

# 17 Life history strategies in fossil cephalopods

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## 1 Introduction

The cephalopods inhabiting today's oceans show a wide variety of morphology, reflecting the great diversity of habits and habitats to which they have adapted. Almost all are shell-less, or have reduced internal shells or organic pens. Of the extant cephalopod genera, only *Nautilus* and *Argonauta* maintain external calcareous shells. In the past, however, the externally shelled, or ectocochliate cephalopods comprised the majority of cephalopod diversity, rather than the very small minority existing today. From the inception of the Cephalopoda during the Cambrian Period, until the extinction of the ammonoids at the end of the Cretaceous, it is fairly certain that the ectocochliate cephalopods were the most diverse cephalopods.

In this chapter we will briefly examine aspects of the life cycles of some of these now-extinct cephalopod groups. Because of the enormous diversity of cephalopod types that have existed in the long interval since the first known cephalopods, we can only scratch the surface of this fascinating group of extinct forms. We intend to concentrate on those features which allow direct comparison with life history strategies of living cephalopods, especially developmental patterns as interpreted from the shells.

## 2 The cephalopod fossil record

The fossil record of the cephalopods is dominated by the ectocochliates. Because of their easily fossilized calcareous shells, these forms left us with a rich fossil record, that is now well understood in its major features (see Teichert, 1967). The evolutionary history of the coleoids, however, is much more poorly understood. Although many coleoids, such as *Spirula*, sepiids, and other minor groups had hard parts, probably the vast majority left



Fig. 17.1 Fossil coleoid collection from Solnhofen Limestone, (Jurassic) Germany. The specimen, housed in the British Museum (BH 865) is an unidentified teuthoid or perhaps an octopod, demonstrating rare preservation of soft parts

fossils only under the most extraordinary, and rare circumstances (Fig. 17.1). Occasionally, certain sedimentary conditions allowed the preservation of soft part remains which give us tantalizing glimpses of life of the past. The Upper Jurassic Solnhofen limestone, Lower Devonian Hunsbruck slate, and several Middle Jurassic claystones in France do show preservation of coleoids, sometimes in exquisite detail. Sadly, these deposits are rare, leaving us with major gaps in our understanding of the history and evolution of the major groups of present day cephalopods.

The major evolutionary transitions within the ectocochliates and endocochliates (internally shelled cephalopods) are shown in Fig. 17.2. The first major group to arise were the nautiloids, which appear to have been derived from non-torted archaeogastropod-like molluscs in the mid to late Cambrian Period (Bandel, 1982). The major adaptive breakthrough was the formation of the phragmocone, or gas-filled chambers within the external shell. As discussed by Yochelson *et al.* (1971), this evolutionary devel-

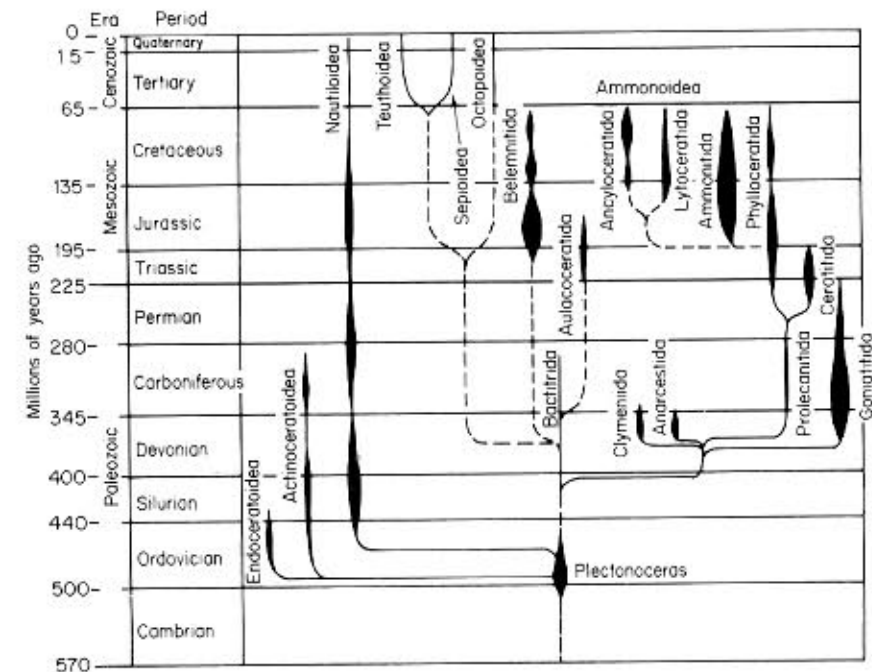


Fig. 17.2 Evolutionary tree of cephalopods, modified from Lehmann, 1981. Recent discoveries include new findings of an extensive suite of Cambrian nautiloids, (Chen & Teichert, 1983), as well as new discoveries of early coleoids of Devonian age (Bandel *et al.*, 1983)

opment involved partially sealing off the back of the shell with calcareous chambers that communicated with the rest of the animal through a strand of flesh. This strand, the incipient siphuncle, then emptied the chambers of liquid. Recent work by Chen & Teichert (1983) has vastly increased our understanding of the Cambrian Period cephalopods.

The Ordovician radiation of the nautiloids was one of the great adaptive radiations of the fossil record. A bewildering array of forms is found in Ordovician strata, and by mid-Ordovician Period time over two hundred genera had evolved. One group of nautiloids, the michelinoceratids, gave rise to the bactritids, a minor group of nautiloid-like forms which differed from other nautiloids in details of juvenile development and septal morphology. The bactritids in turn appear to have been the ancestors of the ammonoids, which first appeared during the early Devonian Period (Erben, 1964). The first coleoids appear at about the same time (Bandel *et al.*, 1983). The ammonoids and nautiloids remained at approximately equal diversity throughout the Paleozoic Era. In the Mesozoic Era, however, the ammonoids far exceeded the nautiloids in species richness and abundance, at least until the end of the Cretaceous, when all remaining ammonoids became extinct. The coleoids are best represented in the fossil record by the belemnoids and aulacoceratids, which appeared in some numbers late in the Paleozoic Era, and became quite abundant during the Mesozoic Era. Virtually all of the belemnoids also went extinct at the end of the Cretaceous Period. The remaining ectocochliates, the nautiloids, remained at low diversity through the Tertiary Period and into the present.

