Cephalic Cartilage of Cephalopoda

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ABSTRACT

The structure of the cephalic cartilage of cephalopods at the light- and electron-microscope levels is briefly reviewed, together with its biochemical properties. The cartilage usually takes the typical hyaline form, but in some cephalopods it is reticulate. A systematic survey includes brief descriptions of the cephalic cartilage in the few cephalopods for which details are available. The very complexity of this structure suggests it could prove valuable as a systematic character.

Introduction

The majority of cephalopods possess a skeletal structure around the central nervous system. Owen (1832:16) noted that "this skeleton is cartilaginous, yields readily to the knife, and in texture and semi-transparency closely resembles the cartilage which constitutes the skeleton of the skate." This interpretation of the tissue was accepted until about the turn of the century, when it was questioned as to whether invertebrates possessed "true" cartilage. A period of doubt and uncertainty lasted until the 1960s, when studies, using various techniques, confirmed the earlier belief that Cephalopoda do possess true cartilage, although it differs in some respects from vertebrate cartilage (for reviews see Person and Philpott, 1967, 1969; Person, 1983).

Although it is small or reduced in some, the cephalic cartilage occupies much of the region between the eyes in most cephalopods. Despite this its gross morphology has been overlooked and is rarely referred to in systematic descriptions. This is perhaps not surprising because isolation of the cartilage is not easy to do after fixation, and it necessitates the destruction of the head.

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Cephalic Cartilage

The word cartilage comes from the Latin *cartilago*, meaning gristle. Person and his colleagues, in a series of experimental studies, demonstrated that the criteria established for this tissue in vertebrates also apply to invertebrates (for reviews see Person and Philpott, 1963, 1967, 1969; Bairati, 1985). The results of these investigations led Person (1983:33) to modify 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."

The basic and constant component of cartilage is the cartilage cell surrounded by a territorial matrix it has itself secreted. Cartilage is a form of connective tissue with polymorphic cells suspended in a matrix (see Moss and Moss-Salentijn, 1983) and is chemically characterized by the presence of collagen, glycosaminoglycan complexes (= mucopolysaccharides) (see Lash and Vasan, 1983), and water.

Cartilage cells, the chondrocytes, are polymorphic and reside in lacunae. Each lacuna may contain one, two, or more chondrocytes, and when several are present it constitutes a cell nest. Young chondrocytes, the chondroblasts, are flattened, becoming rounded when fully mature. Each chondrocyte has a nucleus, well-developed rough endoplasmic reticulum, and Golgi complex; these were described in *Loligo pealeii* Lesueur (Person and Philpott, 1963; Philpott and Person, 1970) using the transmission electron microscope. The chondrocytes have branching processes forming a system of interconnecting canaliculi that extend into the matrix. The matrix consists largely of fibers and an amorphous substance. Ultrastructural studies of the cephalic cartilage of *Loligo pealeii*, *Octopus vulgaris* Cuvier, and *Sepia officinalis* Linnaeus have revealed the presence of collagen fibrils (Philpott and Person, 1970),

