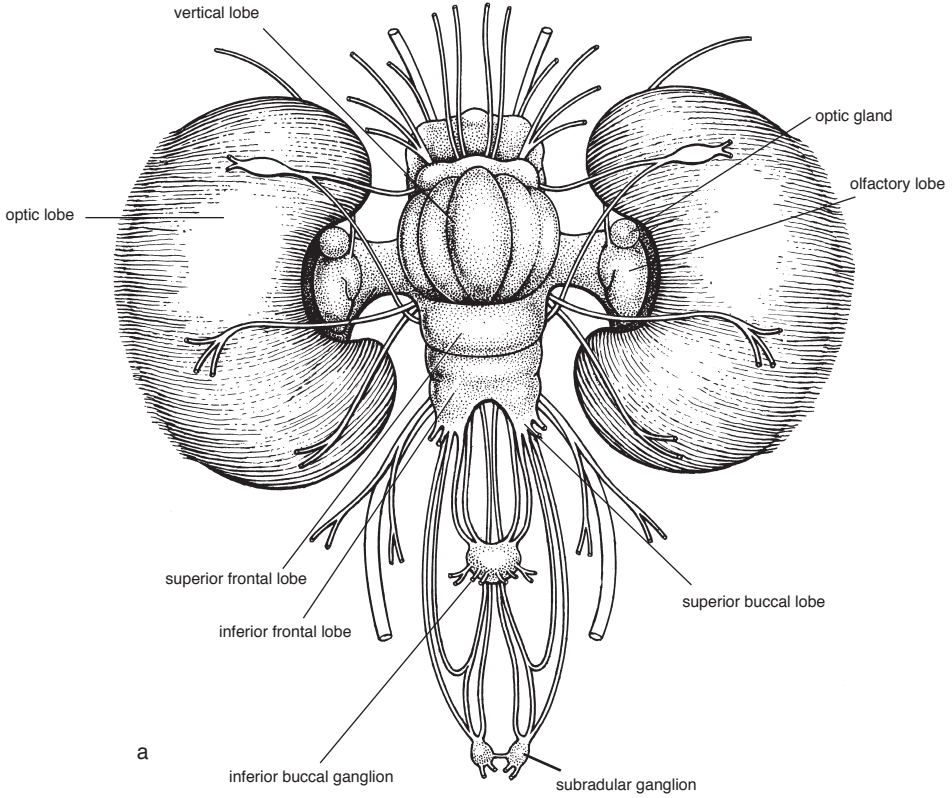
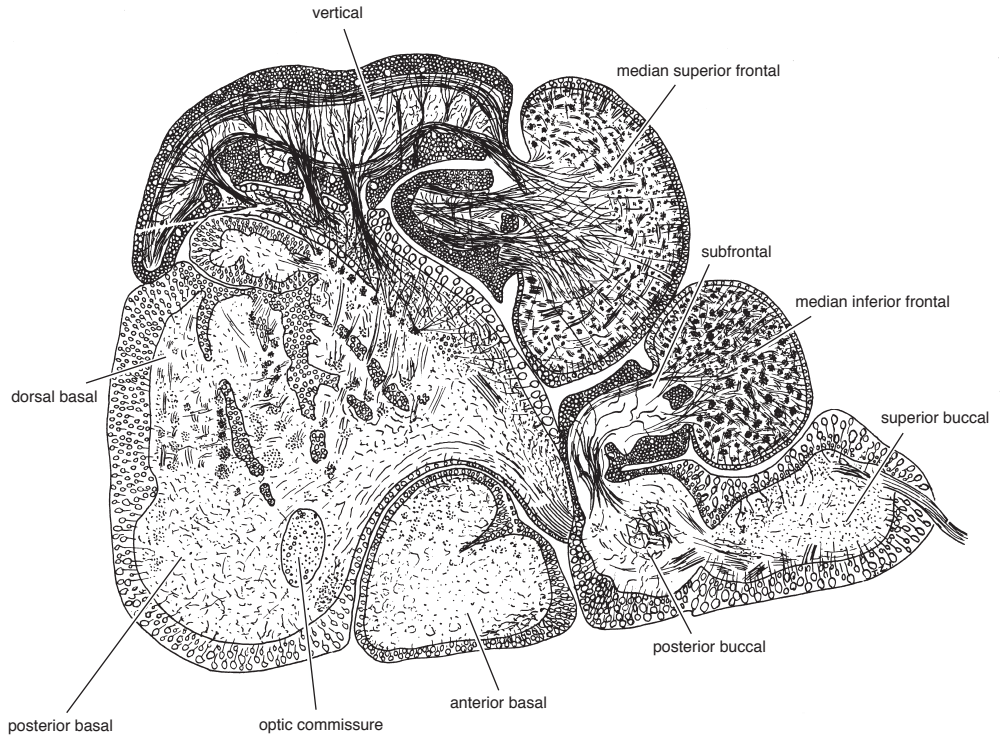
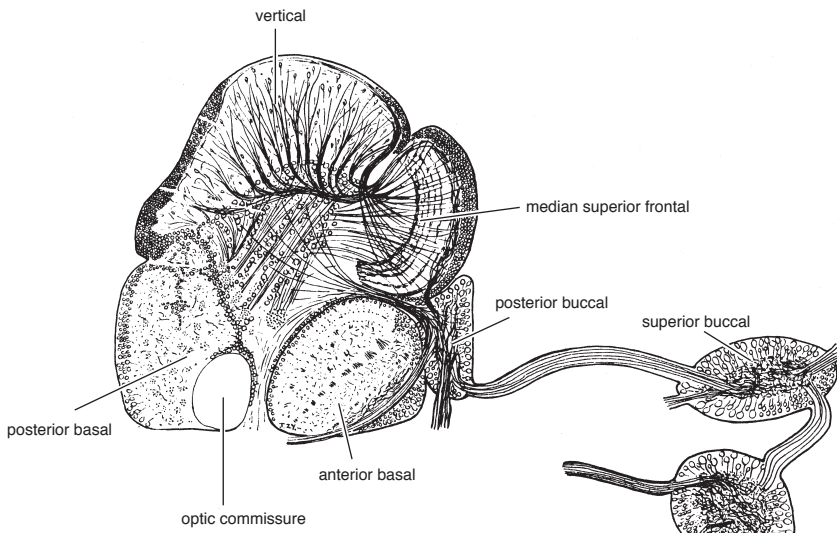


FIG. 15. Brain of *Octopus*; a, from above; b, from right side (Young, 1971).



