Systematics of Cephalopods

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Abstract

Cephalopoda is an extremely diverse class of mollusks that has been evolving since the Cambrian. The extant lineages arose in the late Silurian and diverged into Nautiloidea and Coleoidea in the mid-Palaeozoic. Nautiloidea is represented by a handful of Recent species only. In contrast, Coleoidea has diverged into two superorders, Decapodiformes and Octopodiformes, which together comprise around 800 Recent species. The relationships among orders of Decapodiformes are not well understood, and molecular systematics has failed to provide much resolution, although there is some evidence for a sister-taxon relationship between Spirulida, the ram's horn squid, and Sepiida, the cuttlefishes. A sister-taxon relationship between Bathyteuthida and Oegopsida is well established. The relationships among Octopodiformes are better understood. The vampire squid is placed in a separate order, and all other octopods are placed in Octopoda. Within Octopoda there are well-understood clades: Octopoda is divided into Cirrata and Incirrata; Incirrata is further divided into Argonautoidea and Octopodoidea. Several lineages of cephalopods have been evolving independently for a long time: for example, Spirulida, represented by a single extant species, appears to have diverged from other groups 150 million years ago, nautiloids appear little changed since 300 million years ago, and Vampyromorphida, also represented by a single extant species, appears little changed since 200 million years ago. In contrast, several groups, for example, the sepiids, appear to have undergone recent radiations.

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Introduction

The molluscan class Cephalopoda arose in the Cambrian (Young et al. 1998; Kröger et al. 2011). Arguably the most diverse of all molluscan lineages, cephalopods have adapted to occupy multiple niches in the marine environment, from estuarine bays to shallow neritic shelf seas, to the open ocean, and to benthic abyssal plains.

Cephalopods emerge in the fossil record in Cambrian strata, although there is some dispute over which fossils represent stem cephalopods, a not uncommon problem in paleontology where fossils are rare and where preservation of soft parts is usually far from complete. Reviewing available literature, Kröger et al. (2011) suggested that stem cephalopods were present in the early Cambrian (e.g., *Tannuella*, a mollusk with a chambered shell) and that the earliest undisputed cephalopod fossil is *Plectronoceras cambria*, whose chambered shell probably facilitated buoyancy control as seen in modern nautiloids.

Kröger et al. (2011) place the origin of the lineage that contains all modern (as well as some extinct) cephalopods in the late Silurian. They suggest that this lineage arose from the orthocerids, cephalopods with straight but chambered external shells, and that, in the mid-Palaeozoic, it diverged into the two recognized subclasses that have Recent representatives, Nautiloidea and Coleoidea. The nautiloids found in the Indo West Pacific today are markedly similar to their Palaeozoic ancestors and are widely recognized as living fossils. They retain the external chambered shell and have simple "pinhole camera" eyes (without a lens). In contrast, the coleoids have diverged substantially. Molecular divergence estimates (Kröger et al. 2011) place the initial divergence of coleoids into two extant (Decapodiformes and Octopodiformes) and three extinct (Phragmoteuthida, Belemnitida, and Diplobelida) lineages in the Permian, although undisputed fossils of the extant coleoid lineages are only found in much more recent strata. Further divergence of Decapodiformes and Octopodiformes then appears to have occurred throughout the Jurassic and Cretaceous to provide the variety of forms present in the ocean today (Fig. 1).