### 3 Juvenile development in fossil cephalopods

As is documented elsewhere in this volume, all known living cephalopods undergo direct development. Reconstruction of developmental history in fossil cephalopod groups, based on early shell morphology, indicates that this developmental pattern has been characteristic of the cephalopods since their inception.

Although the fossil cephalopod groups show a bewildering profusion of juvenile and adult shell morphologies, the developmental history of the earliest shell portions appears to have proceeded along one of only two possible paths. As in recent cephalopods, these two developmental strategies appear to be related to egg size. The size, morphology, and sculpture of earliest shell morphology depended on the nature of the yolk substrate on which they grew, and specifically the amount of yolk present within the egg. In those eggs thought to be of 1–3 mm diameter, the initial shell portions were spherical or cap-shaped. In contrast, the initial shell portions

of the fossil cephalopods producing eggs of greater than 3 mm diameter were flattened discs that showed a linear furrow along one side of the shell.

Both types of initial shells are represented among living cephalopods (*Nautilus*, *Sepia*, *Sepiella*, and *Spirula*), allowing us to infer the course of shell development in fossil forms (Bandel & Boletzky, 1979). In both types of early shells, initial shell deposition is accomplished by the shell gland, a rudiment of the mantle. These specialized ectodermal cells differentiate early in development into three distinct types of secretory epithelia, which can be termed periostracum, shell, and muscle mantle. It is still unknown if the periostracum, at least in *Nautilus*, is equivalent to that in other molluscs. Periostracum mantle produces the organic layers of periostracum; these form the outer layer of most mollusc shells, and form the earliest shell stage (Primary shell) in all shelled cephalopods. The shell mantle secretes calcium carbonate crystals and interlayered organic layers on to the organic matrix of the periostracum. This type of mantle cell can produce a variety of aragonitic shell microstructures, such as prismatic, lamellar, or nacreous layers. The final epithelial type, muscle mantle, is used to organize viscera-shell contacts, such as attachment zones of muscles on the shell wall. In ectocochliate cephalopods this mantle is used to organize shell shape, while in endocochliates it evolves into the characteristic muscular mantle, and may produce internal organic or mineral deposits of either calcite or aragonite. All three mantle types arise during development, and their relative size and order of appearance, in large part, dictates the morphology and ultrastructure of the shell that is produced among the various taxa.

In the living endocochliates (such as *Spirula* and *Sepia*, forms with internal shells) as well as the last ectocochliate (*Nautilus*), the primary shell is wholly organic. It is produced entirely by the periostracal mantle epithelium, and shows no growth lines. In the fossil taxa with small eggs, the periostracum mantle is thought to have grown over the spherical, visceral part of the embryo; as the periostracum mantle began to secrete the organic primary shell, it followed the shape of the underlying viscera, and thus took on a spherical shape as well. Irrespective of later juvenile shell shape, which could be straight orthocones (as in some orthoceratid nautiloids and belemnites), slightly curved cryptocones (bactritids, many aulacoceratids), or coiled planispirals (ammonites), the primary shell in these forms was always spherical. This primary shell served as a template for subsequent calcareous deposition growing into, and over the surface of the organic shell. The organic shell maintained its shape during calcification, resulting in a spherical first chamber, or caecum, of the subsequent embryonic shell.

In those cephalopods producing large eggs, the embryo grew at one end

of a large yolk mass, was disc-like, and initially covered only a small portion of the yolk. The embryo in these forms (such as *Sepia* and *Nautilus*) is flattened in shape, and the primary shell forms along one side of the embryo. The middle portion of this flattened, disc-shaped primary shell is attached to the visceral mass along a centrally located, linear groove. This central attachment area leaves a linear scar on the primary shell, called the cicatrix. During embryonic development, the primary shell is deformed by organogenesis of the embryo. Subsequent calcification of the primary shell covers the organic layers, but leaves a record of this central scar. Primary shells with cicatrix are today formed by *Nautilus* and *Sepia*, and can be found in many fossil nautiloids.

In both of these primary shell types, additional development of the shell occurs within the eggs. In both, the hatching juvenile has completed at least one, and usually several functional air chambers. Details of development within the egg are documented below.

#### 4 Ammonoids

Ammonoids are first found in Lower Devonian strata, (Fig. 17.3) and lasted until the end of the Cretaceous Period. They may have evolved as many as



Fig. 17.3 One of the earliest ammonoids, *Gyroceratites* from Devonian strata. This species is transitional between the ancestral bacritids and the true ammonoids. Radiograph of black shales reveals internal structures. Specimen hatched after one half whorl of growth, which on this specimen is at about the point of the sixth septum.

10 000 different species (Lehmann, 1981), making them by far the most diverse group of cephalopods in the fossil record. This large number of species is a direct reflection of the diversity of shell forms evolved. However, in spite of the wide range of shell morphology shown by the adult shell, embryonic development appears to have been relatively similar in all species.

Development of the embryonic ammonoid shell has been the subject of repeated investigation over the last twenty years. Birkelund (1981) and Bandel (1982) have recently published large reviews on the subject, and the reader is directed to these sources for a more complete treatment, including introduction to the very large terminology. The following description will attempt to reduce the paleontological jargon as much as possible, although some terms are unavoidable.

Ammonoids appear to have hatched from small, round eggs of about 1 mm average diameter. Lehman (1967, 1981) and Muller (1969), claimed to have observed fossilized ammonite eggs within the body chambers of well preserved ammonoids. The best evidence for egg size, however, comes from the study of the hatching ammonite shells. The ammonoid shell presumed to have formed within the egg is termed an *ammonitella*, and differs from all later produced shell in its shell organization, especially shell microstructure of the mineral layers. The ammonitella shell wall is composed entirely of prismatic calcium carbonate (aragonite), secreted as distinct shell layers on the original organic template of the initial embryonic shell. All post-hatching shell wall contains a distinct layer of nacreous aragonite as well as prismatic aragonitic layers. The first septum of the ammonitella, which closes off the large protoconch from subsequently produced shell, also differs from subsequent septa in lacking a nacreous layer (Fig. 17.4).

