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PART M, CHAPTER 3: ANATOMY OF RECENT FORMS

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INTRODUCTION

The anatomy of *Octopus vulgaris* (CUVIER, 1817) and that of at least one species from each order of the Coleoidea has been described, but these accounts differ widely, both in scope and detail (Table 1) (MANGOLD, BIDDER, & PORTMANN, 1989a). The main features of *Sepia officinalis* (Decapodiformes, Sepiida), are shown later (see Fig. 5). The microscopic anatomy of many organs, structures, and tissues was given by BUDELMANN, SCHIPP, and VON BOLETZKY (1997), and this review also includes a survey of the external and gross anatomy of cephalopods.

FORM, ORIENTATION, AND SIZE RANGE

Recent coleoids differ widely in shape and form, as a glance through the illustrations of CHUN (1910a, 1915); ROPER, YOUNG, and VOSS (1969); NESIS (1982); and ROPER, SWEENEY, and NAUEN (1984) indicates. They range from elongated, streamlined squids to somewhat rounded octopods, with many variations in between (Fig. 1–2).

It is often difficult to determine the orientation of coleoids. HOYLE (1886) used the position of the body adopted by squids when swimming horizontally to define the head as anterior and the apex of the visceral mass as posterior, with the funnel being ventral (Fig. 3.1). This terminology remains in general use for describing living cephalopods and for morphometric studies (ROBSON, 1929; MANGOLD-WIRZ, 1963; ROPER & VOSS, 1983; ROPER, SWEENEY, & NAUEN, 1984; SWEENEY & others, 1992).

The size of living coleoids is generally expressed as the mantle length. Occasionally, the length of the gladius or the cuttlebone is used for teuthids and sepiids respectively. The mantle extends from the anteriormost point of the mantle to its posterior apex

or to the tip of the fins if they are united, whichever is the longest (ROPER & VOSS, 1983) (Fig. 3). The measurement is made on the dorsal surface: in Decapodiformes, from the dorsal surface; in Decapodiformes, from the posterior apex of the mantle to its anterior edge, and in Octopodiformes, anteriorly to the midpoint of the horizontal diameter of the eye (Fig. 3.4). The general use of mantle length is due to the difficulty of measuring these soft-bodied animals, and the lengths of the head, arms, and tentacles are often omitted. In many species, these structures form a major portion of the length of the whole animal; furthermore, changes may take place during ontogeny in the relationship between the lengths of different parts of the animal. Thus, in addition to the mantle length, the total length, head length, arm lengths, and tentacle lengths should be measured, and the animal should be weighed.

Recent coleoids range from about 20 mm to 2 m or more in mantle length, and from some 0.5 gm in the small sepiolid *Idiosepius* (JACKSON, 1989) to 1,000–2,000 kg in the giant squid *Architeuthis* (ROPER & BOSS, 1982). Records of the latter are understandably inaccurate, as complete animals are rare, and its large size and rather soft tissues make it difficult to measure. The sizes of the remaining coleoids lie between these two extremes.

MANTLE, FUNNEL, AND FINS

The shape and form of the mantle of coleoids results largely from the presence of an internal support in the mantle, although this is absent from some. The support takes the form of an internal, chambered shell in Spirulida; a cuttlebone or sepiion in Sepiida; a shell, gladius, or pen in squids; a dorsal cartilage termed an internal shell, shell vestige, or fin support in Vampyromorpha and Cirrata; and a pair of stylets in some Octopoda

TABLE 1. Sources for descriptions of morphology and/or anatomy of several Recent coleoids.

Order	Family and species	Source
Spirulida	Spirulidae <i>Spirula spirula</i>	Owen, 1848; Huxley & Pelseneer, 1895; Chun, 1910b, 1915; Kerr, 1931
Sepiida	Sepiidae <i>Sepia officinalis</i>	Tompsett, 1939
Sepiolida	Sepiolidae <i>Sepiola robusta</i>	Fioroni, 1981
Myopsida	Loliginidae <i>Loligo pealei</i>	Williams, 1909
Oegopsida	Histioteuthidae Ommastrephidae <i>Todarodes sagittatus</i>	Chun, 1910a, 1915 Posselt, 1891
	Cranchiidae	Chun, 1910a, 1915
Vampyromorpha	Vampyroteuthidae <i>Vampyromorpha infernalis</i>	Pickford, 1949a; Young, 1964
Cirrata	Cirroreuthidae <i>Cirroreuthis umbellata</i> <i>Cirrothauma murrayi</i>	Ebersbach, 1915 Aldred, Nixon, & Young, 1983
	Stauroteuthidae <i>Stauroteuthis</i> sp.	Ebersbach, 1915
	Opisthoteuthidae <i>Opisthoteuthis depressa</i>	Meyer, 1906a, 1906b
Incirrata	Bolitaenidae <i>Bolitaena</i> <i>Eledonella</i>	Chun, 1910a, 1915 Chun, 1910a, 1915
	Octopodidae <i>Octopus vulgaris</i> <i>Eledone cirrhosa</i>	Cuvier, 1817; Wells, 1978 Isgrove, 1909

(Fig. 6–7). These structures are calcareous (aragonite or calcite) or composed of chitin, cartilage, or a combination of both organic and inorganic materials (APPELLÖF, 1893; GRÉGOIRE, 1972; THOMAS & BINGHAM, 1972; HUNT & NIXON, 1981; BIRCHALL

& THOMAS, 1983). They provide sites for the attachment of muscles (Fig. 6) (WELLS, 1988; MANGOLD, BIDDER, & PORTMANN, 1989a). In coleoids, muscles take on the role of support in structures that are largely devoid of hard tissues (KIER, 1988).

The mantle may be conical, spherical, or saclike; in cross section, it ranges from round to dorsoventrally flattened. Some members of the Sepiolidae, Sepiadariidae, Idiosepiidae, and all Octopoda have the ventral part of the visceral mass connected by a longitudinal, muscular septum to the inner surface of the ventral mantle wall. In Vampyromorpha and Octopodiformes, the mantle is fused with the head but not with the funnel. The mantle is muscular and encloses the viscera, which includes the respiratory, digestive, excretory, and reproductive organs. The inner wall of the mantle is continuous with the outer wall of the visceral sac, and the space between these two walls forms the mantle cavity. This lies ventrally and protects the paired gills and the openings of the digestive, excretory, and reproductive systems. The anterior edge of the mantle is free ventrally, and so it forms the mantle aperture, the entrance to the mantle cavity. The mantle opening is divided into three parts by the head dorsally and by the locking cartilages laterally. A cartilaginous ridge, knob, or swelling on each side of the mantle locks into the funnel component of the mantle-locking device (Fig. 4.2) (ROPER, YOUNG, & VOSS, 1969). The funnel-locking cartilage takes the form of a groove, pit, pocket, or depression on each ventrolateral surface of the posterior part of the funnel (Fig. 4–5). Together these structures ensure that all exhalant water is expelled through the funnel. The pelagic octopod *Ocythoe tuberculata* is different in that the mantle aperture is converted to form accessory funnels, so that the propulsive system consists of three jets instead of the usual one, giving improved thrust (PACKARD & WURTZ, 1994). The other locking mechanism, the nuchal cartilage, is a cartilaginous plate on the posterodorsal surface of the

head that articulates with a complementary structure on the mantle but is absent from some coleoids.

The funnel, or hyponome, is a conical tube (Fig. 4–7), wide posteriorly but narrow anteriorly. In cuttlefishes and squids, the funnel lies in a depression on the ventral side of the head and is free over most of its length, but in octopods, it may be partly or largely sunk in the tissue of the head. A rectangular or triangular funnel valve lies inside the funnel of cuttlefishes, most squids, and in Vampyromorpha, but it is absent from octopods and from some slowly moving squids (NESIS, 1982).

Fins are present in all Recent coleoids except the Octopoda (MANGOLD & BIDDER, 1989). They may be attached along part or all of the length of the mantle (Fig. 1). The fins range widely in shape and may be marginal, fringing, ribbed, or rayed and rhomboid, heart shaped, rounded, kidney-shaped, or tonguelike (Fig. 1–2). In *Vampyroteuthis* (Vampyromorpha), two pairs of fins develop; the first pair are present in the paralarva and are resorbed after the juvenile pair develops (PICKFORD, 1949a). The shape of the fins of many coleoids changes during ontogeny, often quite markedly (see *Treatise Online*, Part M, Chapter 5, Fig. 11, 12, 14) (SWEENEY & others, 1992).

HEAD, EYES, AND OLFACTORY ORGANS

The head is usually well defined in Decapodiformes but less so in Vampyromorpha and many Octopodiformes, in which there is often little external indication of division from the body (Fig. 1–2). It may be narrower, equal to, or wider than the diameter of the mantle. The shape of the head is determined mainly by the buccal mass, the cranial cartilage, when present, and the eyes, which together form the major portion of the head, especially at hatching and in the early juvenile.

The eyes are conspicuous and are usually sited laterally. In sepiids, sepiolids, and one group of squids (the myopsids), the

eyes are covered by a very thin, transparent skin. The oegopsid squids have eyes that are open to sea water (Fig. 4.1). Vision is important for the coleoids inhabiting the photic zone and also for those living in depths where they encounter bioluminescent organisms. The eyes of coleoids comprise all the major components of a complex vertebrate eye (BUDELMANN, SCHIPP, & VON BOLETZKY, 1997). A lens is present, although absent from the cirrate octopod *Cirrothauma murrayi* (ALDRED, NIXON, & YOUNG, 1983). It is a spherical, relatively firm structure that may possess growth lines; it is formed of α -, β -, γ -, and δ -crystallin (BON, DOHRN, & BATINK, 1967; NIXON, 1998a). The lens is suspended by ciliary muscles that allow some accommodation for near vision. Decapodiformes have additional eye muscles that are involved in convergent eye movement for binocular vision (BUDELMANN & YOUNG, 1993). In most coleoids, the eyes are nearly spherical, although in a few species they are tubular (CHUN, 1910a, 1915; J. Z. YOUNG, 1991a; LAND, 1992). An orbital cartilage, which supports the eye, is present in many coleoids. In one genus of oegopsid squid, *Histioteuthis*, the left eye is considerably larger than the right and the absorption properties differ (WENTWORTH & MUNTZ, 1989). The giant squid, *Architeuthis*, possesses the largest eyes found in the animal kingdom, each with a diameter of 25 cm in an animal 10 m in total length (ROPER & BOSS, 1982). Proportionally, the eye of *Vampyroteuthis* is larger, and one specimen with a mantle length of 63 mm had an eye with a diameter of 25 mm (PICKFORD, 1949a). The eyes of paralarvae are often larger in relation to the mantle length than in the adult (SWEENEY & others, 1992). Several species have eyes borne at the end of stalks, notably among Cranchiidae (J. Z. YOUNG, 1970; N. A. VOSS, 1980; SWEENEY & others, 1992), but with growth, they become incorporated into the head. The relationship between eye diameter and mantle length often changes during ontogeny (DILLY & NIXON, 1976a). Numerous species have

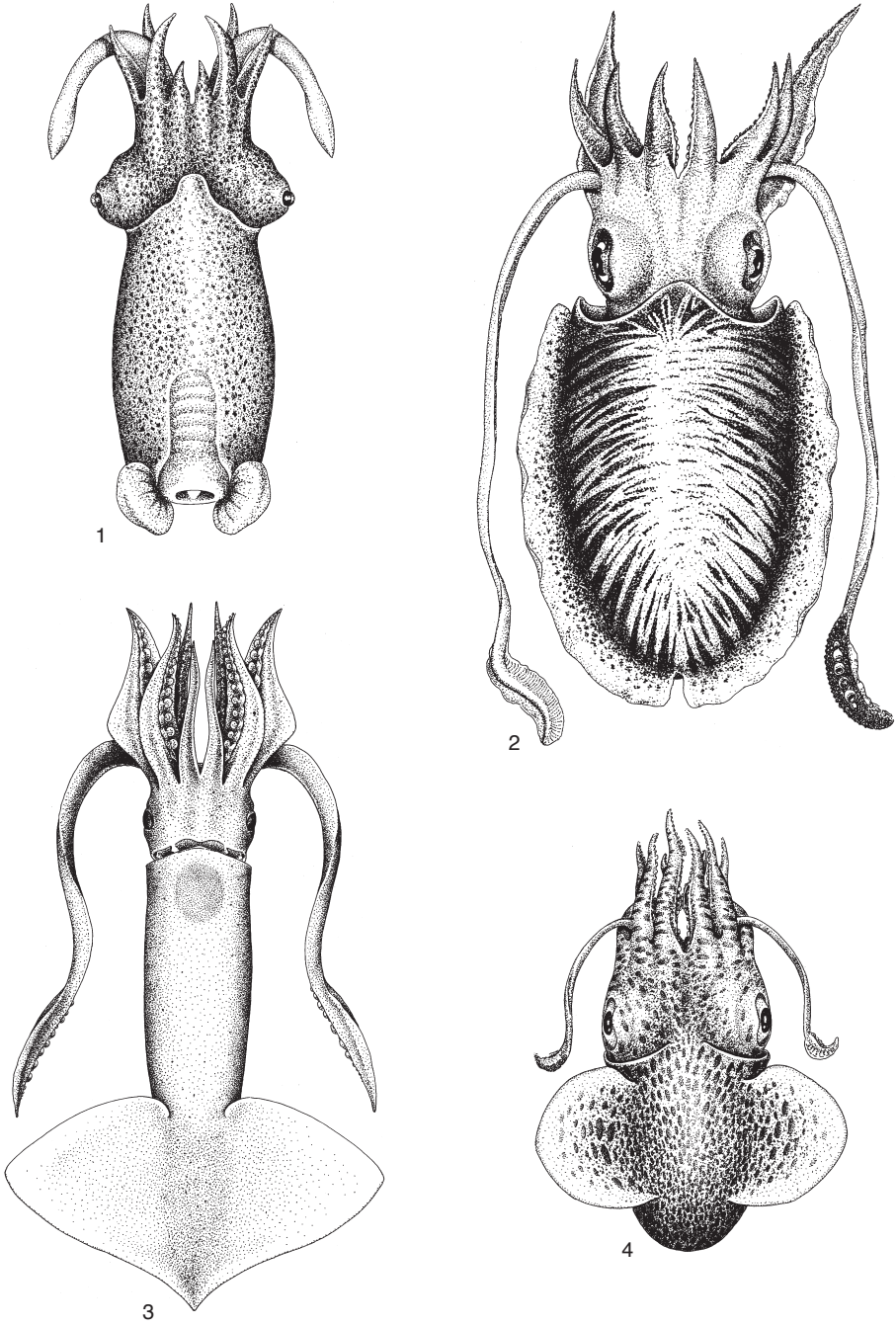


FIG. 1. Recent Coleoidea. 1, *Spirula spirula*, Spirulida; 2, *Sepia officinalis*, Sepiida; 3, *Sthenoteuthis pteropus*, Oegopsida; 4, *Sepioloatlantica*, Sepiolida (Guerra, 1992).