1



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FIG. 16. (For explanation, see facing page.)

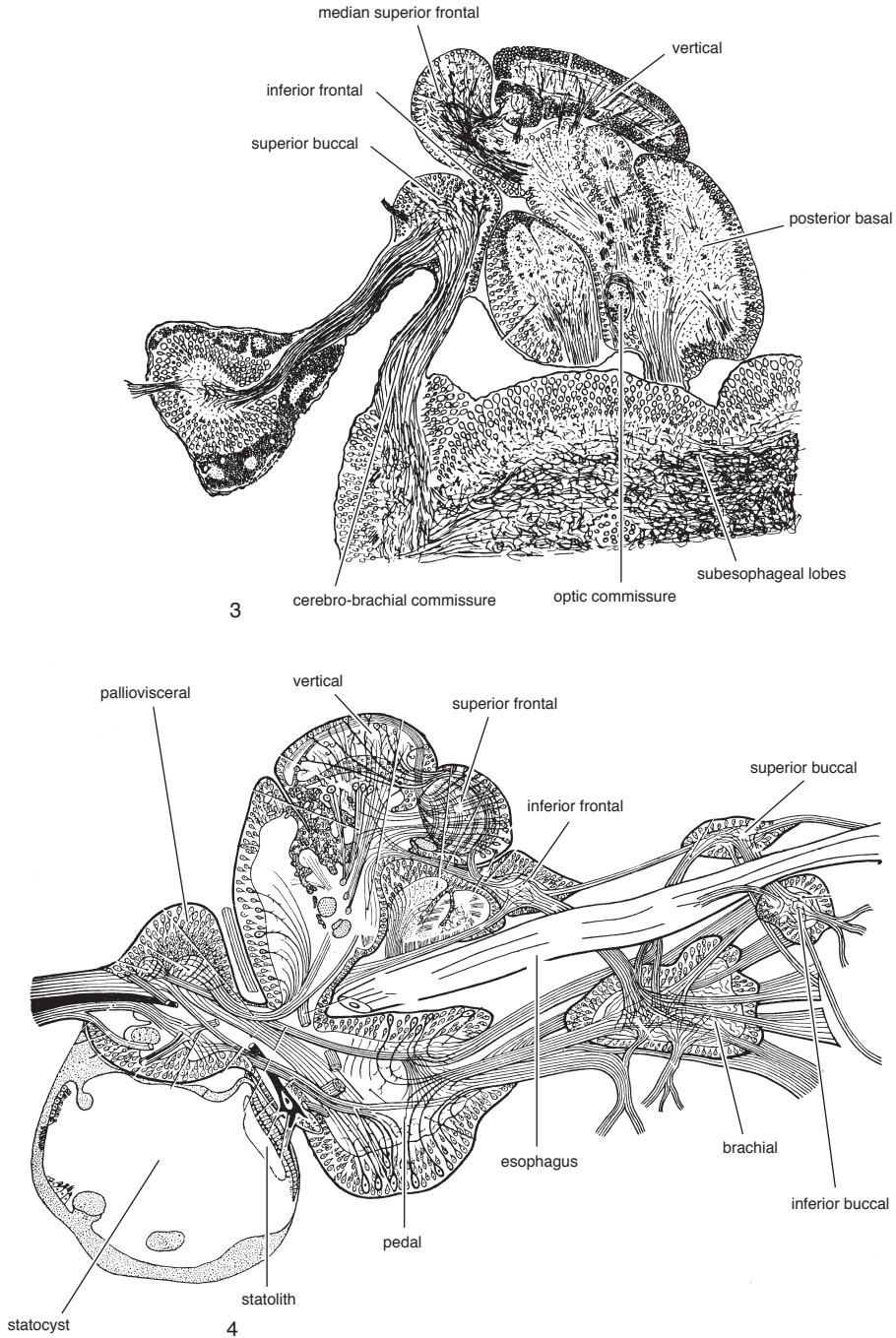


FIG. 16. Median vertical sections through brains of coleoids. 1, *Octopus*, right side view (Young, 1971); 2, *Sepia*, supraesophageal parts only, right side view (Young, 1964); 3, *Tremoctopus*, an octopod that has returned to a pelagic environment but still retains a reduced inferior frontal lobe, left side view (Young, 1964); 4, *Loligo*, where very large optic lobes squeeze center part of brain so that superior buccal and brachial lobes are displaced forward, right side view (Young, 1976).