Decapodiformes comprises about 500 Recent species in between five and seven orders (see Table 1), depending on taxonomic opinion, whereas Octopodiformes comprises approximately 300 species in two orders, with all but one species within the order Octopoda. Within the general bauplan of mantle, head, and arms, the diversity of forms is remarkable: animals may be streamlined or robust,
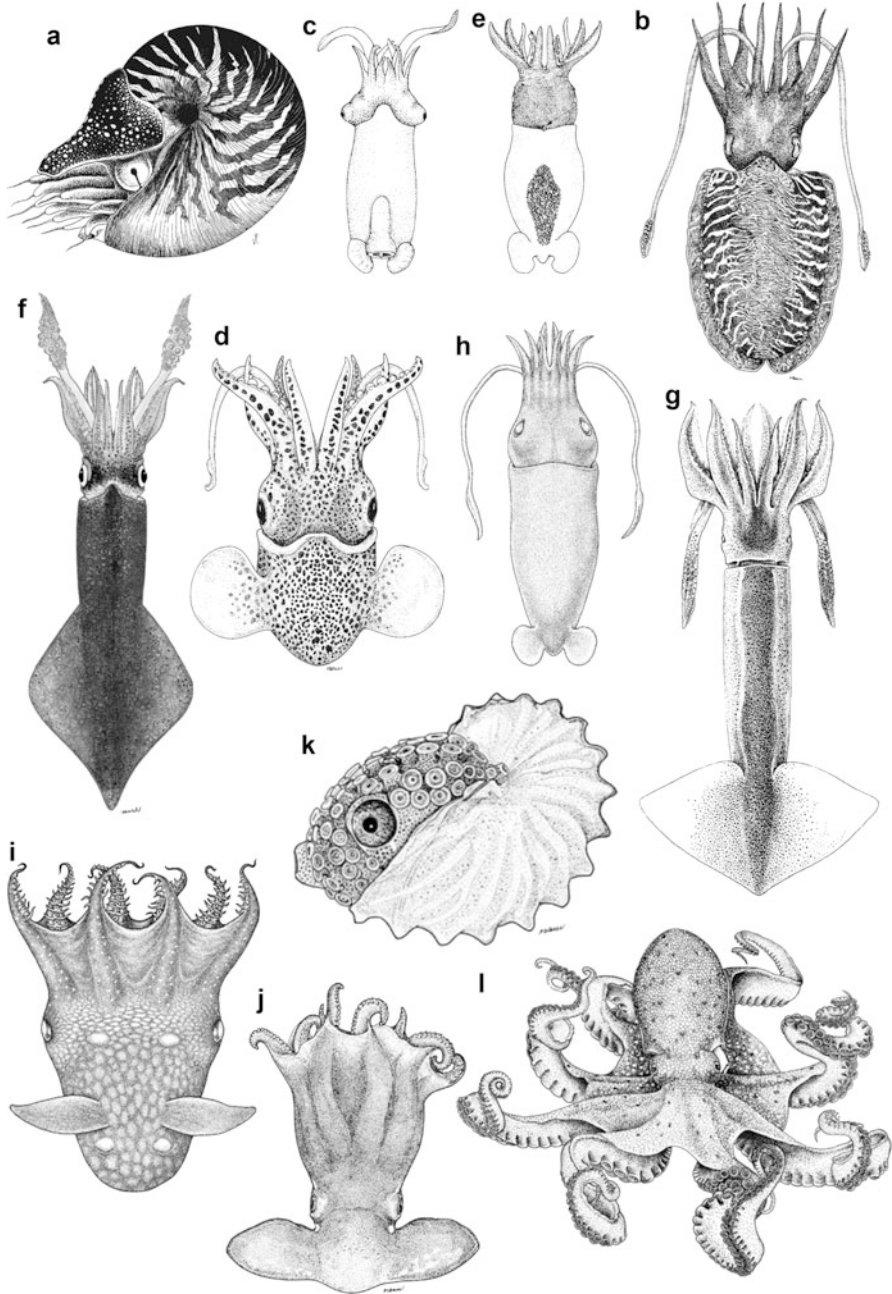
Fig. 1 Representatives of major extant lineages of cephalopods. (**a**) Nautiloidea, *Nautilus macro-mphalus*; (**b**) Sepiida, *Sepia officinalis*; (**c**) Spirulida, *Spirula spirula*; (**d**) Sepiolida, *Sepiola affinis*; (**e**) Idiosepiida; (**f**) Myopsida, *Loligo vulgaris*; (**g**) Oegopsida, *Ommastrephes bartramii*;

Table 1 Major lineages within Decapodiformes. A minimal number of defining characters are provided. For additional characters, see Young et al. (2012a)

Order	Common name	Number of species	Defining characters	Nomenclatural notes
Spirulida	Ram's horn squid	1	Shell as coiled phragmocone, without cornea	Some authors treat at family level as Spirulidae
Sepiida	Cuttlefishes	~120	Shell as flattened phragmocone, with cornea	Some authors treat at family level as Sepiidae
Sepiolida	Bob-tailed squids and bottle-tailed squids	~70	Shell as rudimentary gladius, with cornea	
Myopsida	Squids, often "neritic squids" because of their habitat preferences	~50	Shell as gladius, with cornea	
Idiosepiida	Pygmy squids	~6	Shell as gladius, with cornea, with adhesive organ	Some authors treat at family level as Idiosepiidae
Oegopsida	Squids, often "oceanic squids" because of their habitat preferences	~230	Shell as gladius, without cornea, with carpal locking apparatus	
Bathyteuthida	Squids	~6	Shell as gladius, without cornea, without carpal locking apparatus	Some authors treat at superfamily level as Bathyteuthoidea