The ammonitella consists of a large first chamber (the caecum of protoconch), surrounded by at least one complete whorl of shell deposited on top of it, thus largely covering the initial chamber itself. The outer shell walls of fossilized ammonitellas show a distinctive ornamental pattern of tubercles scattered across a smooth background (Bandel *et al.*, 1982; Bandel, 1982) (Fig. 17.5). The complete lack of shell growth lines, and the lack of shell breaks which characterize later parts of the shell are good evidence that the ammonitella was formed wholly within the egg.

Evolutionary trends within ammonitella morphology, both through time, and between contemporaneous taxa have received scant attention. Russian workers (Drushchits & Khiami, 1970) have noted an interesting trend of decreasing ammonitella size through time with Devonian forms showing diameters of as much as 2 mm, but maximum sizes of less than 1.5 mm in Cretaceous forms. Birkelund (1981), however, noted that even in the



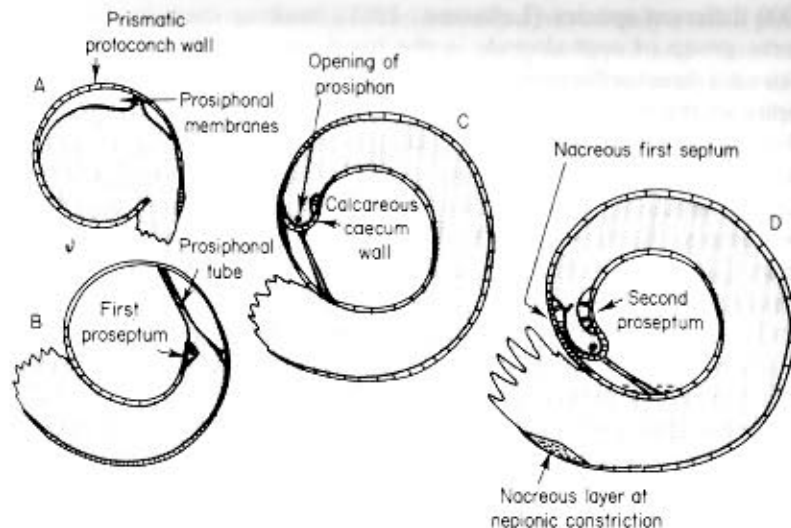


Fig. 17.4 Hypothesized development of ammonite. In A, the protoconch wall is nearly filled with the developing soft parts. In B, the soft parts withdraw from the initially developed shell, leaving behind an attachment of flesh, the prosiphon. The emptied first chamber, or caecum, is closed off with an initial septum. In C, the initial septum is now completely closed off, with the only communication to the initial chamber being a small foramen in the septum itself. Calcification of prismatic aragonite on the original organic shell wall completely covers the caecum as an outer, calcareous shell wall. The body chamber continues to enlarge as the embryo grows forward within the egg. D. At this stage additional septa are secreted, including the first septum with nacreous layers. At the lip of the aperture a thick wedge of nacreous aragonite is also secreted, internal to the prismatic shell wall layer. The thickening of the nacreous layer produces a constriction on the outer shell wall. At this stage the ammonite hatches from the egg. Figure modified from Tanabe *et al.*, 1980

Devonian, ammonitellas as small as those of the Cretaceous had already appeared, as Erben *et al.* (1969) have shown.

The greatest amount of information about ammonitella morphology has been documented for Jurassic and Cretaceous species. The work of Druschits & Doguzhayeva (1981) has especially increased our knowledge, with documentation on 36 genera. These ammonitellas show a range of diameters, and it is conceivable that they have some effect on species dispersal, and possibly some relationship to generic longevity. The range of diameters documented by Druschits and Doguzhayeva, however, shows that no evident relationship between ammonitella diameter and longevity appears to exist.

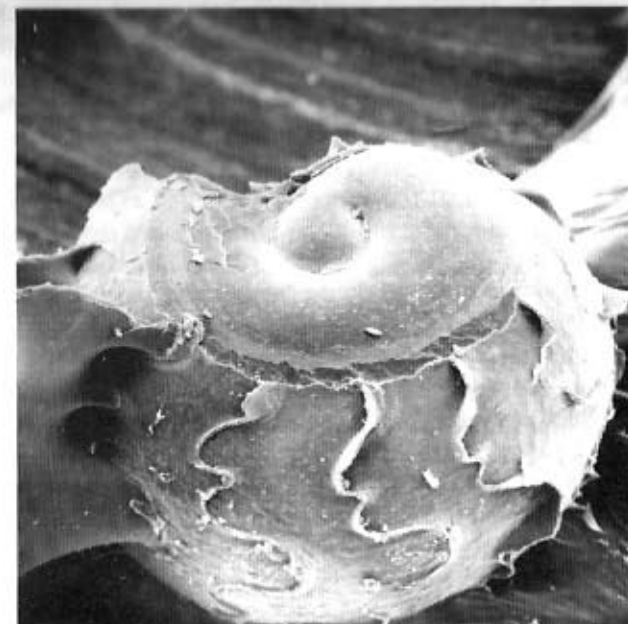


Fig. 17.5 Ammonitella of *Quenstedtoceras* (Jurassic), showing morphology of shell at hatching. The specimen was prepared by peeling back later whorls, leaving a trace of later septa on the ammonitella shell wall. Note the single muscle scars present in the central part of the remaining septa on the outer shell wall. Specimen is 1 mm diameter

Other variation in ammonitella morphology appears to occur mainly in the number of septa produced prior to hatching, and in morphology and position of the siphuncle (Tanabe *et al.*, 1979, 1980; Birkelund, 1981; Bandel, 1985).

The transition from the embryonically produced ammonitella, to hatching shell, is marked by distinct morphological features both within, and on the shell wall exterior. On the outer part of the shell, a distinct constriction of shell material occurs. This mark is followed by the initiation of a different ornament, and growth lines with the first evidence of shell break scars. The constriction, called the nepionic constriction (Hyatt, 1872; Birkelund, 1981), second constriction (Erben *et al.*, 1969), or primary varix (Grandjean, 1910; Landmann & Waage, 1982) is observable in the interior of the shell wall as a point of major shell microstructural reorganization. The constriction area is caused by cessation of the typical ammonitella microstructure of prismatic shell layers; this type of shell wall is succeeded by post-ammonitella layering of outer prismatic, middle nacreous, and inner

prismatic layers. The transition zone itself, between these two shell wall types, is formed by a large swelling of nacreous layer which connects the ammonitella shell with later shell wall.