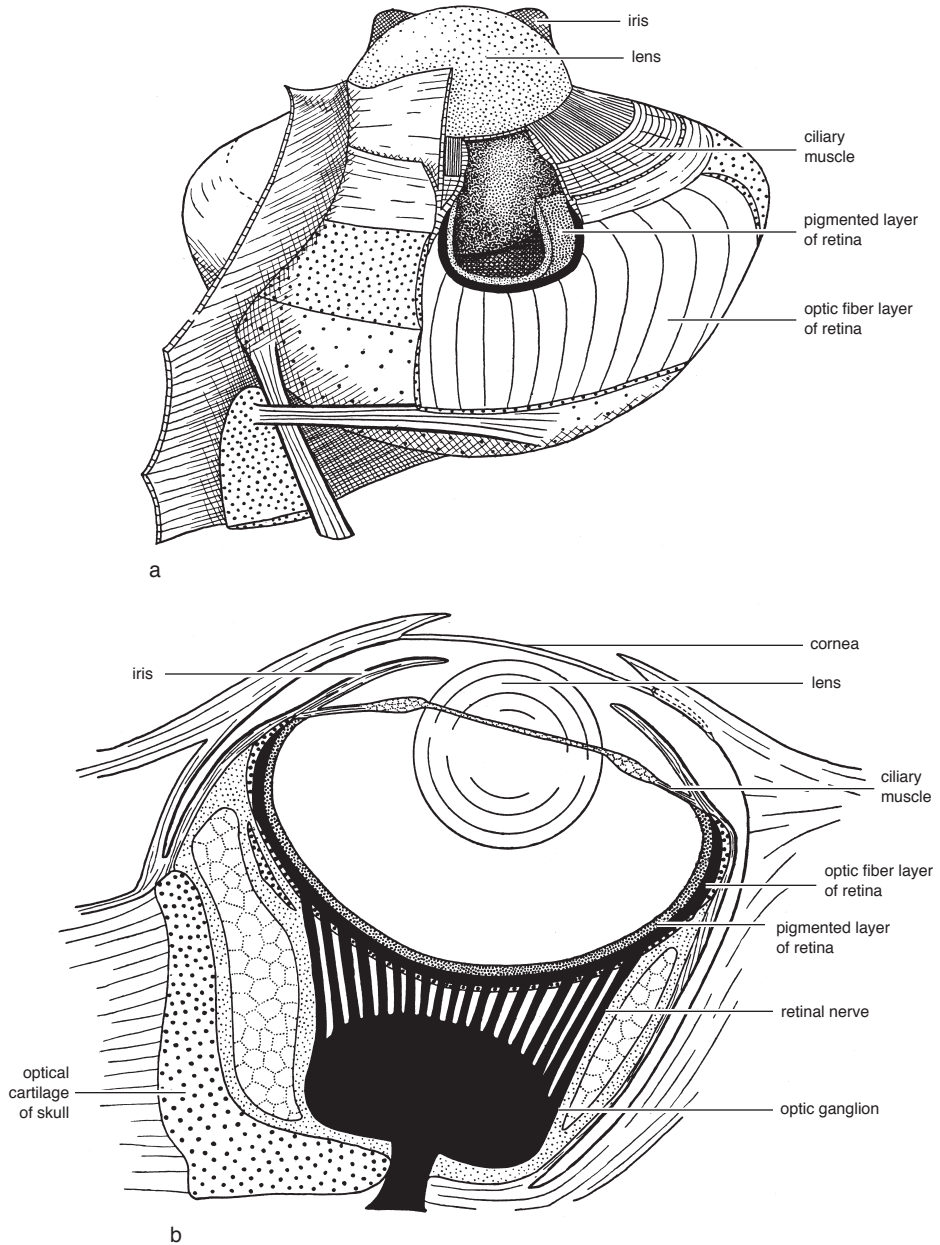


FIG. 17. Structure of eye of *Sepia*; *a*, with skin and corneal membrane removed; *b*, in section. Octopuses and myopsid squid living in sediment-rich waters have a cornea like the sepiids; oegopsids, which are typically oceanic, do not (Tompsett, 1939).

There have been a great many experiments made on visual discrimination, notably with *Octopus*, which can be trained to discriminate by reward and punishment techniques in the laboratory. An extensive literature, generated in the 1960s and 1970s, has been summarized by MESSENGER (1981) and by WELLS (1978); for some later developments, see BOAL (1996). *Octopus*, at least, can distinguish sizes and shapes; it classifies geometric shapes approximately as we would ourselves and makes similar generalizations between shapes. Observations of a wide range of cephalopods in the wild shows that they have complex behavior, based on things that they and we can both see (HANLON & MESSENGER, 1996).

The behavior of squid and cuttlefish appears to be overwhelmingly visually determined. Octopods, living on the bottom, where much of their prey is out of sight, buried or hiding between the rocks, have a well developed touch and taste sense, with chemical acuity exceeding our own (WELLS, 1978). This is reflected in the development of the lobes of the brain; squids have relatively enormous optic lobes; benthic octopods alone have regions, the subfrontal and posterior buccal lobes, uniquely concerned with analyzing tactile data (Fig. 16).

TACTILE AND CHEMOTACTILE SENSES

Octopuses have enormous numbers of sensory cells responding to touch or to chemical stimuli in all areas of the skin but particularly concentrated in the rims of the suckers. They also have receptors in the muscles responding to stretch, but, of course, no equivalent of the joint receptors as found in vertebrates or arthropods. This absence is important; it limits the performance of cephalopods (and other soft-bodied animals) in a number of ways. Much of the behavior of the higher vertebrates and of arthropods depends upon the capacity to measure their own movements accurately. Manipulation of the environment (building spider's webs or skyscrapers), remembering

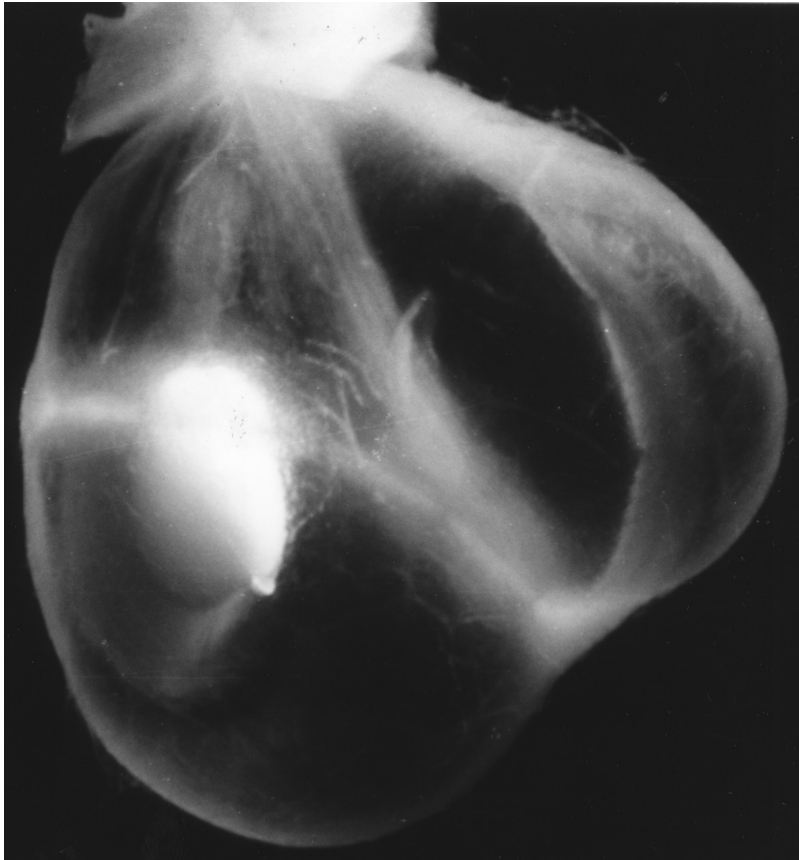
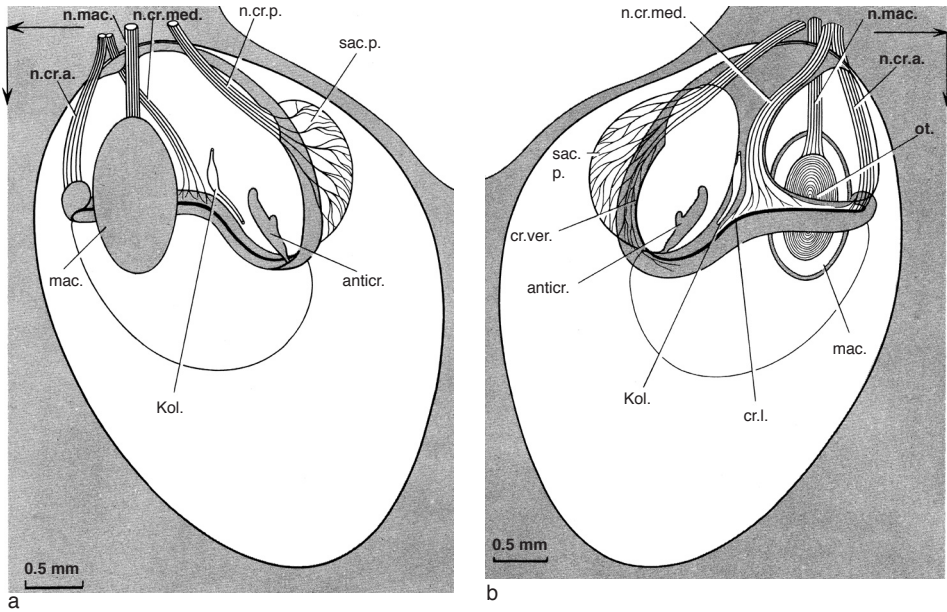
the layout of the habitat (octopuses learn theirs by sight, but presumably could not manage in the dark), or navigation by dead reckoning all depend upon an ability to repeat movements that have yielded a desirable result (WELLS, 1978, 1998).

