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Cephalopoda

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Cephalopoda is one of the most intriguing and diverse classes of molluscs. Modern forms comprise the octopuses, squids, cuttlefish, and pearly nautilus (Figure 8.1). Cephalopods differ greatly from other molluscs—they are more active, fast-moving, intelligent carnivores, with highly advanced visual and nervous systems that allow them to be competitive and efficient predators. Their ability to sense their surrounding environment and adapt rapidly using camouflage or complex behavioral patterns, which have been observed during courtship, reproduction, and mating, demonstrates how complex these animals have become.

All fossil and modern taxa are marine, with a few found in estuarine habitats (as low as 15 ppt salinity). Fossil forms include the ammonoids, which became extinct 65 million years ago; the nautiloids (both orthoconic and coiled), of which *Nautilus* and *Allonautilus* are the only living descendants; and the Coleoidea, the order that accommodates all other living cephalopods.

Modern cephalopods have gained notoriety through being the subject of myths or science fiction (e.g., Verne 1896) and as an important food source. Importantly, they are used as model systems for a large variety of research studies (Hodgkin and Huyley 1952; Makman and Stefano 1984), including areas such as neurobiology, behavior, physiology, development, symbiosis, and growth (Arnold 1962; Hanlon *et al.* 1990; Gilly and Lucero 1992; Boletzky 2002; Forsythe *et al.* 2002; Boletzky 2003; Lee *et al.* 2003). There are close to 1,000 species of living cephalopods (Nesis 1987) found in all oceans, from polar seas to the tropics, with more in the Indo-West Pacific than elsewhere (Norman 2000). They inhabit a variety of marine ecosystems, including estuarine, benthic, pelagic, and the deep (>1,000 m) ocean. Because of their abundance and availability, they are economically important in many of the large fishing industries of Europe, Asia, Australia, New Zealand, and the Americas. It has been estimated that in the western United States alone, 2.7–3.6 million metric tons of squid, worth US $7 billion, are harvested annually (California Department of Fish and Game 2003). They represent a large percentage of the biomass in the ocean and are important in marine food webs, where they play significant roles as predators (mainly of crustaceans, fishes, and other molluscs) as

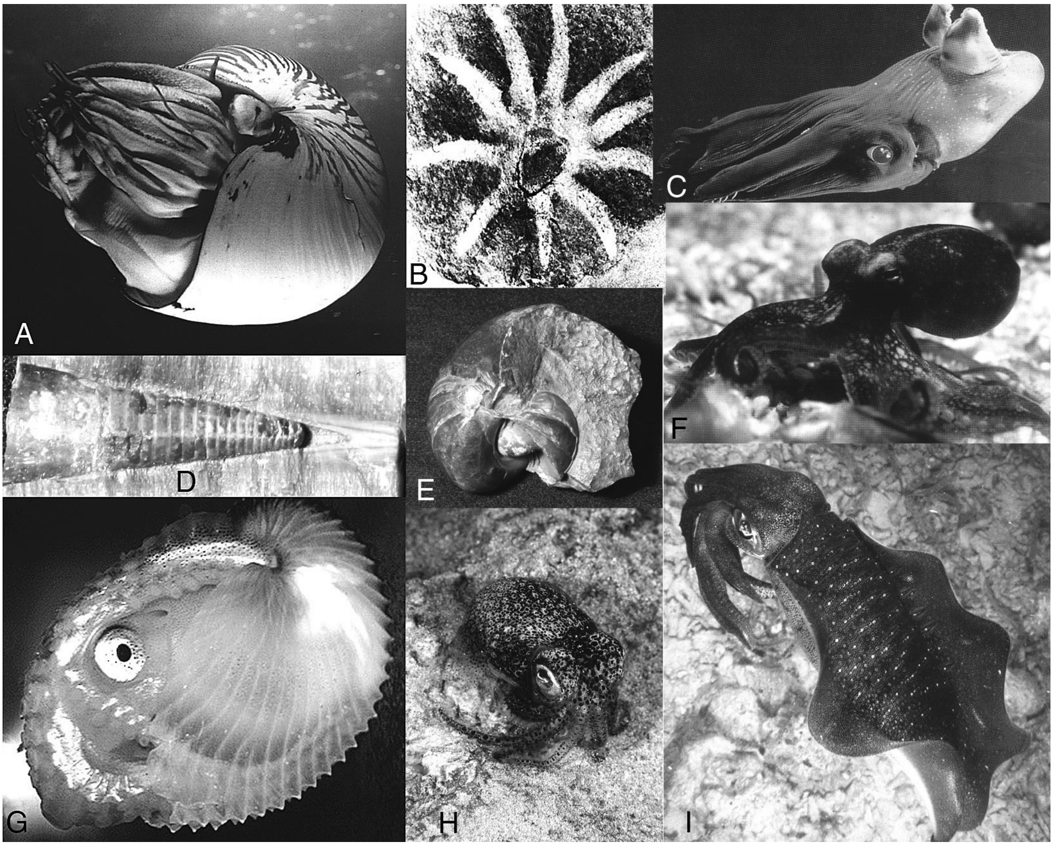


FIGURE 8.1. Cephalopod diversity. (A) *Nautilus pompilius* (M. Norman). (B) *Jeletzkya* (R. Johnson and E. Richardson, Jr.). (C) *Vampyroteuthis infernalis* (K. Reisenbichler). (D) *Pachyteuthis* sp. (D. Lindberg). (E) *Eutrephoceras* sp. (D. Lindberg). (F) *Octopus aegina* (M. Norman). (G) *Argonauta nodosa* (M. Nishiguchi). (H) *Euprymna tasmanica* (M. Norman). (I) *Sepioteuthis lessoniana* (M. Norman).

well as prey for other squids, fishes including sharks, seabirds, and marine mammals (Boyle and Boletzky 1996; Clarke 1996; Croxall and Prince 1996; Norbert and Klages 1996).

The cephalopod fossil record spans more than 450 million years, although this record is patchy because organic remains decrease in quality of preservation and information content with increasing time. Additionally, most fossils are only the remains of the hard, more durable skeletal material, which, in cephalopods as in most other molluscs, is calcium carbonate. Occasional cephalopod-bearing Lagerstätten (i.e., fossil bearing rock units with organisms having exceptional preservation, often including tissues and whole organs; Botter *et al.* 2002) have provided information not seen in typical fossils. In addition to the exceptionally well-preserved cephalopod body fossils from the Konservat Lagerstätten of the Middle Jurassic (Callovian) of England and the Late Jurassic (Tithonian) lithographic limestone of Solenhofen, Germany, fossil cephalopods and their shells are also known from the Lower Carboniferous Bear Gulch Limestone (Hagadorn 2002) in Montana and the Upper Carboniferous Buckhorn Asphalt (Crick and Ottensman 1983; Squires 1973) in southern Oklahoma (both in the United States).

FOSSIL CEPHALOPODS

GROWTH

Like modern *Nautilus* and the coleoids, fossil cephalopods are believed to have determinate growth (i.e., the termination of growth and shell secretion presumably coincided with sexual maturity). Some fossil cephalopods reached large sizes; the largest nautiloid fossil recorded was four meters in length, whereas the largest ammonite was two meters in diameter (Lehmann 1981; Stevens 1988; Nixon and Young 2003). The smallest adult ammonoid shell we are aware of is *Maximites* from the Upper Carboniferous, with maturity attained at about 10 mm diameter (Frest *et al.* 1981).

SHELL MORPHOLOGY AND TERMINOLOGY

Almost always it is only the mineralized shell that is available for study in fossil cephalopods. The terminology for the hard parts of the shell is extensive; a good set of definitions is provided by Teichert (1964b). In general the shell is divided into a chambered phragmocone, used for buoyancy control, and the body chamber, which contained most of the bulk of the animal tissues and organs. In coleoids, the phragmocone and body chamber, if present, are partly or entirely covered by a rostrum or guard if a hard skeleton is present. Variations of these and other features provide the basis of the identification of different taxa. These morphological characters used in fossil cephalopods include the degree of coiling; chamber spacing; siphuncle position; septal neck shape; presence or absence of carbonate deposits within the chambers and, where present, the shape and placement of those deposits; protoconch shape and size; cross-sectional shape of the shell; rate of shell taper; suture pattern formed by the septa on the inside of the shell; mature shell modification of the body chamber that develops at presumed sexual maturity; shell ultrastructure (discussed next), rostrum composition and ultrastructure; guard shape; and numerous other features.

SHELL ULTRASTRUCTURE

The cephalopod shell is composed of aragonite deposited in two ultrastructural forms: nacreous plates (nacre) and prismatic needles (Bandel and Spaeth 1988). The external shell of living nautiloids, like that of most conchiferans, has an outer organic layer, the periostracum, which covers the outer prismatic needle layer and was presumably present in ammonoids and fossil nautiloids. The inner surface of the shell is composed of an aragonitic layer of nacre, as are structures such as septa and septal necks. Other shell layers can be present, depending on the ontogeny of the shell and the position of the outer whorls if the specimen is coiled. In some coleoids, because the mantle tissue covers the exterior of the shell, a layer of prismatic material (sometimes with organic material) is deposited on top of the original prismatic shell layer (the nacreous layer is missing) around the phragmocone or on the dorsal surface of the phragmocone and body chamber, forming the rostrum or guard seen in many fossil coleoids. The coleoid gladius, or proostracum, is composed of organic material or a combination of organic material and aragonite. In the Belemnoidea the rostrum can be composed of calcite, aragonite, and organic material (Bandel and Spaeth 1988).

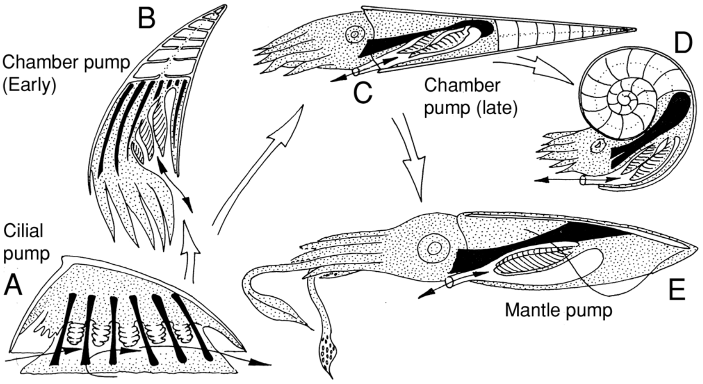
Aragonite, the dominant building material of cephalopod shells, is an unstable mineral and can easily alter to calcite. The oldest unaltered cephalopod shell is from the Lower Carboniferous of Scotland (Hallam and O'Hara 1962). In the United States, the Upper Carboniferous Buckhorn Asphalt (Squires 1973) contains much unaltered cephalopod shell material (e.g., Kulicki *et al.* 2002). Other unaltered cephalopod shell occurrences are rare in the Paleozoic, but they are more common in younger units in the Mesozoic and Cenozoic.

BUOYANCY AND EQUILIBRIUM

The evolution of the morphology of the Cephalopoda was controlled, in large part, by the problems of shell equilibrium and the maintenance of neutral buoyancy while swimming, as described in the preceding section. Buoyancy problems persist despite most modern cephalopods lacking an external or internal shell (Figure 8.2).

Teichert (1988: table 1) listed 14 different mechanisms that modern and fossil cephalopods

FIGURE 8.2. Diagram showing possible evolutionary directions in the methods of achieving more efficient respiratory currents in the history of the Cephalopoda from a hypothetical ancestor (A), through nautiloids (B–D) to modern coleoids (E) (from House 1988). The "chamber pump" alludes to the presence of a muscular hyponome or funnel.



have used to regulate buoyancy and equilibrium. Some of the most important are truncation of the posterior part of the phragmocone; endosiphuncular deposits in the phragmocone; cameral deposits in the phragmocone; replacing liquid-filling of the chambers with gas; shifting the gas-filled chambers to a position over the body chamber by overlap; shifting the liquid- and gas-filled chambers over the body chamber by coiling; using lighter-density chemicals in special tissues to reduce density; changing the shape or reducing the size and complexity of the phragmocone; thinning of the shell, septa, ornament, or other parts to reduce overall shell weight; construction of a rostrum on the phragmocone; and changing the configuration of the chamber by coiling the shell (Figure 8.2).