dorsoventrally flattened or not, and may be adapted to benthic, demersal, or pelagic lifestyles. All coleoids, in contrast to nautiloids, have an internalized shell, but this takes many forms. Cuttlefishes (order Sepiida, superorder Decapodiformes) have a dorsoventrally flattened phragmocone, the "cuttlebone." Ram's horn squids (order Spirulida, superorder Decapodiformes) have a small internal calcareous-chambered open planispiral shell which is used in buoyancy. Most other Decapodiformes have a pen-like gladius, but this may be reduced or absent in some groups. Among Octopodiformes, the vampire squid (which is actually more closely related to octopuses and is the sole representative of the order Vampyromorphida) has a thin gladius, cirrate octopuses have reasonably robust internalized cartilaginous shells,

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Fig. 1 (continued) (**h**) Bathyteuthida, *Bathyteuthis abyssicola*; (**i**) Vampyromorphida, *Vampyromorpha infernalis*; (**j**) Cirrata, Cirroctopodidae; (**k**) Argonautoidea, *Argonauta hians*; (**l**) Octopodoidea, Octopodidae (Figures reproduced with kind permission of the FAO, Rome, from Jereb and Roper (2005, 2010), and Jereb et al. (2014))

and incirrate octopuses tend to have small vestigial internal shell remnants, the "stylets." There is some relationship between shell type and habitat/lifestyle: for example, the buoyancy controls provided by the phragmocones of cuttlefishes and ram's horn squids allow them to exploit the water column, the cartilaginous shells of cirrate octopuses support the fins they use for swimming, and the gladius reflects the streamlined form of squids that facilitates their speed in their pelagic environment. In many cases, the diversity among groups is so great that establishing which groups are most closely related has been a difficult task for systematists and evolutionary biologists.

Nautiloidea

Just a handful of extant nautiloid species exist today, although there is some dispute over the actual number. They are considered to be living fossils, shell morphology having changed little since the late Carboniferous (Wani and Mapes 2010), and they exhibit many of the cephalopod characteristics thought to be plesiomorphic, including an external chambered shell and pinhole eyes as detailed above. Biogeographically, modern nautiloids are restricted to the Indo West Pacific, but nautiloids were more widespread in their earlier history, being both abundant and distributed worldwide from the Jurassic to the Miocene (Teichert and Matsumoto 1987).

Today, they are found on reefs at approximately 100–700 m depth, where they are both scavengers and predators. They are slow growing, and are estimated to reach maturity after about 15 years, and have a life span in excess of 20 years (Dunstan et al. 2011). In captivity, at least, they are slow to reproduce, laying very few eggs throughout the year (Arnold et al. 1990), and this *k*-selected life history strategy makes them particularly susceptible to overfishing (in support of the ornamental shell trade) to which they are subjected through much of their range.

Modern nautiloids are placed in two genera, *Nautilus* and *Allonautilus*, discriminated by differences in gill structure and the male reproductive system, among other characters (Ward and Saunders 1997), within a single family, Nautilidae. The currently recognized species are *Allonautilus scrobiculatus* (Lightfoot, 1786), known from Papua New Guinea and surrounding islands; *Nautilus pompilius* Linnaeus, 1758, originally described from Ambon in Indonesia, with an extensive distribution and possibly comprising a species complex; *Nautilus belauensis* Saunders, 1981, from Palau; *Nautilus macromphalus* Sowerby, 1849, from New Caledonia; *Nautilus repertus* Iredale, 1944, from Western Australia; and *Nautilus stenomphalus* Sowerby, 1849, from the Great Barrier Reef. *Allonautilus perforatus*, which is known from drift shells in Bali, Indonesia, is probably synonymous with *A. scrobiculatus.*

Molecular genetic work on *N. pompilius* across a wide geographic range has shown several populations to be extremely divergent (Sinclair et al. 2007; Bonacum et al. 2011; Williams et al. 2012). Samples from Vanuatu, Fiji, and American Samoa were more closely related to *N. macromphalus* than to other *N. pompilius*, and species from Eastern Australia and Papua New Guinea were clearly divergent

from those from the Philippines, Indonesia, Western Australia, and Palau. Bonacum et al. (2011) suggested that several of these populations actually represented phylogenetic species but did not tackle the nomenclature. Sinclair et al. (2007) found further divergence between *N. pompilius* samples from the Great Barrier Reef and the Coral Sea separated by small geographic distances, and Williams et al. (2012) also found this pattern, as well as separation of these populations from samples from Western Australia, the Philippines, and Indonesia.