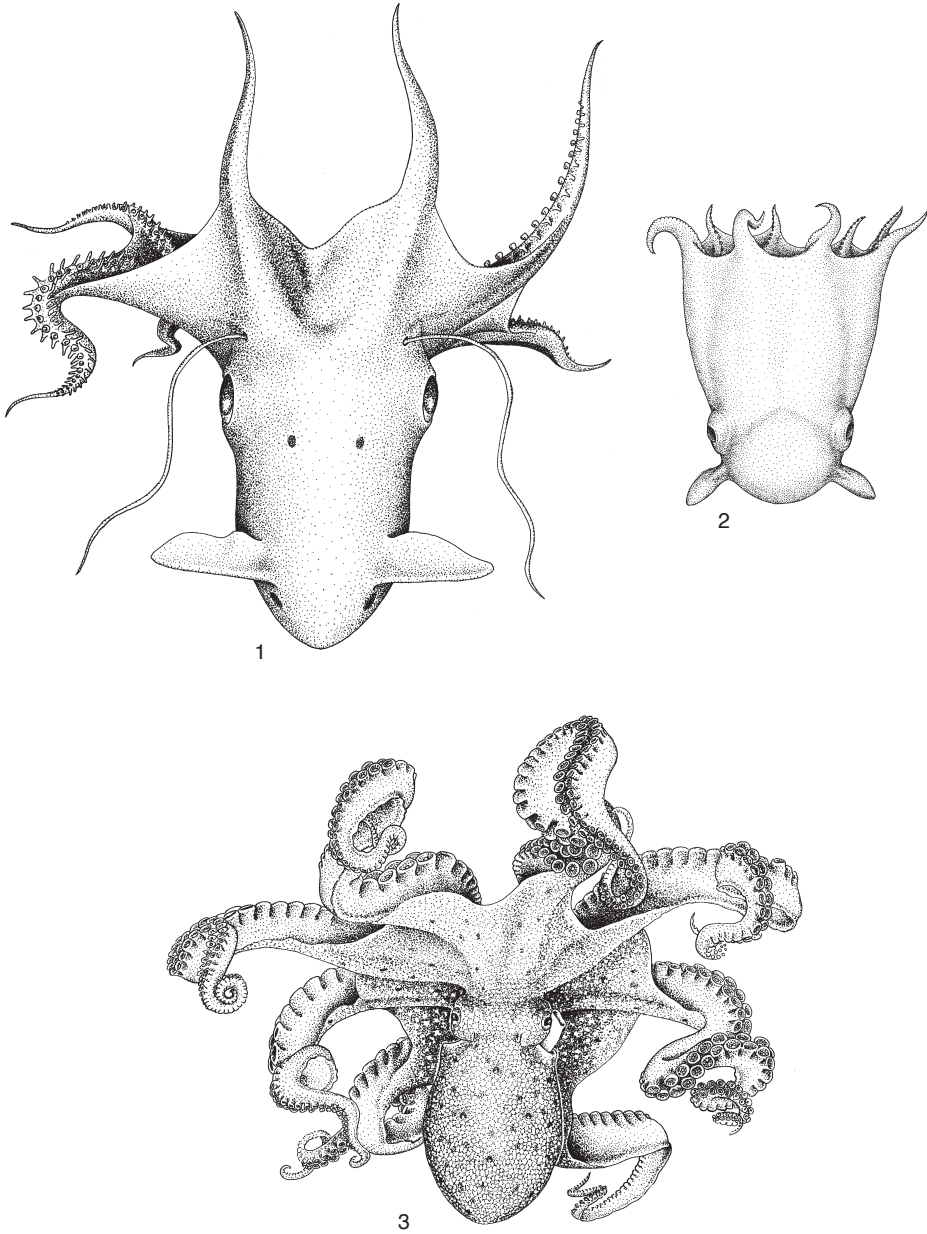


FIG. 2. Recent Coleoidea. 1, *Vampyroteuthis infernalis*, Vampyromorpha; 2, *Opisthoteuthis agassizii*, Cirrata; 3, *Octopus vulgaris*, Incirrata (Guerra, 1992).

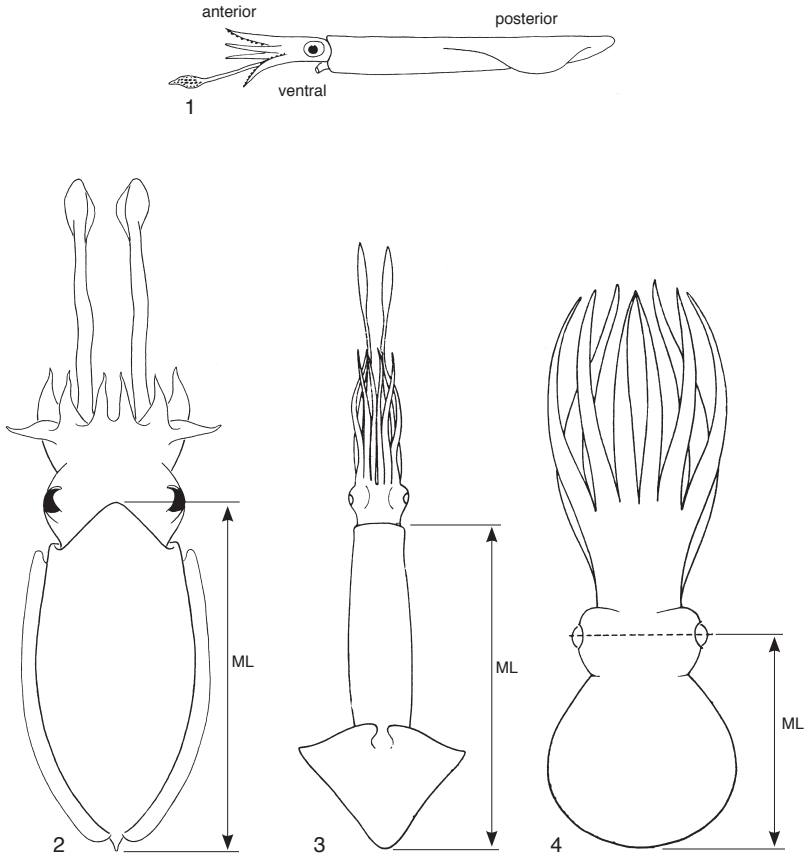


FIG. 3. Orientation of coleoid body for descriptive purposes is that adopted by a muscular squid when swimming horizontally (1); the size of Recent coleoids is usually given as mantle length (ML), but anteriormost point between which this is measured differs between 2,3, Decapodiformes and 4, Octopodiformes; in *Octobranchia*, it is taken as a line from center of eyes (Mangold-Wirz, 1963; Roper & Voss, 1983).

photophores or light organs associated with their eyes (HERRING, 1977).

The head bears a pair of olfactory organs, which usually lie behind the eyes (NAEF, 1923). These are small pits with cilia lining their walls (WOODHAMS & MESSENGER, 1974).

ARMS AND TENTACLES: SUCKERS, HOOKS, AND CIRRI

A fossil coleoid, *Jeletzkyia douglassae*, found in the shale of Mazon Creek (Upper Carboniferous) has clear imprints of ten arms (SAUNDERS & RICHARDSON, 1979). The Lower Jurassic coleoids *Phragmoteuthis conocauda* (RIEGRAF, WERNER, & LÖRCHER, 1984) and *Ostenoteuthis siroi* (GARASSINO

& DONOVAN, 2000) also possess ten arms. Among Recent coleoids, ten appendages are present in Decapodiformes: four pairs of arms and a pair of tentacles, the latter lying between the third and fourth pair of arms. *Vampyroteuthis* has a pair of slender filaments that lie between the first and second pair of arms (Fig. 1–2). Recent Octopodiformes have just four pair of arms.

The arms of Recent coleoids are elongated and taper distally, and their bases surround the mouth. The most dorsal pair are arms I, the dorsolateral pair arms II, the ventrolateral pair arms III, and the ventral pair arms IV (Fig. 4.1); the arms are further designated as right or left (ROBSON,

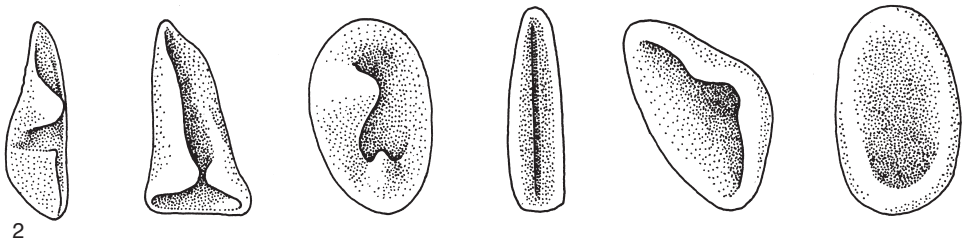
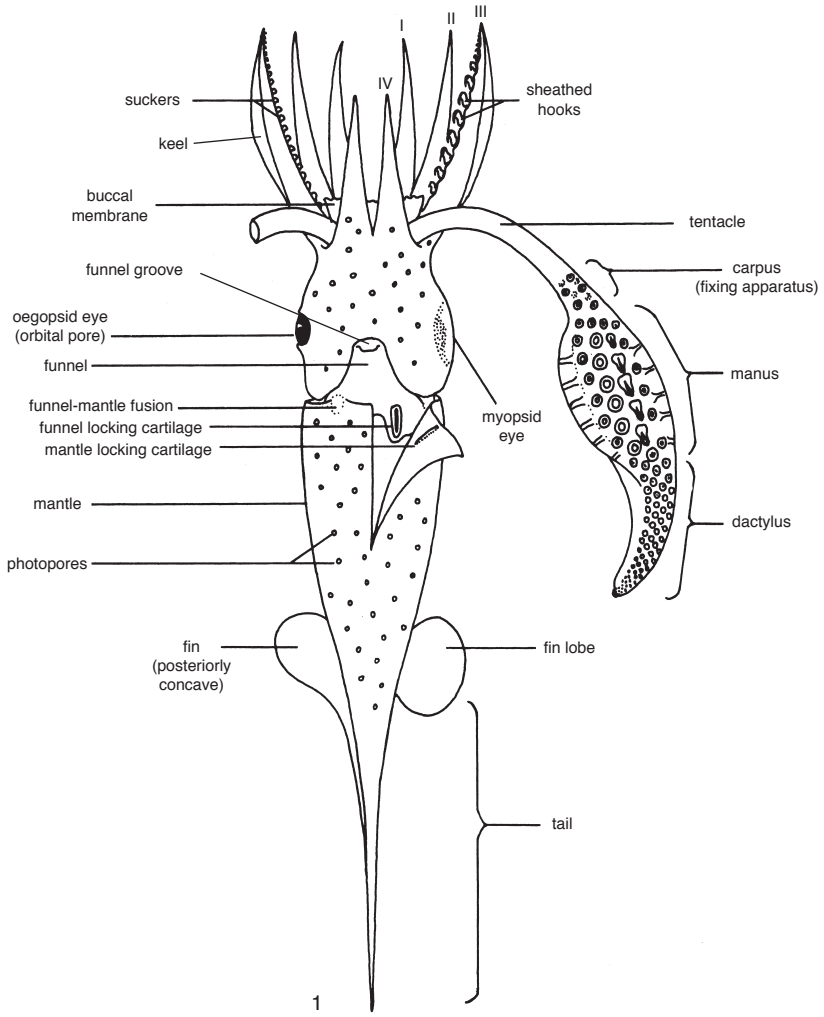


FIG. 4. Composite diagram showing characteristic features of *I*, extant myopsid and oegopsid squids; arm I is dorsal and arm IV is ventral (ventral view) (Roper, Young, & Voss, 1969); and 2, basic types of funnel-locking cartilage (Roper, Sweeney, & Nauen, 1984).

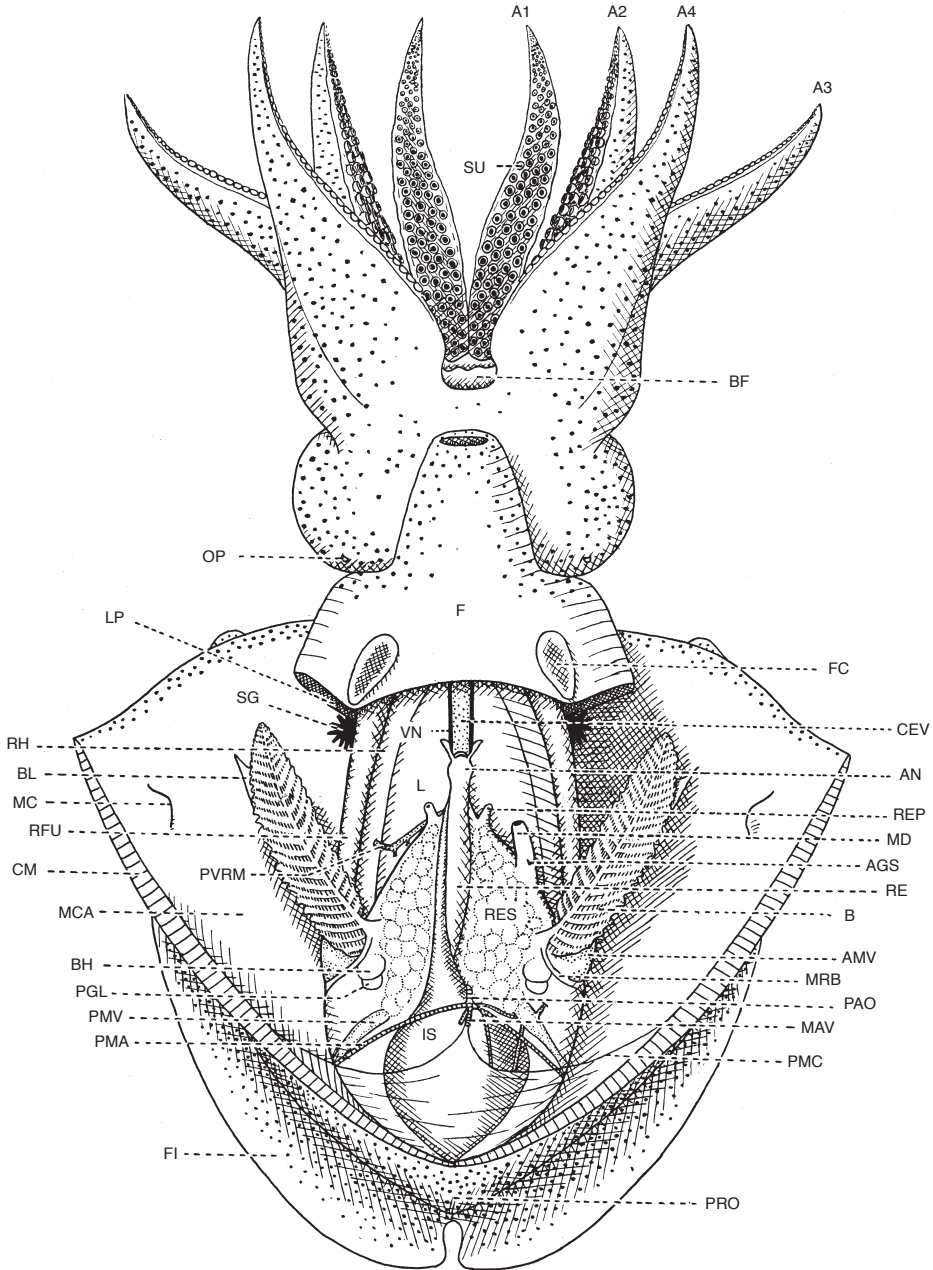


FIG. 5. Main internal features of *Sepia officinalis*, seen from ventral surface. A1–A4, arms I–IV; AGS, opening of genital sac into mantle cavity; AMV, anterior mantle vein; AN, anus; B, branchia; BF, buccal funnel; BH, branchial heart; BL, branchial membrane and ligament; CEV, cephalic vein; CM, cut wall of mantle; F, funnel; FC, funnel cartilage; FI, fin; IS, ink sac; L, digestive gland; LP, lateral pocket or valve funnel; MAV, median mantle artery and vein; MC, mantle cartilage; MCA, mantle cavity; MD, male genital duct; MRB, marginal part of retractor muscle of branchia; OP, olfactory pit; PAO, posterior aorta; PGL, pericardial gland; PMA, posterior mantle artery; PMC, posterior elastic boundary of mantle cavity; PMV, posterior mantle vein; PRO, position of rostrum of shell; PVRM, posterior vein to retractor muscles of head and funnel; RE, rectum; REP, renal papilla; RES, renal sac; RFU, retractor muscle of funnel; RH, retractor muscle of head; SG, stellate ganglion; SU, sucker; VN, visceral nerve (Tompsett, 1939).

1929; ROPER, YOUNG, & VOSS, 1969). The lengths of the arms usually differ and can be expressed in a formula, each pair being given in order of decreasing length; for example IV>III>II>I, where arms IV are the longest. Modification of one or two arms or a pair of arms of the male results in a hectocotylus in many species. The hectocotylus is involved in the transportation of spermatophores to the female. It is absent in some species. The spirulid, *Spirula spirula*, has a most distinctive hectocotylus, as both arms IV are modified, and their distal tips are morphologically quite different (KERR, 1931). Histoteuthid squids have both arms I hectocotylized, and the sepiolid *Heteroteuthis dispar* has both arms III hectocotylized, but in most only one arm is so modified (MANGOLD, 1989b).

The newly hatched young of numerous species of coleoids have small, short arms, often barely visible, especially in planktonic forms. Other species have relatively long, well-developed arms, and this is usually found among those that adopt benthic habits immediately after hatching (see *Treatise Online*, Part M, Chapter 5, Fig. 8) (SWEENEY & others, 1992). The relationship between the lengths of the arms and the mantle changes considerably during ontogeny in many species. In cross section, the arms may be almost square, triangular, or nearly round; but the inner, sucker-bearing surface is usually somewhat flattened. A keel or swimming membrane, represented by a ridge or a triangular protuberance on the outer, aboral side of the arm, is found in many squids. The oral side of the arm may be bordered laterally by thin, protective membranes, and this fold of integument is supported by muscular rods or trabeculae (SWEENEY & others, 1992).