OLFACTORY PIT

There is a group of sensory organs close to the entrance to the mantle on either side. This has long been known as the olfactory pit, presumably because of its similarity in position to the osphradium in other mollusks. A nerve runs from the pit to the small olfactory lobe at the base of the optic lobe on each side of the brain (Fig. 15). Squid ink released onto this group of sense organs provokes immediate escape jetting in *Loligo opalescens*, a response lost if the organ is removed or anesthetized (GILLY & LUCERO, 1992).

ORGANS OF BALANCE

Coleoids have an elaborate series of sense organs responding to gravity and angular accelerations. These are housed in a pair of fluid-filled sacs on either side of and below the brain and surrounded by extensions of the cranial cartilage (Fig. 18–19). A great deal of elegant electrophysiological work has shown that the calcareous statoliths lie on beds of sensory hairs, the maculae, that respond to shear forces created by the weight of the statoliths. There is one macula and one statolith in each statocyst in octopuses and three maculae and a single statolith in squids. In addition, there are sensory hair cells that respond to angular accelerations underlying a series of flaps extending into the fluid of the statocyst. The flaps (cupulae) attached to the tips of the hair cells form a continuous series, the crista, arranged in three planes at right angles. When the animal accelerates in any plane, the fluid in the statocyst lags behind the rotation of the animal, bending the relevant flaps. There is an abundant efferent nerve supply, from the brain to the maculae and to the cells underlying the crista, as well as the sensory



c

FIG. 18. (For explanation, see facing page.)

nerves running inward. The animal can thus modify the output from the sense cells and so distinguish between movements that it has itself initiated and those occurring passively (BUDELMANN, 1970, 1977, 1990). A series of cartilagenous baffle plates (anticristae) within the statocyst that vary greatly in shape and number (0 to 43, depending on the species) presumably modify the flow within the sac, but the details of their action are as yet unknown.

EXTERNAL DETECTORS OF FLUID FLOW

It was long believed that cephalopods had no equivalent of the lateral lines of fish. More recent work (BUDELMANN, RIESE, & BLECKMANN, 1991) has shown a tracery of lines of cilia on the head of *Sepia* (Fig. 20) and *Alloteuthis*, with underlying sensory cells that respond to the movement of water over the skin that are morphologically and physiologically analogous to the mechanoreceptive lateral line system of fish. By analogy with fish, one might expect this sensory input to be used in predator and prey detection, particularly in the dark or under murky conditions. Behavioral experiments show that cuttlefish with the epidermal lines 75 percent destroyed have no difficulty catching shrimps in the light but perform poorly compared with controls in the dark (BUDELMANN, RIESE, & BLECKMANN, 1991).

DEFENSES

Coleoid defense is primarily dependent on crypsis. Many of the animals are partially transparent, although some structures, such as the ink sac and the reflective screens backing the eyes or photophores (see below), cannot be hidden in this way. Coleoids too large or too solid to be hidden by transpar-

ency can generally match the intensity of light reflected by the background (sand, weeds, rocks, and so on) by adjusting the expansion of the chromatophores that are under direct nervous control from the brain. Figures 21 and 22 show the appearance of the chromatophores in *Octopus*. MIROW (1972a, 1972b) illustrated the corresponding structures in squid. Coleoids can, moreover, display a repertoire of patterns of chromatophore expansion so as to break up their own outline or mimic the light and dark patterns in their background.

The chromatophores are all in the yellow-red-brown (almost to black) range. Colors that are not represented but present in the background are reflected by the contents of two types of reflecting cells (Fig. 22–23). Iridophores are multilayered stacks of thin chitin (DENTON & LAND, 1971) or protein platelets separated by cytoplasm (COOPER, HANLON, & BUDELMANN, 1990); they produce colors by interference or diffraction. Iridophores are probably also responsible for patterns such as the warning colors shown by the blue-ringed octopus *Hapalochlaena*. They may also be under (indirect) nervous control, since the thickness of the platelets and the state of the material within the platelets, and thus the reflected colors, change when the iridophores are bathed in acetylcholine (COOPER, HANLON, & BUDELMANN, 1990).

Finally, in some octopuses, cuttlefish, and *Sepioteuthis*, cells containing white granules underlie the rest. These act, apparently passively, as broad-band reflectors of light that have passed through the overlying structures in the skin (MESSENGER, 1974). Figure 22 shows the appearance of the chromatophores, iridophores, and leucophores at high magnification in the skin of *Octopus*. In squids, the leucophores are missing, and

FIG. 18. Statocyst from right side of *Octopus*, *a*, from midline of animal (adapted from Young, 1971); *b*, from right side; *arrows* show anterior and ventral. *anticr.*, anticrista; *cr.l.* and *cr.ver.*, lateral and vertical sections of crista; *kol*, Kollikers canal, connecting endolymph and perilymph; *mac.*, macula; *n.cr.a.*, *n.cr.med.*, and *n.cr.p.*, nerves to anterior, median, and posterior sections of crista; *n.mac.*, macular nerve; *ot.*, otolith (=statolith); *sac.p.*, posterior sac (adapted from Young, 1971); *c*, photograph of right side statocyst sac, seen from midline (adapted from Budelmann, Sachse, & Staudigl, 1987).