Other species not currently considered valid have been described, and Young (2010) provides a complete list of nominal species. Many of these names do not, in fact, refer to nautilids and some are *nomen nudum,* but a few are nomenclaturally valid and may be applied in the future, particularly to widely separated populations that are found to merit specific status. Thus, it is important to note that nautilid systematics is in a state of flux. Given their status as living fossils and the fact that they have been evolving independently for hundreds of million years, nautilids may prove very interesting in comparative studies of venom with other cephalopods and indeed other mollusks. Therefore, knowledge of their more recent radiations and the current diversity within this group may be important for venom studies.

Coleoidea: Decapodiformes

There are seven main groups of decapodiforms (Table 1). Herein they are all recognized as separate orders, but differing opinions exist as to their ranks. In two of these groups, Spirulida and Sepiida, the shell is a phragmocone (i.e., chambered as in nautiloids, although internal as in all coleoids). However, the form of the phragmocone is highly divergent between Spirulida and Sepiida. Spirulida comprises the single species *Spirula spirula* Linnaeus, 1758. It is a midwater species that seems to be most abundant over bottom depths of 1,000–2,000 m (e.g., continental slopes or slopes associated with volcanic islands). *Spirula* has a long fossil record, extending back to the latest Jurassic (Kröger et al. 2011). Often also referred to as a "living fossil," its lineage is estimated to have diverged from that of other decapodiforms 150 mya (Warnke et al. 2011). Species of the order Sepiida are characterized by the presence of a cuttlebone. Sepiida comprises more than 100 species of cuttlefishes that live in continental shelf waters although they may extend onto the slope to depths of about 600 m. They are present along tropical and temperate coasts of the world including Australasia, Asia, Africa, and Europe but are totally absent from North and South America. Sepiids have a benthic or demersal lifestyle, are short lived, and spawn large eggs for an extended period once they reach maturity. Cuttlefishes are dorsoventrally flattened as is their internal phragmocone, the cuttlebone, which runs the length (or most of the length) of the body. The phragmocone of spirulids is superficially very different: the planispiral calcareous phragmocone is situated rostrally and occupies a much smaller portion of the body.

The temptation to unite these two groups on morphological grounds is resisted not only because of superficial differences but also because the phragmocone is a

plesiomorphic structure. Nonetheless, the wall structure of their phragmocones is similar and differs from that of extinct coleoids such as Belemnitida and non-coleoid ectocochleate cephalopods (Doguzhaeva 1996; Young et al. 1998). Furthermore, Spirulida and Sepiida share other morphological characters such as statolith shape and the structure of the tentacular clubs (Clarke and Maddock 1988; Young et al. 1998).

Young and Vecchione (1996) conducted a cladistics analysis of extant coleoid cephalopods based on 50 morphological characters. Their analysis neither resolved relationships within Decapodiformes nor found a sister-taxon relationship between Sepiida and Spirulida. In fact, in their analysis, all decapodiform taxa branched as a polytomy from a single node in a strict consensus tree. Molecular studies have often also failed to recover deep cephalopod relationships. However, two studies (Strugnell et al. 2005; Lindgren and Daly 2007) have found support for a sister-taxon relationship between Spirulida and Sepiida. These studies used different nuclear genes (Pax6, octopine dehydrogenase, rhodopsin versus 18S rRNA), but it should be noted that bootstrap support values for the 18S rRNA tree were relatively low (66 %). Nonetheless, conflicting topologies have not been found either. The major problem with molecular studies to date is that they have failed to yield topologies with notable bootstrap or posterior probability support on deep nodes.