SEXUAL DIMORPHISM AND MATURITY

Many fossil cephalopods exhibit changes in shell morphology during growth, especially as the animal approaches and attains full size at maturity. Sexual dimorphism can be expressed by differences in shell size or modifications (Davis *et al.* 1996). Most research on maturity and sexual dimorphism in fossil cephalopods has been done on the Ammonoidea (see Davis *et al.* 1996 for references). Maturity and sexual dimorphism in fossil nautiloids, despite the numerous observations on living nautiloids (Collins and Ward 1987; Ward 1987), have received only modest study. This is also the case for the fossil coleoids.

From the Devonian (416–359 Mya) through the Cretaceous there are numerous cases in which mature ammonoid shells with nearly identical morphologies except for size are found in the same deposits; such cases are usually interpreted as different sexes rather than different species. Other shell morphology changes that have also been used as identifying maturity and sexual dimorphic characteristics include modification of the opening of aperture; septal approximation (i.e., septa becoming closer together); changes in the rate of coiling, ornament or in the cross-sectional shape of the body chamber; simplification of the suture pattern formed by the septa on the inside of the shell; and development of muscle scars (see Davis *et al.* 1996 for a more complete discussion). Additionally, there is approximation of transverse color bands and different patterns on the shells of some otherwise morphologically identical taxa that were presumably mature Triassic ammonoids (Mapes 1987a), which suggests that these specimens are different sexes.

INK

Buckland first described fossil ink from a Jurassic coleoid in 1836. Since then only modest numbers of coleoids from the Mesozoic have been recorded that contain ink (Doguzhaeva *et al.* 2004a) because the preservation of such material requires exceptional geologic conditions. The location and color of black or brown masses in the body chambers of fossil cephalopods is suggestive that the material could be fossil ink; however, proving that the material is ink has, until recently, been impossible without destroying the specimen, because identification of the melanin-based ink was previously dependent on destructive chemical analysis. The discovery of a new method of identifying fossil ink was made by Doguzhaeva *et al.* (2004a). Doguzhaeva independently discovered that ink from a Jurassic coleoid had a globular ultrastructure when viewed under the scanning electron microscope (SEM) at high magnification (×10,000 to ×20,000) like that of modern coleoid ink from squid, octopus, and cuttlefish. Similar results were obtained on ink from Carboniferous coleoids (Doguzhaeva *et al.* 2004a; Doguzhaeva *et al.,* in press, a). To date the oldest confirmed coleoid ink is from the Upper Carboniferous in the United States (Oklahoma and Illinois), indicating that the use of ink as a method of predator avoidance has been long utilized (Doguzhaeva *et al.* 2004a; Doguzhaeva *et al.,* in press, a).

Although only some fossil coleoids are known to have ink, this is not surprising given the rarity of suitable preservation. It is possessed by most, but not all, modern coleoids, so some extinct coleoid taxa may also have not possessed it. No nautiloids are known to have ink, but there are unconfirmed reports that some Ammonoidea did possess it (Lehmann 1967; Doguzhaeva *et al.* 2004a). However, Lehmann (1988) reinterpreted his original material and concluded that his 1967 report was in error. Later Doguzhaeva *et al.* (2004b; in press, b) analyzed a Jurassic ammonoid using SEM techniques and identified preserved mantle tissue and the possible presence of ink. Thus, the debate as to whether some ammonoids had ink remains unresolved.

BEAK AND RADULAE

In general details, the beak (or mandibles, a modified jaw) and radulae of fossil cephalopods are known for most geological time periods, with many reports back to the Carboniferous (Mapes 1987). There are few reports of Devonian beaks and none of radulae, and no reports of either structure prior to the Devonian. Reported occurrences of beaks are much more common than those of radulae; most are from ammonoids (Kennedy *et al.* 2002), with only a few nautiloid jaws having been recovered (Mapes 1987; Müller 1974). Jaws, in general, appear to be moderately conservative structures in regards to evolutionary innovations with all known Upper Paleozoic examples being chitinous. In the Mesozoic, some ammonoids replaced the chitinous lower jaw with two massive calcareous plates. The function of these plates is debated, with suggestions that either they functioned only as lower jaws or they had a dual function by acting as a lower jaw and as a protective operculum, equivalent to the hood on modern *Nautilus* (Lehmann 1981; Morton 1981; Seilacher 1993; Kennedy *et al.* 2002; Tanabe and Landman 2002). Radulae are known from several species of ammonoids (e.g., Saunders and Richardson 1979; Nixon 1996; and their citations) and coleoids (e.g., Saunders and Richardson 1979). These structures are similar to those found in extant coleoids. In general it is possible to separate nautiloid, ammonoid, and coleoid mandibles and radulae by their morphologies; however, it is seldom possible to separate them on a generic or specific level.

TISSUES AND ORGANS

Only a few reports have been published on the organs and soft tissues of ammonoids and nautiloids, with most being from fossil coleoids. Impressions of tentacle-bearing bodies assigned to octopods have been described from the Cretaceous and Jurassic of the Middle East and Europe (Kluessendorf and Doyle 2000; Haas 2003; Fuchs *et al.* 2003). The oldest impression of soft body tissues we are aware of is from the Mazon Creek Lagerstätte (Upper Carboniferous) in Illinois. This deposit has yielded several important coleoids. One is *Jeletzkya*, the famous ten-armed impression of a coleoid with arm hooks but without a well-preserved phragmocone (Figure 8.1). Another is an octopus-like form described as *Pohlsepia,* which has eight arms, two modified arms, a poorly defined head (including eyes, funnel, and beaks with a radula preserved between them) and fins; there is no evidence of any internal or external shell associated with the fossil. Other coleoids from this Lagerstätte are also known (Saunders and Richardson 1979; Allison 1987; Doguzhaeva *et al.*, in press, a). However, there are numerous reports of Mesozoic coleoids with preserved soft parts including arms with arm hooks, mantle tissue, gills, beaks, and radulae (e.g., Naef 1922; Doguzhaeva *et al.* 2002a; and citations therein). Gills are known only from Mesozoic coleoids (Bandel and Leich 1986; Mehl 1990).

Internal organs such as the stomach, crop, intestines, and circulatory system have been rarely reported in fossil cephalopods. In all reported cases involving the digestive system, the actual organs are not preserved. Instead, the undigested calcareous, chitinous, or phosphatic skeletal remains of meals are found clustered in specific areas of the body and are interpreted to mark the positions of the crop, stomach, or the intestine. In ammonoids, Lehman (1981) reported crinoid fragments, aptychi (lower beak/operculum) from smaller ammonoids, foraminiferans, and ostracods (Lehmann 1981; Nixon 1988). In orthoconic nautiloids, Quinn (1977) and Mapes and Dalton (2002) reported that the ammonoid clusters surrounding the body of large (1–3 meters in length) actinoceratid nautiloids from the Lower Carboniferous of Arkansas were the stomach contents of the nautiloid (Mapes and Dalton 2002). The oldest crop/stomach contents were discovered in an "orthoconic nautiloid" from the Lower Carboniferous Bear Gulch Lagerstätte (Landman and Davis 1988); these contents appear to be mostly composed of macerated fish scales. Subsequent study has shown that this specimen is a new coleoid (Mapes *et al.* 2007).

The circulatory system in fossil cephalopods is known only from impressions or grooves on the internal parts of mineralized structures such as the shell, cameral deposits, or rostrum and the siphuncle in fossil nautiloids and ammonoids, which contained arteries and veins. In Permian ammonoids from Nevada, segments of the siphuncular tissues replaced by phosphate have been discovered and described (Tanabe *et al.* 2000).

COLOR PATTERNS

It is unknown whether fossil cephalopods had chromatophores like those seen in the mantle tissue of many modern coleoids. *Nautilus* and *Allonautilus* have reddish-colored transverse bands across the shell, and the tissue of the hood has reddish markings, which are not capable of changing in life (in contrast to modern coleoids). While it is unknown whether the head-foot region of ammonites and extinct nautiloids had similar coloration to modern nautiloids, the shells of different fossil cephalopod taxa exhibited a variety of different color patterns.

The actual color of the patterns on the fossil ammonoid and nautiloid shells is unknown because fossilization has destroyed the pigments, leaving patterns of gray in different shades (Teichert 1964a; Mapes and Evans 1995; Mapes and Davis 1996; Gardner and Mapes 2001); such patterns have not been discovered on fossil coleoid shells. Patterns include zigzag lines, transverse bands, longitudinal bands, and uniformly colored shells. Interestingly, while modern *Nautilus* and *Allonautilus* have transverse bands that do not follow the growth lines, all transverse bands on ammonoid forms do. Additionally, at maturity, in *Nautilus* and *Allonautilus* the transverse bands are confined to the umbilical sides of the shell, leaving the lateral and ventral sides of the shell uniform creamy white. In mature shells of ammonoids with transverse color bands, the color pattern extended entirely across the shell and covered the body chamber to the edge of the aperture at maturity.

In addition to the color patterns on nautiloids and ammonoids, a different kind of coloration was present in some fossils. This is not the product of a pigment but instead the result of scattering and differential absorption of light by the ultrastructure of the outer layers of the shell. Unaltered ammonoid shells from Poland,

FIGURE 8.3. Longitudinal color pattern on *Cadoceras* sp., an ammonoid from Jurassic sediments near Luków, Poland. Except in the places where the shell is broken (white areas), the conch also exhibits an overall dark (reddish) iridescence; a longitudinal band of lighter iridescence can be seen on the darker (red) background around the umbilical region.

Russia, and Madagascar (all Mesozoic; precise ultrastructural and stratigraphic details are under study; Mapes, personal observation) with narrow longitudinal bands of red to reddish green on a darker red background have been observed (Figure 8.3). Such external colors would appear dark brown or dark gray at water depths below 10 meters. Interior shell layers appear to exhibit only deeper blue to purple colors; however, these colors would not be exposed during normal living conditions. The use of different refractions and reflections at different wavelengths of light to produce color patterns is not known in modern cephalopods, and indeed, we are not aware of any cases in modern taxa belonging to the phylum.

BIOLOGY OF LIVING CEPHALOPODS

Living cephalopods are divided into two major groups usually treated as subclasses: the Nautiloidea, containing *Nautilus* and *Allonautilus*, and the Coleoidea with all remaining taxa. Characteristics that distinguish these two subclasses are the presence of an external, many-chambered shell and multiple (60–90) suckerless tentacles in nautiloids, whereas coleoids have reduced (*Spirula*), internalized, or no shell, bearing eight to ten prehensile suckered appendages (arms and tentacles). Coleoids have a modified seven-element radula and a chitinous beak (similar to many ammonoids, see previous discussion), whereas nautiloids have a 13-element radula with a chitin and calcium carbonate beak. The nautiloid funnel has two separate folds, and they have two pairs of ctenidia (tetrabranchiate) and nephridia. Coleoids have a closed single tube for a funnel and one pair of ctenidia (dibranchiate) and nephridia. Coleoid eyes are more complex than the pinhole-camera eyes of nautiloids, and some even contain a cornea and lens (much like vertebrate eyes, an excellent example of convergent evolution). Modern nautiloids have no ink sac or chromatophores, whereas most coleoids have both. *Nautilus* has a simple type of statocyst, an oval cavity completely lined with hair cells (Young 1965). Coleoids have two types of statocysts: the "octobrachian" statocyst, which contains a spherelike sac with one gravity receptor system and an angular acceleration receptor system subdivided into nine segments (Young 1960; Budelmann *et al.* 1997), or the "decabrachian" statocyst, which is irregularly shaped with three gravity receptor systems and an angular acceleration receptor system subdivided into four segments (Budelmann *et al.* 1997). Both octobrachian and decabrachian statocysts are species specific in size and levels of organization and have been used in phylogenetic comparisons (Young 1984).