Although Erben (1964, 1966) has suggested that ammonoids hatched with only the protoconch formed, and thus underwent metamorphosis in the plankton, most workers now agree that the nepionic constriction marks the hatching event, and that the ammonoid hatched as a miniature, adult-like form. Thus, ammonoids would have had direct development as in all present-day cephalopods. The habitat of the hatchling ammonoids is unknown. Perhaps they hatched on the bottom of the sea, and underwent a demersal, but largely benthic existence. Alternatively, it is possible that they hatched into the plankton, and spent some unknown period of time feeding at or near the surface, either passively floating (it is known that from one to six air chambers were completed during embryonic development, the 'pseudolarval stage' of Kulicki, 1979), or perhaps as active swimmers and predators within the plankton, in the manner of hatchling octopuses. The wide geographic distribution of some ammonoid species does suggest that much dispersal did take place at the newly hatched stage. Although many ammonoids were streamlined in shell form, and thus were probably capable of rapid swimming and dispersal as adults, many others had shell shapes that probably reduced adult movement. Chief among these latter forms were the numerous Cretaceous heteromorphic ammonites, with non-planispiral shells that have been variously interpreted as to function and habitat. Some of these shell types, such as the many helicoid shells, must have precluded long-term swimming or voyaging by the adults; in many cases, however, such as the Cretaceous *Turrillites costatus*, these taxa are virtually world wide in distribution. Such distribution could be accomplished largely by hatchling movement while in the plankton, either moving along the edges of continents, or perhaps as teloplantic forms capable of crossing seas and oceans.

The small size of the ammonitella indicates that egg sizes were small for cephalopods, and therefore, brood size or egg numbers per individual may have been comparable to those present-day cephalopods which produce eggs of 2 mm or less. With their small eggs, ammonoids may have produced thousands of eggs per female. This possibility is strengthened by the great size dimorphism evident among ammonoids. In Paleozoic forms, one adult conch of the dimorphic pair of macroconchs (thought to be female) and microconchs (thought to be male) can be two to four times the diameter of the other; in Jurassic forms, the difference can be as great as five times (Lehmann, 1981). This great size difference would produce even greater volume differences between the body chambers of the dimorphic pairs. Almost all workers tend to regard the larger shells as belonging to females

(macroconchs). Westermann (1969) has pointed out that among living cephalopods, such extreme cases of dimorphism (*Argonauta* is an example) always involve the larger of the pair being female, and producing hundreds or usually thousands of eggs.

## 5 Nautiloids

The subclass Nautilacea is composed of a wide variety of greatly differing taxa. Unlike the ammonoids, which in spite of variation in conch morphology show unmistakable evidence of a common origin, the various groups referred to as 'nautiloids' appear to be very different types of animals, and may be polyphyletic. Not surprisingly, they showed a variety of embryonic shell morphology. In spite of the diversity of embryonic structures, however, two fairly consistent features unite the vast majority of nautiloid embryonic conchs: most were of large size (greater than 2 mm egg diameter), (Fig. 17.6) and of these larger forms, all show a cicatrix on the apex of the earliest found shell. Although many nautiloid species still remain to be investigated, it appears at this time that only some orthoceratids (especially the Michelinoceratidae) produced spherical or bulbous protoconchs of small size, and without a cicatrix.

Within the early shell of *Nautilus*, and in some well preserved fossil forms as well (*Pseudorthoceras*, *Aturia*) there appears to be a lesser degree of shell ultrastructural reorganization between pre- and post-hatching shell (Erben *et al.*, 1969) than in ammonoids. The earliest shell wall in these forms shows the major ultrastructural features of prismatic and nacreous layers that characterize later shell growth, although discontinuities may occur between the embryonic and post-embryonic nacreous layers in some species, or the nacreous layer may even be absent in the earliest shell portion. The septa of the nautiloids appear to be structurally similar throughout growth, although major changes in fine-scale morphology of the septal prismatic layers is apparent.

A feature uniting most nautiloids is the presence of cancellate shell sculpture on embryonically produced shell wall (Fig. 17.7). This faint cross-hatching is visible on the interior and exterior of recent *Nautilus*. The shell wall in this region is notably without the presence of healed shell break scars that characterize post-hatching shell material. In *Nautilus*, the pre- and post-hatching shell is also marked by a colour change in the shell colour pigment (Ward, volume I). Finally, our recent studies have shown there to be distinct differences in prism morphology between the pre- and post-hatching spherulitic prismatic layer on *Nautilus* septa. Neither of these latter two observations has been confirmed from fossil species (Ward, 1984).



Fig. 17.6 Early shell portions of the Pennsylvanian orthoconic nautiloid *Pseudorthoceras knoxense*. Specimen hatched at a shell length of approximately 5 mm total length

As in ammonoids, the pre- and post-hatching shell in most nautiloids is separated by a distinct shell constriction (nepionic or primary constriction) visible on the outer shell wall. This growth discontinuity is analogous to the constriction found in ammonoids, but is not accompanied by the thick prism of nacreous shell material that occurs at this point in the ammonoid shell. Analysis of shell material before and after the constriction shows a distinct difference in oxygen isotopic concentrations (Eichler & Ristedt, 1966; Cochran *et al.*, 1981; Taylor & Ward, 1983). This isotopic 'step' is interpreted to be the result of the hatching event, and has recently been confirmed for the first time from fossil material (*Eutrephoceras dekayi*, of the Upper Cretaceous; Landman *et al.*, 1983).