Khromov (1998) discussed the biogeography of Recent sepiids (which are absent from the Americas) in light of paleoceanography and concluded they had a very recent origin in the Old World, a conclusion that fits with the available fossil data (Young et al. 1998). Naef (1921–1923) concurred, suggesting similarly recent origins for idiosepiids and sepiolids. Although a close relationship between these taxa is far from certain, if correct, these conclusions have implications for the length of time the various branches have been diverging when considering comparative studies of their venom.

Naef (1921–1923) studied fossil, morphological, and embryological evidence and recognized a close relationship between Spirulida and Sepiida but also considered these taxa to be closely united with Idiosepiida and Sepiolida. Idiosepiida is a monogeneric taxon of pygmy squids. These tiny squids are circa 2 cm long as adults, and the synapomorphic character for the group is an adhesive organ on the dorsal surface of their mantle, which they use to attach to sea-grass blades or other algae in their inshore habitat. Sepiolida is a more diverse order, comprising the bob-tailed and bottle-tailed squids. These small round cephalopods have broad posteriorly placed fins and may be benthic, demersal, or pelagic. Naef treated Spirulida, Sepiida, Idiosepiida, and Sepiolida as families and placed them together in the superfamily Sepioidea. Although sepiolids have a gladius rather than a phragmocone, Naef (1921–1923), who conducted meticulous embryological studies, concluded that a phragmocone anlage could be deduced from the form of the embryological shell sac. Naef did not conduct embryological studies on *Idiosepius* but concluded that a similar form would be seen. Naef (1921–1923) noted other similarities between Sepiolida and Idiosepiida, including the similarity of the shell, and the presence of an adductor pallii medialis and suggested that Sepiolida developed from an "*Idiosepius*-like predecessor." Strugnell et al. (2005) did find some support from nuclear genes

for a sister-taxon relationship between *Idiosepius* and sepiolid species, particularly when just the third codon positions were used in the analysis. Note that the nomenclature is somewhat confusing, since more recent authors (e.g., Young et al. 2012a) use the name Sepioidea to describe a clade containing just Sepiolida and Sepiida, although this two-taxon grouping is not widely accepted.

The neritic squids, Myopsida, and the oceanic squids, Oegopsida, the latter sometimes assumed to include the bathyteuthids, have often been combined into the taxon Teuthida. However, support for this taxon is equivocal. Superficially, the morphology of Myopsida and Oegopsida is similar. The shell (or gladius) is similar, they share the same long streamlined body, and they have similar tentacular clubs. However, myopsids share several characters with sepiids and sepiolids that oegopsids do not have, the most notable of which is the presence of a cornea. Thus, despite their superficial similarity to oegopsids, some authors consider myopsids to be more closely related to sepiids and sepiolids. Once again, molecular data have failed to resolve this issue. In many cases, phylogenies have even failed to recover these orders as monophyletic. This is not believed to reflect confused systematics as these orders are well defined morphologically. Furthermore, these orders tend to resolve as well-supported clades in studies based on multiple nuclear genes (e.g., Strugnell et al. 2005; Lindgren and Daly 2007; Strugnell and Nishiguchi 2007; Lindgren 2010; Lindgren et al. 2012). Molecular studies do recognize the close relationship between Bathyteuthida (which many authors do not treat at order level) and Oegopsida, but this has anyway long been recognized. Naef (1921–1923) suggested that Bathyteuthidae possesses characters primitive for all Oegopsida and *Bathyteuthis* has historically been placed in Oegopsida.

Multigene phylogenies (Strugnell et al. 2005; Strugnell and Nishiguchi 2007; Lindgren 2010; Lindgren et al. 2012), combined morphological and molecular analyses (Lindgren et al. 2004), and analyses based on mitochondrial genome rearrangement (Allcock et al. 2011) have failed to resolve deep relationships among Decapodiformes lineages (for review see Allcock et al. 2015). It is likely these will only be resolved by genomic studies (Albertin et al. 2012). Fortunately, relationships within some of these orders are better understood.

Sepiida

Cuttlefishes are perhaps best known for their remarkable camouflage, signaling patterns, and behavior, all of which are relatively easy to study, given their presence in shallow coastal waters. There are just three genera in a single family Sepiidae within the order Sepiida, with species distributed unevenly among the genera. There are two species within the genus *Metasepia*, which is characterized by a reduced cuttlebone. Species of *Metasepia* are only found around Australia and in the Western Pacific. There are seven species with the genus *Sepiella*, which is characterized by a subcutaneous gland opening through a pore between the fins, the function of which is unknown. *Sepiella* is also found in the Pacific with species as far north as Japan and Korea and as far south as northern Australia, but the distribution of this genus also extends westward with two species known from the Mozambique coast and a

third species extending down the west coast of Africa from Mauritania to Namibia (Barratt and Allcock 2012).