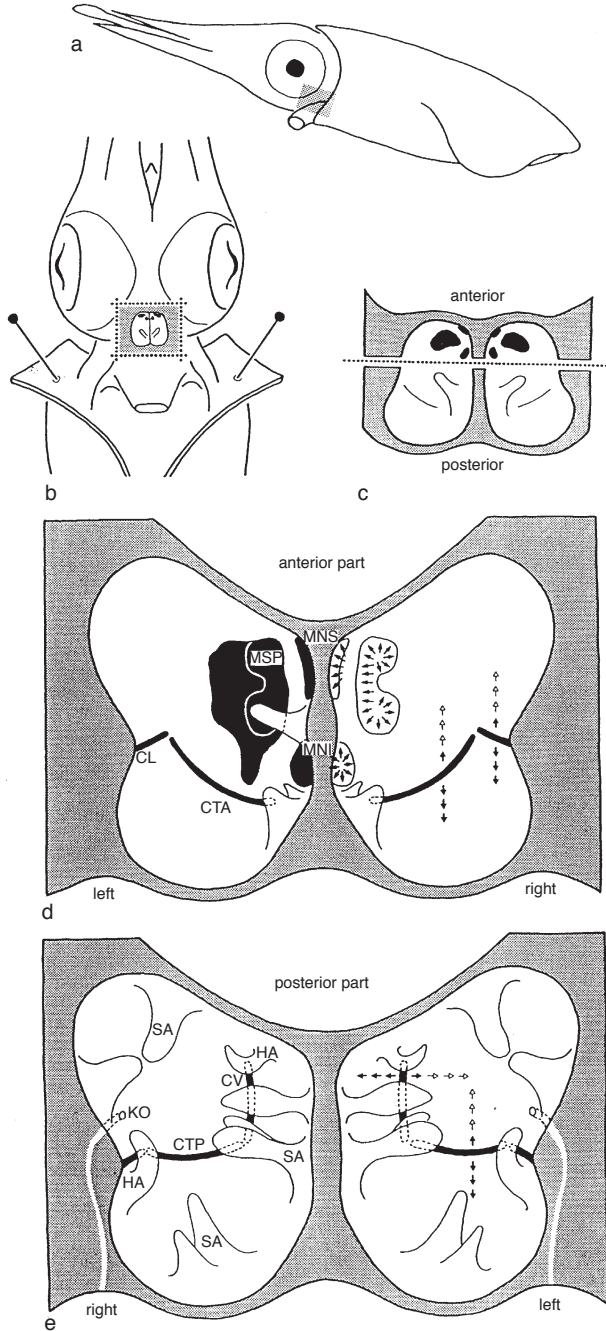


FIG. 19. Statocysts from *Loligo*. *a*, Position of statocysts seen laterally; *b–c*, from below; dotted line in view *c* shows position of a vertical cut; *d–e*, details of statocysts seen looking anteriorly and posteriorly from plane of cut in view *c*; diagrams on left show three gravity receptor systems; *MSP*, macula superior princeps; *MNS*, macula neglecta superior; *MNI*, macula neglecta inferior; angular acceleration detectors of crista lie in three planes at right angles; *CTA*, anterior transverse crista; *CL*, longitudinal crista; *CTP*, posterior transverse crista; *CV*, vertical crista; arrows (Continued on facing page).

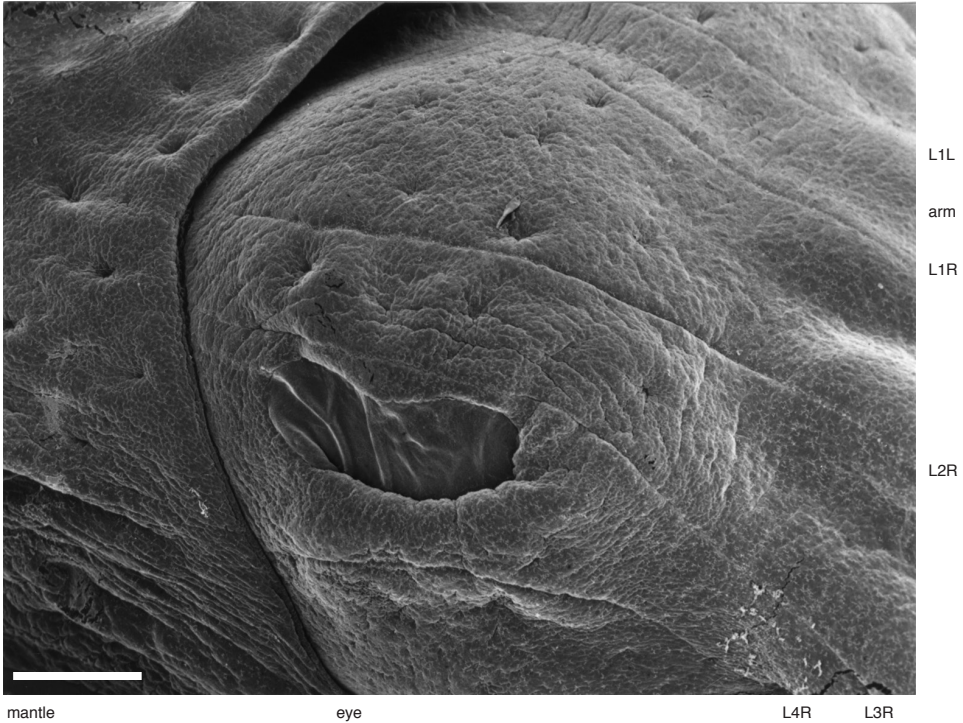


FIG. 20. Epidermal lines (lateral line analogue) on the head of a 14-day-old *Sepia officinalis*. Scanning electron micrograph of oblique lateral view of head, showing four lateral lines on right side (L1R–L4R) and one on left side (L1L); lateral lines (1–3) that run in anterior-posterior direction continue onto an arm; scale bar, 0.3 mm (Budelmann & Fertl, unpublished observations, 1989; Budelmann, Schipp, & Boletzky, 1997).

the iridophores may take the form of long strands of platelets (MIROW, 1972b).