EGG LAYING

Laying of fertile eggs by modern *Nautilus* has been observed only in aquariums (Arnold 1987; Uchiyama and Tanabe 1999). Under these conditions single large (about 25 mm in diameter), yolky eggs are attached to a hard substrate. Embryo maturation takes 269 to 362 days, and the hatchling is a miniature of a full-sized adult.

Egg laying for modern coleoids is usually in two basic modes: those whose life histories are restricted to coastal and shelf habitats and those that are pelagic (Boyle and Rodhouse 2005). Cephalopods such as cuttlefish, most octopuses, and loliginid squids lay eggs that are attached to some type of substrate such as coral or kelp. Most of these squids ensheath their eggs with material from the nidamental glands and usually attach the eggs in areas where they are inconspicuous. Octopus eggs are more individually attached by a short stalk into strings or festoons, which are then attached to the substrate (Boyle and Rodhouse 2005). All octopod species brood their eggs, no matter whether or not they are attaching them to a specific substratum, and this characteristic has been used to delineate species complexes (i.e., *Octopus*; Boletzky, personal communication). For pelagic species, some ommastrephid squids extrude their eggs in a gelatinous mass, and some, such as the gonatid squids, are known to carry their eggs (Seibel *et al.* 2000). Young hatch directly from this gelatinous mass and are then fledged into the water column as paralarvae (see below). Other pelagic species, such as the Enoploteuthidae, release eggs singly into the water column (Young 1985), and the juvenile squids are then hatched in a pelagic state.

EARLY DEVELOPMENT

All cephalopods are direct developers; there is no larval stage (although juvenile cephalopods are referred to as paralarvae) or metamorphosis. This direct development is linked with the advent of swimming using jet propulsion (Boletzky 2003). Because coleoids lack an external shell, the development into a free-living, jet-propelled swimmer may have selected for direct development, rather than keeping the shell that would hinder this type of behavior. Cephalopod eggs are laden with yolk and vary in developmental time from a few days (O'Dor and Dawe 1998) to more than one year (Voight and Grehan 2000). The development time is dependent not only on species but on temperature (Boletzky 2003). Juvenile development is also variable with respect to arm crown morphologies among species. Hatchlings that develop from species with large eggs generally have fully developed arms, whereas species that produce smaller eggs have juveniles with short arms and tentacles with fewer suckers that cannot be immediately used like adult tentacles to capture prey (Boletzky 2003). Therefore, these juveniles use their arms to capture prey until the tentacles and suckers fully develop.

In *Nautilus*, the hatchlings have a shell diameter of about 25 mm. At maturity, shell diameters can exceed 210 mm diameter in the largest species, with estimates ranging from 2.5 to 15 years for *Nautilus* to achieve maturity depending on the species and the method of study (Landman and Cochran 1987). In *Nautilus* the sexes are separate and laying the single eggs continues for the life span of the female, which can be years or perhaps decades. In modern coleoids sexes are also separate and, while most species spawn their eggs only once, there are species that have several spawning events throughout their adult life span.

GROWTH

Modern cephalopods are the largest known invertebrates, reaching total lengths (mantle plus tentacles) ranging from 15 mm in pygmy squids (*Idiosepius*) to 20 m (*Architeuthis*). Some cephalopods grow rapidly, depending on temperature and age to senescence (Pecl and Moltschaniwskyj 1997; Semmens and Moltschaniwskyj 2000; Jackson and Moltschaniwskyj 2001; Moltschaniwskyj 2004). Often, in one season, there are two separate breeding cohorts that reach sexual maturity within a few months of one another (Moltschaniwskyj 2004), demonstrating that modern cephalopods can accelerate their growth rates depending on both environmental and physiological constraints.

MOVEMENT

Early cephalopods had a ventral apertural sinus that enabled jet propulsion for movement (House 1988). In all living cephalopods, the funnel enables movement through jet propulsion.

In squids and cuttlefishes, the funnel tube and collar close the entire length of the mantle. In some oegopsid squids (mainly Ommastrephidae), the funnel tube sits in a depression (funnel groove) mainly located in the lower head region. Certain aspects of the funnel groove (folds or ridges within the groove) can be used to distinguish subfamilies from one another. In myopsids, the groove is more like a depression and not as well defined as in Oegopsida, whereas in some octopuses the funnel tube is partially or fully embedded in the head tissues and is free only at the head end. In many of the fast-swimming squids, the anterior part of the funnel groove is bordered in front of the funnel aperture by a cuticular ridge. A pair of anterior adductor muscles are attached to the funnel anteriorly, and the posterior-lateral sides of the funnel are connected to the sac of the gladius or to the dorsal side of the mantle cavity by much stronger retractor muscles. For example, in the Jumbo Flying Squid, *Dosidicus,* the swimming velocity can increase from 4 to 14 knots (2–7.2 m/s) between becoming airborne and re-entering the sea as a result of the rapid expulsion of water from the mantle cavity (Packard 1985; House 1988). In most squids, cuttlefishes, and vampyromorphs, there is a funnel valve that supposedly strengthens or supports the funnel wall when the squid is swimming. There is no valve in octopuses or in some oceanic squids (Cranchiidae). The valve is also used to change the shape of the ink cloud when it is ejected through the funnel. Along with this, a funnel organ (Verrill's organ) is located on the dorsal side of the funnel just behind the valve. Its function is unknown, but it has been hypothesized that the mucus it secretes helps in maintaining the structure of the funnel or decreasing turbulence while swimming. The shape of this organ is species specific, and thus it is another useful character for taxonomy and systematics.

Fins are also used for locomotion in squids, even those that are not good swimmers. There are mainly five types of fin shapes, which can be used as a good taxonomic character for delineating families. These include marginal or fringing, rhomboidal or heart-shaped (cordate), kidney-shaped (reniform), round, and tonguelike fins (Nesis 1980). Smaller fins are usually less adapted to speed than larger ones but are better at maneuverability. It was previously thought that fins could be a good synapomorphy for Coleoidea (Young *et al.* 1998), and this may be true for modern forms, but they are preserved in very few fossils, so their distribution in fossil coleoids is uncertain.

FEEDING MODES

The mouth (buccal aperture) is highly adapted for predatory behavior. In the Devonian and Carboniferous and in most later fossil forms the mandibles (jaws) are a horny beak divided into an upper (shorter) and lower (longer) halves. In modern cephalopods, both mandibles contain pharyngeal plates and a frontal plate covering the lateral walls. These plates fuse, forming the rostrum and the cutting edges of the mandibles. Relative size and structure of the mandibles, as well as indentations along the cutting edge, differ greatly among cephalopods and are useful characters for the study of cephalopod evolution. In dibranchiate cephalopods, the radula consists of seven longitudinal rows of teeth, with a median (= central or rhachidian) tooth and the first, second, and third lateral teeth. Marginal plates may be present on either side but are not present in all species (they are absent in sepiolids and most oegopsids but are more developed in octopuses). Radulae are highly reduced in *Spirula* and finned octopuses. In other squids, such as *Gonatus,* the radula consists of five rows of teeth and the first lateral tooth is absent. Radulae have also been useful in determining differences among closely related species (Lindgren *et al.* 2005). The radula in most coleoids is used for gripping pieces of food torn by the beak and transferring it to the pharynx.

MODIFICATION OF ARMS AND TENTACLES

Cephalopods have the most modified foot among molluscs. The large muscular appendage has been divided into several appendages that can be used to manipulate and capture prey or be used for mating. The main characteristic that separates the Decabrachia from the Octobrachia is the number of arms, with the squids and cuttlefishes having ten arms, of which two are modified as retractable tentacles, and the octopuses having eight. There is debate on whether vampyromorphs are sister to the decabrachians (with their two reduced arms considered to be "squid-like") or whether they are more like octopuses. Arms and tentacles are attached to the outer lip surrounding the mouth by the buccal membrane. There are initially eight lappets or small triangular flaps that support the buccal membrane during development, at which point the first and sometimes fourth arms may merge together. Where the buccal lappet supports are attached is of great taxonomic significance for decabrachians, since in eight families of oegopsids, the supports are attached to the fourth arms dorsally, while in the remaining families of Oegopsida and Myopsida, they are attached ventrally (Nesis 1980).

Tentacles are always positioned between the third and fourth arms and not connected to the buccal funnel. In cuttlefishes, the tentacles are very elastic and can be retracted into special pockets, whereas in other squids the tentacles can be retracted slightly, but not entirely. Although all squids have tentacles (synapomorphic character), they may lose this feature as adults (as in the Octopoteuthidae and some Gonatidae), or obtain them later during juvenile development (Idiosepiidae). Arms have also been modified for functionality; not only are they used for capturing prey, but in the octopod *Argonauta* they are used for building a pseudo-shell (the "paper nautilus") to brood eggs.

The presence of arms or tentacles around the mouth is a synapomorphic character of the Cephalopoda. The oldest tentacle preservation is *Pohlsepia* from the Carboniferous period (Mazon Creek) (Klussendorf and Doyle 2000) and *Jeletzkya* (Johnson and Richardson 1968). No ammonoid or nautiloid tentacles or impressions made by tentacles are currently known. Suckers on the arms of squids and cuttlefishes are stalked and are hemispherical in shape, and the stalks can either be long or short, thin or thick, with outgrowths in the middle forming a cup (Nesis 1980). They are often arranged in two rows, but can also be found in four rows, particularly in the Sepiidae, Sepiolidae, and Gonatidae. The suckers can also increase in number toward the base of the arm and enlarged suckers may be found in both or one of the sexes. Suckers can also be absent or rearranged into one row. Squids with hectocotylzed arms (used for passing spermatophores to the female) have modifications of the suckers, with the larger ones found in the middle or near the tips and growing smaller towards the ends of the arms. Suckers also differ on the tentacular club and can vary in the number of rows (four and up to fifty, in some Sepiolidae and Mastigoteuthidae). Larger suckers are found in the center of the club (manus) and are smaller at the ends of the club (dactylus). Most suckers of squids and cuttlefishes are armed with horny rings but are smooth in Crahnchiidae or armed with teeth in some Loliginidae. Suckers are also modified into hooks (some Gonatidae and all Enoploteuthidae) and are either on median parts of the arms or only on a few arms. Hooks always develop from suckers by uneven elongation, bending, and longitudinal folding of the distal edge of the ring or by elongation of one or two teeth during the later stages of ontogenesis. Arms of octopuses and vampyromorphs have only suckers with neither stalks nor horny rings. Finned octopods and vampyromorphs have suckers flanked by a small row of cirri, which alternate between the suckers.

NERVOUS SYSTEM

Cephalopods have a more developed nervous system than any other invertebrate, with a highly developed brain and optic lobes (Budelmann *et al.* 1997). It has been previously noted that certain octopuses are capable of learning by observation (Fiorito and Scotto 1992) as well as by testing (Wells and Wells 1977). Of importance to neural biology was the discovery and subsequent use of the giant axon in *Loligo* *vulgaris* (J. Z. Young 1936, 1977). In addition, a highly advanced visual system, particularly in the coleoids, gives the capacity to recognize surroundings. *Nautilus* eyes are of the pinhole type, in which the lumen is filled with seawater. Both House (1988) and Lehmann (1985) speculated that this was probably the same for the ancestral Ammonoidea. Coleoids have a lens and a cornea, which improve their vision and is coupled with the ability to camouflage and signal using their chromatophores. This feature probably evolved within the endocochleate (having an internalized shell) Coleoidea, in which the development of chromatophores led to a change in defensive and offensive strategies for seeking or hiding from prey and predators (House 1988).

Not only is the visual system used to match surrounding habitats, but other adaptive features such as light organs, used for counter-illumination and signaling, exist in a number of squids and a few octopuses (Young and Roper 1976; R. E. Young 1977; Young *et al.* 1979b; Jones and Nishiguchi 2004; Nishiguchi *et al.* 2004). Cephalopods have either autogenic bioluminescence (luminescence produced by themselves with a eukaryotic luciferase) or bacteriogenic light organs (luminescence produced by symbiotic bacteria with prokaryotic luciferase). Squids are capable of visually detecting changes in light attenuation and can thereby mask their shadow so that predators or prey below cannot easily see them. This is especially important at night when many cephalopods are active and the only potential illumination is moonlight (Young *et al.* 1980; Jones and Nishiguchi 2004).