A major unifying feature of all forms with a cicatrix is the apparently

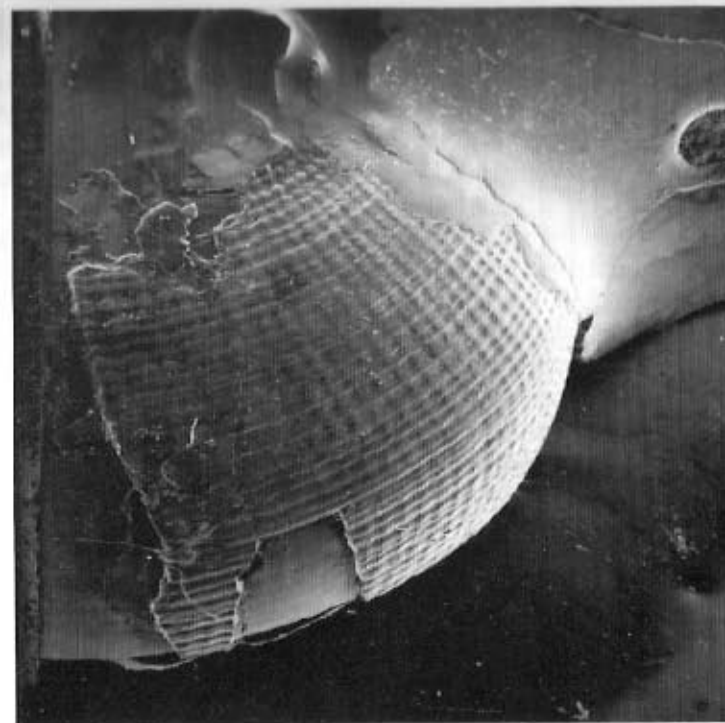


Fig. 17.7 Cancellate shell wall structure on pre-hatching shell of the Cretaceous nautiloid *Eutrephoceras dekayi*. The nepionic constriction, occurring at about 8 to 9 mm shell diameter, (not shown in this photo) marks the hatching event. Post-constriction shell wall is composed of growth lines, often with rehealed shell breaks. The pre-hatching outer shell wall can be seen to be free of shell breaks

large size at hatching. *Nautilus* may be the largest shelled cephalopod at hatching, with an egg of 45 mm, and shell diameter at hatching presumed to be 25 mm average diameter (Ward, volume I). While no other hatching nautiloids of this size are known, virtually all appeared to be larger than the 0.6 to 2 mm ammonitellas. The larger size of the nautiloid eggs suggests that perhaps they laid fewer eggs than the ammonoids. These differences in juvenile morphology probably reflect major differences in reproductive strategies in these two groups. Today, *Nautilus* appears to lay between 10 and 15 eggs per year (Ward, volume I), but may ameliorate this low reproductive potential by producing eggs over several breeding seasons, rather than reproducing once and then dying.



## 6 Belemnites

Each coiled ammonoid contains an ammonitella preserved within its middle, and hence a great deal of material has been available for study. In belemnoids, the largest group of fossil coleoids, the same is unfortunately not true. Belemnite early shell stages are preserved within the aragonitic phragmocone, which is rarely preserved within the calcitic rostrum. Belemnite development is thus less well known than in ammonoids, and is based on a few, exceptionally well preserved specimens (Jeletzky, 1966; Bandel *et al.*, 1985).

The normal skeletal parts of a belemnite were composed of an aragonitic phragmocone extending into a pen-like structure that ran along the dorsal side of the animal, and which probably functioned as a support for the animal in much the same way that the cuttlebone or pen does in modern cephalopods. The proostracum and phragmocone were attached to a massive, calcitic, cone-shaped guard. The phragmocone was of relatively low volume compared to the guard.

From well preserved fossil material belonging to the genus *Hibolithes* (Middle Jurassic), Bandel *et al.*, (1985) recently reconstructed the course of the development of a typical belemnite, and discussed older literature in detail. Shell development can be summarized as follows.

The hatching belemnite possessed an internal shell consisting of a hemispherical first chamber connected anteriorly to a living chamber and posteriorly to a primordial guard (Fig. 17.8). The conch was composed of shell layers deposited by the different mantle epithelia in a manner resembling shell deposition in *Sepia* (Bandel & Boletzky, 1979). The spreading shell gland initially produced a wholly organic shell that encompassed the whole of the embryonic shell in its outline. This first conch was secreted by gland cells of the mantle edge only (periostracum gland) during its growth across the visceral mass and within the forming muscle mantle. When growth was completed the gland tissue detached from the shell edge. Calcification of this organic shell was by the formation of aragonitic prismatic layers, which were deposited on the inside of the organic shell.

Body attachment to the calcifying shell was on a longitudinal ribbon on the dorsal side of the conch interior, very similar to that seen in recent *Spirula* (Bandel, 1982). Following calcification, the visceral mass retracted from the first chamber, secreting liquid into it while withdrawing. A septum closed off this space. This first septum was composed of thin organic sheets that were attached to each other forming a solid organic wall. This initial septum was attached by prismatic crystals to the shell wall at the aperture of the first chamber.

The muscle mantle surrounding the embryonic shell secreted a thin outer

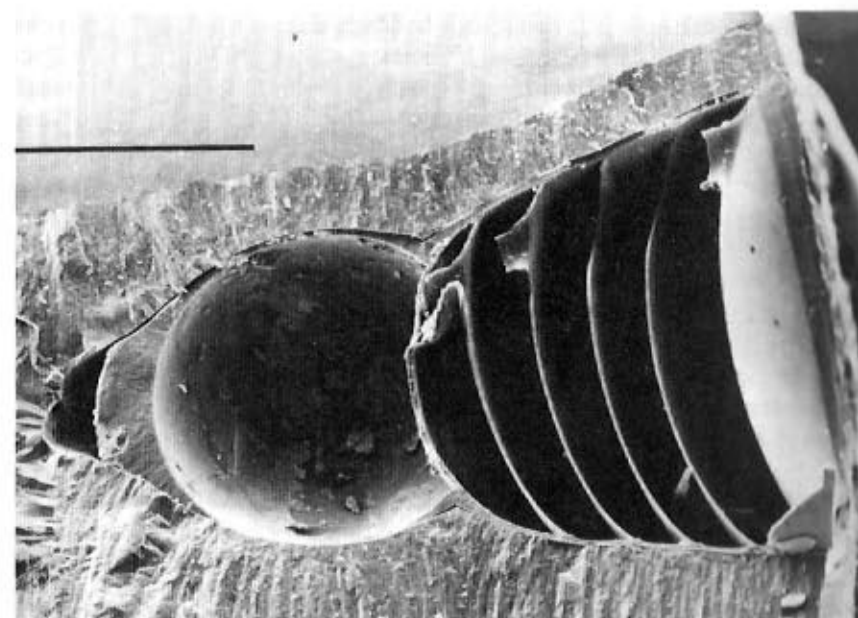


Fig. 17.8 Embryonic shell of belemnite *Hibolithes* (Jurassic). Rounded initial chamber is attached to primordial guard, which serves as an initial counterweight. The belemnite hatched with the large protoconch and early formed guard. Later septa grew anterior to the protoconch. Scale bar 400µm

mineral layer covering the whole conch. Along the posterior portion a primordial guard was formed at the same time. Thus, the hatching animal carried a shell with one chamber functioning. Liquid could be pumped out of this chamber via a porous organic closing membrane, representing the first septum. The pumping epithelium was spread on the posterior side of the visceral mass and thus was not restricted to a siphuncle. The hatchling probably took up a basically benthic life, just like *Sepia*.