The color pattern repertoires of open-water squid tend to be simpler than those of forms living close to the bottom, but many squid (and other coleoids when small) make up for this by being semitransparent. *Sepia*, and probably many other squids and sepiids, show counter-shading, with chromatophores expanding on the lit side if the animal is rolled (FERGUSON, MESSENGER, & BUDELMANN, 1994). Octobrachiates and sepiids can, in addition, change their surface texture, raising papillae by contraction of muscles in the skin.

Since chromatophore and skin texture changes are under direct nervous control, changes in appearance can be made within milliseconds. This makes coleoids very difficult to follow underwater because of repeated disruptions of the search image of any would-be predator.

If crypsis fails, the animals can squirt ink. The structure of the ink sac is described in *Treatise Online*, Part M, Chapter 3 (Anatomy of Recent Forms, p. 31–34). The black component of the ink is melanin. Ink can typically be delivered in two modes, either dispersed, forming a smokescreen, or discharged, bound into a ball with mucus,

FIG. 19. (Continued from facing page).

in diagrams on the right indicate polarizations of hair cells of three maculae and four crista sections; processes from the walls of the statocyst, which are assumed to modify flow over cristae: HA, the curved hamuli; SA, straight anticristae; KO, ciliated Kölliker's canal, runs out of statocyst and may be concerned in regulation of fluid content of statocyst (Budelmann, 1990).

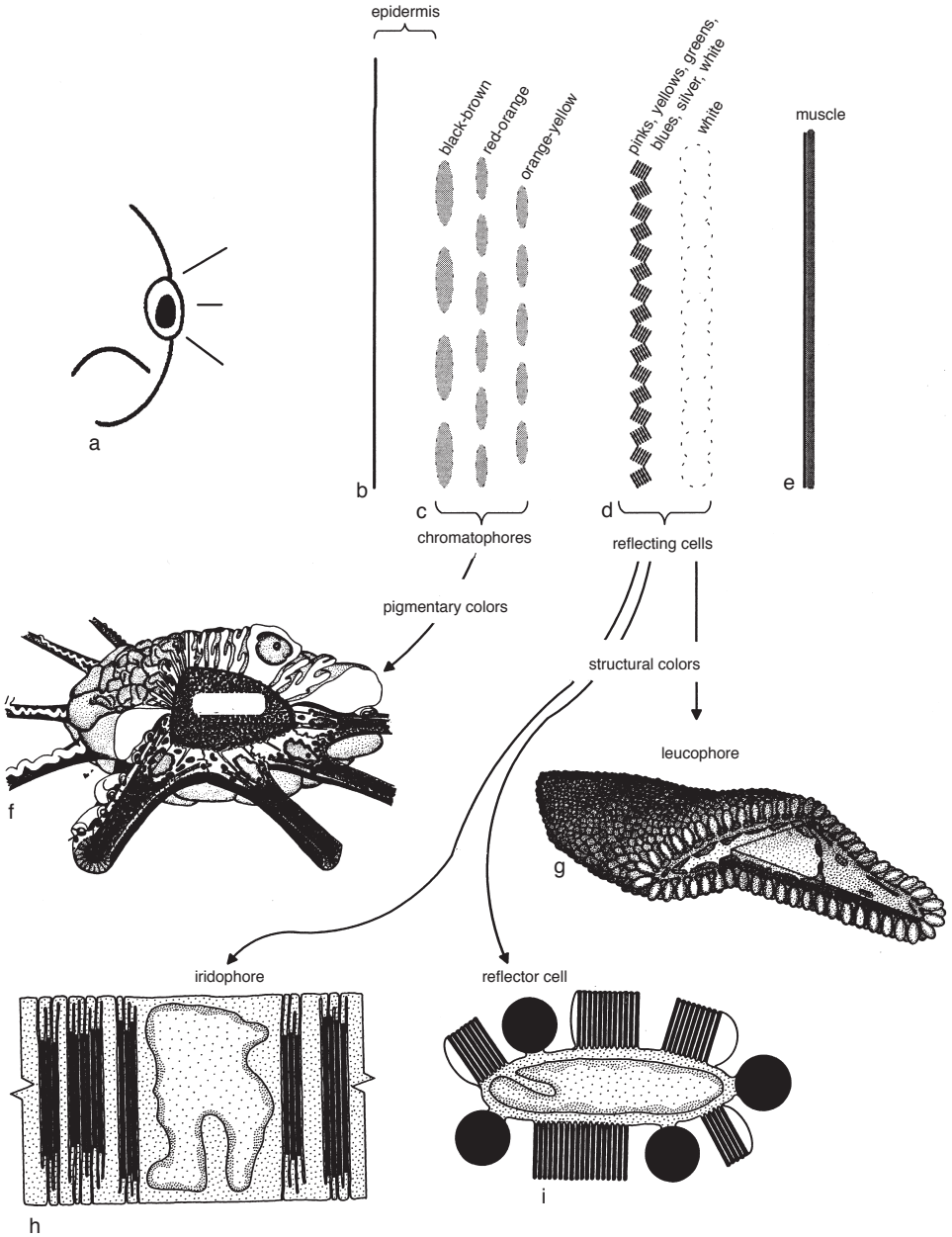


FIG. 21. Elements that give rise to colors seen in skin of a cephalopod (*b-f*), and *a*, being viewed by a fish. Reflector cells, reflecting blue and green, are found only in the skins of octopuses; *f*, chromatophore organ, showing central cytoelastic sac containing pigment granules and array of muscle fibers; *g*, leucophore, which reflects mainly white light; *b*, iridophore with iridosomal platelets that reflect iridescent colors; *i*, reflector cell with reflectosomes composed of lamellae and reflective platelets around periphery (Hanlon & Messenger, 1996).