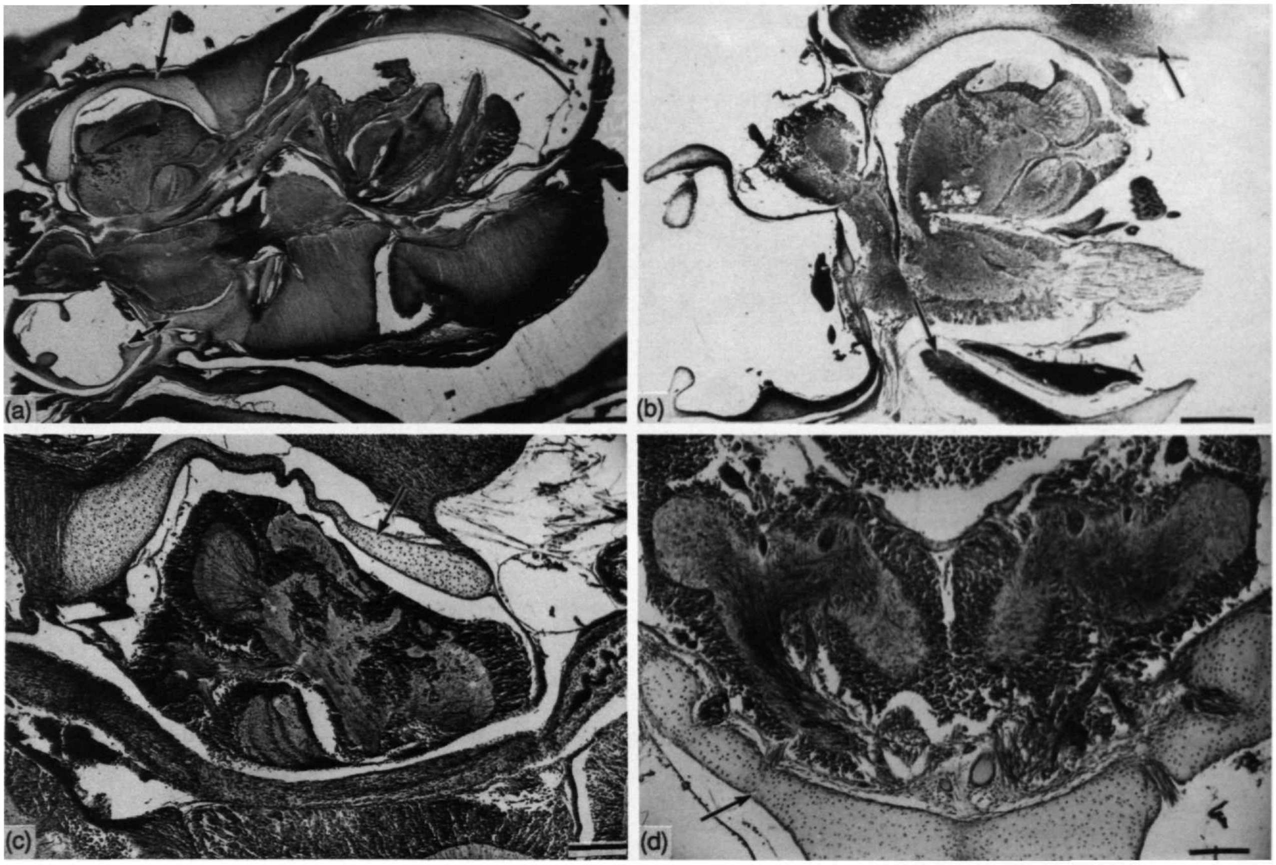

FIGURE 1.—*a, Alloteuthis subulata* (bar = 1 mm); *b, Chtenopteryx sicula*, note very thick dorsal portion of cartilage (bar = 0.5 mm); *c, Gonatus fabricii* (bar = 0.2 μm); *d, Teuthowenia megalops* (bar = 0.2 μm). Cephalic cartilage like that of vertebrate hyaline cartilage.

10–26 nm in diameter, with an indistinct periodicity and separated by a constant space (Bairati et al., 1987). The collagen fibrils were found to have a periodic structure similar to that of one of the types found in mammals (Bairati et al., 1989). The fibrils are arranged parallel to the surface in the superficial zones of the cephalic cartilage. Electron dense bodies of varying diameter and length are irregularly distributed among the collagen fibrils. These bodies are interpreted as anchoring devices for the collagen fibrils. Proteoglycan aggregates (30–45 nm in diameter, electron dense, and granular) adhere to the collagen fibrils, the anchoring devices, and the cellular surfaces (Bairati et al., 1987).

Few investigations have been made of the biochemistry of this cartilage in cephalopods, and the works by Person and Philpott (1969), Mathews (1967, 1975), Hunt (1970), Person (1983), and Kimura and Karasawa (1985) encompass most of the meager data available. Amino-acid analyses are available for *Loligo pealeii* (Philpott and Person, 1970) and *Todarodes pacificus* (Steenstrup) (Kimura and Karasawa, 1985); some differences are apparent between the two species. The composition of polyanionic glycosaminoglycans for four species of cephalopods is summarized by Person (1983).

The cephalic cartilage is glass-like in living cephalopods, being translucent, colorless, and clear to the naked eye, and cannot be discerned visually as a distinct structure. After death, or shortly after removal, this cartilage becomes opaque and bluish white. The cartilage encases the central nervous system and is perforated for the passage of nerves, blood vessels, and oesophagus (see Willey, 1900). Various sectors have muscle fibers and connective laminae deeply inserted in the superficial zone.