The paired tentacles of Decapodiformes lie between arms III and IV. Each tentacle consists of a long stalk with a club at the distal end, bearing longitudinal rows of suckers (or hooks in some species) on the oral surface (Fig. 4.1) (ROPER, YOUNG, & VOSS, 1969). When the club is wide, it may have a keel and protective membranes. The

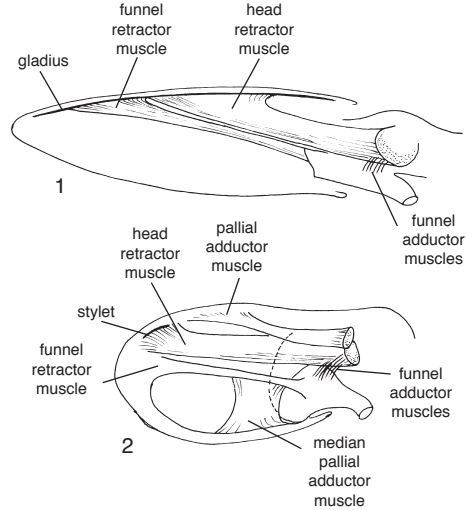
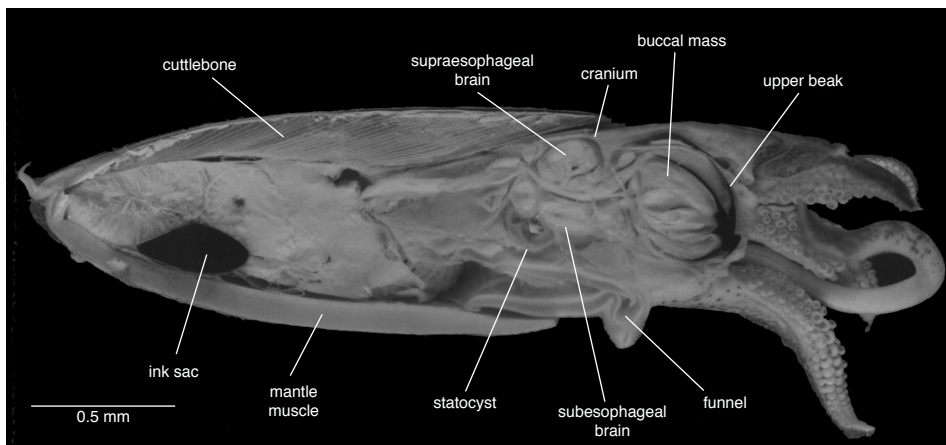


FIG. 6. Major muscles of mantle of 1, *Loligo*, with gladius, and 2, *Octopus* with stylet, or shell vestige (new).

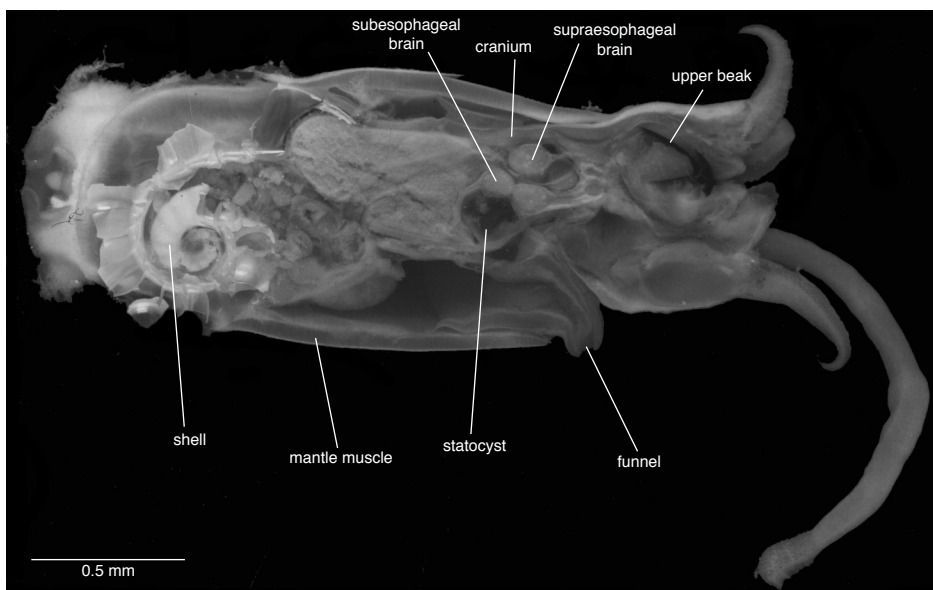
tentacles are retractile or partially retractile into pockets or sheaths on the head. In the so-called eight-armed squids [(*Gonatopsis* (Gonatidae), *Chaunoteuthis* (Onychoteuthidae), *Lepidoteuthis* (Lepidoteuthidae), and *Octopoteuthidae*)], the tentacles are resorbed or remain as rudimentary stumps. The tentacles of *Chaunoteuthis mollis* are reduced to short stumps, 1 to 2 cm long, when the mantle reaches about 40 cm in length (OKUTANI & IDA, 1986), and in *Octopoteuthidae*, only rudiments remain when the mantle is 4 to 4.5 cm long (NESIS, 1982).

Vampyroteuthis infernalis (Vampyromorpha) possesses a pair of long, slim filaments entirely without armature that lie between arms I and II. Each filament is mobile and extensile for a considerable distance (PICKFORD, 1949a) and is retractile into a pocket on the aboral surface of the web (Fig. 2).

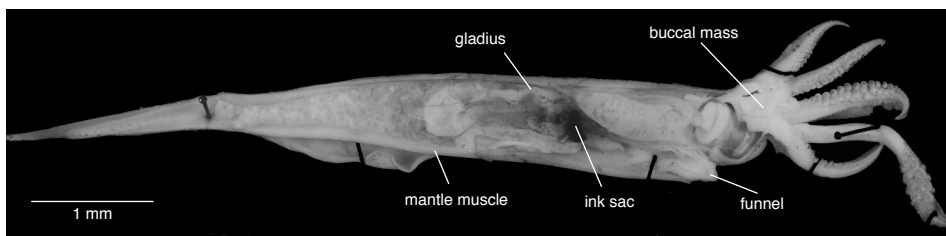
The suckers are a distinctive feature of all living Coleoidea (GIROD, 1884; NIXON & DILLY, 1977) and are unique derivatives of the skin (PACKARD, 1988). They are usually arranged along the arms in one, two, or four longitudinal rows, rarely more. The suckers range from being numerous and closely arranged to few and well separated. In



1



2



3

FIG. 7. Recent Decapodiformes. 1, Hemisection of *Sepia officinalis* (Sepiida), juvenile specimen, showing cuttlebone and other main features; 2, hemisection of *Spirula spirula* (Spirulida); 3, hemisection of *Alloseuthis subulata* (Myopsida) (new).

Decapodiformes, the sucker has a chamber or acetabulum with a wall lined with a stiff chitinous inner ring, which may bear teeth around its outer perimeter (Fig. 8.1). The inner ring is surrounded by the infundibulum, a cuticular covering bearing polygonal processes, each with a projecting peg. The suckers of Octopodiformes lack a cuticular inner ring, and the pegs of the infundibulum are much less conspicuous than those of the Decapodiformes (Fig. 8.2). The arrangement of the suckers has been preserved in some fossil coleoids. The arms of *Rhomboteuthis lehmani* had two longitudinal rows of suckers, and the tentacular club of *Gramadella pive-teaui* had five rows of suckers (FISCHER & RIOU, 1982). The suckers of the fossil coleoid *Belemnoteuthis antiquus* may have had chitinous rings (DONOVAN & CRANE, 1992). During embryonic development of Recent coleoids, the suckers appear first as protuberances of the skin (FIORONI, 1982a; NOLTE & FIORONI, 1983). With growth, changes may be seen in the infundibulum and the inner ring of suckers, and there is usually an increasing complexity of this surface (DILLY & NIXON, 1976a).

Hooks have been found isolated but associated with the remains of belemnites (ENGESER & CLARKE, 1988). The Lower Jurassic *Paraglycerites*, perhaps the oldest belemnite, possessed hooks, as do the coleoids *Phragmoteuthis conocauda* (RIEGRAF, 1996) and *Ostenoteuthis siroi* (GARASSINO & DONOVAN, 2000). The last two species both have ten arms, all bearing hooks.

The tentacles of Recent Decapodiformes have clubs that bear suckers, and sometimes hooks; their number and arrangement varies (ROPER, YOUNG, & VOSS, 1969). Hooks are present on the tentacles or arms of Onychoteuthidae (Fig. 9), Enoploteuthidae, Octopoteuthidae, Gonatidae, and Cranchiidae; and the armature may be present in all or only some species of these families. Onychoteuthids have 12 to 38 hooks in two longitudinal rows on the tentacle club, those of the most dorsal row being much longer than those in the other row; the

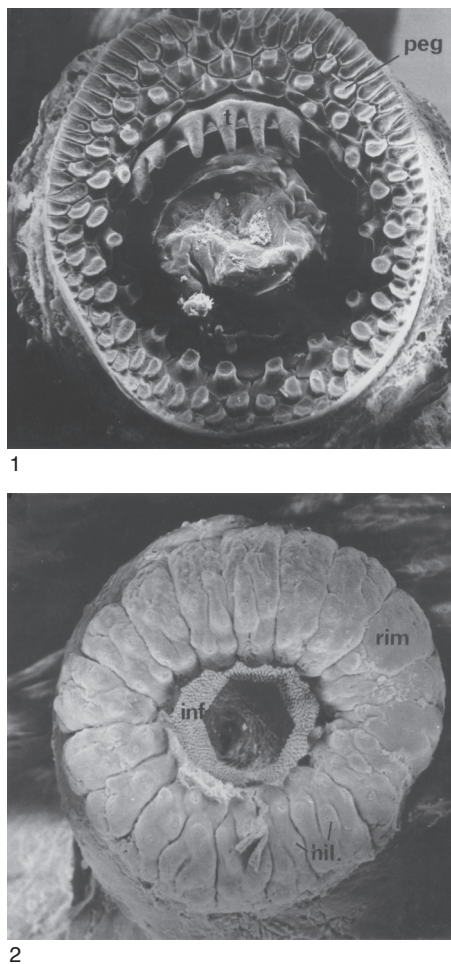


FIG. 8. Scanning electron micrographs of arm suckers of 1, *Mastigoteuthis* sp. (Oegopsida), showing dentition of chitinous inner ring and infundibulum with polygonal processes, the majority of which have a peg projecting from the surface (field width, 1203 μm); 2, small *Octopus vulgaris* (Incirrata) showing rim encircling infundibulum, the surface of which is covered with small pegs (field width, 500 μm); *hil*, hillock; *inf*, infundibulum; *peg*, projecting peg of polygonal process; *rim*, encircles infundibulum (Nixon & Dilly, 1977).

arrangement is similar in all species of this family. Enoploteuthidae have hooks on the arms and tentacles, except in one species in which they are absent from the tentacles. Gonatidae have a few large, central hooks on the tentacular club and two medial rows of hooks on arms I to III. The hooks develop by modification of the inner ring in *Gonatus*

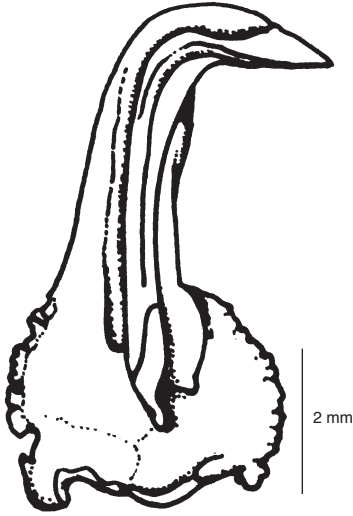


FIG. 9. Largest ventral tentacular hook of onychoteuthid squid *Moroteuthis knipovitchi* (Clarke, 1980).

(KRISTENSEN, 1977). Octopoteuthidae have biserial hooks along the arms, and some Cranchiidae have hooks on their tentacles (N. A. VOSS, 1980; NESIS, 1982). The shape, form, development, and mode of attachment of hooks in Recent and fossil coleoids were described by ENGESER and CLARKE (1988).

Cirri are a characteristic feature of Cirrata and Vampyromorpha. They are slender, tapered, and arranged in pairs along the arms, alternating with the suckers. *Cirrothauma murrayi* has long cirri, and they are especially elongated in young animals (Fig. 10) (ALDRED, NIXON, & YOUNG, 1983). In the deep sea, these coleoids hold the cirri erect and away from the arms (ROPER & BRUNDAGE, 1972; P. J. HERRING, personal communication, 1979).

THE SKIN: DERMAL STRUCTURES, CHROMATOPHORES, LEUCOPHORES, IRIDOCYTES, AND PHOTOCYTES

The skin is a barrier, as well as an interface at which selective exchange can take place between the animal and the external environment. In addition, it has developed into

an organ for concealment and behavioral expression (PACKARD, 1988). Epithelial, glandular, and sensory cells are present in the skin, as well as various specialized dermal tissues and structures, including papillae, Kölliker's tufts, adhesive pads, dermal cushions, tubercles, chromatophores, iridophores, and photophores, and suckers, hooks, and cirri (MANGOLD, BIDDER, & PORTMANN, 1989b; BUDELMANN, SCHIPP, & VON BOLETZKY, 1997).

Papillae are often temporary and mostly serve for concealment. They are raised by the actions of muscles lying below the skin. Kölliker's organs, tuft- or bristle-like structures about 50 μm in height, are present in hatchlings of Incirrata. They are transitory and small and not readily seen unless greatly magnified (VON BOLETZKY, 1973; BUDELMANN, SCHIPP, & VON BOLETZKY, 1997).

An unusual adhesive pad is present on the posterodorsal region of the mantle of the smallest coleoid, *Idiosepius pygmaeus*, enabling it to attach itself to algal fronds in the coastal waters (SASAKI, 1923). The small sepiolid *Euprymna scolopes* has an area of specialized epithelial cells on the dorsal surface of the mantle to which small particles adhere, providing the animal with camouflage (SINGLEY, 1982).

Dermal cushions are a characteristic feature of the skin of the scaled squids *Lepidoteuthis grimaldi* and *Pholidoteuthis adami*. In the former, they are diamond shaped and overlap rather like roof tiles, but in the latter they do not overlap (CLARKE & MAUL, 1962; ROPER & LU, 1990). Tubercles occur on the mantle of many Cranchiidae; in *Cranchia scabra*, they are cartilaginous and develop from a simple nodule into a complex Maltese-cross form (Fig. 11) (PERSON, 1969; DILLY & NIXON, 1976b). Tubercles of cartilage, elastic cartilage, or fibrocartilage are found in other families; their shapes range from simple cones to complex forms (ROPER & LU, 1990).

A vertical section through the skin shows that the chromatophores are superficial, with tiny iridophores and leucophores below, the last being deepest of all (PACKARD, 1988).

Each chromatophore is a thin, cytoelastic sac containing granules of pigment, with muscles radiating around the periphery of the sac. When the muscles contract, the sac expands so the pigment spreads and becomes conspicuous (FLOREY, 1969). Relaxation of the muscles results in contraction of the sac. Chromatophores range from about 0.3 mm to 1.5 mm in diameter (HANLON & MESSENGER, 1996). The contained pigments are ommochromes (LINZEN, 1967) with traces of calcium, nickel, and sulphur (FROESCH & PACKARD, 1979). Chromatophores are present in all coleoids but one, although those of *Vampyroteuthis* lack muscles (J. Z. YOUNG, 1977). The exception is *Cirrothauma murrayi*, in which there is pigment in the skin but no chromatophores (ALDRED, NIXON, & YOUNG, 1983). Iridophores comprise multilayered stacks of thin plates or iridosomes separated by cytoplasm (MIROW, 1972); the platelets are 75 nm thick (FROESCH & MESSENGER, 1979). In *Octopus* and *Sepia*, leucophores are branched structures with many ovoid, stalked clubs over their surface (FROESCH & MESSENGER, 1979).

Light organs or photophores occur sporadically, and one or more genera possessing them are found in most orders of the Coleoidea. The greatest development of photophores is among the oceanic oegopsid squids (HERRING, 1977, 1988; R. E. YOUNG, 1983; R. E. YOUNG & BENNETT, 1988). Photophores can be discrete or take the form of minute photogenic spots that may be organized into strips or bands or may be scattered. Photophores display great variety in their structure, from simple to morphologically and optically complex, and one or more types of photophore can occur in the same animal.

CENTRAL NERVOUS SYSTEM AND MAJOR RECEPTORS

The nervous system of Coleoidea, formed from a system of nerve cords, has become centralized and consists of a mass of tissue closely surrounding the esophagus

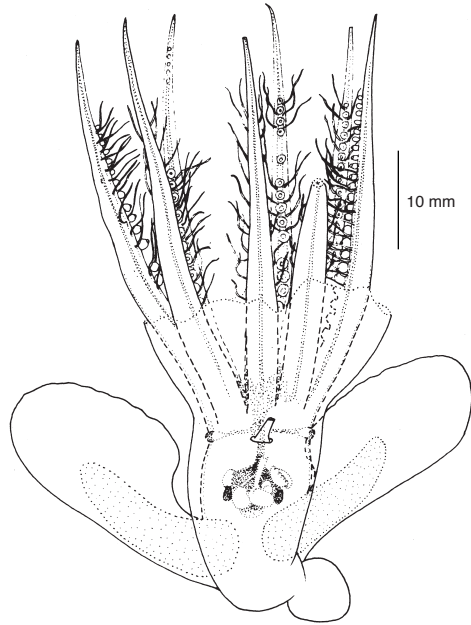


FIG. 10. Young specimen of *Cirrothauma murrayi*, Cirrata, showing long cirri arranged on either side of suckers on arms (Aldred, Nixon, & Young, 1983).