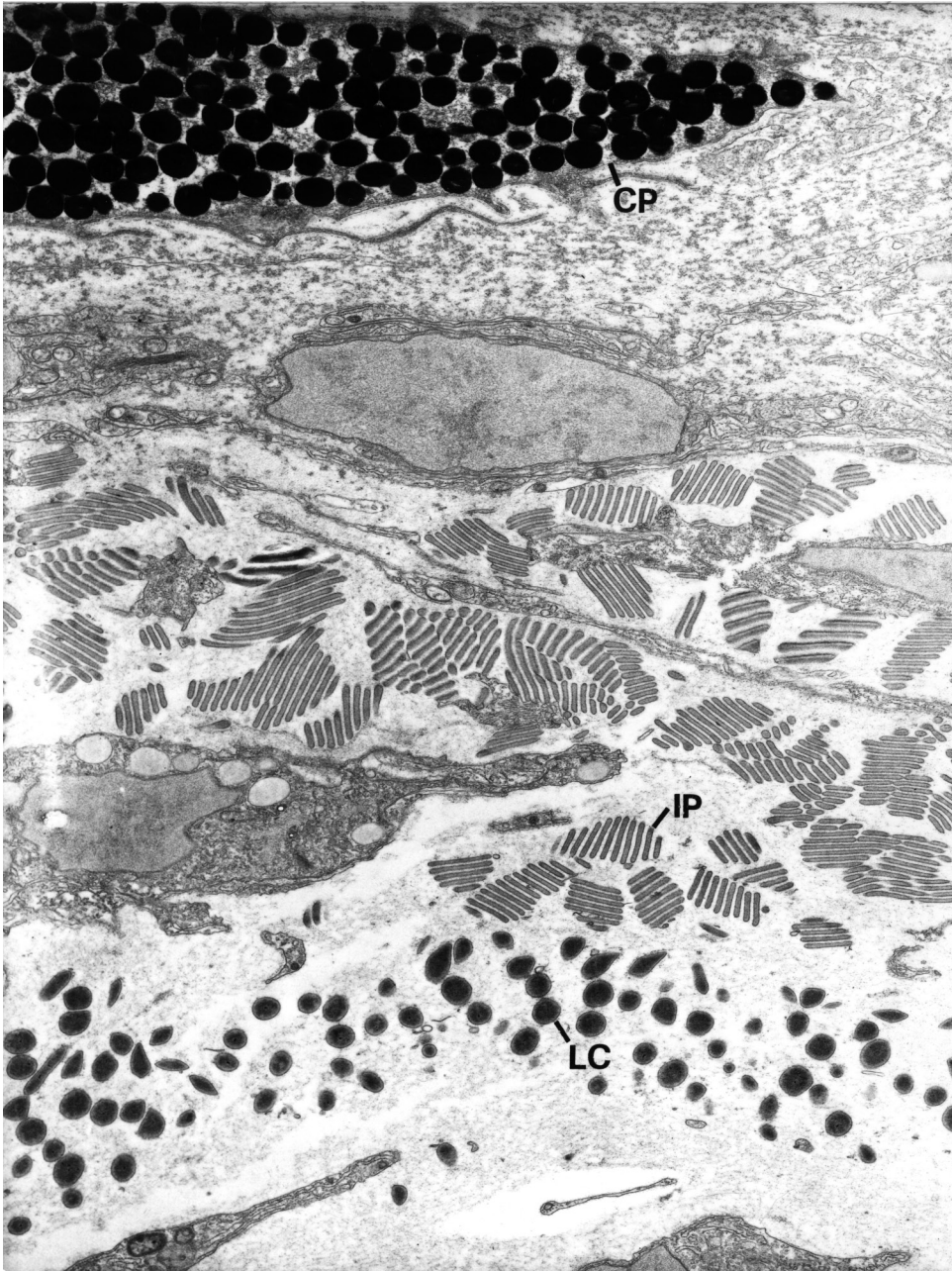


FIG. 22. Electron micrograph of a section through skin of *Octopus*; *CP*, part of a chromatophore, with pigment granules; *IP*, iridophore platelets; *LC*, leucophore clubs; in squids, iridophore platelets are sometimes arranged in long strings, with reflective elements predominantly parallel to skin surface, $\times 6100$ (Froesch & Messenger, 1978).