Histological sections of this cartilage in cephalopods have shown two types; the more usual form resembles hyaline cartilage (Figure 1) (Young, 1971), but the other form is

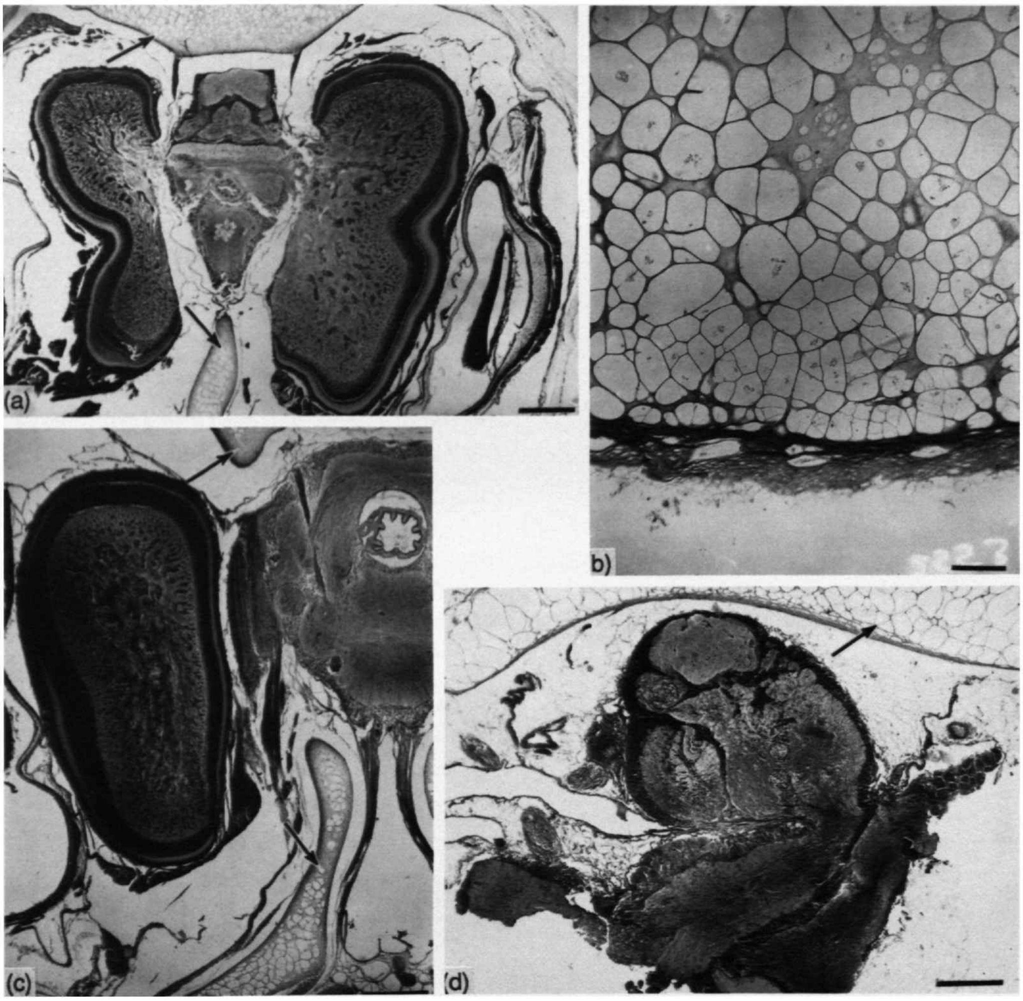

FIGURE 2.—*a*, *Abraliopsis* sp. (bar = 0.5 mm); *b*, *Architeuthis* sp. (bar = 0.5 mm); *c*, *Onychoteuthis* sp. (bar = 0.5 mm); *d*, *Mastigoteuthis* (bar = 0.5 mm). Cephalic cartilage reticulate and differs notably from that of cephalopods shown in Figure 1.

reticulate (Figure 2). Reticulate cartilage is encountered mainly in the neutrally buoyant oegopsid squids (Clarke et al., 1979). In some squids the network is very loose (Figure 2), but at the surface, where growth occurs, the appearance is that of typical cartilage. From a study in progress (Nixon and Young, in prep.), the type of cartilage present in the head has been tabulated for a number of cephalopods (Table 1). It is notable that of the squids possessing reticulate cephalic cartilage most are neutrally buoyant, but *Onychoteuthis* and perhaps *Lycoteuthis* are nonbuoyant forms (Clarke et al., 1979).