(BOYCOTT, 1961; J. Z. YOUNG, 1971; MANGOLD, 1989a). The brain of numerous Coleoidea and *Nautilus* has been described (NIXON & YOUNG, 2003). It is protected by a cranium of cartilage in most coleoids (Nixon, 1998a) (see Fig. 25) but not

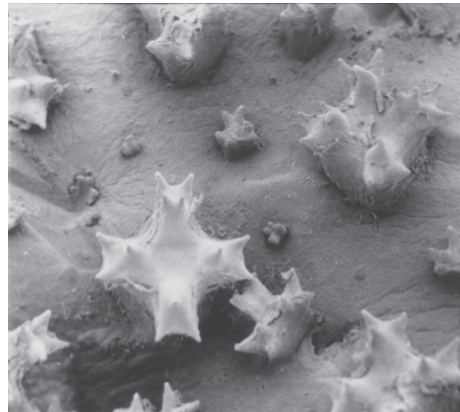


FIG. 11. Scanning electron micrograph of cartilaginous tubercles on mantle of cranchiid squid, *Cranchia scabra* (field width, 900 μm) (Dilly & Nixon, 1976b).

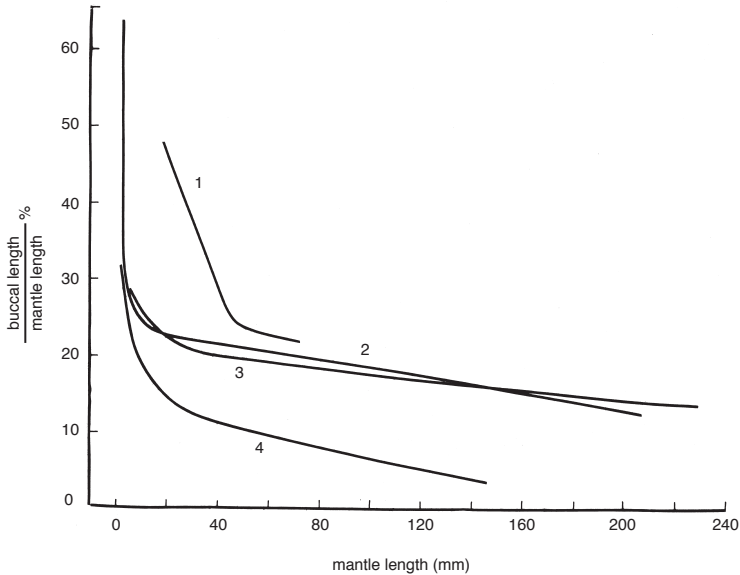


FIG. 12. The anteroposterior length of buccal mass shown as a percentage of mantle length and plotted against mantle length of 1, *Argonauta argo*, 2, *Octopus vulgaris*, 3, *Sepia officinalis*, and 4, *Alloteuthis subulata*; the buccal mass often forms a large proportion of a late embryo and a newly hatched animal, but this diminishes with growth (new).

in Cirrata (J. Z. YOUNG, 1977; ALDRED, NIXON, & YOUNG, 1983; NIXON, 1998b). The brain is compact and consists of sub- and supraesophageal masses (Fig. 7.1) and a periesophageal lobe. The subesophageal mass has three main portions: the anterior (prebrachial and brachial lobes), middle (pedal lobe), and posterior (palliovisceral) lobes. The supraesophageal mass is divided into numerous lobes, some forming higher centers. The periesophageal or magnocellular lobes lie far laterally, around the sides of the brain (J. Z. YOUNG, 1939). In addition, the optic lobes on each side of the brain can be regarded as special developments of the central brain, to which they are joined by the optic tracts.

A considerable part of the nervous system lies outside of the main central brain. This is especially apparent in the coastal-living *Octopus vulgaris* (Octopoda), as the nerve cords in the eight arms contain nearly 350 million cells, whereas the two optic lobes together have 130 million cells and the brain itself 40 million cells (YOUNG, 1963). There is a complex system of nerve fibers

serving all parts of the animal (ISGROVE, 1909; WILLIAMS, 1909; CHUN, 1910a, 1915; TOMPSETT, 1939; J. Z. YOUNG, 1971, 1977; ALDRED, NIXON, & YOUNG, 1983).

Coleoids possess elaborate motor and receptor centers and sense organs (WILLIAMSON, 1995; BUDELDMANN, SCHIPP, & VON BOLETZKY, 1997).

Balance and orientation are provided by the statocysts, which can also detect vibrations. Paired statocysts are usually attached to the cephalic cartilage (Fig. 7), but in Cirrata and Vampyromorpha, they take the form of large sacs that lie behind and below the brain itself (J. Z. YOUNG, 1977; ALDRED, NIXON, & YOUNG, 1983). The shape and form of the statocysts vary widely among the coleoids (J. Z. YOUNG, 1989). Each statocyst is fluid filled with a calcareous statolith suspended in the cavity and has special sensory areas to detect gravity and angular acceleration (BUDELDMANN, 1994). The statolith is a hard, calcified (aragonite) structure, and its form is useful in Recent forms for generic and even specific identification (CLARKE &

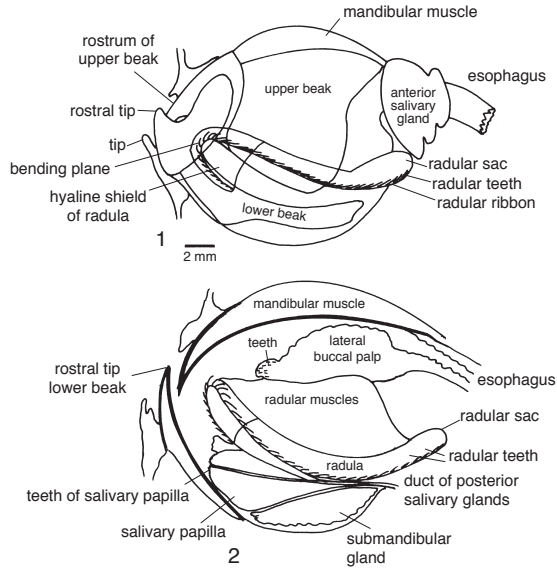


FIG. 13. Buccal mass of *Octopus vulgaris* showing 1, main features, and 2, hemisection illustrating main features of buccal cavity (new).

MADDOCK, 1988b) and in fossil coleoids to the generic level (CLARKE & MADDOCK, 1988a).

A system capable of detecting local water movements has been described for young *Sepia* (WILLIAMSON, 1995) and is probably present in other coleoids. Chemical signals are received via ciliated cells in the lips and the suckers of the arms (WELLS, 1978). Olfactory signals are received by the olfactory organs (WILLIAMSON, 1995).

BUCCAL MASS, BEAK, AND RADULA

The buccal mass of living Coleoidea is spherical and lies in a hollow formed by the bases of the arms (Fig. 7). Its antero-posterior length can range from 60 percent of the mantle length in a late embryo to 4 percent in an adult (Fig. 12) (NIXON, 1969; MORTON & NIXON, 1987; NIXON, 1988a, 1988b). Much of the beak is enclosed by the mandibular muscles, leaving only the tip exposed anteriorly within the encircling lips; the rostrum of the upper beak passes inside the lower (Fig. 13–14) (NIXON, 1988a; KEAR, 1994).

VERRILL (1882) described the main features of the upper and lower beaks. The beaks show wide variation in shape and form (Fig. 14) (CLARKE, 1986; NIXON, 1988a). The lower beak possesses characteristic features, and CLARKE (1962, 1986) modified and supplemented the terminology to describe them (Fig. 15). The size of the lower beak ranges widely, from a rostral length of 19.0 mm in the giant squid *Architeuthis* to only 0.35 mm in the small coastal squid *Pickfordiateuthis* (CLARKE, 1986). The beak can be almost black, brown, or pale and translucent amber; in some species, only the exposed tips are tanned. The beak is a chitin-protein complex (HUNT & NIXON, 1981) secreted by a single layer of columnar epithelial cells, or beccublasts, that also attach the mandibular muscles to the beak (see Fig. 26) (DILLY & NIXON, 1976c). Within the cell layer, there are three types of cells. The most numerous contain cell-long fibrils; these cells are closely associated with the mandibular muscles and may have contractile properties. The second group of cells contains masses of endoplasmic reticulum and dense granules; these cells are probably the major source of

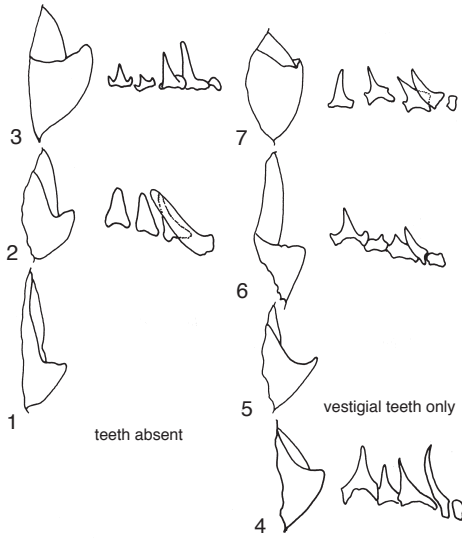


FIG. 14. Anterior part of beaks and radulae of some Recent Coleoidea; tips of beaks are seen in profile, upper being largely enclosed by lower; to right is part of a single transverse row of teeth, including central rhachidian tooth with lateral and marginal teeth and marginal plate of left side only; 1, *Spirula spirula*; 2, *Sepia officinalis*; 3, *Loligo vulgaris*; 4, *Vampyroteuthis infernalis*; 5, *Cirrothauma murrayi*; 6, *Octopus vulgaris*; 7, *Argonauta argo* (new).

the hard tissue of the beak. The third group of cells contains a mixture of secretory tissue and fibrils. The surface of the beak has aligned polygonal imprints of the beccublast cells (Fig. 16). Distinct lines are discernible to the naked eye on the surface of the beak, and an attempt was made to correlate the lines with growth (CLARKE, 1965). An upper beak was preserved in a fossil, *Plesioteuthis prisca*, and NAEF (1922) commented that it was of typical decapodiformean form. It occupied a relatively small portion of the animal, as is true of the adults of many living squids.

The radula consists of a long ribbon bearing numerous rows of teeth with a regular arrangement (NIXON, 1995). The ribbon runs from the back of the buccal mass forward, over the bending plane, to end below and just posterior to the anteriormost tip of the radula (Fig. 13). Each transverse row consists

of a central rhachidian tooth, with lateral and marginal teeth and a marginal plate on either side (Fig. 17), except in a few species in which the teeth or the marginal plates are reduced in number or are absent. Some gonatid squids have only five teeth in each transverse row. In Cirrata, the radula is vestigial, and it is absent in *Spirula*. On either side of the rhachidian tooth, the teeth show differentiation in shape and form across each transverse row. Decapodiformes tend to have few lateral cusps on their teeth compared with Octopoda; a few members of the latter have teeth with numerous cusps (Fig. 14, 17). The teeth are secreted by odontoblast cells, which line the radula sac at the back of the buccal complex (Fig. 13). The most recently formed teeth move forward from the sac, and new ones develop behind them. The newest are always larger than those formed earlier (NIXON, 1969). The old and often worn teeth are lost after passing over the bending plane. The teeth increase in size between hatching and the adult stage. This is most notable between the first and last formed of the rhachidian teeth (NIXON, 1973). In *Teuthowenia megalops*, an oegopsid squid (Fig. 18), the teeth are small and simple in the smallest specimens, as they lack cusps that are present on the teeth of the nearly mature animals (DILLY & NIXON, 1976a). A survey of radulae has revealed something of their variety and complexity among living Cephalopoda (NIXON, 1998b; and see *Treatise Online*, Part M, Chapter 12). The radula from a fossil, *Jeletzkyia douglassae*, is preserved and has a small, triangular, rhachidian tooth and triangular lateral teeth 1 and 2. The marginal tooth is crescentic and elongate, and the marginal plate is wide (SAUNDERS & RICHARDSON, 1979). The affinities of this fossil have been variously interpreted. The radular apparatus of several coleoids has been described (MESSENGER & YOUNG, 1999).

Lateral buccal palps lie on either side of the radula. They are relatively large and mobile and can extend far forward and then sweep back toward the esophagus (Fig. 13.2). They have a chitinous covering that

often has small, backward-pointing teeth that may be thin, delicate, and small, or stout and large. The spirulid, *Spirula spirula*, lacks a radula but has large, robust teeth on these palps (KERR, 1931).

A papilla lies below the radula and carries the single duct from the posterior salivary glands (Fig. 13.2). This papilla has small teeth on its anterior face, and in at least two coastal-living, incirrate octopods, it is involved in some stages of the excavation of small cavities in mollusk shells and the carapaces of crustaceans, aided by secretions from the posterior salivary glands (NIXON & MACCONNACHIE, 1988).

The structures of the buccal complex, lying within the buccal cavity, have a cuticular covering, with the exception of the glandular tissues. This cuticle is continuous from the buccal cavity into the digestive tract (HUNT & NIXON, 1981).

DIGESTIVE SYSTEM

Living coleoids are active predators, feeding mainly on crustaceans, fish, and other mollusks and capturing prey with their tentacles or arms (NIXON, 1987, 1988b; CLARKE, 1996). The food to be ingested has to be in pieces small enough to pass along the esophagus without damage to the surrounding brain.

The organs of the digestive tract consist of the buccal mass, the salivary glands, the esophagus, the stomach, the caecum, the intestine, the digestive gland, and the appendages of its duct (MANGOLD & YOUNG, 1998). The esophagus runs directly to the stomach in sepiids, squids, and cirrate octopods; but incirrates have a pocketlike diverticulum or crop before the stomach (Fig. 19) (BIDDER, 1950, 1966; ALDRED, NIXON, & YOUNG, 1983; BOUCHER-RODONI, BOUCAUD-CAMOU, & MANGOLD, 1987). The digestive tract, from the buccal mass to the stomach, including the esophagus and crop, with the exception of the glandular areas, is lined with a chitin-protein complex in coleoids (HUNT & NIXON, 1981). The stomach (or crop) has been found preserved with contained prey in

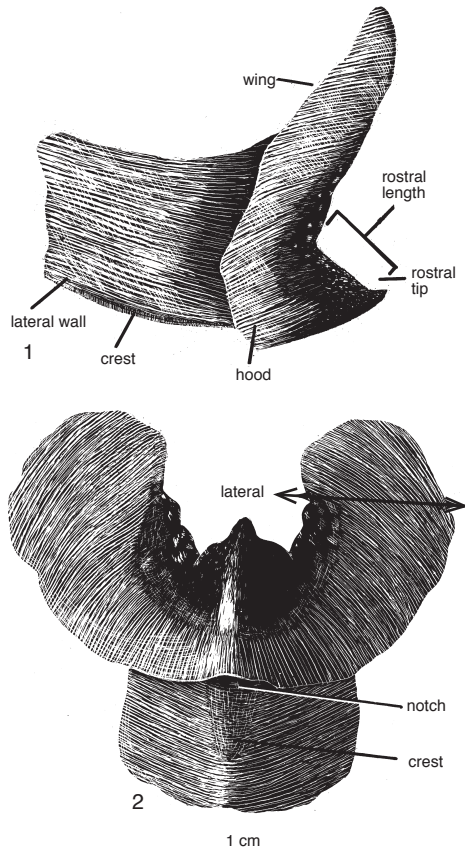


FIG. 15. Lower beak of loliginid squid (*Loligo forbesi*, 241 mm mantle length), with terms used to describe most important features; 1, in profile; 2, view of ventral surface (Clarke, 1977).

some ammonite fossils (LEHMANN, 1976). The midgut region is formed of stomach, caecum, intestine, and digestive gland (Fig. 19). The intestine runs into a short rectum. The ink sac opens into the rectum, which runs forward, and the anus lies just posterior of the funnel.

CIRCULATORY, RESPIRATORY, AND EXCRETORY SYSTEMS

The morphology of these systems has been described for the common cuttlefish *Sepia officinalis* (TOMPSETT, 1939); an oegopsid squid, *Todarodes sagittatus* (POSSELT, 1891); a myopsid squid, *Loligo pealei* (WILLIAMS,

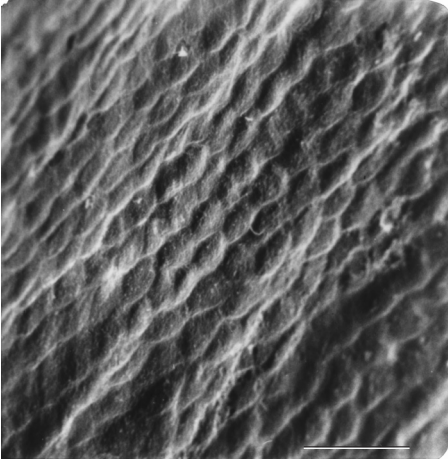


FIG. 16. Scanning electron micrograph of surface of crest region of the upper beak of the myopsid squid, *Alloteuthis subulata*, showing aligned polygonal imprints of beccublast cells; scale bar, 10 μ m (Dilly & Nixon, 1976c).