All other species of sepiid are grouped in the large (with more than 100 species) genus *Sepia*. Khromov (1998) attempted to diagnose subgroups within the genus *Sepia*. He defined and provided keys to six species complexes within the genus: *Hemisepius*, *Acanthosepion*, *Sepia* sensu stricto, *Anomalosepia*, *Rhombosepion*, and *Doratosepion*. He further allocated all (at that time) recognized species to one of these species complexes and provided keys to the species within each complex. There have been no large-scale molecular studies with extensive taxon sampling of sepiids to date to verify these subdivisions. Nonetheless, Yoshida et al. (2010), in a relatively small-scale study, did find molecular support for *Doratosepion* and *Acanthosepion*. However, molecular phylogenies have also highlighted an unexpected relationship between *Sepia officinalis* and *Sepiella* (Bonnaud et al. 2006; Yoshida et al. 2010; Lindgren et al. 2012), suggesting that our current understanding of generic level relationships is not totally correct.

The genus *Sepia* has the widest distribution of all the sepiid genera, perhaps not surprisingly, since it contains very many more species than the other genera. It occurs off the coasts of Europe, Asia, Africa, and Australasia; however, as mentioned above, it is absent from the coasts of North and South America. Khromov (1998) analyzed biogeographic patterns in sepiids. He found greatest diversity in the Indo West Pacific, which was home to 91 species, 86 of which were endemic to the region. In contrast, the Northeast Atlantic, including the Mediterranean Sea, was home to just nine species, five of which were endemic. He concluded that the northern and southern limits of the family were governed by temperature. Low diversity in parts of Indonesia was attributed to poor faunal knowledge of that region; however, Khromov (1998) found clear evidence of a decrease in species numbers from inshore waters of the Pacific and Indian Oceans to more remote island habitats, with sepiids absent from Hawaii, the Seychelles, and the Chagos Archipelago. The inability of sepiids to colonize habitats separated by deep water likely reflects their lack of dispersal phase: adults lay large eggs that give rise to miniature benthic hatchlings which inhabit the same habitat as the adult phase. Molecular investigations of island endemics from places such as Guam and the Marshall islands may therefore show evidence of founder populations.

The earliest fossil sepiids are found in US deposits but their identification is disputed. *Voltzia* from the Upper Jurassic and *Actintosepia* from the Cretaceous have been considered not to be sepiids by some authors (e.g., Waage 1965). However, of the five genera reported from the Eocene (*Archaeosepia*, *Belosepia*, *Pseudosepia*, *Sepia*, *and Stenosepia*), two are known from US deposits (Roeleveld 1972; Khromov 1998), but only *Sepia* is known from more recent strata (Roeleveld 1972). Hence, it is likely that low water temperatures, particularly in the western Atlantic in the Oligocene, led to the extinction of sepiids from the Americas. Although the genus *Sepia* later radiated out of Europe, Roeleveld (1972) suggests that temperatures would have been too low on the only suitable routes for recolonization (i.e., via the Bering Straits or from Europe to Greenland via the Faroe Islands and Iceland). Khromov (1998) proposed that *Sepia* subsequently

radiated from the Mediterranean Ocean, spreading to the developing Indian Ocean in the Oligocene and then radiating throughout Southeast Asia. He suggests that the African fauna and that of the Japan Sea (i.e., those species on the periphery of the range) are therefore the youngest in evolutionary terms. There is considerable concordance between the subgeneric classification and geographic location, presumably reflecting these different radiations.

Sepiolida

There are two families within Sepiolida: the eponymous Sepiolidae and Sepiadariidae. Sepiadariidae is a small family of bottle-tailed squids in just two genera: *Sepioloidea* and *Sepiadarium*. Neither genus has a shell remnant, and the members of the genera are colorful small squids that live on the seafloor in mostly shallow tropical seas of the Indo West Pacific. *Sepioloidea* is known from Australia, Indonesia, and New Zealand, with the distribution of one species extending along submarine ridges as far as Easter Island (Reid 2005, 2009). *Sepiadarium* has a slightly broader distribution with species occurring from South Australia northward through the Pacific to Japan and westward to east India and Sri Lanka.