BEHAVIOR

Behavior is also presently used as a way to distinguish not only species, but populations as well (Hanlon 1988; Packard 1988; Hanlon and Messenger 1996). There is a multitude of behaviors that have been documented by cephalopod researchers and are related to the complexity of the nervous system and the brain. Some of these include camouflage and body patterning, defense, communication, reproduction, and interspecies interactions (Hanlon and Messenger 1996). These intricate behaviors are not found in any of the other molluscan classes and have been key features that render the Cephalopoda unique within the phylum. Most of their behavioral features are ecologically similar to those of modern fishes, and probably the evolution of modern teleosts was largely responsible for the decline of cephalopods since the Mesozoic (Aronson 1991). Supposedly, many behavioral features were selected when fishes and reptiles living in coastal waters forced ectocochleate (having an external shell) cephalopods into deeper habitats (Packard 1972), but this is now refuted for modern cephalopods, with the exception of *Nautilus* (Aronson 1991).

Given such selective pressures, cephalopods have evolved a variety of behavioral traits linked to many of the senses (mechano-, chemo-, and photoreceptors) that allow the effectors (such as muscle, chromatophores, reflectors, photophores and the ink sac) to work in response to external stimuli. The brain, which has been mapped in a few key species (*Nautilus*, *Octopus*, and *Sepia*), forms a much more developed central nervous system and concentrated ganglia than in any other mollusc (Budelmann *et al.* 1997; Young 1988a), enabling the animal to efficiently organize the information received from all the sensory structures. This leads to the ability of matching habitat complexity, detecting and capturing prey, defense against predators (crypsis, flight, aggression), communication, learning, as well as complex mating rituals (which may be species specific) and subsequent brooding of eggs prior to hatching (Hanlon and Messenger 1996). Many of these behaviors can also be specific to species or even populations of individuals, which may then lead to subsequent sympatry and genetic differentiation between populations.

SHELL REDUCTION AND LOSS

Shell reduction (i.e., the change from having an external shell to having a reduced internal shell or no internal shell or supporting structure) was accomplished by the Carboniferous (*Pohlsepia*), and, based on the fossil record, the reduction did not appear to have a major impact on cephalopod evolution (Kluessendorf and Doyle 2000). Because of *Pohlsepia* (Kluessendorf and Doyle 2000) from the Upper Carboniferous, it is probable that shell reduction in the Coleoidea may have occurred at different times within different coleoid lineages. For example, a single evolutionary event giving rise to the Decabrachia as presented by Hass (2003) does not appear to be resolvable using a single lineage and the known fossil record.

In the *Pohlsepia* lineage, which is not well understood at this time, the complete loss of the internal chambered phragmocone, rostrum, and any kind of supporting structure (such as a pen), occurred much earlier in the overall evolution of the Coleoidea than had been expected given knowledge of the fossil record prior to 2000. With recognition of the early geologic age of this evolutionary internal shell reduction condition, it would appear that loss of buoyancy and equilibrium control by gas-filled chambers in the phragmocone or even a simple mineralized supporting structure did not provide a major evolutionary advantage to the coleoids. However, the coleoids did manage to survive three major extinction events (the Permian-Triassic, the Triassic-Jurassic, and the Cretaceous-Cenozoic), whereas the externally shelled ammonoids, which are the most abundant cephalopod group from the late Paleozoic to the end of the Mesozoic, survived only two of these extinctions. Interestingly, the ancestors of modern *Nautilus* and *Allonautilus* with their external shells managed to survive all three extinction events. The observation that the ammonoids were more abundant than the coleoids and that they were the dominant cephalopod group in the Late Paleozoic and Mesozoic is supported by the numerous marine Lagerstätten and other marine deposits around the world that preserve fossil cephalopods. Based on a nonquantifiable impression of collecting fossil cephalopods for decades and the understanding that externally shelled cephalopods were more easily fossilized, coleoid fossils are considered to be very rare through the Late Paleozoic and Mesozoic; whereas, ammonoids are relatively common and are the dominant (in terms of abundance, diversity, and geographic distribution) fossil cephalopod group.

EVOLUTION AND PHYLOGENY OF CEPHALOPODS

SISTER GROUP RELATIONSHIPS

The two main competing hypotheses for cephalopod relationships with other molluscan classes have considered the placement of Cephalopoda with Gastropoda (as the Cyrtosoma) within the Conchifera (Haszprunar 1996; Salvini-Plawen and Steiner 1996; Haszprunar 2000) or whether the Scaphopoda are sister to the gastropod+cephalopod clade (Lindberg and Ponder 1996; Haszprunar 2000). Most recently, cephalopods have been widely accepted as sister to both Scaphopoda and Gastropoda based on molecular and morphological data (Waller 1998; Giribet and Wheeler 2002; Steiner and Dreyer 2003; Giribet *et al.* 2006).

FOSSIL GROUPS

In fossil cephalopods, the general higher-level details of the overall evolution and phylogeny of many of the nautiloid taxa (variably treated as orders, superorders, or even subclasses; Figure 8.4) appear to be moderately stable, though little research has been done since the 1970s (Orlov 1962; Teichert 1964a, 1967). Although most of the main details of cephalopod evolutionary trends appear to be well established, presumed ancestral links between many higher groups remain uncertain. Ammonoid evolution is known to be very complex because these animals have durable shells that quickly evolved complex features. These animals also had a worldwide distribution over a long span of geologic time, and they have received much more attention over the past two centuries because they are very useful in determining the age of different rock units (Moore 1957, 1964;

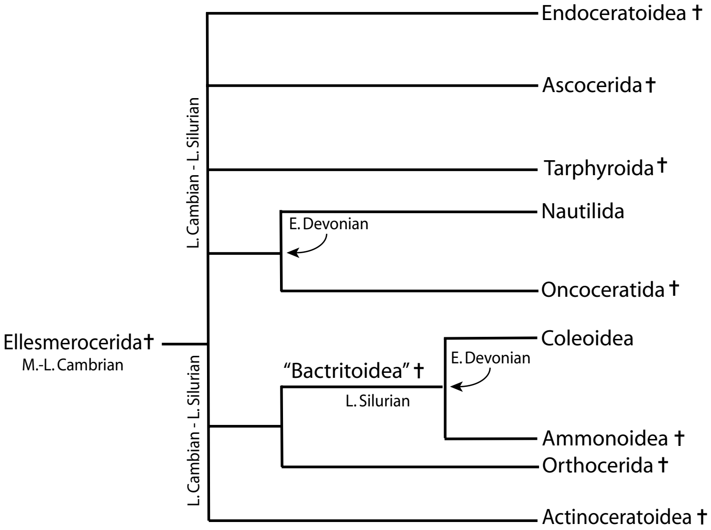


FIGURE 8.4. Generalized cephalopod phylogeny through time showing the general evolutionary trends from an Ellesmerocerida ancestor in Middle to Late Cambrian time to the extant Nautilida and Coleoidea in today's oceans. The ancestral molluscan that gave rise to the Ellesmerocerida was probably a monoplacophoran. The Ellesmerocerida lineage developed into a number of distinct subclasses, superorders, and orders, including the Orthocerida, between Late Cambrian and Late Silurian time. Only two genera with external shells (*Allonautilus* and *Nautilus*), which belong to the Nautilida, survive today. The Bactritoidea arose out of the Orthocerida in the Early Devonian. Slightly later in the Early Devonian, the Bactritoidea gave rise to the Ammonoidea, which became extinct at the end of the Cretaceous. Additionally, the Bactritoidea gave rise to the Coleoidea, which is the only other cephalopod group to survive today. The timing of the evolutionary origin of the Coleoidea from the Bactritoidea is presently unknown, with the majority of authorities suggesting a Devonian or Early Carboniferous timing for this significant evolutionary event. In order to clearly show the extant nautiloid and coleoid placements on the tree, some major groups are omitted from the diagram; all major cephalopod groups and their known geologic ranges are shown in Figure 8.7. Extinct taxa are designated with a dagger (†). E. = Early; L. = Late.

Orlov 1962; House 1981; Becker and Kullmann 1996; Page 1996; Wiedmann and Kullmann 1996; Kullmann 2002) (Figure 8.5). Even though the Nautiloidea have similar characteristics, the evolution of this group has received only modest attention because they evolved more slowly (Woodruff *et al.* 1987; Wray *et al.* 1995; Ward and Saunders 1997). To our knowledge only segments of the Ammonoidea phylogeny have been evaluated using cladistic analysis.

In contrast to the research pattern seen in the Nautiloidea, new coleoid material has been described during the past ten years that has significantly altered parts of the classifications proposed by pre-1995 coleoid researchers (e.g., Naef 1922; Jeletzky 1966; Donovan 1977). New classifications, including some using cladistic methodologies, have been proposed (Engeser 1996; Pignatti and Mariotti 1996; Mariotti and Pignatti 1999; Haas 2002) (Figure 8.6). Despite this, the early phylogeny of the Coleoidea remains poorly understood.

The oldest cephalopod fossils are from the lower and middle part of the Yenchou Member of the Fengshan Formation (late Middle Cambrian) of northeast China (Chen and Teichert 1983). Only the genus *Plectronoceras* has been recovered from the lower part of this unit. This genus represents what is probably the best cephalopod archetype and presumably arose from ancient monoplacophorans with longiconic or breviconic shells similar to the

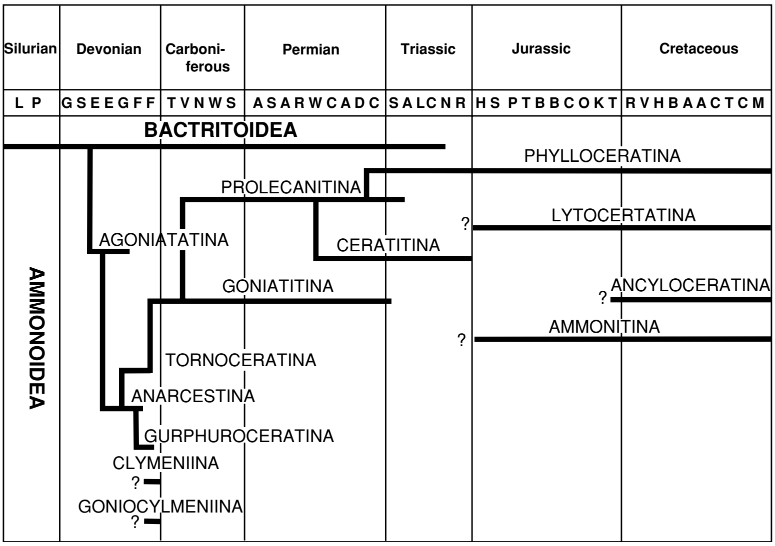


FIGURE 8.5. The evolutionary phylogeny of the Ammonoidea at the ordinal and subordinal level as derived from the Bactritoidea based on published data by Gordon 1966; Donovan *et al.* 1981; Glenister and Furnish 1981; Kullmann 1981; Tozer 1981; Wright 1981; House 1981, 1993; Wiedmann and Kullmann 1988, 1996; Becker and Kullmann 1996; Page 1996; and Kröger and Mapes 2007. Based on these works, there has been general agreement on most the phylogenetic relationships among most authorities, but some differences are unresolved. The overall relationships between the ammonoid suborders look deceptively simple; however, note that five of the 13 ammonoid suborders begin their origination with a question mark, indicating that the ancestral origins are presently unknown. There are also many unresolved ancestor and descendant relationships at the superfamily and family levels. A total number of ammonoid species is not yet available; however, Wiedmann and Kullmann (1996) indicated there are over 3,700 described ammonoid species in the Devonian, Carboniferous, and Permian. Given this impressive diversity and the fact that this cephalopod order has been studied for more than 250 years, it is surprising that subordinal ancestral-descendant relationships within the order are still unknown. This problem is even more complicated and extensive when one attempts to determine the phylogenies of the Bactritoidea, Nautiloidea, Coleoidea, and the other cephalopod orders.