1909); and for the incirrates *Eledone cirrhosa* (ISGROVE, 1909), *Octopus dofleini*, and *O. vulgaris* (HARRISON & MARTIN, 1965; WELLS, 1978, 1988).

Coleoids possess one median systemic and two branchial hearts (Fig. 20). The systemic heart has a pair of auricles and a muscular ventricle. Two major vessels, the anterior and posterior aortae, originate from the heart, and these two arterial vessels with their

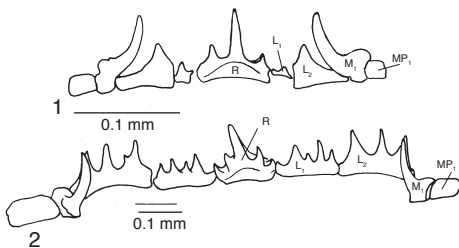


FIG. 17. Transverse row of teeth from radula of 1, *Vitreledonella richardi* and 2, *Eledonella*. Both are Incirrata, but in the latter, all teeth are cuspidate except marginal tooth; *L1*, *L2*, lateral teeth 1 and 2; *M1*, marginal tooth 1; *MP1*, marginal plate 1; *R*, rhachidian tooth (new).

numerous branches provide the tissues with oxygenated blood (Fig. 20). Blood returns via the venous system to two vena cavae and to the two branchial hearts. The branchial hearts lie laterally, and each has a single chamber, the muscular action of which propels blood into an afferent branchial vessel to be oxygenated during its passage through the gills (Fig. 5). The branchial hearts exert a pressure to force an ultrafiltrate of the blood through the branchial heart appendages into a pericardium. The filtrate passes through a duct to the kidney sac, where it comes into contact with the renal appendages, before the urine is discharged through the renal papilla into the mantle cavity (WELLS, 1978, 1988).

The gills are paired and lie on either side of the visceral mass in the mantle cavity, each attached to the visceral mass and the mantle (Fig. 5). Each gill is a long, pinnate structure with numerous gill leaflets or lamellae, a branchial artery, and vein (Fig. 20). Each leaflet is attached to the core of the gill by a triangular sheet of tissue, whose free edge is stiffened by delicate, curved rods of hard tissue [chitin in *Loligo* (WILLIAMS, 1909), cartilage in *Sepia* (TOMPSETT, 1939)]. The blood passing through the gill leaflets is separated by only a thin, delicate membrane from the oxygenated and constantly changing water in the mantle cavity. The gills of deep-water forms and of some shallow-water inhabitants may be reduced in overall size or in the number of leaflets (G. L. VOSS, 1988b). An x-ray of a Lower Jurassic coleoid, *Phragmoteuthis conocauda*, shows the outline of the support for the two gills (REITNER & MEHL, 1989; MEHL, 1990).

REPRODUCTIVE SYSTEM

The female genital tract consists of ovary, oviduct(s), and oviducal and nidamental glands (ARNOLD & WILLIAMS-ARNOLD, 1977; WELLS & WELLS, 1977; MANGOLD, 1989b). The ovary is single and lies in the posterior part of the mantle; it is conical in squids and hemispherical and saclike

in sepiids and octopods (Fig. 21–22). The ovary increases in size with maturation and comes to occupy most of the mantle cavity, pushing the remaining organs anteriorly. Ovarian eggs may be uniform or of various sizes (see *Treatise Online*, Part M, Chapter 5). In the oceanic, pelagic incirrate *Ocythoe tuberculata*, the fertilized ova complete their development in the long oviduct, and the young are born alive (ovoviviparity) (STEENSTRUP, 1880; NAEF, 1923). The oviduct may be single or paired, and the oviducal gland corresponds in number. Secretion from the oviducal gland(s) contributes to the envelope around the egg. A pair of nidamental glands is present in sepiids, sepiolids, and oegopsid squids, with the exception of the Enoplo-teuthidae; and small, accessory nidamental glands are present in cuttlefish and myopsid squids (NESIS, 1982).

The male reproductive tract consists of a testis, seminal vesicle (vas deferens), spermatophoric organ (vas efferens), accessory gland, spermatophoric sac (Needham's sac), and penis (Fig. 22.2) (MANGOLD, 1989b; NORMAN, HOCHBERG, & LU, 1997). In most coleoids, the male genital organs are unpaired and lie in the left half of the mantle. The mature testis is a median structure and lies in the posterior apex of the mantle; it is spherical in octopods and is elongated and flattened against the gladius in squids and sepiids. From the testis, sperm pass into the seminal duct, which joins the spermatophoric organ. This organ is a complex of glandular tissue and laminae where the sperm are formed into a spiral mass and coated with a tough, elastic membrane to form the spermatophore (MANN, MARTIN, & THIERSCH, 1970). Each spermatophore is tubular and consists of two parts, one largely filled with compacted sperms and the other an invaginated, folded tube forming the ejaculatory apparatus. Extending from the anterior extremity is the cap thread (Fig. 23) (AUSTIN, LUTWAK-MANN, & MANN, 1964). Spermatophores are transferred singly into the spermatophoric sac for storage until copulation

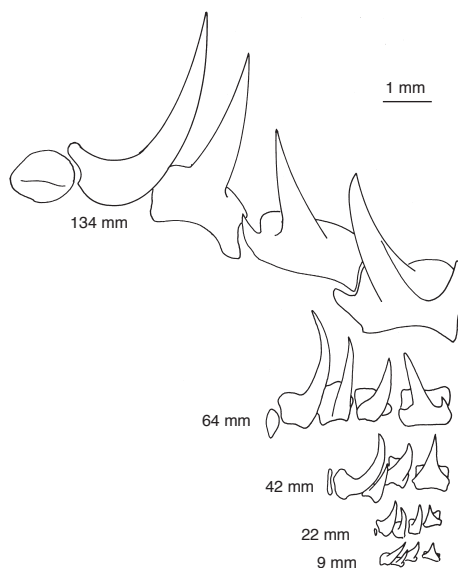


FIG. 18. Central rhachidian tooth, with lateral and marginal teeth and marginal plate of right side only of radula of *Teuthowenia megalops*, showing change in size of teeth, with growth of animal from 9 mm to 134 mm, dorsal mantle length (Dilly & Nixon, 1976a).

takes place, when it passes to the female (Fig. 22). Each spermatophore has a brittle outer coat and a complicated internal structure; the features of spermatophores are of taxonomic value (MANGOLD, 1989b). The spermatophores range in size from 16 to 18 mm in length in *Sepia officinalis* and *Loligo vulgaris* of 300 to 400 mm mantle length, to 65 mm in *Octopus vulgaris* of 200 mm mantle length, to more than 1 m in *Octopus dofleini* of about 1.5 m total length (MANGOLD-WIRZ, 1963; MANN, MARTIN, & THIERSCH, 1970). The spermatozoa, within the spermatophore, have complex features, and their morphology has been found to support the accepted taxonomic divisions of the subclass (HEALY, 1995).

CARTILAGE AND CHITIN

Cephalopods have several structures consisting entirely or partly of hard tissue that are referred to as cartilaginous or chitinous. Only a few have been described when isolated from the animal or analyzed

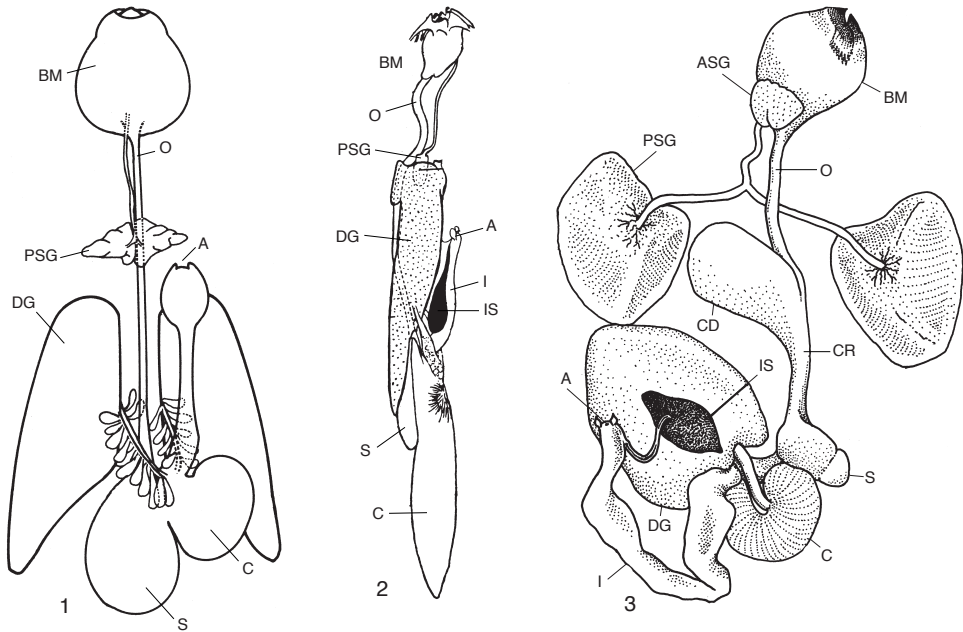


FIG. 19. Digestive system of 1, *Sepioli atlantica*, 2, *Loligo vulgaris*, and 3, *Octopus pyrum*; A, anus; ASG, anterior salivary glands; BM, buccal mass; C, caecum; CD, crop diverticulum; CR, crop; DG, digestive gland; O, esophagus; I, intestine; IS, ink sac; PSG, posterior salivary gland; S, stomach (Bidder, 1950; Norman, Hochberg, & Lu, 1997).

chemically. Notably, some have been found preserved in fossil cephalopods. The supports of the gill lamellae have been revealed by x-rays in the fossil coleoid *Phragmoteuthis conocauda* (REITNER & MEHL, 1989; MEHL, 1990). The hooks of the arms or tentacles of teuthids survive both the digestive process and fossilization, since some have been found in the gastric contents of predators (ENGESER & CLARKE, 1988). Both radula and beaks, sometimes together, have been found in fossil cephalopods, including some ammonoids (NIXON, 1996) and at the center of the arm crown of the coleoid *Jeletzkyia douglassae* (SAUNDERS & RICHARDSON, 1979), although the affinities of this species are uncertain.

OWEN (1832, p. 16) noted of the cranium of *Nautilus*, "Like that of the Dibranchiate Cephalopods, this skeleton is cartilaginous . . . and in texture and semitransparency closely resembles the cartilage which constitutes the skeleton of the skate." The apparent similarity of cartilage in cephalopods and

vertebrates was accepted until around the end of the 19th century when it began to be questioned. Doubt continued until the 1960s, when several experimental and structural studies indicated that the earlier belief was correct and that cephalopods possess true cartilage, although differing in some respects from vertebrate cartilage. Criteria established for the latter were found to apply to invertebrate cartilages and led to the modification of the definition of cartilage to "an animal tissue, usually endoskeletal, but also exoskeletal. . . . Physically, cartilages are gristle-like, relatively rigid, and resistant to forces of compression, shearing, and tension" (PERSON, 1983, p. 33).

The cartilage cell is the basic and constant component of cartilage, and it is surrounded by a territorial matrix it has itself secreted. Cartilage is a form of connective tissue with polymorphic cells suspended in a matrix (Fig. 24.1) and chemically includes chondroitin sulphate, keratosulphate, and hyaluronic acid (BUDELMANN, SCHIPP, & VON

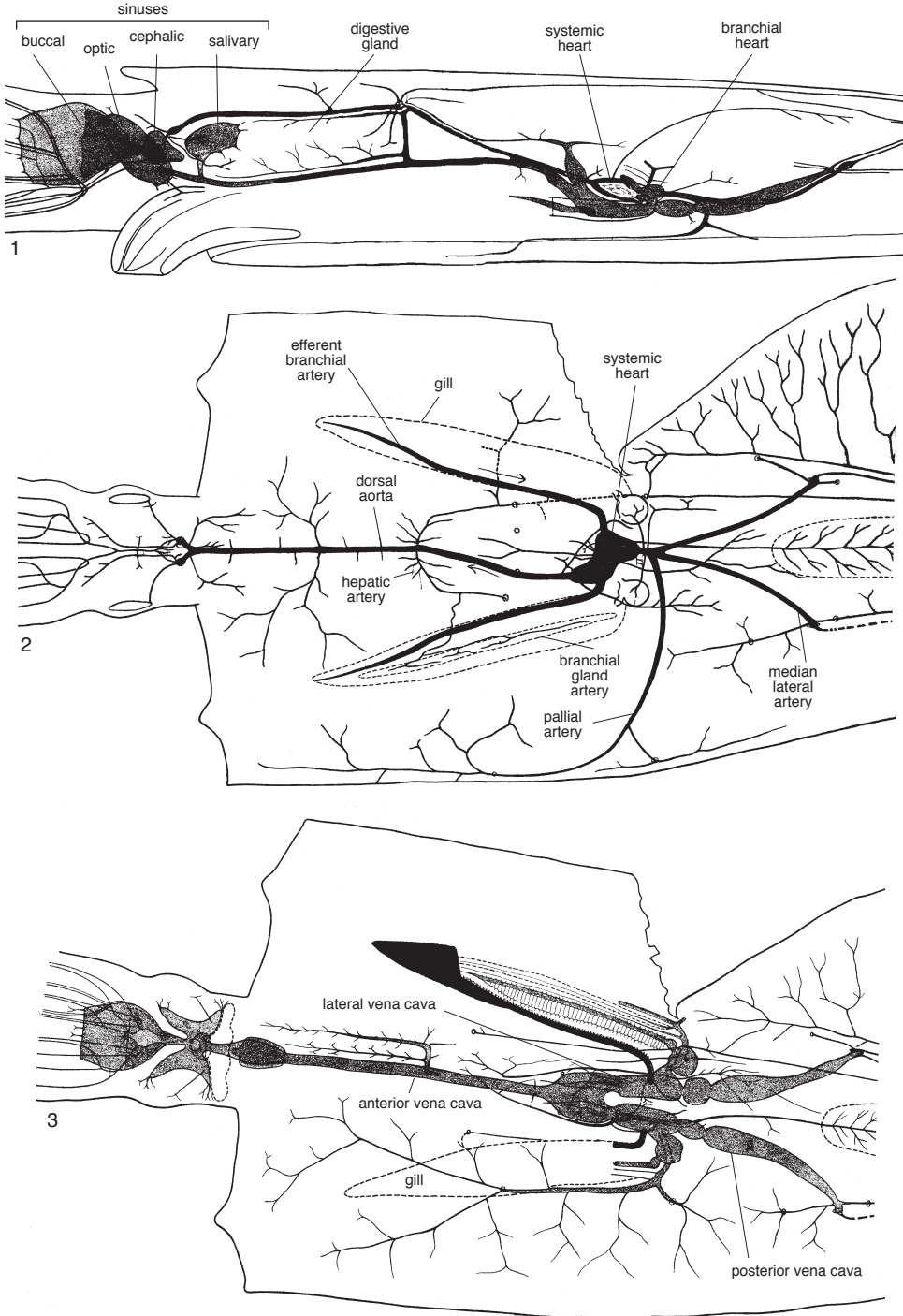


FIG. 20. Vascular system of *Loligo pealei*; arterial system seen from side showing 1, position of aorta and gills and 2, middle region seen from ventral surface; venous system seen from ventral side showing 3, venous return to gills (Williams, 1909).

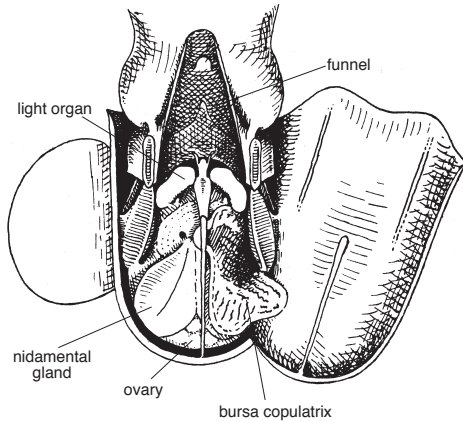


FIG. 21. Pallial cavity of mature female *Sepioloidea rondeleti* (Sepiolida) after mating, opened to show ovary, nidamental glands, and enlarged bursa copulatrix and its extension to inner side of mantle (Naef, 1923).