In contrast, the family Sepiolidae is more diverse, comprising 16 genera divided into three subfamilies. Sepiolids are small-rounded squids, with a rudimentary gladius, which may be absent, and posterior fins, not dissimilar in overall shape to the sepiadariids. Members of two of the subfamilies, Rossiinae and Sepiolinae, are benthic, while members of Heteroteuthinae are pelagic or benthopelagic. All heteroteuthins have a large visceral photophore, and Naef (1921–1923) believed this subfamily to be the most derived form. Unfortunately, because of the very delicate shell in this group, there is no fossil evidence with which to consider evolutionary pathways.

The relationships among genera are not completely clear. Young (2007) placed *Sepiola*, *Euprymna*, *Inioteuthis*, *Rondeletiola*, and *Sepietta* in Sepiolinae; *Heteroteuthis*, *Nectoteuthis*, *Stoloteuthis*, *Iridoteuthis*, *Amphorateuthis*, and *Sepiolina* in Heteroteuthinae; and *Rossia*, *Austrorossia*, *Neorossia*, and *Semirossia* in Rossiinae. This reflects Naef's (1921–1923) placements with the exception that *Sepiolina* is placed in Heteroteuthinae rather than Sepiolinae. Young (2007) left *Choneteuthis* unplaced, noting its similarity to *Sepiolina* but also the differences of *Sepiolina* to other Heteroteuthinae. Young (2007) also highlighted the presence of an as-yet undescribed subfamily whose affinities are not clear, specimens of which are currently only known from fish stomachs.

A multigene molecular phylogeny of Decapodiformes (Lindgren et al. 2012) suggests that our understanding of sepiolid relationships may not yet be complete. The phylogeny supported monophyly of Sepiadariidae and confirmed Sepiadariidae and Sepiolidae to be sister taxa. This study, which included representatives of eight genera of Sepiolidae (Rossiinae, *Rossia*; Heteroteuthinae, *Heteroteuthis*, *Stoloteuthis*, *Sepiolina*; Sepiolinae, *Euprymna*, *Sepiola*, *Sepietta*, *Rondeletiola*), found *Stoloteuthis* as sister taxon to *Rossia* and consequently did not support the monophyly of Heteroteuthinae. Only two species of Rossiinae were included, but they did group as sister taxa. The 13 included species of Sepiolinae formed a clade,

but within this clade, the genera *Sepiola* and *Sepietta* were not monophyletic, although included members of the genus *Euprymna* did form a clade. Groenenberg et al. (2009) also failed to recover monophyletic genera within Sepiolinae in a study using the cytochrome oxidase subunit I (COI) barcode gene. Importantly, Groenenberg et al. (2009) highlighted the presence of several misidentified sequences on GenBank that could confound future studies: see Groenenberg et al. (2009) and Lindgren et al. (2012) for details.

Idiosepiida

Represented by the single genus *Idiosepius* in the family Idiosepiidae, pygmy squids also have an Indo West Pacific distribution. However, the delimitation of species is not clear, and researchers conducting comparative studies on venom should be aware of this. The currently known specimens probably comprise a single species (*Idiosepius minimus*) off the coasts of Africa, a species endemic to Australia (*Idiosepius notoides*), and at least four species in the Indo West Pacific whose precise ranges and overlaps have not been elucidated (*I. picteti*, *I. thailandicus*, *I. paradoxus*, and *I. pygmaeus*). *Idiosepius biserialis* is probably a junior synonym of *I. minimus* and confined to African coasts, and species treated under this name from the Indo West Pacific likely refer to *I. thailandicus*. DNA barcoding has helped clarify the distribution of some species (Byern et al. 2012), but much further work is required.