The calcitic rostrum was later added by secretions coming from the muscle mantle that covered the internal conch. In its mineral composition and structure this rostrum resembled very much the conch formed by the recent *Argonauta*.

## 7 Development of the oldest known coleoids

Two different types of endocochleate (coleoid) cephalopods from the Lower Devonian of Germany (Hunsruckschiefer) have recently been dis-



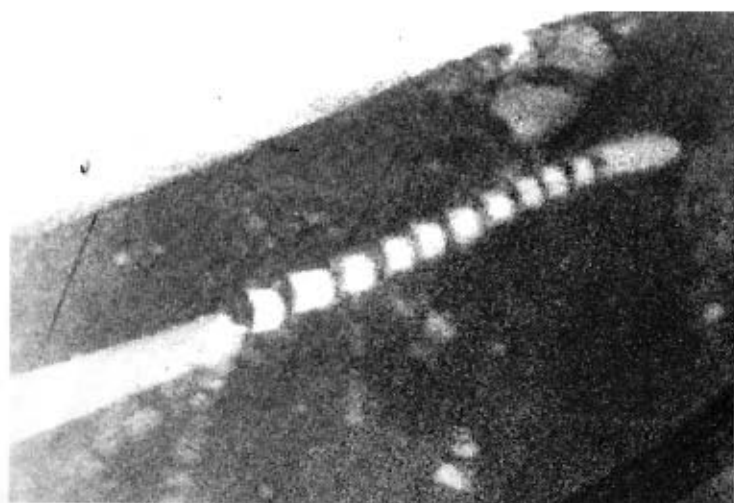


Fig. 17.9 Radiograph of *Protoauloceras*, (Devonian) interpreted as an early coleoid. The protoconch is elongated and oval; the hatchling is thought to have had a conch of 3 mm in total length, but had only a single chamber. Specimen magnified approximately 30 times

covered and described (Bandel *et al.*, 1983). One, *Protoauloceras*, represents the earliest rostrum bearing form, while the others, *Boletzky* and *Naefiteuthis*, have been interpreted as the oldest teuthids which developed into gladius-bearing forms.

*Protoauloceras* (Fig. 17.9) is interpreted to have hatched with a 3 mm long conch. Only the first, ovoid chamber of 1 mm length and 0.4 mm width was closed by a septum, probably pierced by the blindly ending siphuncular tube, similar to that of some representatives of the michilinoceratids and related orthocerid cephalopods of the Upper Silurian age (Ristedt, 1971). During growth a thin, needle-like conch formed with chambers almost as high as wide. Up to 40 chambers formed and the conch grew to over 5 cm length before an organic rostrum formed. The rostrum increased in thickness rapidly with further shell growth; when about 16 mm long, the conch had a width about 1 cm. As in the later Aulococerida of the Triassic (Jeletzky, 1966), the rostrum covered the whole conch up to the apertural end of 'living chamber'.

*Boletzky* and *Naefiteuthis* hatchlings had one or two septa completed in conchs of about 2 to 4 mm length. During early life *Boletzky* produced 6–10 septa and chambers a bit wider than high in a quite normal 'orthocerid' conch. Shells with 8 mm length had a phragmocone as long as the living chamber. However, a subsequent metamorphosis of the shell is noted. The

initially round early conch changed into an oval cross-section, while the shell showed evidence of a median dorsal and two lateral keels. The flattening of the entire shell made it the functional equivalent of an internal pen.

#### 8 Shell form and mode of life

Various sources have estimated that about 10 000 species of externally shelled cephalopods have so far been identified from the fossil record (Ruzhentsev, 1962; Lehman, 1981) and about 500 internally shelled species (Ruzhentsev, 1962).

Perceptible evolutionary trends are apparent in the course of ecto-cochliate cephalopod evolution. The most apparent are related to the shape of the shell itself, and others include the type of internal supports between the individual chambers, and the nature of ornamentation. These factors suggest that buoyancy, shell strength, and mobility have been important in determining the shell shapes evolved by individual species. The wide spectrum of Paleozoic, Mesozoic, and Cenozoic shelled cephalopods can be viewed as different solutions to these adaptive pressures.

The most important function of the external shell is that it provides the animal with neutral buoyancy in the sea by lowering overall animal density. The pioneering work of Denton and Gilpin-Brown on *Sepia* (1961), *Spirula* (1971) and *Nautilus* (1966) have provided a model for the chamber formation and subsequent liquid removal which probably has applicability to all chambered cephalopods. Details of this process have undoubtedly differed from group to group, as evidenced by differing positions of siphuncle and shape of septa (Ward, 1982), but the overall process has probably been a conservative feature of the class (Ward *et al.*, 1980).

Shell strength has been of great importance in determining the habitat of various groups of external cephalopods, and, as has been demonstrated in the elegant studies of Westermann (1971, 1973, 1975) is interrelated to buoyancy of the shell. Thicker shells obviously provide more strength, but had the attached penalty of greater weight, thus decreasing buoyancy. Two major, and greatly differing solutions to this problem have been attempted: the simple, thick shell and septa of the nautiloids, and the more complexly fluted, but thinner septa and conch of the ammonoids.

Balance and stability have also provided constraints on the form of the external shell. The well known cameral deposits of the diverse suite of orthoconic and cryptoconic nautiloids of the Paleozoic have greatly increased mass, and necessitated increased phragmocone volume, but were necessary for correct orientation of the animal in the sea. Planispiral shells have, by virtue of their coiling, corrected balance considerations without the need

for internal deposits. This shell plan, however, varies in stability according to coiling morphology (Raup, 1967).