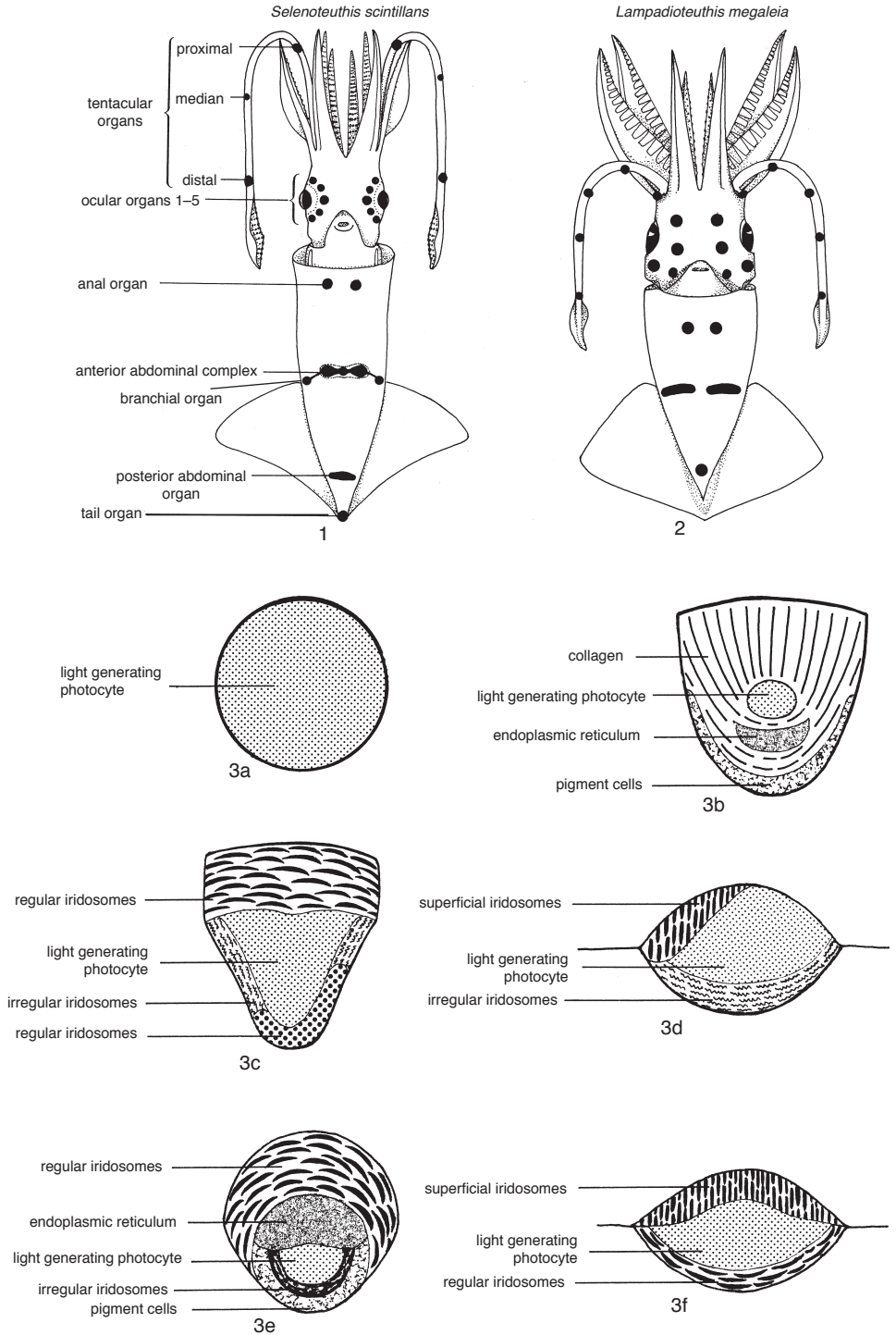


FIG. 23. Distribution of photophores in two species of deepwater squid, 1, *Selenoteuthis* and 2, *Lampadoteuthis*; 3a-f: structure of photophores from *Selenoteuthis*; view 3a is from tail (Herring, Dilly, & Cope, 1985).

as a decoy, while the cephalopod makes good its escape.

As a last resort, the animals can produce threat or startle (deimatic) displays in which they adopt postures that make them appear larger than they really are or patterns that enhance the size of the eyes or produce prominent eyespots on other parts of their anatomy (HANLON & MESSENGER, 1996).

Deepwater coleoids very often have photophores producing light (Fig. 23). The structure and distribution of these often complex organs is highly variable (HERRING, 1988; HERRING, DILLY, & COPE, 1992). Many photophores are on the underside of the animals shining downward. Their purpose appears to be to conceal the silhouette of the animal from predators approaching from below. Experiments with *Abraliopsis* show that the light emitted is accurately matched to the faint ambient light from above (Fig. 24; R. E. YOUNG, 1977; YOUNG, ROPER, & WALTERS, 1979; YOUNG & others, 1980). Other photophores produce brighter lights in a variety of colors and sometimes in flashes. We can only guess at their functions, which probably range from sexual identification and the attraction of mates to startling displays aimed at deterring predators (HANLON & MESSENGER, 1996).

REPRODUCTIVE PHYSIOLOGY

There are no hermaphrodite cephalopods. Differences between the sexes are described in *Treatise Online*, Part M, Chapter 5 (Reproduction and Lifespan, p. 1); males can be larger or smaller, sometimes in pelagic species of octobrachiates being very much smaller than females (*Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, Fig. 1, p. 2). The animals hatch from eggs that vary greatly in size from one species to the next, and the hatchlings may be pelagic or benthic. Sometimes the form of the paralarvae may be very different from that of the adults (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, p. 9).

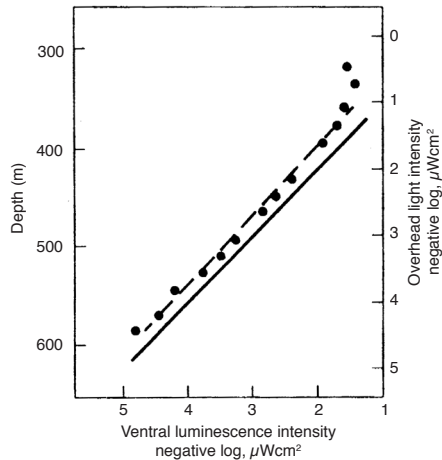


FIG. 24. Intensity of light produced by photophores on undersurface of young *Abraliopsis* (dots) increases as overhead light intensity (line) increases and depth decreases; at about 350 m, light emitted can no longer match the downwelling light (Young & others, 1980).

The sex organs originate as unpaired structures with paired gonoducts in the posterior part of the abdomen. In female octopods and in most female oegopsids, both ducts persist. Elsewhere, only a single duct develops (MANGOLD, 1987). The structure of the male and female sex organs is described in *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 18–19. Females lay eggs enclosed in individual capsules from material secreted by oviducal (octobrachiates) or nidamental (sepiids) glands or enclosed in gelatinous masses secreted by nidamental glands (other Decabrachia). Males package sperm into spermatophores, elaborated in coiled ducts and stored, often hundreds at a time, in Needham's sac (see *Treatise Online*, Part M, Chapter 3, Anatomy of Recent Forms, p. 19). Spermatophores are passed to the females in a variety of ways (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, Fig. 3–4, p. 4); males may court females and fight other males for the privilege of passing spermatophores (HANLON & MESSENGER, 1996).

Both iteroparous and semelparous species exist. *Nautilus* is iteroparous. Eggs of varying

sizes and states of development can be found in the ovaries and ducts of species scattered through all of the orders of coleoids, suggesting that iteroparity is probably the primitive condition (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, p. 8). Some of the best-known species of octopuses and squids spawn only once. Female *Octopus* seek shelter individually and lay and brood their eggs over a period of weeks or months, during which time they feed little or not at all. The emaciated females die soon after the eggs have hatched. Males seek females over a prolonged period, generally maturing earlier than females. In the final weeks of their lives, they too become emaciated and die. Such squids as *Loligo* gather in huge shoals to mate and deposit their egg capsules in common masses that they then abandon, both sexes dying, exhausted, after a reproductive holocaust that can leave the seafloor thick with corpses. These gatherings generally include not only fully grown males and females but also a proportion of small sneaker males, who achieve matings by stealth. It seems likely that the semelparous condition is an adaptation to the same grow fast and die young, high metabolic rate strategy discussed in the introduction to this chapter.

Hormonal control of reproduction has been studied in *Octopus vulgaris*. In this semelparous species, and probably in all other coleoids, sexual maturation is triggered by a secretion of the optic glands, small rounded bodies on the stalks of the optic lobes of the brain, which increase in size with the approach of sexual maturity (Fig. 15). Optic-gland secretion is in turn dependent upon a nerve supply from the brain, which appears to be inhibitory, since section of the nerves to the glands causes them to secrete (WELLS & WELLS, 1959). The hormone released simultaneously causes maturation of the gonad and breakdown of tissues elsewhere, notably muscle tissue (O'DOR & WELLS, 1978).

In the laboratory, sexual maturity can also be accelerated by blinding, which suggests

that day length might play an important role in determining the season of sexual maturity in the wild (WELLS & WELLS, 1959). Subsequent results with different species of *Octopus*, *Eledone*, *Sepia*, and *Illex* kept in the laboratory have indicated that the relationship to day length is by no means simple, and that such other factors as temperature and the availability of prey may be important. The matter has been reviewed by MANGOLD (1987).

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