Upper Cambrian *Hypseloconus* (Teichert 1988). During late Yenchou time, almost all nautiloid genera became extinct. This extinction was followed by a large evolutionary radiation seen in the overlying Wanwankou Member of the Fengshan Formation (Teichert 1988). By the Middle Ordovician, the nautiloids had diversified to the greatest morphological diversity recorded in the fossil record for ectocochleate cephalopods (Teichert and Matsumoto 1987). Almost all of the established major clades arose from Ellesmerocerida ancestors. These are the Intejocerida, Endocerida, Actinocerida, Discosorida, Ascocerida, Orthocerida, Barrandeocerida, Nautilida, Tarphycerida, and Oncoceratida (for details of these nautiloid groups see Moore 1964: fig. 7). Two were the ancestors to all the living cephalopods: the Nautilida, which gave rise to modern nautiloids (*Nautilus* and *Allonautilus*), the two living externally shelled cephalopod genera, and the Bactritoidea, which gave rise to the ammonoids and the coleoids (Chen and Teichert 1983) (Figures 8.5, 8.7).

The coleoids are generally thought to consist of eleven ordinal-level taxa, of which six are extinct (House 1988). The extinct groups with internal phragmocones are the Donovaniconida (Doguzhaeva *et al.*, in press, a), Aulacocerida, Phragmoteuthida, Belemnitida, Hematitida and Belemnoteuthida (Jeletzky 1966; Engeser and Reitner 1981; Teichert 1988; Figure 8.6, Table 8.1). The five living orders are the Octopoda, Sepiida,

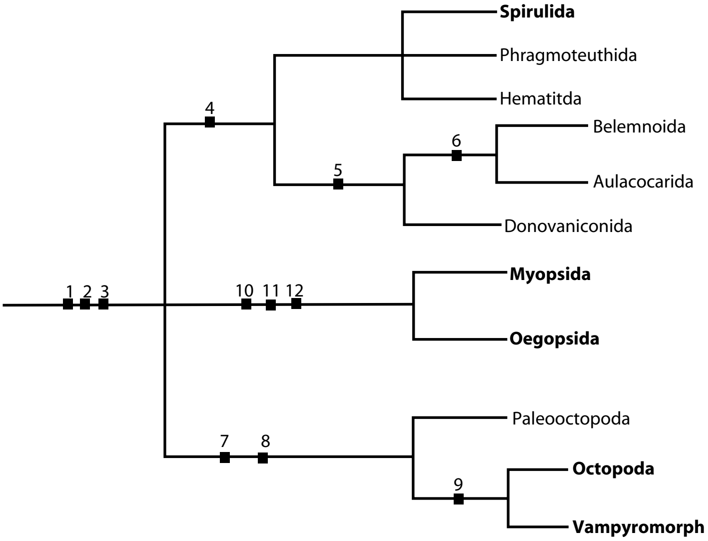


FIGURE 8.6. Proposed evolution of extinct and modern coleoids. Apomorphic characters include: (1) external shell; (2) 10 undifferentiated arms; (3) no suckers; (4) interior phragmocone; (5) arm hooks; (6) closing membrane in first chamber (suppression of prosiphon and cecum); (7) no internal shell; (8) modified arms; (9) presence of suckers; (10) arm 2 modified; (11) suppression of phragmocone; and (12) arm 4 modified. The ancestral bactritoid form probably had apomorphic characters (1), (2), and (3). This analysis evaluates most of the lineages of the Coleoidea. However, many other characters have not yet been evaluated, and we recommend that additional study of these evolutionary pathways is necessary to delineate the phylogeny of the Coleoidea more completely and accurately. Extant taxa are indicated in bold. See also Table 8.1.

Spirulida, Teuthida, and Vampyromorpha. Of these, the best documented in the fossil record is the Sepiida, since they retain all the morphological elements of the belemnitid shell (Jeletzky 1966, 1969). There are no known transitional taxa showing clear intermediate features between any of the higher coleoid groups.

Most characters used for classification of fossil coleoids include the phragmocone, rostrum or guard, and so forth. However, in general the Teuthida lack shelly hard parts but do have a modified proostracum (pen or gladius) made of organic material or a combination of organic and some carbonate material (Teichert 1988). These gladii typically do not fossilize well, and other hard parts such as phragmocones, although calcareous, are also rare as fossils. The Carboniferous coleoid taxon *Pohlsepia*, assigned to Palaeoctopoda, (Kluessendorf and Doyle 2000), lacks hard parts, and reveals the existence of coleoids without shells at that time. However, from the Middle Carboniferous through the last of the late Paleozoic and through the early Mesozoic there has been no other recovery of coleoid material assignable to the Octopoda. Significantly, below the Middle Carboniferous there are no transitional forms from the primitive bactritoid stock that presumably gave rise to this important coleoid order.

New techniques to identify fossils as coleoids include the SEM analysis of fossil ink (see the section on ink above) and the identification of unique coleoid shell ultrastructures using SEM. For example, a Carboniferous "*Bactrites*" from Texas (Miller 1930) was reinterpreted as a coleoid belonging to the Spirulida (Doguzhaeva *et al.* 1999), extending the range of Spirulida from the Cretaceous (the oldest previously known spirulid) to the Carboniferous. Such discoveries, however, are rare (especially in the Paleozoic and early Mesozoic), given the generally poor fossilization potential of most coleoids.

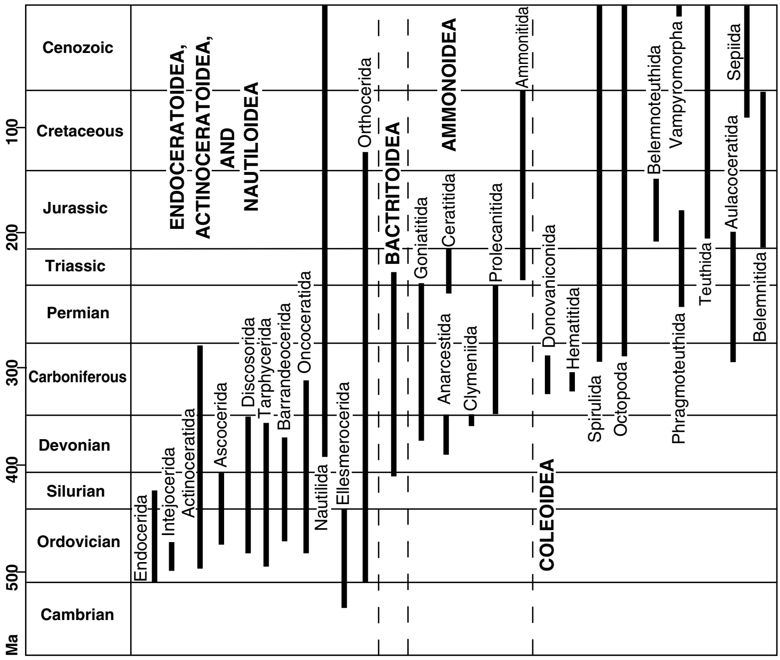


FIGURE 8.7. Geologic ranges of the major extinct and extant subclasses, superorders, and orders of the Cephalopoda (modified from House 1988; note that the terminology as to rank varies considerably in the literature). Some of the ancestor-descendant relationships within the Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea, and Ammonoidea are known. However, the recent discovery of numerous new fossil coleoids from the Carboniferous has put to question some of the geologic ranges and the proposed origins of some of the fossil coleoid orders. Also, the fact that the origin of the earliest coleoids is unknown remains an unresolved evolutionary problem that complicates the development of a unified phylogeny for the Coleoidea.

The origin of the Coleoidea (Figure 8.4) is presently accepted as being from the Bactritoidea in the Paleozoic (Devonian and/or Carboniferous) (Figure 8.7). The Bactritoidea (Silurian to Triassic) have an egg- or ball-shaped protoconch in which the typical phragmocone of the genus *Bactrites* has a ventral marginal siphuncle with simple disk-shaped septa and an orthoconic (i.e., straight) shell (e.g., Mapes 1979). Primitive coleoids have phragmocones with these same characteristics. *Lobobactrites,* another bactritoidean, is similar in gross morphology to *Bactrites* except that the subspherical protoconch is twice as large in diameter and length as that of *Bactrites. Lobobactrites* is considered the probable ancestor of Ammonoidea because the earliest known ammonoids also have large, egg-shaped protoconchs (Erben 1964; Teichert 1988). The main difference between the Bactritoidea and the Ammonoidea is that all bactritoids have orthoconic shells, whereas those of the most primitive ammonoids are cyrtoconic (slightly curved) shells. By the end of the early Devonian, the ammonoid protoconch had generally begun to reduce in size and the shell became more tightly coiled. By the end of the Devonian, all ammonoids had a small, more or less spherical protoconch, and the shell was tightly coiled.

The ammonoid groups underwent several major extinctions and re-radiations from the early Devonian to the end of the Cretaceous (e.g., House 1988). The first extinction was near the end of the Devonian, the second at the Permo-Cenozoic boundary, and the third at the Triassic-Jurassic boundary. After surviving these three extinctions, ammonites became extinct at the Cretaceous-Cenozoic boundary (Figure 8.5). At

TABLE 8.1

Classification of Paleozoic and Modern Coleoids

- Subclass Coleoidea Bather, 1888
  - Superorder Belemnoida Gray, 1849 (Carboniferous–Cretaceous)
    - Order Hematitida Doguzhaeva, Mapes, and Mutvei, 2002[a] (Carboniferous)
      - Family Hematitidae Gustomesov, 1976
        - Hematites (Flower and Gordon 1959): Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovan), Utah, Arkansas, United States
        - *Bactritimimus* (Flower and Gordon 1959): Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovan), Arkansas, United States
        - *Paleoconus* (Flower and Gordon 1959): Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovan), Arkansas, United States
    - Order Phragmoteuthida Jeletzky in Sweet, 1964 (Upper Permian–Jurassic)
      - Family Phragmoteuthididae Mojsisovics, 1882
        - *Permoteuthis groenlandica* Rosenkrantz, 1946: Upper Permian, Foldvik Creek Formation, Clavering Island, East Greenland
    - Order Donovaniconida Doguzhaeva, Mapes, and Mutvei[b] (Carboniferous)
      - Family Donovaniconidae Doguzhaeva, Mapes and Mutvei, 2002[c]
        - *Donovaniconus* (Doguzhaeva *et al.* 2002a): Upper Carboniferous, Desmoinesian, Oklahoma, United States
        - *Saundersities* (Doguzhaeva *et al.*, in press, b): Upper Carboniferous, Desmoinesian, Illinois, United States
      - Family Rhiphaeoteuthidae Doguzhaeva, 2002
        - *Rhiphaeteuthis* Doguzhaeva, 2002: Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan Republic (former USSR).
      - Family Uncertain
        - New genus: Lower Carboniferous, Bear Gulch Limestone, Montana, United States (Mapes *et al.* 2007)
    - Order Aulacoceratida Stolley, 1919 (Carboniferous–Jurassic)
      - Family Mutveiconitidae Doguzhaeva, 2002
        - *Mutveiconites* Doguzhaeva, 2002: Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan Republic (former Soviet Union).
  - Superorder Decembrachiata Winckworth, 1932 (Carboniferous–Holocene)
    - Order Spirulida Haeckel, 1896 (Carboniferous–Holocene)
      - Family Shimanskyidae Doguzhaeva, Mapes, and Mutvei, 1999
        - *Shimanskya* (Doguzhaeva *et al.* 1999): Upper Pennsylvanian, Virginian (= Stephanian); Texas, United States
      - Family Spirulidae Owen, 1836
    - Order Oegopsida Leach, 1917
      - Family Architeuthidae Pfeffer, 1900
      - Family Brachioteuthidae Pfeffer, 1908
      - Family Batoteuthidae Young and Roper, 1968
      - Family Chiroteuthidae Gray, 1849
      - Family Joubiniteuthidae Naef, 1922

TABLE 8.1
(continued)