METHODS.—The simplest method for extracting the cephalic cartilage without damage is to take fresh material and, after appropriate external measurements, remove the whole head and place it in sea water at room temperature until the tissues fall away to leave a clean skeleton. Animals frozen immediately after capture can be treated in the same way because the musculocartilage attachments are readily broken in cephalopods after such low temperature treatment. After fixation, proteolytic enzymes can be used to break down the tissues and adhering muscles, but, if possible, chemical macerating agents should be avoided because many lead to loss of skeletal material. An alternative is the use of thick serial sections of the whole head so that graphic reconstructions of the cephalic cartilage can be made (see Pantin, 1946), aided by a suitable computer program.

TABLE 1.—The distribution of reticulate cartilage among cephalopods for which histological sections are available (Nixon and Young, in prep.).

Family	Genus	Cartilage tissue	
		normal	reticulate
Sepiidae	*Sepia*	×	
Sepiolidae	*Sepiola*	×	
Loliginidae	*Loligo*	×	
	Alloteuthis	×	
Lycoteuthidae	*Lycoteuthis*		×
Enoploteuthidae	*Abraliopsis*		×
	Pyroteuthis	×	
	Pterygioteuthis	×	
Octopoteuthidae	*Octopoteuthis*		×
Onychoteuthidae	*Onychoteuthis*		×
Cycloteuthidae	*Discoteuthis*		×
Gonatidae	*Gonatus*	×*	
Architeuthidae	*Architeuthis*		×
Histioteuthidae	*Histioteuthis*		×
Neoteuthidae	*Neoteuthis*		×
Chtenopterygidae	*Chtenopteryx*	×	
Brachioteuthidae	*Brachioteuthis*	×	
Ommastrephidae	*Illex*	×	
	Todarodes	×	
Chiroteuthidae	*Chiroteuthis*		×
Mastigoteuthidae	*Mastigoteuthis*		×
Grimalditeuthidae	*Grimalditeuthis*		×
Joubiniteuthidae	*Joubiniteuthis*		×
Cranchiidae	*Leachia*	×	
	Liocranchia	×	
	Taonius	×	
	Egea	×	
	Sandalops	×	
	Liguriella	×	
	Teuthowenia	×	
	Helicocranchia	×	
	Galiteuthis	×	
	Bathothauma	×	
Octopodidae	*Octopus*	×	
Tremoctopodidae	*Tremoctopus*	×	
Argonautidae	*Argonauta*	×	
Vampyroteuthidae	*Vampyroteuthis*	×	

* small species.

Systematic Survey

SUBCLASS NAUTILOIDEA

Nautilus.—Owen (1832:16) described the internal skeleton of the head region of *N. pompilius* Linnaeus as "incomplete behind and the brain is protected only by its membraneous sheath. ... The central mass of the cartilage ... is situated on the ventral aspect of the oesophagus." Later, Keferstein (1862) sectioned the cartilage and illustrated its histological structure, and Griffin (1900) briefly described its morphology.

The cartilage is H-shaped and shows contiguity only with the more ventral parts of the central nervous system; its main relations are with the motor system and the funnel. The anterior pair of projections extend into the funnel and the posterior pair project upward to support the perioesophageal nerve ring. After examining and describing this structure, Willey (1900) commented that the cartilage surrounds no part of the central nervous system, is not perforated by any nerves, and is only traversed by one pair of blood vessels. The cartilage does, however, provide some support for the central nervous system and the statocysts.

ORDER SEPIOIDEA

Spirula spirula (Linnaeus).—The cephalic cartilage was described briefly by Huxley and Pelseneer (1895) and was included in their illustrations of the head region. It is a capsule, enveloping the central nervous system, from which prolongations extend laterally to support the optic lobes. Ventrally and anteriorly, the median projection provides attachment sites for brachial muscles. Anteriorly, the cartilaginous capsule is continued as an envelope of connective tissue at the junction of the pedal and brachial lobes of the brain. Retractor muscles of the funnel attach to the aboral face of the cartilage.