BOLETZKY, 1997; NIXON, 1998b). The polymorphic cartilage cells, the chondrocytes, reside in lacunae. Each lacuna may contain one, two, or more chondrocytes. Within one cartilage alone (the nuchal cartilage of *Lolliguncula brevis*), the chondrocytes may vary from ovoid with fine processes in an abundant matrix to amoeboid with irregular processes in less abundant matrix (BUDELMANN, SCHIPP, & VON BOLETZKY, 1997). This type is called hyaline cartilage. A second type is found in some coleoids and is reticulate or lacelike (Fig. 24.2) (CLARKE, DENTON, & GILPIN-BROWN, 1979).

The structural features of cephalopods said to be cartilaginous are mostly internal and may include all or several of the following: the cephalic or cranial cartilage, the postcephalic cartilage, the brachial cartilage, the nuchal cartilage and dorsal cartilage, the funnel- and mantle-locking cartilages, the brachial cartilages, and the fin cartilages, the number varying between taxa. The gross morphology and the microanatomy of these cartilaginous structures is known for only a very small number of species. Cartilage also occurs in dermal structures such as cushions (e.g., in *Lepidoteuthis*) and tubercles (e.g., *Cranchia*, *Mastigoteuthis*) (NIXON, 1998a). The tubercles of *Cranchia scabra* have been

shown by structural and chemical studies to be of cartilage that is in the more usual hyaline form (Fig. 24.1).

Most notable of these structures, and usually the largest, is the cephalic or cranial cartilage. It is present in most, but not all, Recent coleoids. The gross morphology of the cephalic cartilage of a few coleoids has been described, the most detailed description available being that for *Sepia officinalis* by TOMPSETT (1939). The cephalic cartilage is symmetrical and has a complex form, with major anterior and posterior openings for the esophagus, as well as numerous orifices for the passage of nerves and blood vessels (Fig. 25). It serves for the attachment of the head-retractor and funnel-adductor muscles and the arm and tentacular muscles. The shape and form of the cephalic cartilage tends to follow that of the central nervous system. The numerous lobes of the brain show differences in size and shape between genera and even species (J. Z. YOUNG, 1971; MADDOCK & YOUNG, 1987), and these differences may be reflected in the cephalic cartilage. Histological sections of numerous coleoid species reveal the cephalic cartilage to be hyaline or reticulate (Fig. 24.2) (NIXON, 1998b), although the significance of the difference is not known. In some coleoids, such as *Chtenopteryx* and most especially *Architeuthis* (Oegopsida), the cephalic cartilage is extremely thick; this contrasts with many in which it is relatively thin.

A brachial cartilage, if present, lies anteroventral to the cephalic cartilage (Fig. 25). It is small, closely associated with the complex muscles of the bases of the arms, and may be of hyaline cartilage. On either side of the cephalic cartilage are posterolateral expansions with winglike extensions forming the orbital cartilages (Fig. 25). The statocysts are usually enclosed within cartilage and lie at the back of the cranium. Two cartilages are found in the neck region, the nuchal and the dorsal cartilages, which together form a locking device.

Best known of all the cartilaginous structures in coleoids is the funnel-locking cartilage, because it has features of taxonomic

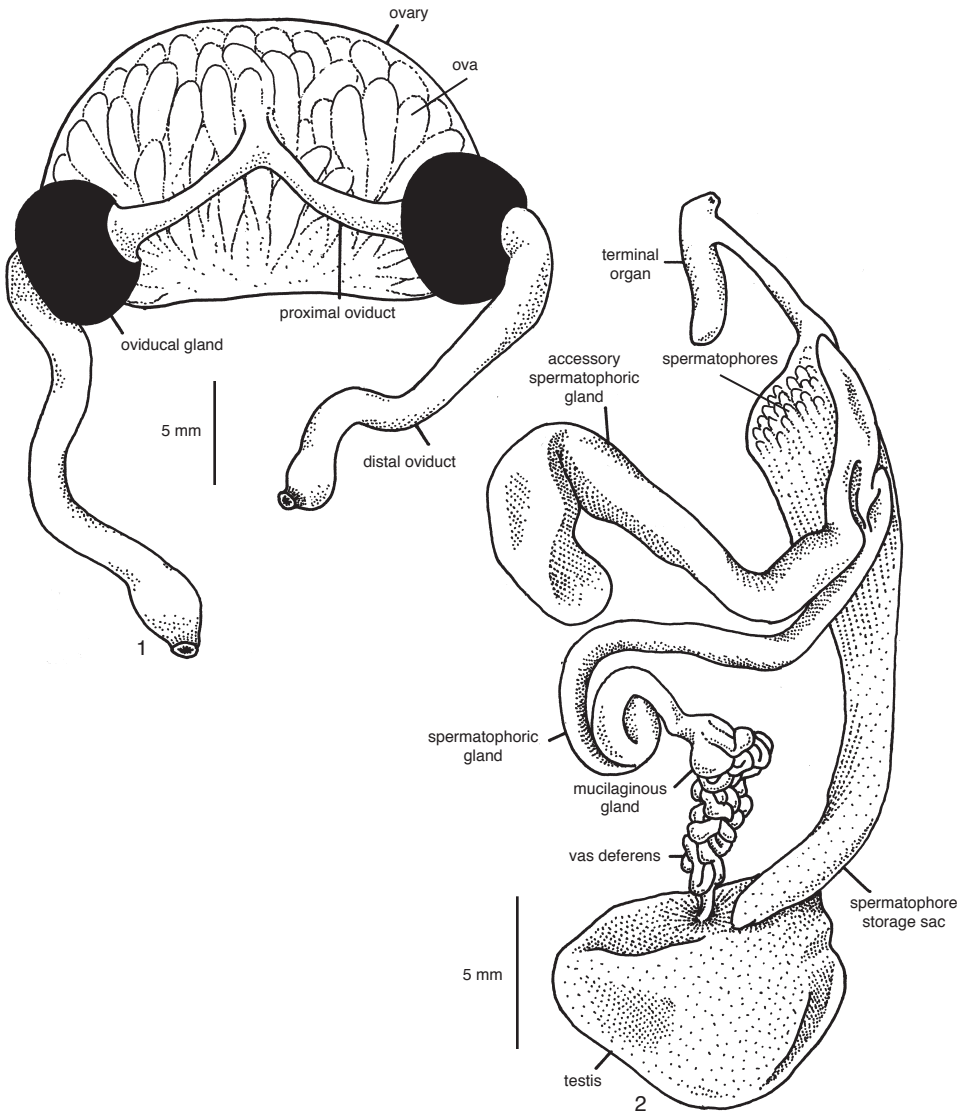


FIG. 22. Reproductive system of *Benthoctopus karubar* (Octopoda); 1, nearly mature female (97 mm mantle length) and 2, mature male (60 mm mantle length) (Norman, Hochberg, & Lu, 1997).

value (ROPER, YOUNG, & VOSS, 1969). One cartilage is sited on either side of the ventrolateral side of the funnel (Fig. 4-5). This is a cartilaginous pad with variously shaped depressions of grooves, pits, or pockets. The following types of funnel cartilage structure are known: a simple (straight) cartilage; triangular; oval; earlike; cup shaped; and an

inverted T-shape (Fig. 4.2). This component locks into a corresponding cartilage on either side of the ventrolateral internal surface of the mantle, the mantle-locking cartilage (NESIS, 1982). This is a cartilaginous ridge, knob, or swelling that, by locking into that of the funnel, locks funnel and mantle together during locomotion.

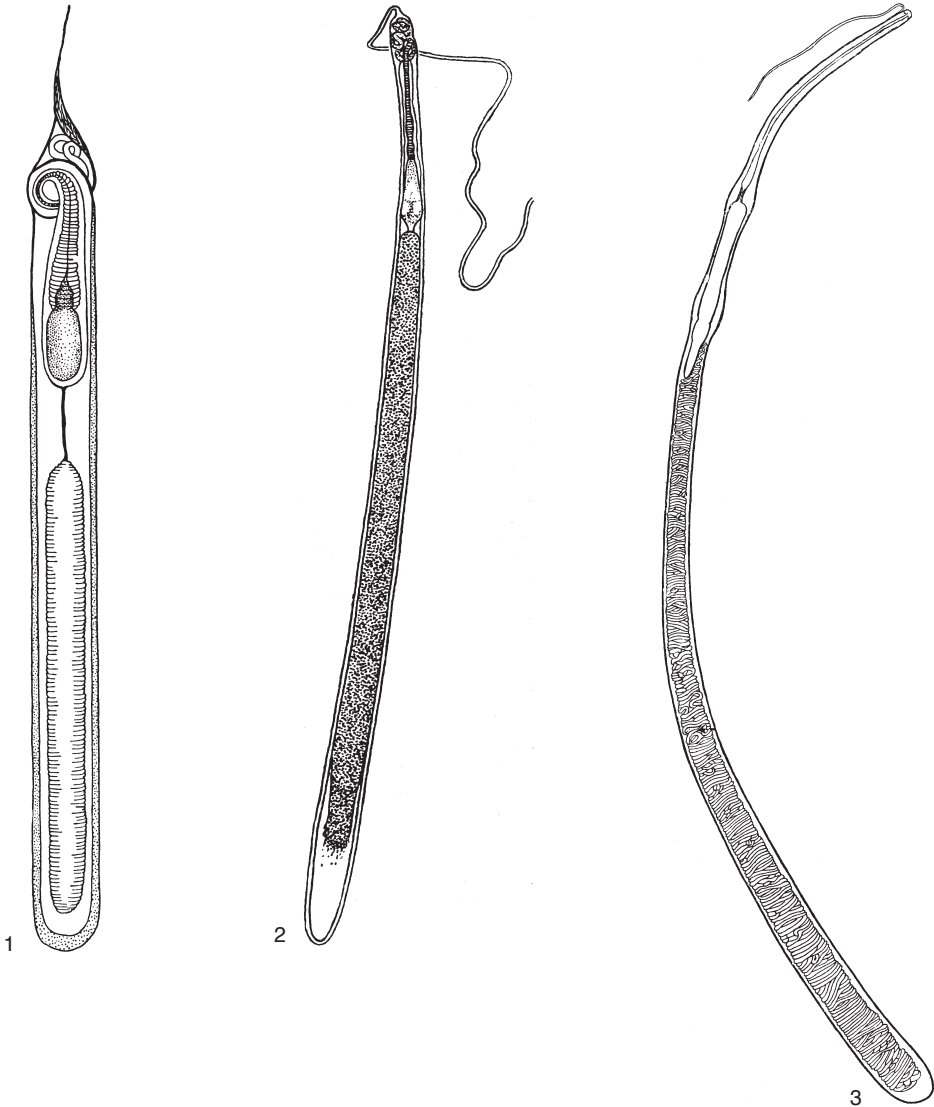


FIG. 23. Diagrams of spermatophores of 1, *Sepia officinalis* (Sepiida), 2, *Loligo pealei* (Myxosida), and 3, *Eledone cirrhosa* (Incirrata); sperm mass occupies most of internal space, ejaculatory apparatus lies anterior to this and consists of globular cement body and ejaculatory tube, beyond which extends the cap thread (Fort, 1937; Tompsett, 1939; Austin, Lutwak-Mann, & Mann, 1964).

Cartilaginous tissue may be present along the base of the fins, for example, in sepiids and in *Vampyroteuthis* (Vampyromorpha) and in the strange fins of *Chtenopteryx* (Oegopsida) (J. Z. YOUNG, 1991b).

The gills have numerous leaflets or lamellae, and each is attached by means of a small, hard tissue structure, which is

composed of cartilage in *Sepia* (TOMPSETT, 1939) and chitin in *Loligo* (WILLIAMS, 1909).

Several structures have been termed chitinous in cephalopods. A few have been analyzed and found to be chitin-protein complexes. These include the gladius, beak, radula, and the sucker discs of octopods (HUNT & NIXON, 1981; HUNT & HUCKERBY,

1987). In squids, the gladius is the largest of these structures. The beak, radula, and esophageal lining have survived in fossil ammonites (NIXON, 1996). The hooks of the arms or tentacles of oegopsids are of tough tissue that, like the beaks, can survive both digestive and fossilization processes (ENGESER & CLARKE, 1988; GARASSINO & DONOVAN, 2000), although the chemical composition is not known. Chitin is difficult to section for histological examination, as it often fractures.

The gladius varies greatly in shape, size, and complexity. It has been described in *Vampyroteuthis*, three cirrates, and eight incirrates by BIZIKOV (2004). One of the sepiolids has the smallest gladius, as it extends over only the anterior half of the mantle. The loliginid and some oegopsid squids have broad gladii that are almost the length of the mantle. The gladius of other oegopsid squids is slender with longitudinal ribs and a cone-shaped posterior end, so that it resembles the conotheca of fossil squids (BUDELMANN, SCHIPP, & VON BOLETZKY, 1997; see *Treatise Online*, Part M, Chapter 10). The composition of the gladius, or shell, is little known. In the myopsid *Loligo*, it is a chitin-proteoglycan structure (HUNT & NIXON, 1981), and transmission electron micrographs reveal layers of striated material interspersed with diffusely banded or unstriated layers, suggestive of plywood (HUNT & EL-SHERIEF, 1990). The vampyromorph *Vampyroteuthis infernalis* and the cirrates have chitinous supporting structures, and in some incirrates, a much reduced pair of stylets.

Successful histological sections of the beak show few features, except some indication of layers as the chitin is laid down by the tall, columnar, epithelial, beccublast cells (Fig. 26). These cells leave aligned polygonal outlines on the outer surface of the beak that are readily seen with the scanning electron microscope (Fig. 16) (DILLY & NIXON, 1976c). The outer surface of the beak shows lines of development, but their value in aging has not been determined (CLARKE, 1965).

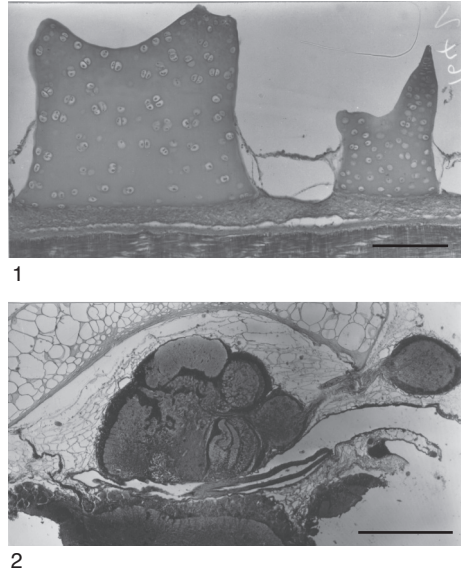


FIG. 24. 1, Skin with two tubercles seen in histological section, showing hyaline cartilage, with chondrocytes, some dividing, in matrix; scale bar, 100 μ m; 2, sagittal section through head of *Mastigoteuthis* (Teuthida) showing cranium of reticulate cartilage above brain; scale bar, 0.5 mm (new).

The radula and its teeth are secreted by the tall odontoblast cells that lie within the radular sac. The teeth form and develop in the radular sac and move forward to the front of the mouth (NIXON, 1988a). The radula has a support on either side, and these are usually said to be cartilaginous. These are, however,

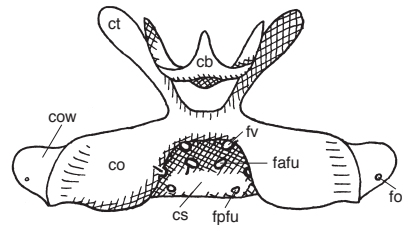


FIG. 25. Cephalic cartilage of *Sepia officinalis*; ventral surface showing orbital and trochlear cartilages; *cb*, brachial cartilage; *co*, orbital cartilage; *cow*, wing of orbital cartilage; *cs*, statocyst cartilage; *ct*, trochlear cartilage; *fafu*, foramen of anterior funnel nerve; *fol*, foramen of olfactory nerve; *fpu*, foramen of posterior funnel nerve; *fvf*, foramen for vein of olfactory nerve (Tompsett, 1939).

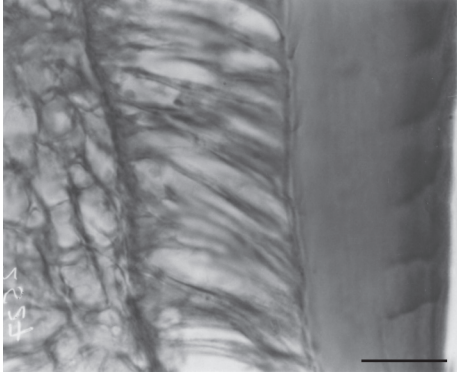


FIG. 26. Histological section through chitin-protein tissue of beak of *Alloseuthis* (Myopsida) secreted by tall, columnar, beccublast cells; exposed surface of beak showing fractures resulting from section cutting; scale bar, 10 μm (new).

muscular hydrostats and are devoid of cartilaginous tissue (MESSENGER & YOUNG, 1999).