Finally, buoyancy and balance are interrelated with mobility. The necessity of cameral deposits in orthocones must have exacted a high price in terms of mobility. Even though these organisms were undoubtedly at, or near neutral buoyancy, the incorporation of the heavy cameral deposits necessitated larger phragmocones, and hence longer conchs. The added weight also increased the inertia of the specimens, necessitating a higher energy expenditure for initiating and ending movement, or changing course.

Planispiral shells must have had much greater mobility than orthoconic or other heteromorphic shapes of equal mass. Mobility, however, was directly related to the shell geometry, and to such factors as streamlining as well as stability (Chamberlain, 1981). In addition to being poorly streamlined, an evolute shell shape has the added disadvantage of low stability, so that a great deal of the energy provided by hyponome action would be transferred to rocking or spinning of the shell on its centre of gravity, rather than as forward movement.

### 9 Shell form through geological time

The earliest cephalopods had externally chambered shells (Yochelson *et al.*, 1971) and probably many of the morphological features present in modern cephalopods are modified from adaptations originally developed for life within a calcareous shell. The shell shape itself must have been the most dominant morphological factor in determining the mode of life of the organism. The most prominent shell shape difference among the ectocochliates was between those forms evolving uncoiled, or heteromorphic shell types, such as orthocones, brevicones, cryptocones, and planispiral shell types.

The percentages of the various shell shape categories for the Paleozoic and Mesozoic Eras is shown in Fig. 17.10, with data assembled for genera listed in the Treatise on Invertebrate Paleontology, parts 3 and 4 (Cephalopoda). The earliest ectocochliates were all non-planispiral. Teichert (1967) has described the major evolutionary feature of the initial nautiloid radiations. More recently, Chen & Teichert (1983), have described large, newly discovered nautiloid faunas from the Cambrian of China. These new discoveries shed important new information about the earliest nautiloids, and show that even in the Cambrian as many as 35 genera were already present. In the Cambrian, Ordovician, and Silurian Periods, planispiral shells showed less diversity than the non-planispiral shell shapes.

The dominance of the heteromorphic shell shapes ended in the Devonian Period. With the evolution of the first ammonoids in early Devonian time,

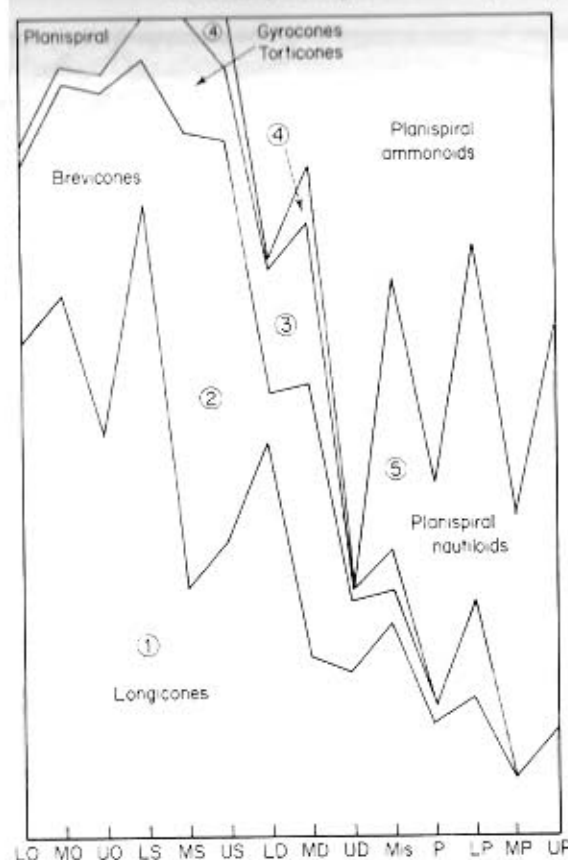


Fig. 17.10 Shell shape categories for nautiloids and ammonoids of the Paleozoic Era. The early Paleozoic dominance of non-planispirally coiled shells is replaced by planispirals during the middle and later Paleozoic periods. The abscissa gives the initial letters of the geological period from Lower Ordovician (LO) through to Upper Permian (UP). See Fig. 17.2.

followed by their rapid radiation, the proportion of planispiral shapes increased. Nautiloids of the Devonian and later during the Paleozoic also showed an increase in the number of planispiral as compared to heteromorphic forms. By the late Paleozoic, planispiral shells dominated both the nautiloid and ammonoid faunas.

The Mesozoic history of the chambered cephalopods differs markedly from the Paleozoic. Following the mass extinction at the end of the Permian Period, which exacted a heavy toll on cephalopods as well as most other Paleozoic marine invertebrate species, new radiations of ammonoids occurred in the Triassic. In contrast to the later parts of the Paleozoic,

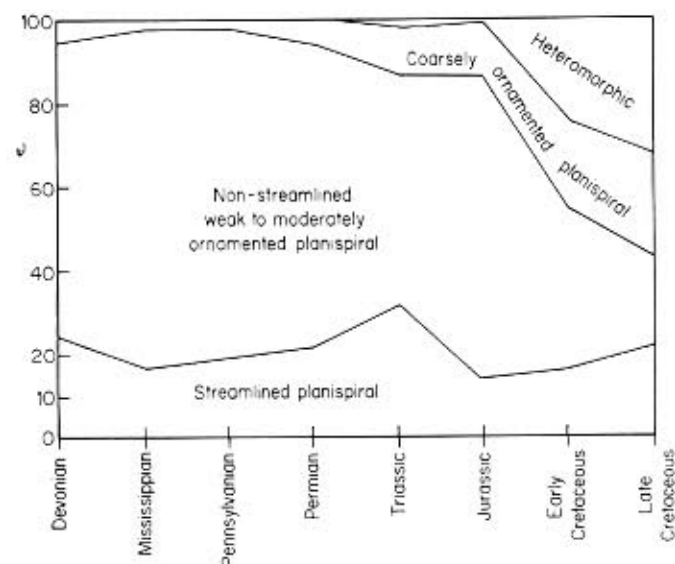


Fig. 17.11 Shell shape categories for Paleozoic and Mesozoic ammonoids

when the ammonoids and nautiloids remained at varying, but approximately similar generic diversity, the ammonoids of the Triassic far eclipsed the nautiloid in numbers. During this time, all but a tiny fraction of both the ammonoids and nautiloids had planispiral shells.