Sepia officinalis.—Early recognition and description of the cephalic cartilage was by Owen (1832:16), who wrote that "in *Sepia* this cartilaginous part completely encircles the oesophagus and on the dorsal aspect of that tube is dilated into a large cavity, which contains the brain." Later, the cartilage was isolated and illustrated by Keferstein (1862), who noted foramina for the passage of the nerves, flanges forming cups for the eyes, and statocysts attached posteroventrally.

Tompsett (1939) provided the most detailed description of cephalic cartilage yet available for any cephalopod (Figure 3*a*). The cephalic cartilage is symmetrical and complicated in form, and it serves for the attachment of the head retractor, the funnel adductor, the oculomotor, and the brachial and tentacular muscles. The orbital cartilages are formed by posterior lateral expansions with thin, wing-like extensions. Anteriorly, a stout, triangular bridge of cartilage unites the orbital cartilages ventrally. From this bridge a pair of delicate, wing-like blades, the trochlear cartilages, project anteriorly and dorsolaterally. Posteriorly, the statocyst cartilage lies between the orbital cartilages. Dorsally, the cerebral cartilage partly encloses the central nervous system and connects the orbital cartilages.

A number of foramina are present of which the single foramen magnum is the largest (Figure 3*a*). Through it pass the oesophagus, the perioesophageal sinus, the paired buccal arteries, the single duct from the paired posterior salivary glands, the paired visceral and pallial nerves, and the posterior head retractor nerves. The rim of the foramen has slight grooves where the nerves emerge. The remaining foramina are paired, those for the optic nerve being the largest, and they are as follows:

1. Optic tract foramen (incomplete), which also carries the olfactory, posterior oculomotor, and superior anterior ophthalmic nerves.

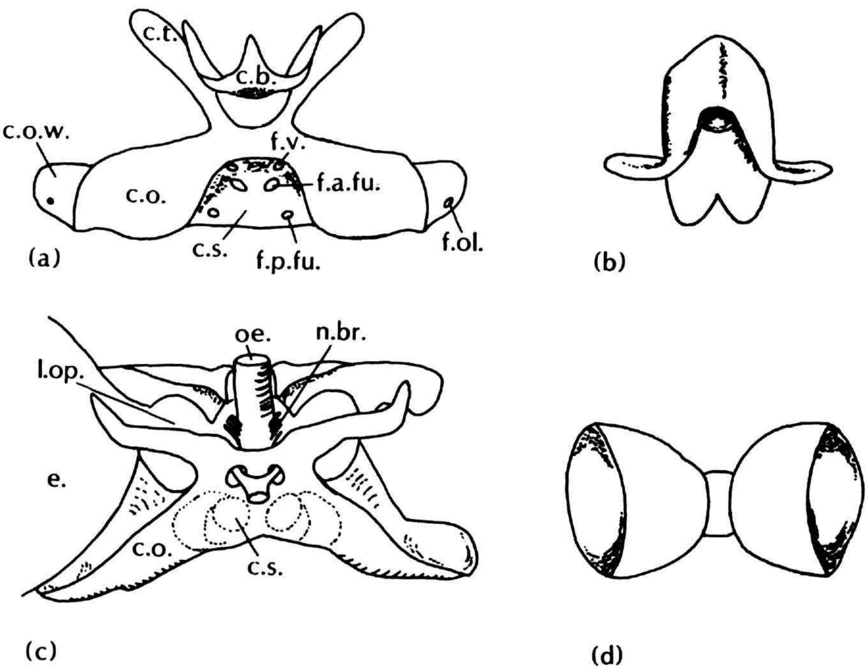

FIGURE 3.—Cephalic cartilage: *a, Sepia officinalis*, ventral surface (redrawn from Tompsett, 1939); *b, Gonatus fabricii*, dorsal surface (redrawn from Hoyle, 1889); *c, Vampyroteuthis infernalis*, ventral surface, with eye remaining in position on one side (optic lobes, oesophagus, and statocysts (dotted outline) remain to show relationships to cartilage (redrawn from R.E. Young, 1964)); *d, Eledone cirrhosa*, dorsal surface and orbital cartilage (redrawn from Isgrove, 1909). (Abbreviations: c.b., brachial cartilage; c.o., orbital cartilage; c.o.w., wing of orbital cartilage; c.s., statocyst cartilage; c.t., trochlear cartilage; e., eye; f.a.fu., foramen of anterior funnel nerve; f.ol., foramen of olfactory nerve; f.p.fu., foramen of posterior funnel nerve; f.v., foramen for vein from head sinuses to cephalic vein; oe., oesophagus; n.br., brachial nerve; l.op., optic lobe.)