The sucker discs of incirrate octopods also consist of chitin-protein complexes (HUNT & NIXON, 1981; HUNT & HUCKERBY, 1987).

MUSCLES

CUVIER (1802), in his sixth lecture on comparative anatomy entitled "Organs of motion in Mollusca Cephalopoda," described the muscles of the body, feet, and suckers. As there is little hard or skeletal tissue in many coleoids, this is formed largely of muscles that function as a muscular-hydrostat support system (KIER, 1988). The muscles are usually a complex, dense, tightly packed, three-dimensional array of fibers. Changes in the dimension of the muscle fibers transmit the force of muscular contraction into movement and muscular antagonism (KIER, 1988). The major muscles of *Loligo pealei* have been described by WILLIAMS (1909) and of *Sepia officinalis* by TOMPSETT (1939); those involved in locomotion and jet propulsion by WARD and WAINWRIGHT (1972) and BONE, PULSFORD, and CHUBB (1981); those of the arms and tentacles and their suckers by GUÉRIN (1908), KIER (1982, 1985), KIER and SMITH (1990); of the mantle by WELLS

(1988); and of the fins by KIER (1989). An overview of the muscular system was given by MANGOLD and BIDDER (1989) and that of the ultrastructure by BUDELMANN, SCHIPP, and VON BOLETZKY (1997). Muscle tissues have been found preserved in some fossil coleoids (DONOVAN, 1995; KEAR, BRIGGS, & DONOVAN, 1995).

The mantle is supported by a chambered internal shell (Spirulida) (GRÉGOIRE, 1961; THOMAS & BINGHAM, 1972), a calcified cuttlebone (Sepiida) (GRÉGOIRE, 1972; BIRCHALL & THOMAS, 1983), an organic, chitinous gladius, shell, or pen, or paired stylets (Fig. 6–7) (APPELLÖF, 1893; HUNT & NIXON, 1981), and the muscles are attached to a layer of connective tissue covering the support. They have been described in a number of coleoids by BIZIKOV (2004).

The paired head-retractor muscles are large and have their origin at the edge of the cuttlebone of *Sepia*, about halfway along its length (TOMPSETT, 1939). Anteriorly, the head retractor muscles are added to by fibers originating on the whole of the ventral surface of the nuchal cartilage. These muscles become fused into a continuous muscle sheath on the dorsal surface of the cartilage. Dorsally, these muscles are partly continuous with the bases of the arms, and ventrally, they are inserted partly on to the orbital and cranial cartilages and partly on the posterior surface of the brachial cartilages, where the right and left retractor muscles of the head fuse together. The head-retractor muscles of *Loligo* are relatively very large, and these muscles, together with the funnel-retractor muscles, are attached to the lower surface of the gladius (Fig. 6.1) (WILLIAMS, 1909). In *Octopus*, the head-retractor muscles, also large, are attached to the pair of small chitinous stylets buried laterally in the muscle of the mantle wall; the funnel-retractor muscles are smaller and lie below; and there is a pallial adductor muscle, which is not present in squids (Fig. 6.2) (WELLS, 1978, 1988).

The mantle muscle of *Sepia officinalis* (Sepioidea) has its origin along the horny

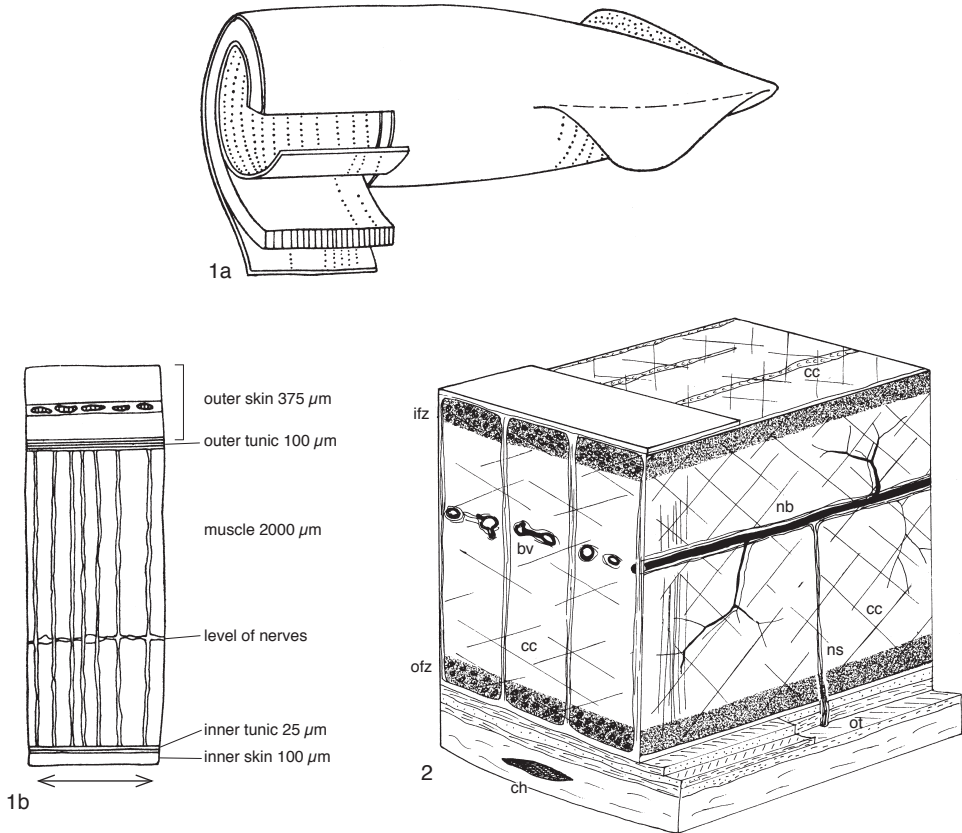


FIG. 27. Mantle of Myopsida; *1a*, diagram of mantle of *Loliguncula* (120 mm mantle length) showing thick muscle layer between inner and outer tunics; *1b*, longitudinal radial section showing relative thickness of its parts (Ward & Wainwright, 1972); *2*, disposition of connective tissue fibers in mantle of *Aloteuthis*; skin at bottom of figure; *bv*, blood vessels; *cc*, connective tissue fibers; *ch*, chromatophore; *ifz*, inner fiber zone; *nb*, nerve bundle; *ns*, nerves to skin; *ofz*, outer fiber zone; *ot*, outer tunic (Bone, Pulsford, & Chubb, 1981).

margin of the cuttlebone and consists of a thick sheet of muscle (TOMPSETT, 1939). The muscles of the mantle of *Loligo* (Myopsida) are attached to the upper surface of the gladius, and the large funnel-, nuchal-, and head-retractor muscles to the lower surface of the gladius (Fig. 6.1). The loliginid squids have circular muscle bands that extend from one side of the gladius around the mantle cavity to the opposite side or pass outside of the gladius and so encircle the body completely. The mantle is attached to the visceral mass by a pair of ligaments that arise near the middle of the visceral mass and extend over the edge of the gladius to the mantle (WILLIAMS, 1909). The large and

powerful retractor muscles of the funnel are fused at their origin with those of the head-retractor muscles and the walls of the mantle. They run forward on either side, expanding gradually over the ventral surface of the digestive gland to merge into the walls of the exhalant siphon. The ventral part of the mantle is concerned with respiration and with the expulsion of water during locomotion; it has elastic properties provided by collagen fibers (GOSLINE & SHADWICK, 1983).

The circular muscle fibers of the mantle are divided, more or less regularly, by thin partitions of radial muscle fibers. In addition, there are muscle fibers running along

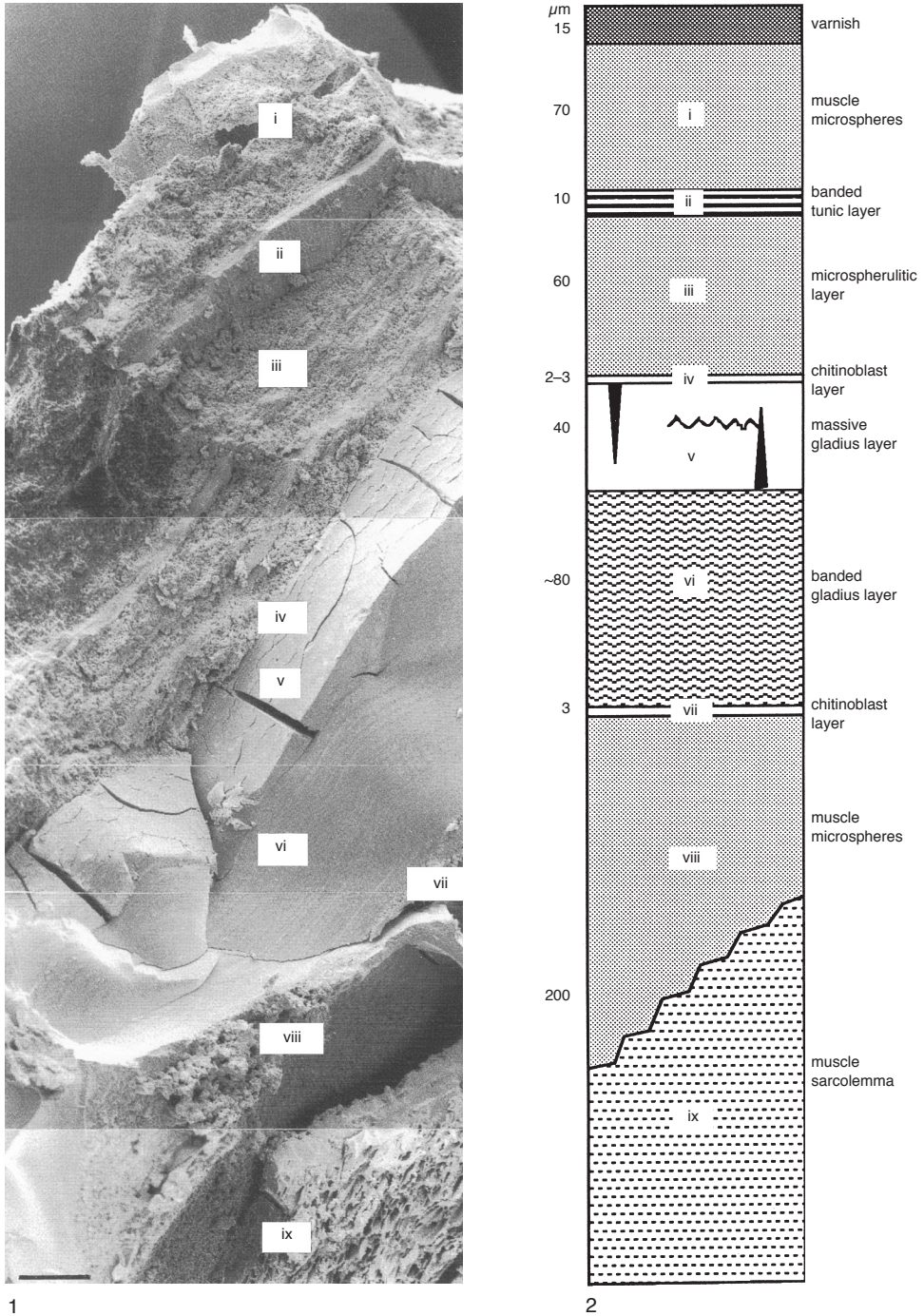


FIG. 28. 1, Scanning electron micrographs of a section through mantle of fossil coleoid, *Mastigophora brevipinnis* (Callovian, Jurassic), showing muscle and inner tunic, and muscle forming sheath around digestive gland (scale bar, 40 μm); 2, diagrammatic representation of section (Kear, Briggs, & Donovan, 1995).

the long axis of the animal. The longitudinal fibers lie superficially just inside the connective tissue and epithelial layer lining the mantle cavity (WARD & WAINWRIGHT, 1972) (Fig. 27). The partitions of radial fibers also contain connective tissue fibrils (BONE, PULSFORD, & CHUBB, 1981). The inner and outer surfaces are covered by layers of collagen, called the tunics (GOSLINE & DEMONT, 1985), and there is a complex network of connective tissue fibers (BONE, PULSFORD, & CHUBB, 1981) (Fig. 27.2). Two incirrate octopods, *Eledone* and *Pteroctopus*, have circular and radial muscle fibers in the mantle (MANGOLD & BIDDER, 1989). Squids such as *Lepidoteuthis* (CLARKE & MAUL, 1962) and *Mastigoteuthis* (DILLY, NIXON, & YOUNG, 1977) have layers of muscle separated by vacuolated or reticulate tissues in the mantle; whereas others, such as the cirrate octopod *Cirrothauma* (ALDRED, NIXON, & YOUNG, 1983), have muscles interspersed among loose tissues. Such reticulate or loose tissue may contain fluids of a lower density than seawater and so contribute to neutral buoyancy in coleoids (CLARKE, DENTON, & GILPIN-BROWN, 1979).

The mantles of the Jurassic coleoids *Phragmoteuthis* (DONOVAN, 2006), *Geopeltis*, *Loligosepia*, *Belemnoteutis*, *Mastigophora*, and *Plesioteuthis* have radial and circular muscles. In addition, the last three genera have longitudinal muscles, the fibers of which are associated with the gladius in *Mastigophora* (Fig. 28) and *Plesioteuthis* (KEAR, BRIGGS, & DONOVAN, 1995).

The tentacles of Decapodiformes have dense and variously oriented muscles surrounding the axial nerve cord (Fig. 29.1) (KIER, 1988). From the muscle mass, groups of fibers or trabeculae radiate between bundles of peripherally arranged, longitudinal muscle fibers. Surrounding the layer of circular muscle are two thin layers of helically oriented muscle fibers, and these, in turn, are covered with a layer of longitudinal muscle (KIER, 1982). The transverse muscles produce rapid extension of the tentacles, which are ejected from the sac and

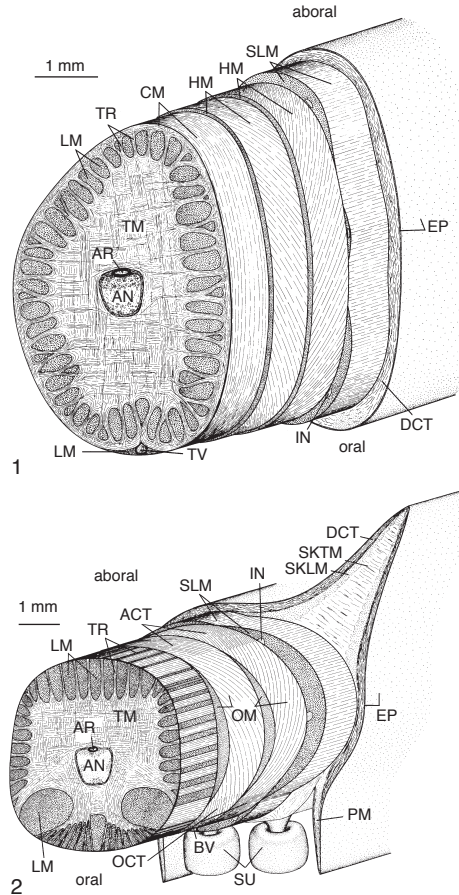
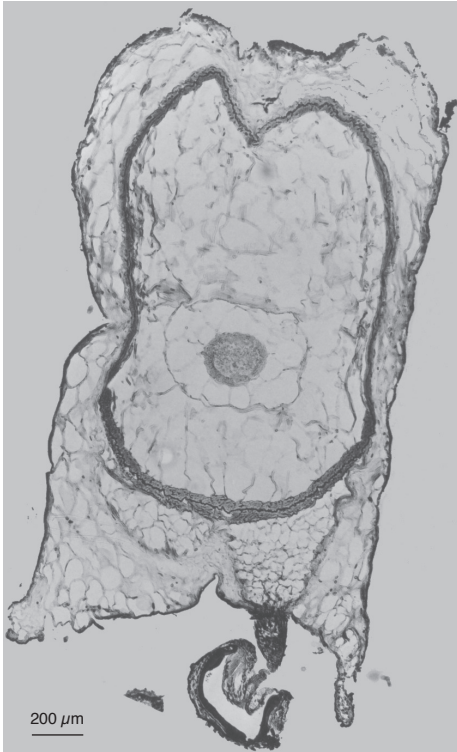
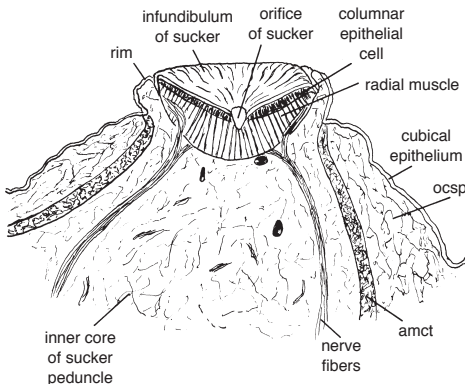


FIG. 29. 1, Tentacular stalk (left) and 2, arm (left) of loliginid squid in cross section; *ACT*, aboral connective tissue; *AN*, axial nerve cord; *AR*, artery; *BV*, brachial vein; *CM*, circular muscle; *DCT*, dermal connective tissue; *EP*, epithelium; *HM*, helical muscle; *IN*, intramuscular nerve cord; *LM*, longitudinal muscle; *OCT*, oral connective tissue; *OM*, oblique muscle; *PM*, protective membrane; *SKLM*, swimming keel longitudinal muscle; *SKTM*, swimming keel transverse muscle; *SLM*, superficial longitudinal muscle; *SU*, suckers; *TR*, trabeculae; *TM*, transverse muscle; *TV*, superficial tentacular vein (Kier, 1982).

elongated to capture prey in as little as 15 msec (MESSENGER, 1968; KIER, 1982). These muscles differ in their ultrastructure from all other cephalopod muscles (KIER, 1991), and their specialized fibers have cross striations, short sarcomeres, and thick filaments (KIER & SCHACHAT, 1992).