- Family Magnapinnidae Vecchione and Young, 1998
- Family Mastigoteuthidae Verrill, 1881
- Family Promachoteuthidae Naef, 1912
- Family Cranchiidae Prosch, 1847
- Family Cycloteuthidae Naef, 1923
- Family Ancistrocheiridae Pfeffer, 1912
- Family Enoploteuthidae Pfeffer, 1900
- Family Lycoteuthidae Pfeffer, 1908
- Family Pyroteuthidae Pfeffer, 1912
- Family Gonatidae Hoyle, 1886
- Family Histioteuthidae Verrill, 1881
- Family Psychroteuthidae Thiele, 1920
- Family Lepidoteuthidae Naef, 1912
- Family Octopoteuthidae Berry, 1912
- Family Pholidoteuthidae Voss, 1956
- Family Neoteuthidae Naef, 1921
- Family Ommastrephidae Steenstruup, 1857
- Family Onychoteuthidae Gray, 1847
- Family Thysanoteuthidae Keferstein, 1866
- Order Myopsida Naef, 1916
  - Family Australiteuthidae Lu, 2005
  - Family Loliginidae Lesueur, 1821
- Order Sepioidea Naef, 1916
  - Suborder Sepiida Keferstein, 1866
    - Family Sepiidae Keferstein, 1866
  - Suborder Sepiolida Naef, 1916
    - Family Sepiadariidae Fischer, 1882
    - Family Sepiolidae Leach, 1817
- Superorder Vampyropoda Boletzky, 1992 (Carboniferous–Holocene)
  - Order Octopoda Leach, 1817 (Carboniferous–Holocene)
    - Family Palaeoctopodidae Dollo, 1912
      - *Pohlsepia mazonensis* (Kluessendorf and Doyle 2000): Middle Carboniferous, Desmoinesian, Francis Creek Formation, Illinois, United States
    - Suborder Cirrata Grimpe, 1916
      - Family Cirroteuthidae Keferstein, 1866
      - Family Stauroteuthidae Grimpe, 1916
      - Family Opisthoteuthidae Verrill, 1896
    - Suborder Incirrata Grimpe, 1916
      - Family Amphitretidae Hoyle, 1886
      - Family Bolitaenidae Chun, 1911
      - Family Octopodidae Orbigny, 1840, in Ferussac and Orbigny, 1834–1848

TABLE 8.1
(continued)

        - Family Vitreledonellidae Robson, 1932
      - Superfamily Argonautoida Naef, 1912
        - Family Alloposidae Verrill, 1881
        - Family Argonautidae Cantraine, 1841
        - Family Ocythoidae Gray, 1849
        - Family Tremoctopodidae Tryon, 1879
    - Order and family uncertain
          - "*Bactrites*" *woodi* (Mapes 1979: pl. 18: figs. 8, 12): Upper Carboniferous, Missourian, Kansas, United States
          - Undescribed Stark coleoids (see Doguzhaeva *et al.* 2002c): Upper Pennsylvanian, Missourian (= Kasimovian), Nebraska, United States
      - Superfamily Bathyteuthoida V
        - Family Bathyteuthidae Pfeffer, 1900
        - Family Chtenopterygidae Grimpe, 1922
        - Family Idiosepiidae Fischer, 1882
- Problematic specimens
  - *Boletzkya longa* (Bandel *et al.* 1983): Devonian (Emsian), Hunsrückschiefer, Kaisergrube, Hunsrück, Germany
  - *Naefiteuthis breviphragmoconus* (Bandel *et al.* 1983): Devonian (Emsian), Hunsrückschiefer, Kaisergrube, Hunsrück, Germany
  - *Protoaulacoceras longirostris* (Bandel *et al.* 1983): Devonian, Hunsrückschiefer, Kaisergrube, Hunsrück, Germany
  - *Eoteuthis* sp. (Termier and Termier 1971): Devonian of Morocco, North Africa
  - *Aulacoceras*? sp. (de Konick 1843): Locality and age (?Devonian/Carboniferous)
  - *Eobelemnites caneyensis* (Flower 1945): Unknown locality and age
  - *Jeletzkya douglassae* (Johnson and Richardson 1968): Upper Carboniferous, Desmoinesian, Francis Creek Formation, Illinois, United States
  - Unnamed coleoid from Czech Republic (Kostak *et al.* 2002): Early Carboniferous, Moravica Formation, Northern Moravia, Czech Republic
  - Unnamed coleoid by Allison (1987): Upper Carboniferous, Desmoinesian, Francis Creek Formation, Illinois, United States
  - *Palaeobelemnopsis sinensis* Chin, 1982:Upper Permian from China

NOTE: From Doyle 1993, Doyle *et al.* 1994, Pignatti and Mariotti 1995, Young *et al.* 1998, Doguzhaeva *et al.* 1999, 2002a,b, 2003, in press a, Haas 2002, and the web site maintained by T. Engeser (http://userpage.fu-berlin.de/~palaeont/fossilcoleoidea/hhierarchicalclassification.html) and by R. Young (http://tolweb.org/tree?group=Cephalopoda&contgroup=Mollusca).

[a] Doguzhaeva *et al.* 2002b.

[b] Doguzhaeva *et al.*, in press, b.

[c] Doguzhaeva *et al.* 2002a.

Taxa without stratigraphic ranges are Recent.

each extinction event, only one or a few genera survived, and it was those survivors that rapidly diversified into the empty ecological niches in the world's oceans. Thus, the Ammonoidea have an important place in invertebrate paleontology and stratigraphy, not only because of their diversity but through their pelagic development, which facilitated the attainment of worldwide distributions.

There are literature reports of putative coleoids from the Devonian (de Konick 1843), *Eoteuthis* from Morocco (Termier and Termier 1971) and *Protoaulacoceras, Boletzkya,* and *Naefiteuthis* from Germany (Bandel and Boletzky 1988, Bandel *et al.* 1983). Unfortunately, none of these have been confirmed as being coleoids. De Konick's (1843) specimens were inadequately illustrated and are apparently lost, and the specimen identified by Termier and Termier (1971) has been determined to be a bactritoid (Doyle *et al.* 1994). The identification of specimens reported by Bandel *et al.* (1983) and reanalyzed by Bandel and Boletzky (1988) are questionable (Doyle *et al.* 1994), making the coleoid evolution of the Devonian period difficult to assess.

Of the known fossil coleoids, the oldest are *Hematites, Paleoconus,* and *Bactritimimus* (Flower and Gordon 1959; Gordon 1964) from the lower Carboniferous of Arkansas and Utah, United States, with only *Hematites* represented by numerous, well-preserved specimens. Doguzhaeva *et al.* (2002b) determined that *Hematites* and probably the other two genera were unique in many ways and established a new order, Hematitida. Some unique characteristics included the thick, blunt rostrum, which was partly calcified and organic. During early ontogeny, the animal initially grew the breviconic phragmocone with chambers containing internal cameral deposits and a short body chamber. The rostrum was secreted only as the animal neared maturity. Of over 100 *Hematites* specimens examined with rostrums, only one retained a visible protoconch,[1] described as relatively large and spherical in shape. A spherical protoconch and the characteristics of the phragmocone support the interpretation that the bactritoids were the ancestral stock of the coleoids, which probably originated in the earliest Carboniferous or perhaps the Devonian.

The Carboniferous is now known to contain several additional different coleoid genera. Many of these taxa have been described in the past ten years and have lead to the establishment of a number of new families (Table 8.1) complicating previous hypotheses of the early coleoid phylogeny (e.g., Teichert and Moore 1964: K101, fig. 70; Teichert 1967: 198–199, fig. 20; Engeser and Bandel 1988; Pignatti and Mariotti 1996) (Figure 8.6). There has been general agreement that the origination of coleoids occurred in either the Early Carboniferous or the Devonian and that they were derived from a bactritoidean, with the implication that the group is monophyletic, arising from a paraphyletic Nautiloidea (Figure 8.4). Little consideration has yet been given to the possibility that several different taxa belonging to the Bactritoidea may have been involved in the origin of the Coleoidea at different times in the Devonian and Carboniferous. A polyphyletic origin of Coleoidea might help to explain the great diversity of different morphologies seen in the Carboniferous coleoids and why no closely related coleoid taxa have been conclusively documented from the Devonian.

Currently, there is little agreement among coleoid researchers as to how the higher groups are related to each other and how and when their originations occurred. In part, this lack of agreement is due to the lack of suitable fossils. Additionally, the understanding of the phylogeny of fossil Coleoidea may also have been confused by the premature application of cladistic analysis using data sets subject to major changes with the discovery of new fossils. This is not to suggest that cladistic analysis should not be applied to the coleoid data set, but rather that the results of such preliminary analyses should be treated with caution.

LIVING GROUPS

The first attempt at understanding cephalopod relationships among extant species began in the early 1800s, with the establishment of the subclasses Tetrabranchiata and Dibranchiata based on the number of ctenidia present (Owen 1836). Both Decapoda (Decabrachia, *sensu* Boletzky 2003) and Octopoda (Octobrachia, *sensu* Boletzky 2003) have been acknowledged since the works of d'Orbigny (d'Orbigny 1845) and are distinguished by a number of characters including the number of arms, presence or

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[1] Specimen now misplaced.

absence of chitinous sucker rings and sucker stalks, presence or absence of a buccal crown and lappets, a wide canal between the afferent and efferent vessels of the gill, reduced internal shell (common in both groups), broad neck fusion (found in both groups), and a mediodorsal sac of the mantle cavity (Clarke 1988). These "superorders" were further subdivided into several groups usually treated as orders (Spirulida, Sepiida, Sepiolida, and Teuthida in the Decabrachia; Octopodida and Vampyromorphida in the Octobrachia) (e.g., Sweeney and Roper 1998). The majority of the earliest classifications were initiated by Naef (1921–1923, 1928), who used a large amount of detailed morphological, embryological, and paleontological data in his monographs. Although many of his groupings are still currently recognized today, some of his classification schemes have since been challenged. He did not use many of the adult morphological characters that are commonly used today, but nonetheless his observations provided a solid foundation and are some of the most influential and important works on cephalopod evolution.

Numerous characters have provided information in delineating family- to species-level differences (Clarke 1988), such as the gladii (Donovan and Toll 1988), mouth parts such as the buccal mass and beaks (Clarke and Maddock 1988a; Nixon 1988), statoliths (Clarke and Maddock 1988b; Young 1988b), ontogenetic development (Boletzky 1997, 2002, 2003), brain morphology (Budelmann *et al.* 1997; Nixon and Young 2003; Young 1988a) and photophores or the presence of a light organ (Young *et al.* 1979a; Young and Bennett 1988; Nishiguchi *et al.* 1998, 2004; Nishiguchi 2002). Since many of these characteristics are shared among sister taxa (e.g., bacteriogenic light organs—those that produce light by symbiotic luminous bacteria—are found only in two families of squids, the Loliginidae and the Sepiolidae), they provide additional information regarding the evolution of such structures and whether those features are derived, are synapomorphic, or have evolved independently several times.

EVOLUTION AND PHYLOGENETIC ANALYSIS OF RECENT CEPHALOPODS

CURRENT CLASSIFICATIONS

Overall, there has been strong support for the monophyly of Cephalopoda (Berthold and Engeser 1987; Salvini-Plawen and Steiner 1996; Lindgren *et al.* 2004; Passamaneck *et al.* 2004; Giribet *et al.* 2006). Most research in the past century has focused solely on describing groups, from levels of orders to species. In living cephalopods, Nautiloidea has one family (Nautilidae) and Coleoidea has two major groups (Octopodiformes and Decapodiformes). Several ordinal-group taxa have been recognized: Vampyromorpha (vampire squids) and Octopoda (shallow-water benthic and deep-water and pelagic octopus) within the Octopodiformes, and Oegopsida, Myopsida, Sepioidea (cuttlefish and bobtail squids) and Spirulida (ram's horn squid) (Young *et al.*, 1998). There are many variations on this classification that differ in detail (number of orders, suborders, superfamilies recognized, and their rank). For example, the orders Cirroctopodida and Octopodida have also been classified as suborders Cirrata and Incirrata, using Octopoda as the order designation and Octopodiformes as the superorder designation (Young and Vecchione 1999; Norman 2000). An additional level of controversy exists when fossil taxa are incorporated in classifications (see also previous section) and different classifications result (Berthold and Engeser 1987) (Figure 8.6).