2. Superior posterior ophthalmic nerve foramen, on the posterodorsal surface of the orbit.
3. Inferior posterior ophthalmic nerve foramen.
4. Anterior oculomotor nerve foramen, close to the base of the trochlear cartilage.
5. Olfactory nerve foramen, which passes through the wing of the orbital cartilage.
6. Anterior funnel nerve foramen, which also carries the anterior funnel artery.
7. Posterior funnel nerve foramen, near the base of the posterior surface.
8. Postorbital nerve foramen, on the posterodorsal surface.
9. Collar nerve foramen, near the emergence of the pallial and posterior head retractor nerves.
10. Anterior head retractor nerve foramen, near the collar nerve foramen.
11. Crista nerve foramen and macular nerve foramen, which lead into the statocyst. Two further foramina permit blood vessels to pass through.
12. Ophthalmic vein foramen, on the posteroventral surface.
13. Large foramen for the vein from the head sinuses, anteromesial to the ophthalmic vein foramen.

The histological structure of the cartilage of *Sepia* was described by Nowikoff (1912) and is of typical hyaline form (Table 1). Transmission electron microscopy has revealed a network of collagen fibrils, with well-defined periodic banding, embedded in a great quantity of proteoglycans (Bairati et al., 1987).

ORDER TEUTHOIDEA

SUBORDER MYOPSIDA

A study of the cephalic cartilage, including a morphometric analysis, has been carried out in nine myopsid squids, namely *Uroteuthis duvauceli* (Orbigny), *Doryteuthis plei* Blainville, *Loligo pealeii, Alloteuthis africana* Adam, *Loliolus investigatoris* Goodrich, *Loliopsis diomedeae* (Hoyle), and *Sepioteuthis sepioidea* (Blainville) (deMaintenon, 1990). Anatomical landmarks on the posterior surface of the cranium were used to make a series of measurements. These were analyzed statistically and indicated that the morphology of the cephalic cartilage did differ between the species examined.

Loligo pealeii.—The cephalic cartilage was described by Williams (1909). It has a large foramen magnum through which the oesophagus, visceral nerves, and head arteries pass. Laterally, a concavity provides support for the eyes and the optic lobes. The preorbital cartilages, attached side by side, extend outward and forward between the eyes for attachment of the eye muscles. The statocysts are embedded in a pair of rounded projections posteroventrally.

Two or three pairs of foramina for statocyst nerves pierce the ventral wall of the capsule. A foramen at the edge of the depression for the pedal lobe allows the passage of the crista nerves. Close to this lies the macular nerve foramen. Two pairs of foramina penetrate the cartilage just anterior to the statocysts; one pair for the funnel nerves and the other for veins from the orbital sinuses to the anterior vena cava. The presence of several small foramina to allow the passage of blood vessels and nerves were noted but were not described.

SUBORDER OEGOPSIDA

Gonatus fabricii (Lichtenstein).—Hoyle (1889) illustrated the cephalic cartilage of this oceanic squid after reconstructing its form from serial sections of one specimen and the damaged head of another. The head cartilage resembles an elongated box, open anteriorly and with the statocysts attached posteriorly (Figure 3*b*). Lateral flanges provide support for the eyes. The cartilage is of the typical hyaline form (Figure 1*c*, Table 1).

Architeuthis sp.—The head of *Architeuthis* consists largely of cartilage, on either side of which lie cavities for the eyes and optic lobes. The central nervous system, which is relatively small, proved almost impossible to find and extricate from this massive cartilage (Nixon and Young, in prep.).

Many tissues of *Architeuthis* float, and analyses have shown an accumulation of ammonium ions so that the animal can achieve near-neutral buoyancy (Denton and Gilpin-Brown, 1973; Clarke et al., 1979). This chemical aid to buoyancy is augmented by reticulate tissues present even in the cephalic cartilage (Figure 2*b*, Table 1).