1



2

FIG. 30. 1, Transverse section of arm of *Mastigoteuthis* (Oegopsida) showing reticulate tissues (Nixon & Dilly, 1977); 2, sucker and peduncle of *Cirrothauma murrayi* (Cirrata), drawn from a histological section showing loose tissues and thin band of muscle; *amct*, acid-mucopolysaccharide-containing tissue; *ocsp*, outer core of sucker peduncle (Aldred, Nixon, & Young, 1983).

The eight arms are similarly organized. Each has an axial nerve cord surrounded by obliquely striated, transverse muscle fibers (Fig. 29.2) (KIER, 1985), which extend peripherally as trabeculae, to insert on fibrous connective tissue sheets on the oral and aboral sides of the arms, and laterally, on oblique muscles (Fig. 29.2). Bundles of longitudinal muscle fibers lie between the trabeculae. In octopods, the transverse muscle mass is deepest aborally, thinnest orally, and intermediate laterally, and there are three sets of oblique muscles: internal, median, and external. Histological staining shows the tissues of the arms of a number of coleoids to have little organization, for example, *Cirrothauma* (ALDRED, NIXON, & YOUNG, 1983) and *Vampyroteuthis*; and in some, the tissue is reticulate or lacelike, for example, *Mastigoteuthis* (Fig. 30) (DILLY, NIXON, & YOUNG, 1977) and *Histioteuthis* (CLARKE, DENTON, & GILPIN-BROWN, 1979). The arms or tentacles of a Jurassic coleoid, *Belemnoteutis*, have longitudinal muscle fibers throughout; fibers with other orientations were not observed (KEAR, BRIGGS, & DONOVAN, 1995).

The musculature of the suckers was first described by GIROD (1884), and more recently by KIER and SMITH (1990). There are radial, circular, and meridional muscles. The suckers of Decapodiformes and many Octopodiformes possess a sphincter muscle (GUÉRIN, 1908; KIER & SMITH, 1990), but in those of Vampyromorpha and some Octopodiformes, this is absent, so the chamber is simple (Fig. 31) (NIXON & DILLY, 1977). The peduncle or stalk of the sucker is usually muscular, but in *Cirrothauma* (ALDRED, NIXON, & YOUNG, 1983), *Argonauta* (NIXON & DILLY, 1977), and a few other coleoids, there is reticulate or loosely organized tissue.

The muscles of the fins of *Sepia officinalis* and of two loliginids have been shown at the ultrastructural level to consist of highly organized, tightly packed, obliquely striated fibers arranged in three mutually perpendicular planes (Fig. 32) (KIER, 1989). Different arrangements occur in the fins of

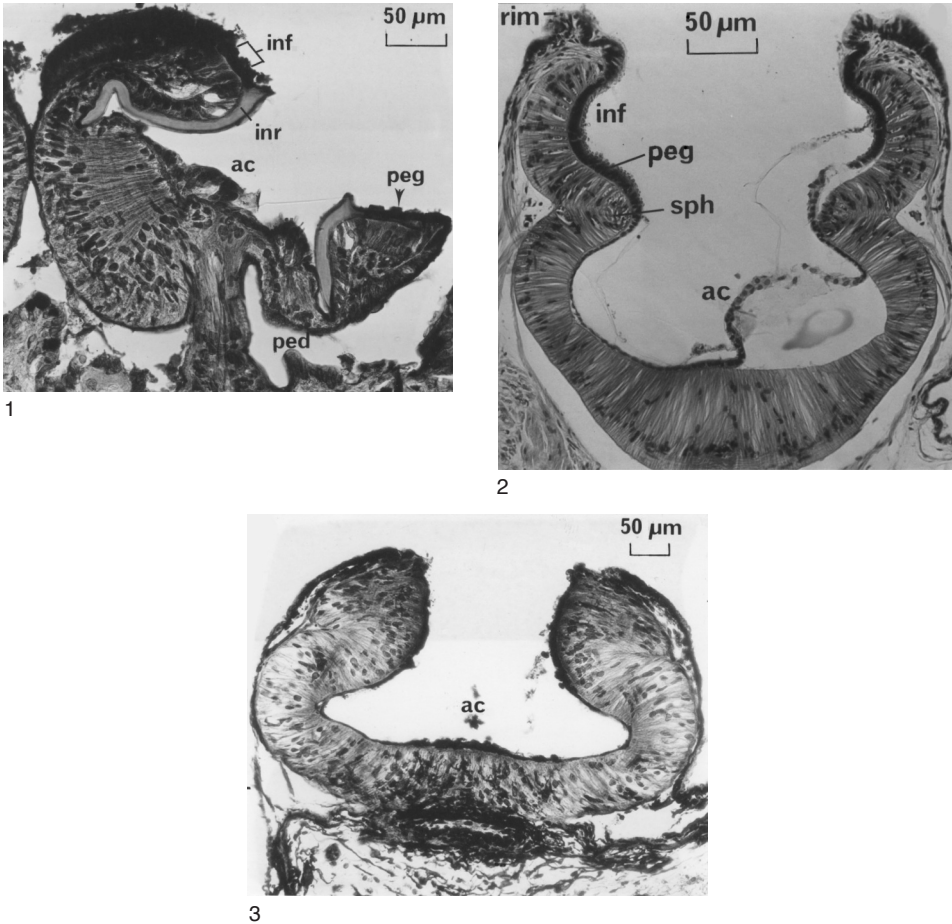


FIG. 31. Sagittal sections through suckers of arms of 1, *Teuthowenia megalops* (Oegopsida), showing muscles, acetabulum, infundibulum, and inner chitinous ring; 2, *Octopus vulgaris* (Incirrata) showing sphincter muscle between acetabulum and infundibulum; 3, *Vampyroteuthis infernalis* (Vampyromorpha) showing its relative simplicity; *ac*, acetabulum; *hil*, hillock; *inf*, infundibulum; *inr*, inner ring; *ped*, peduncle; *peg*, projecting process of infundibulum; *sph*, sphincter; *rim*, surface of small sucker with tiny hillocks superimposed on many of the radially arranged cushions (Nixon & Dilly, 1977).

other coleoids. The strange fin of the dorsoventrally flattened oceanic oegopsid squid *Ctenopteryx* (*Ctenopteryx*) has so-called fin rays. These consist almost entirely of muscles and connective tissue forming muscular-hydrostat supports (KIER, 1988) and serving both for support and movement; the fin muscles are attached to small, toothlike supports of hyaline cartilage at their base and a double web of membranous sheets (J. Z. YOUNG, 1991b). The arrangement of the muscles of the fin of an Upper Jurassic fossil

coleoid, *Trachyteuthis* (DONOVAN, 1995), is similar to that found in extant *Vampyroteuthis*, Cirrata, and Decapodiformes (R. E. YOUNG & M. VECCHIONE, personal communication, 1995).

INK SAC AND INK

ARISTOTLE (384–322 BCE; see translation by THOMPSON, 1910) recorded that the ink sac is largest and the ink most abundant in the cuttlefish, and that the animal discharges the ink when frightened. In some countries,

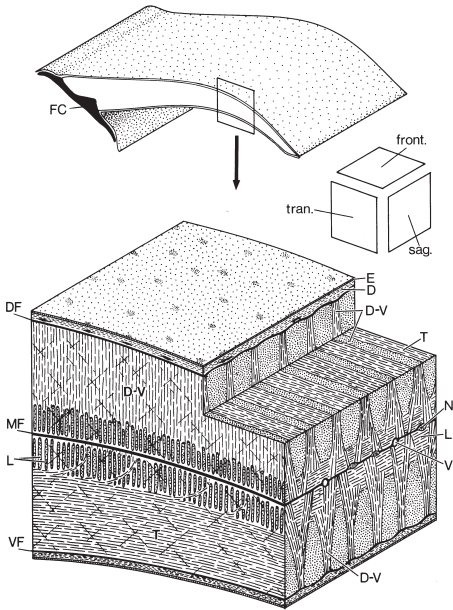


FIG. 32. Schematic diagram showing microanatomy of fin of *Sepia officinalis*; D, dermis; DF, dorsal fascia; D-V, dorsoventral muscle; E, epidermis; FC, fin cartilage; L, longitudinal muscle; MF, median fascia; N, fin nerve; T, transverse muscle; V, blood vessel; VF, ventral fascia (Kier, 1989).

the common name for the cuttlefish is derived from the word for ink, for example, Tintenfische (German) and Inktvis (Netherlands), and yet there is a paucity of information about the ink sac. SCHNEIDER (1784), in an early classification, used the term *Blakfisch* for the cephalopods, presumably from their capacity to expel ink. Although included in many descriptions, the ink sac is usually noted as being present or absent with rarely any further comment. This oversight is particularly unfortunate, as the ink sac can survive fossilization (for example, CRICK, 1897; NAEF, 1922; DONOVAN, 1977; and *Treatise Online*, Part M, Chapter 21D).

An ink sac or ink reservoir is present in most living Decapodiformes and Octopoda (except very deep-living species) but is absent from Cirrata (G. L. VOSS, 1988b) and Vampyromorpha (J. Z. YOUNG, 1977). The ink sac is one part of the ink-gland

complex, the others being the ink gland and the ink-sac duct. The complex usually lies ventral to the visceral mass, the duct running anteriorly along the right side of the rectum, which it enters on the dorsal side, close to the anus. During ontogeny, the ink-gland complex of *Sepia officinalis* is displaced from its typical position above the hind intestine to the right and grows toward the posterior end of the mantle sac, into which the ink sac fits in more mature animals (Fig. 5) (TOMPSETT, 1939). *S. officinalis* has an ink sac 30 to 40 mm in diameter, with a capacity of 20 to 30 cl and a duct 8 to 15 mm in length. Those of *Loligo vulgaris* and *Octopus vulgaris* are 8 to 12 mm and 12 to 17 mm in diameter respectively; unfortunately, the sizes of the animals were not recorded (GIROD, 1882). The ink sac is partially embedded in the digestive gland in some species; and in a few, for example, *Cycloteuthis*, photophores are associated with the ventral side of the ink sac (HERRING, 1977).

Among extant coleoids, the position of the ink sac varies between the anterior and the posterior end of the mantle; its shape ranges from being round and saclike to pear shaped. It may be large or small, relative to the size of the animal and appears to differ between genera and perhaps even species (CHUN, 1910a, 1915; NAEF, 1922, 1923), but no studies have been made as to its possible value as a characteristic feature. The ink sac is well preserved in a number of fossil coleoids, and illustrations show variations in its position, shape, and size but also similarities among various specimens of the same species. One example is *Plesiotheuthis prisca* (NAEF, 1922; DONOVAN, 1977; MEHL, 1990), in which the ink sac is small relative to the mantle length and is round and saclike. It is somewhat similar in *Mastigophora brevipinnis* (DONOVAN, 1983). The ink sac of *Lioteuthis* is an elongated pear shape (NAEF, 1922). It is similarly shaped in the belemnite *Belemnoteutis antiquus* and is moderately large in relation to the whole animal; it is situated immediately anterior to the phragmocone (approximately halfway

along the mantle) (DONOVAN & CRANE, 1992).

The morphology of the ink sac of several living coleoids was described by GIROD (1882) and the ultrastructure in *Loligo pealei* by VOGEL and MCGREGOR (1964). The dorsal glandular portion of the ink complex consists of membranous trabeculae and a glandular epithelium, which secretes the ink; a large conical reservoir for the ink; and a duct leading from the reservoir to the anal chamber (Fig. 33). The epithelium consists of two types of cells. One predominates in the central region of the gland and is responsible for the production of granules of the pigment melanin. The distal end of the duct of the ink sac may have valves or be surrounded by a sphincter. The wall of the sac is formed of an inner sheet of epithelium, a muscular layer, and an outer sheet of connective tissue (WILLIAMS, 1909). Circular muscle fibers can be seen in the wall of the ink sac of *Plesiotenthis* (D. T. DONOVAN, personal communication, 1998). In translucent or semitranslucent coleoids, the reservoir portion of the ink sac has an additional thick layer formed of iridophores, giving it a silvery sheen so that the darkly pigmented ink within the sac is obscured (MANGOLD, BIDDER, & PORTMANN, 1989a).

The ink is a suspension of nearly pure melanin; it is usually black and serves as a visual cloaking device as it hangs suspended like a cloud in the water after ejection as a plume. In some loliginids, it also acts as a defensive olfactory or alarm substance (LUCERO, FARRINGTON, & GILLY, 1994). The ink of the cuttlefish, *Sepia officinalis*, consists of uniformly spherical granules of melanin, 56 to 161 nm in diameter (FLOOD, DEIBEL, & MORRIS, 1990). An ink sac found in the phragmocone of an unnamed coleoid of the Middle Pennsylvanian is divided into compartments. The substance within the sac has a globular ultrastructure that is identical to the dried ink of a Recent loliginid squid, *Loligo forbesi* (DOGUZHAIEVA, MAPES, & MUTVEI, 2010). The infrared spectra of the ink sacs from a fossil, *Loligosepia (Geotheutis)*

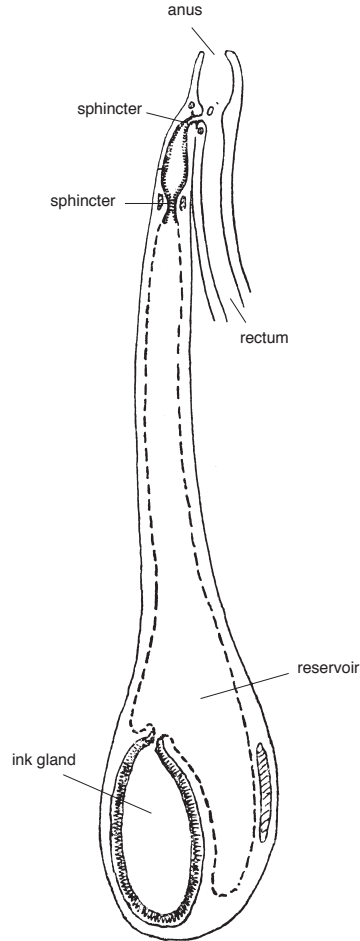


FIG. 33. Ink sac of *Sepia officinalis* (Girod, 1882).

bollensis (180 Ma), and from a Recent *Sepia officinalis*, indicate that the fossil ink is unchanged melanin (BEYERMAN & HASENMAIER, 1973). Ultrastructural studies of the ink sac of *Loligo pealei* show that melanogenesis is heralded by the aggregation of cytoplasmic granules forming melanin spheres that range from 40 to 50 nm (BUDELMANN, SCHIPP, & VON BOLETZKY, 1997); these group into packets to be expelled into the ink reservoir (VOGEL & MCGREGOR, 1964). Spherical granules of several sorts, differing in size and electron density, are present in the ink sac of *Heteroteuthis dispar* (DILLY & HERRING, 1978). The melanins of coleoid

ink have a high molecular weight and no exact stoichiometric chemical structure or corresponding assignable formula (FOX, 1966, 1983). The amino acids tyrosine and DOPA (3,4-dihydroxyphenylalanine) are involved and are converted by enzymes to melanin in the ink sac (WAITE, 1992). The enzyme tyrosinase is present in the ink sac (PROTA & others, 1981). The highest absorbance spectrum of the ink of *Sepia officinalis* is 230 to 270 nm (PAULIJ & others, 1991). The ink is relatively opaque to infrared rays (MITCHELL, 1937) and x-ray (W. STÜRMER, personal communication, 1981).

Ink made from *Sepia* was referred to by Romans in classical texts (MITCHELL, 1937). BUCKLAND (1836) commented that GEORGES CUVIER (1817) drew his illustrations of extant *Sepia* with ink extracted from its own ink sac. BUCKLAND (1836), too, used the ink extracted from fossil specimens to draw the remains of extinct species, including *Loligosepia* from the lower Lias of Lyme Regis, Dorset.

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