MORPHOLOGICAL DATA

The most extensive morphological phylogenetic analysis of coleoids is that of Young and Vecchione (1996), who examined 50 morphological characters of 24 species from 17 families to determine whether Cirrata, Incirrata, and Decabrachia were monophyletic and whether vampyromorphs were included within the Octobrachia or Decabrachia. Because of problems with character independence, lack of apomorphic characters, and possible presence of homoplasy among several key features, many characters were disregarded prior to analysis. Their analysis resulted in a better understanding of the relationships between incirrate and cirrate octopods, as well as the placement of Vampyromorpha as sister to the Octobrachia. Taxa within the Decabrachia were unresolved, although that group was not the primary focus of this analysis. In the ten years since their study, numerous Paleozoic coleoids have been described (see previous section and Table 8.1), which will undoubtedly have an impact on our understanding of early coleoid evolution. Other morphological studies focused on one or a few key characters for higher-level relationships (Roper 1969; Toll 1982; Boletzky 1987; Hess 1987; Nesis 1987; Voight 1997; Young *et al.* 1998; Vecchione *et al.* 1999; Haas 2002), but none were able to provide robust phylogenies for family-level relationships (e.g., within the Decabrachia).

MOLECULAR PHYLOGENETICS

SINGLE-GENE TREE PHYLOGENIES

The first attempt at using molecular data to determine family-level relationships of coleoids was by Bonnaud and co-workers (Bonnaud *et al.* 1994) using a 450–580 bp sequence of the 16S rDNA locus from 27 species of decabrachian squids, representing eight families. This study supported many of the higher order-level relationships resolved in some of the previous morphological studies (e.g., Young and Vecchione 1996; Young *et al.* 1998), yet it unsuccessfully delineated many of the family-level relationships. Following this, three more extensive molecular phylogenetic analyses were completed using loci from the mitochondrial genome; the cytochrome *c* oxidase subunit I (COI) and combined cytochrome *c* oxidase subunits II and III for 48 and 17 taxa respectively (Bonnaud 1995; Bonnaud *et al.* 1997; Carlini and Graves 1999). These studies demonstrated the monophyly of Coleoidea, Octobrachia, Vampyromorpha, and Decabrachia; that Vampyromorpha is sister to the Octobrachia; the polyphyly of Sepioidea; and the lack of resolution of lower-level taxa, particularly within the Decabrachia. *Spirula,* which was previously included within the Sepioidea (e.g., Voss 1977), was separated in both studies and grouped with the teuthoids. There were also some discrepancies between the analyses, with placement of Idiosepiidae either with Sepiadariidae (Carlini and Graves 1999), or within the Oegopsida (Bonnaud *et al.* 1997). A separate study used the actin gene family to determine coleoid phylogeny from 44 representative taxa (Carlini *et al.* 2000). The results recognized that multigene families of actin existed with the Cephalopoda (therefore producing gene trees more than taxon-specific trees), and the information had little resolution of decabrachian relationships, particularly within the orders of Teuthoidea, Sepioidea, and the teuthid suborder Oegopsida, but gave support to the Myopsida.

MULTILOCUS AND COMBINED PHYLOGENETIC ANALYSES

Concurrently, there has been a recognition that additional genes, or a combination of genes and morphology, was needed to provide more resolution, not only at the higher levels within coleoid cephalopods but also within "orders" of the Decabrachia. The first analysis using both molecular and morphological data sets (Carlini *et al.* 2001) reevaluated previous COI data (Carlini and Graves 1999) for octopod phylogeny in light of previous morphological evidence (Young and Vecchione 1996). Although a number of congruencies were supported using both data sets (monophyly of the Octopoda and of Cirrata), other discrepancies have not yet been resolved (monophyly of Incirrata). Studies using additional mitochondrial loci (Takumiya *et al.* 2005) or entire mitochondrial genomes (Yokobori *et al.* 2004; Akasaki *et al.* 2006) supported higher-level coleoid relationships but were still not able to resolve family-level hierarchies, particularly in the Decabrachia.

Because of conflict between molecular and morphological data sets, more recent analyses have used a combination of molecular data (using multiple genes) and morphology with a variety of analyses to determine both higher- and lower-level relationships within cephalopods (Lindgren *et al.* 2004; Strugnell *et al.* 2005). Morphology has been successfully used to define higher-level classification among the Octobrachia and Decabrachia, but

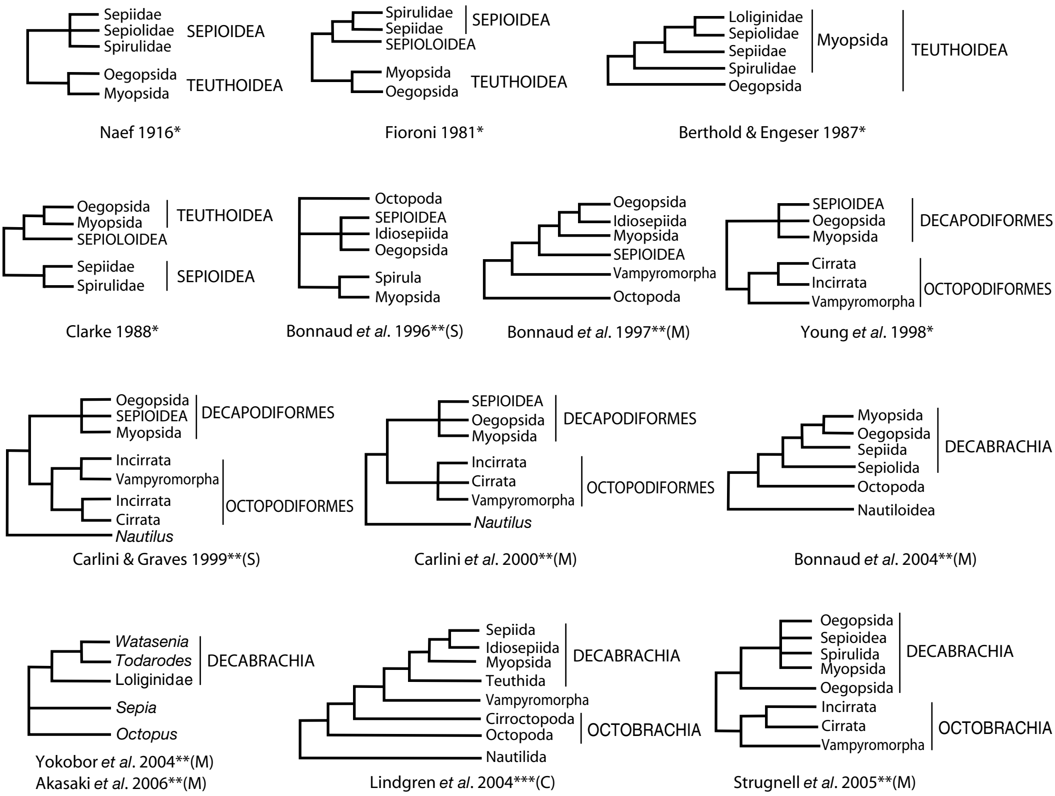

FIGURE 8.8. Summaries of phylogenetic hypotheses of several models of cephalopod evolution based on morphological (*), molecular (**), and combined data (***). Note the differences between many of the morphologically based phylogenies, as well as those using various molecular (single [S] or multiple [M] genes) and combined (molecular and morphology, [C]) data sets.

the lower-level relationships have been better resolved using molecular systematics. This has also been true for other metazoan groups where the diversity among classes is quite high (Giribet *et al.* 2001; Giribet and Edgecombe 2006). Incongruence between morphological and molecular data is not uncommon in other phylogenetic studies (Giribet 2003), and therefore, further investigation of the resolution between individual genes, synonymous and non-synonymous substitutions, and the use of coding genes (Strugnell *et al.* 2005) may help increase support for unresolved relationships. Inclusion of fossil data to "fill in" information regarding rapid radiations or extinctions may also help support nodes that contain problematic taxa (e.g., Vampyromorpha).

Comparisons of individual trees derived from a variety of analyses of single genes and morphological data have provided information regarding which loci/characters have more or less resolution. This can be of use, since genes that evolve faster will have higher resolution at the family/species/population level, whereas slower-evolving or more conserved genes (such as the ribosomal genes) will have more resolution at the basal nodes of larger groups. For example, more conserved loci, such as 18S and 28S rDNA, provide information regarding the monophyly for Cephalopoda and Coleoidea but have little resolution among the lower-level relationships among orders and families (Lindgren *et al.* 2004, table 1). Combined analyses (Lindgren *et al.* 2004), along with several other studies (Bonnaud *et al.* 1994, 1997; Carlini and Graves 1999; Nishiguchi *et al.* 2004; Strugnell *et al.* 2005) have demonstrated that relationships among Sepiolida, Sepiida, Idiosepiida, and the Loliginidae are well supported by the addition of molecular data, while the position

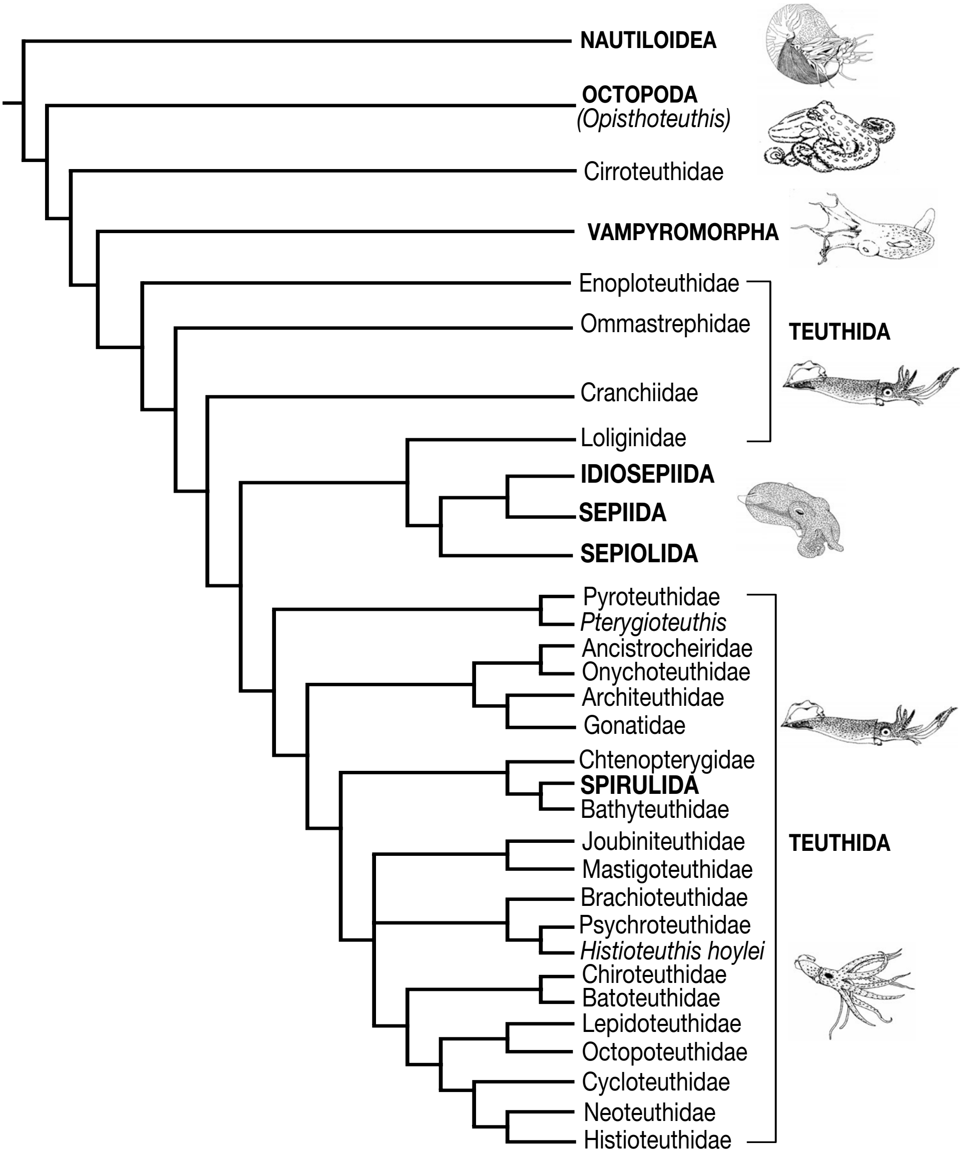

FIGURE 8.9. Schematic representation of modern cephalopod relationships based on the optimal parameter set using direct optimization (via parsimony) for the combined analysis of 101 morphological characters and molecular data from four loci (mitochondrial cytochrome *c* oxidase subunit I, nuclear 18S rDNA, the D3 expansion fragment of 28S rDNA, and histone H3). Taxa in capitals represent orders of cephalopods that appeared monophyletic in the analysis (from Lindgren *et al.* 2004). Drawings by G. Williams.

of *Spirula* within the sepioid groups remains to be resolved (Figures 8.8, 8.9). Although the molecular data has added increased resolution between the orders, it still does not resolve relationships between large family groups, such as the Oegopsida. This is probably because this order radiated rather quickly and, because sampling some of the deeper water families is difficult, they are under-represented in most molecular studies to date.