The end of the Triassic, as at the end of the Permian, was marked by a widespread mass extinction that decimated the cephalopod stocks. The ammonoids were reduced to about five genera. In the early Jurassic, however, these survivors again showed a major adaptive radiation, and as during the Triassic, all but a small number of genera were again planispiral. The Late Jurassic record of the chambered cephalopods is essentially a continuation of the early Jurassic record, with most ammonoids and all nautiloids continuing to produce planispiral shell shapes. In the Lower Cretaceous, however, increasing numbers of heteromorphic ammonites appeared. This fact alone differentiates the Cretaceous history of the ammonites from all previous periods (Fig. 17.11). An additional morphological feature also characterized the Cretaceous record. During this time, increasing numbers of heavily ornamented forms also appeared. Ward (1981) has documented this trend (Fig. 17.12), and has interpreted it to mean that increasing predation on ammonites was occurring during the Cretaceous.

The Cretaceous period appears to have been a time of modernization for many marine faunas. One of the most important trends was the evolution of shell crushing predators in many vertebrate and invertebrate groups. Examples of organisms which actively feed on molluscs, and which radiated during this time frame, include brachyuran crabs, spiny lobsters, teleost fish and large numbers of skates and rays.

Recent work on *Nautilus* suggests that shell breakage in the apertural region is of great danger to the organism, because of the rapid buoyancy changes which result (Ward & Greenwald, 1982; Ward, 1983). *Nautilus*, and probably most or all ancient chambered cephalopods as well, maintains a delicate balance of approximately neutral buoyancy in the sea. This balance is disturbed either by heavy feeding, which increases density, or by some density reduction caused by starvation or, more commonly, by loss of shell material near the aperture. Ectocochliate shell material has an average specific gravity of  $2.7 \text{ g cm}^{-3}$ , as compared to a mean value of 1.07 for the soft parts (Heptonstall, 1971). The removal of even small volumes of shell from the apertural region immediately decreases the overall specific gravity of the organism, making it lighter. In *N. macromphalus*, decrease of as little as 5 g of the weight in water (from neutrally buoyant) is sufficient to force an adult specimen to the surface; in this case, no amount of swimming effort allows resubmergence. As the surface of the sea is an especially dangerous place for a chambered cephalopod (predation from seabirds, elevated temperature, surface sharks, and mechanical breakage) such shell breaks are of great potential danger. It has been shown that immediately after shell breakage, *N. macromphalus* can partially refill emptied chambers with liquid secreted from the siphuncle (Ward and

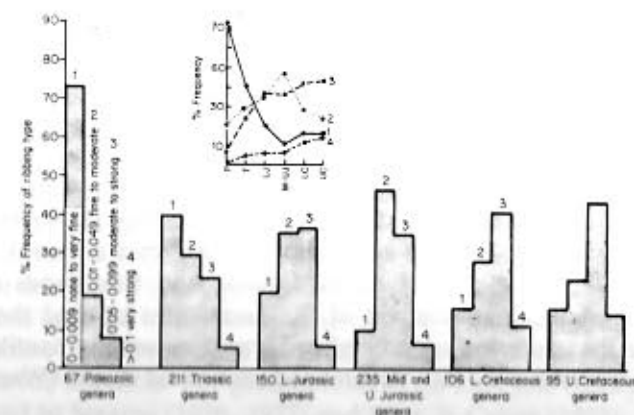


Fig. 17.12 Shell ornament frequencies among ammonites



Greenwald, 1982). More recent work (Ward, in press) shows that this refilling mechanism is quite slow, and limited in the ultimate volume of liquid replaced to between 3 and 6 ml, for the entire phragmocone. As *Nautilus* and the ammonites have approximately equivalent siphuncular surface to chamber volume relationships (Ward, 1982), and as this value appears to be the major factor influencing the rate of liquid emptying as well as refilling, we assume that ammonites, as well as modern *Nautilus*, would be susceptible to catastrophic buoyancy change due to apertural shell breakage. Unless the siphuncular epithelium in ammonites was greatly different in morphology and function than in *Nautilus*, refilling mechanisms in ammonites would not be sufficient to forestall some sort of involuntary ascent to the surface after an unsuccessful predatory attack involving shell breakage. Breaks on ammonite shells are quite common (Kennedy & Cobban, 1976).

Two new shell trends occurred among Cretaceous ammonites. Both may be related to avoiding predation. The first, a great increase in the proportion of ammonites with large ribs and spines may have been an adaptation towards reducing the chance or magnitude of shell breakage. The second, the evolution of the Upper Cretaceous heteromorphic ammonites, may in part be an ecological shift, involving the move of cephalopods off the shelves, and into the midwater regions (Packard, 1972; Ward, 1979; Klingler, 1981; Ward, 1983).

By Maastrichtian time, the last interval of the Cretaceous Period, ammonite diversity was extremely reduced compared to even ten million years previously in the Cretaceous (Wiedmann, 1969; Kennedy, 1977). Ward and Signor (1983) have shown that most diversity reduction occurred among the heavily ornamented and non-streamlined planispiral forms. Most Maastrichtian faunas are composed either of heteromorphic forms, or highly compressed planispiral ammonite forms suggestive of being rapid swimmers. The last ammonites thus roughly paralleled two important components of modern-day cephalopod faunas: streamlined swimmers, such as loliginids, and poor floaters or swimmers that live in midwater regions, such as *Spirula* and the cranchiids. Curiously, the nautiloids passed the Cretaceous-Tertiary boundary unchanged in diversity and even show a modest radiation in the lower Tertiary (Ward, volume I). Nautiloid shell shapes of the Lower Tertiary appear to be somewhat different than the majority of shell shapes evolved by Jurassic and Cretaceous nautiloid species, suggesting that removal of the ammonites opened the way, if briefly, for the evolution of streamlined, rapid-swimming nautiloids that very much resembled the last, streamlined ammonoid shapes (Ward, 1980).