Todarodes sagittatus (Lamarck).—Posselt (1891) described the cephalic cartilage of this ommastrephid squid as a transversely oblong, flat, broad cup-shaped ring, with the dorsal and ventral surfaces strongly curved anteriorly, the lateral parts being flat (see also Knudsen and Roeleveld, 1991). There is a large foramen for the passage of the oesophagus, salivary duct, blood vessels, and nerves, and there are openings for the olfactory, collar, and other nerves. The concave anterior and lateral parts of the head cartilage support the eyes with, in addition, two delicate, curved cartilaginous supports on each side.

ORDER VAMPYROMORPHA

Vampyroteuthis infernalis Chun.—The central nervous system is encased on the posterior and ventral surfaces by the cartilage but not on the anterior and dorsal sides (Figure 3*c*) (R.E. Young, 1964). A foramen magnum, on the posterior surface, allows the oesophagus, major nerves, and arteries to pass through. A foramen for the cephalic vein lies on the ventral surface. Much of the posterior side of the cartilage is occupied by the statocysts. Three projections form the orbital fossa and provide support for the eye. The cartilage itself is reticulate in form (Table 1).

ORDER OCTOPODA

Eledone cirrhosa (Lamarck).—Isgrove (1909:66) described "a tubular cartilaginous capsule, the anterior and posterior ends of which are closed by tough membranes ... pierced for the passage of the oesophagus, posterior salivary duct, pharyngeal arteries etc.," but she did not indicate any foramina in her figure (Figure 3*d*). Sections of the cartilage were described as being "built up of oval cells surrounded by a clear matrix." The cells have large oval nuclei and fine cytoplasmic processes that run down canals allowing intercommunication.

The cephalic cartilage of *Eledone cirrhosa, E. moschata* (Lamarck), and *Octopus vulgaris* is of the typical hyaline form (Young, 1971).

Discussion

This brief survey of the cephalic cartilage in cephalopods shows, from the most detailed account available, that it is a complex structure with many specialized features. It is difficult to make comparisons but some similarities can be seen in the cephalic cartilage of *Vampyroteuthis* and *Sepia* (Figure 3*a,c*), although the morphological details are insufficient to discuss their relationships. Reconstructions of the central nervous system of *Nautilus* (Young, 1965), *Sepia* (Tompsett, 1939), *Loligo* (Young, 1976), *Mastigoteuthis* (Young, 1977), *Vampyroteuthis* (R.E. Young, 1964; Young, 1977), *Octopus* (J.Z. Young, 1964), and *Argonauta* (Boycott and Young, 1956), for example, show that the morphology of the brain and the arrangement of the nerves do vary and, by implication, so must the gross morphology of the cephalic cartilage, although this remains to be investigated. The central nervous system differs markedly among the Coleoidea in its size and shape, as well as in the position of its major lobes and the emerging nerves (Nixon and Young, in prep.); by implication there are likely to be considerable variations in the shape and orifices of the cephalic cartilage. The eyes, buccal mass, encircling arms, and other features of the animal vary, as do the position and size of the foramina for the oesophagus and blood vessels in relation to the cephalic cartilage. Morphometric investigations of the relationships between various anatomical features of the cephalic cartilage and of the foramina should prove of value in taxonomic studies.

The cartilage may, or may not, enclose the central nervous system. The H-shaped cartilage of *Nautilus* lies below part of the ventral surface of the circumoesophageal nerve ring (Young, 1965), and Lankester (1891) named it the capitopedal cartilage. In the coastal coleoids, such as *Octopus,* *Sepia,* and *Loligo,* the cartilage does encase the brain and has been variously called perineural, cephalic, cranial, and head cartilage, and the chondrocranium. Although recognizing these two forms of cartilaginous skeleton associated with the brain, it is proposed that the term cephalic cartilage be used for both and for any new forms that may be found with further investigation.

Recommendations

An initial investigation of the cephalic cartilage as a systematic character should be a comparison of this structure in readily available cephalopods. The gross morphology of this structure in coastal genera, such as *Sepia, Loligo,* and *Octopus,* could be described, and selected features could be subjected to morphometric analyses to determine the value of the cephalic cartilage as a systematic character. If it should prove useful, the study could be extended to several genera of the same family and to species of the same genus. The major disadvantage in using the cephalic cartilage is the necessary destruction of the head region in order to extract it without damage.

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