One of the most debatable relationships is the placement of Vampyromorpha within the Decabrachia (Figures 8.8, 8.9). Earlier studies have placed Vampyromorpha with the Octobrachia based on embryological and developmental data (Naef 1928, Young and Vecchione 1996;

Boletzky 2003) as well as several morphological, including ultrastructural, characters (Toll 1982, 1998; Healy 1989, Lindgren *et al.* 2004). However, molecular studies (Bonnaud *et al.* 1997; Carlini and Graves 1999; Lindgren *et al.* 2004) have shown different results depending on which molecular loci were tested and which outgroup taxa and parameter variations were used. The main conflict for this work was between the morphological and the molecular/combined data. Morphological data suggests a sister relationship between Vampyromorpha and the Octobrachia, whereas the molecular and combined data suggest a closer relationship between Vampyromorpha and the Decabrachia. Additional studies are needed to resolve these and other internal relationships, and the inclusion of more taxa (particularly from those groups that have been poorly sampled and therefore under-represented in previous results) will help provide a more detailed phylogeny of cephalopod evolution.

Additional molecular studies have recently been used to investigate decabrachian evolution with respect to the placement of *Spirula* using 18S rDNA (Warnke *et al.* 2003); lower-level relationships within families (16S rDNA for cirrate octopod relationships [Piertney *et al.* 2003] and microsatellite and 16S rDNA for loliginid relationships [Shaw *et al.* 1999; Anderson 2000; Reichow and Smith 2001]); identification of juvenile and adult gonatid squids (Seibel *et al.* 2000; Lindgren *et al.* 2005); as well as investigating the evolution of species complexes among octopods (Söller *et al.* 2000; Strugnell *et al.* 2004; Allcock *et al.* 1997; Guzik *et al.* 2005) and sepiolids (Nishiguchi *et al.* 2004), to name a few. Population genetic studies have also helped provide information regarding the migration of specific haplotypes and the phylogeography of sister species (Anderson 2000; Herke and Foltz 2002; Jones *et al.* 2006).

DEVELOPMENT

More recently, sophisticated techniques have improved our understanding of the development and neontology of cephalopods. Naef provided much of the foundation for the embryology of many cephalopod species, which is elegantly presented in his monograph (Naef 1928). This work provided cephalopod researchers with a large number of characters that were useful for morphological comparisons and, subsequently, cephalopod systematics and evolution. Recent techniques using *in situ* hybridization have allowed the expansion of a new field of research, namely evolutionary developmental biology, to help understand how specific genes are expressed among related taxa. This information can provide insight as to whether the same gene in a variety of organisms controls key developmental traits, or whether these genes have been co-opted to function for other developmental programs. For instance, master control genes such as *Hox* and *Pax6* have demonstrated the relationship of closely related molluscs and the conservative nature of these sequences (Halder *et al.* 1995, see also Wanninger *et al.*, Chapter 16). Although the genetic information may not give the resolution needed to solve internal cephalopod nodes, the observation of protein expression can provide insights into the differentiation of cephalopod morphology and the co-option of genes for numerous functions (Tomarev *et al.* 1997; Callaerts *et al.* 2002; Hartmann *et al.* 2003; Lee *et al.* 2003).

Following developmental programs and combining them with phylogenetic information may also give insights as to the evolution of specific morphological features and provide evidence for relationships that are linked only by these features, such as bacteriogenic light organs in both sepiolids and loliginid squids (Foster *et al.* 2002; Nishiguchi *et al.* 1998, 2004) and symbiosis between squids and bacteria in accessory nidamental glands (Grigioni *et al.* 2000; Pichon *et al.* 2005). Elegant work has recently provided detailed maps of the neurodevelopment of myopsid, oegopsid, and idiosepiid squids (Shigeno *et al.* 2001a, b; Shigeno and Yamamoto 2002), exhibiting major differences among these squids. Protein regulation and gene expression has recently been examined in squids for use in diagnosing induction of tissue morphogenesis and apoptosis (Crookes *et al.* 2004; Doino and McFall-Ngai 1995; Foster and McFall-Ngai 1998; Montgomery and McFall-Ngai 1992; Small and McFall-Ngai 1998; Zinovieva *et al.* 1993). Finally, advanced tracer techniques, biochemical analyses, and direct *in situ* measurements of growth and other physiological attributes are providing information regarding the growth, life history strategies, and behavior of squids, both from the wild and in the laboratory (Forsythe *et al.* 2001, 2002; Hanlon *et al.* 1997; Huffard *et al.* 2005; Jones and Nishiguchi 2004; Kasugai 2000; Landman *et al.* 2004; Moltschaniwskyj 1994; Pecl and Moltschaniwskyj 1997; Shea 2005; Steer *et al.* 2004).

All these comparative studies have proven to be useful in providing additional information not only for delineating function and life history characteristics but also to delve into the possible evolutionary trajectories that may explain similar characteristics shared among distantly related cephalopods. Combining this information with molecular studies may help evolutionary biologists test homology hypotheses of morphological features or shared developmental patterns in gene expression, which may be evolutionarily derived. These can then be used as key innovations and included in cladistic analyses.

ADAPTIVE RADIATIONS

In fossil cephalopods, the focus of the few studies on adaptive radiation have been on the progressive changes of the external shell through geologic time as predators became more efficient (for an extended discussion of the theory of evolution and escalation see Vermeij 1987; also see Mapes and Chaffin 2003). Ward (1981) determined that the ornament on the shells of ammonoids became rougher through time (Devonian to Cretaceous). Signor and Brett (1984) analyzed the tarphycerids, barrandeocerids, and nautilids in part of the Paleozoic and determined that the origin of the durophagous (shell-crushing) predators in the Silurian and Devonian coincided with a gradually increased robustness of the ornament in these nautiloid orders. As an additional observation on fossil cephalopod evolutionary radiations, Vermeij (1987) observed that the external shells of ancient nautiloids have not proven to be an effective counter to predation in the long run. The rationale behind this observation is that, given the evolutionary success of durophagous predators through time, and given that modern cephalopods without external shells (i.e., the Coleoidea) are so much more abundant, diverse, and worldwide in their distribution today as compared to modern *Nautilus* and *Allonautilus* with their external shells and limited geographic distribution, the externally shelled cephalopods were not competitive in the long run. This conclusion seems obvious given the then-known fossil record of ectocochleate cephalopods versus the abundance of endocochleate cephalopods living today. However, the externally shelled cephalopods (e.g., the Nautiloidea and Ammonoidea) had a long and diverse history (see Figure 8.5, for example, showing the complexity of ammonoid phylogeny) and that these lineages survived many extinction events and reradiated to refill and dominate the world's oceans. Notably, we now know that the evolution of shell-less coleoids occurred prior to the Upper Carboniferous and that, while these shell-less coleoids must have also survived the same extinction events in the Late Paleozoic and Mesozoic as the externally shelled cephalopods, they did not overwhelm them and become the dominant cephalopod group after those extinction events. It was only after almost all the externally shelled forms had become extinct (all the Ammonoidea and virtually all of the Nautiloidea) at the end of the Mesozoic that the coleoids radiated to become the dominant cephalopod group in the world's oceans.

Cephalopods, with their sensory/nervous/visual systems, are excellent predators, being entirely carnivorous on a large variety of prey species. Not only does their advanced nervous system allow for a great ability for capturing prey, but it also increased their ability to invade a multitude of niches. Based on observations of modern coleoids, the evolution of a complex visual system and chromatophores was probably related to the development of a well developed nervous system (Budelmann *et al.* 1997; Hanlon and Messenger 1996), which, through integration with a highly developed system of dermal chromatophores, enables most coleoid cephalopods to change color rapidly. Such color changes are used for camouflage; to display specific patterns toward predators, prey, other cephalopod species; or for intraspecific behavioral interactions, such as sexual displays (Hanlon and Messenger 1996), and presumably played a large part in the success of the group. The static presumed cryptic coloration of the shell and animal of living *Nautilus* is in marked contrast. The evolution from a shelled to a nonshelled coleoid probably began in the Devonian and/or early Carboniferous (see above) because more efficient and active predators evolved at that time. By shell reduction and the evolutionary selection of other advanced traits (i.e., complex brain driving other characters), the coleoids evolved elaborate sensory systems fulfilling tasks achieved by effectors (i.e., camouflage) to counter the evolutionary pressures created by efficient and more active predators (Nixon and Young 2003).

Along with major changes in behavior due to a highly advanced nervous system, cephalopods have evolved various mechanisms for controlling buoyancy and propulsion. As previously mentioned, buoyancy in cephalopods is controlled by the presence of gas spaces (as in taxa such as *Nautilus, Spirula,* and *Sepia,* which have a shell or cuttlebone). Cephalopods with no gas-filled compartments must rely on using jet propulsion to move continually through the water column to maintain buoyancy, or they achieve it by an increase in solutes such as ammonium chloride within the coelomic space or in vacuoles within their tissues (Boyle and Rodhouse 2005). The evolution of fins also helped to orient and maneuver the body during swimming, depending on the lifestyle of the squid (epipelagic fast swimmers versus slower, coastal species). Finally, the evolution of arms and tentacles enabled cephalopods to possess the ability to handle prey efficiently, allowing them to feed on a large variety of prey items. The arm crown, which is derived from the mouth of cephalopods (Packard 1972), is much more versatile for capturing and handling prey (Boyle and Rodhouse 2005). Along with arms and tentacles that possess suckers for holding and attaching onto prey, these adaptive characteristics contributed to the success of cephalopods as predators compared to other molluscan groups.

FUTURE STUDIES

The largest unresolved problems in the fossil Coleoidea are the problematic origins of the order and the relationships between the different families and genera that are assigned to the orders. To refine our understanding of the evolutionary events that gave rise to the Coleoidea will require new material, especially from Devonian-aged rock units. Efforts should focus on Lagerstätten where tissues can be preserved and there is excellent shell preservation. Paleoenvironments that had well-oxygenated water columns and anoxic conditions at the water/sediment interface are likely candidates for yielding well-preserved fossil coleoids.

There are also significant problems with obtaining living taxa. Many species do not survive commonly used collection techniques (such as deep-water trawls), suffering extensive damage and frustrating morphological studies. Similarly, there are difficulties in obtaining eggs or juveniles to study development with pelagic taxa and in obtaining rare or deep-water taxa for molecular studies.

The resolution of the problem of whether the coleoids have a monophyletic or paraphyletic origin will require additional research on existing specimens and the collection and analysis of new living and fossil material. Increased taxon sampling (both extinct and extant species) as well as the addition of larger molecular data sets (complete mitochondrial genomes, additional nuclear genes) will provide resolution both at the higher level relationships and those that have been particularly problematic (e.g., Decabrachia). Thus, we need to obtain and combine more fossil, morphological, developmental, and molecular data in order to increase our understanding of the interrelationships of these amazingly diverse and ecologically important molluscs.

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