Myopsida

Myopsid squids are found in neritic zones where they inhabit pelagic or demersal waters. They number, in total, about 50 species and there have been several major rearrangements of myopsid systematics. The currently accepted classification has all species except one in the family Loliginidae, with a second monospecific family Australiteuthidae restricted to northern Australia and Papua New Guinea. Eleven genera, and a number of subgenera, are currently recognized as valid within Loliginidae. Intriguingly, most of these genera appear to affiliate with particular geographic regions, much as the subgenera of sepiids do. *Loligo*, *Afrololigo*, and *Alloteuthis* are associated with Europe and Africa. *Doryteuthis*, *Lolliguncula* and *Pickfordiateuthis* are associated with the Americas. *Heterololigo* is associated with the northern Pacific. *Loliolus*, *Uroteuthis*, and *Photololigo* are associated with the Indo West Pacific. The exception is *Sepioteuthis* which is distributed in the western Atlantic, the Mediterranean, the Indo West Pacific, and around the coasts of Australia as far south as Tasmania. This distribution led Brakoniecki (1986) to suggest that *Sepioteuthis* is a Tethyan relic, and molecular data (Anderson 2000; Sales et al. 2013) support this, indicating *Sepioteuthis* to be the sister taxon to all other loliginids. Anderson (2000) further suggested subsequent dispersal from the Indo West Pacific to East Pacific American waters, possibly along the continental shelf on the northern periphery of the Pacific, and then further radiation in the Americas, possibly driven by the uplift of the isthmus of Panama. This could explain the sister-taxon relationship between *Heterololigo* and *Doryteuthis* found in molecular studies and the sister-taxon relationship between *Doryteuthis opalescens* (Berry, 1911) in American Pacific waters and *Doryteuthis pealeii*

(Lesueur, 1821) in American Atlantic waters. To date, no molecular studies have included Australiteuthidae.

There is marked genetic structure among populations of some loliginid species (Dai et al. 2012; Sales et al. 2013; Zheng et al. 2012), possibly indicative of a number of cryptic species or ongoing speciation in these taxa.

Oegopsida

Oegopsid squids are found in the open ocean, and this taxon comprises the largest order of cephalopods with more than 200 species in 24 families and 69 genera. Seven families are monospecific (Architeuthidae, *Architeuthis dux* Steenstrup, 1857; Batoteuthida, *Batoteuthis skolops* Young and Roper, 1968; Joubiniteuthidae, *Joubiniteuthis portieri* (Joubin, 1912); Ancistrocheiridae, *Ancistrocheirus lesueurii* (d'Orbigny, 1842); Psychroteuthidae, *Psychroteuthis glacialis* Thiele, 1920; Lepidoteuthidae, *Lepidoteuthis grimaldii* Joubin, 1895; Thysanoteuthidae, *Thysanoteuthis rhombus* Troschel, 1857), and a further three families are mono-generic (Promachoteuthidae, Magnapinnidae, Pholidoteuthidae). The families with greatest diversity are Cranchiidae (13 genera, circa 60 species), Ommastrephidae (11 genera, circa 22 species), Onychoteuthidae (7 genera, circa 25 species), and Gonatidae (4 genera, circa 19 species). Relationships among families are not well understood, but some families are believed to be closely associated.

Young and Vecchione (2004) propose four groupings of multiple families. They highlight loss of the true tentacular club as a feature shared by Batoteuthidae, Chiroteuthidae, Joubiniteuthidae, Magnapinnidae, Mastigoteuthidae, and Pro-machoteuthidae. However, they note that monophyly of this group is far from certain. Lindgren et al. (2012), in a total evidence molecular study, found five of these families formed a clade that also included Pholidoteuthidae; Pro-machoteuthidae was not included in the study. This clade was not strongly supported, but a subclade containing Batoteuthidae and Chiroteuthidae received bootstrap support >90 %, and a subclade containing Joubiniteuthidae, Mastigoteuthidae, and Magnapinnidae received bootstrap support >50 %.

Small mesopelagic squids in the families Ancistrocheiridae, Enoploteuthidae, Lycoteuthidae, and Pyroteuthidae may be related (Young and Vecchione 2004). Lindgren et al. (2012) found that members of Enoploteuthidae and Pyroteuthidae formed a clade, which had good bootstrap support >90 %. However, members of Lycoteuthidae fell together, but no support was found for a relationship between Lycoteuthidae and any other family. Ancistrocheiridae was not included in the study.

Histioteuthidae and Psychroteuthidae share the same tentacular club structure, and their relationship is supported by 100 % bootstrap support in a total evidence molecular study (Lindgren et al. 2012).

The fourth family-level relationship is among Lepidoteuthidae, Octopoteuthidae, and Pholidoteuthidae. There is no single uniting character for this grouping (Young and Vecchione 2004), and it is not supported as a monophyletic group by molecular work. Nevertheless, there is some bootstrap support (>50 %) for a relationship between Lepidoteuthidae and Octopoteuthidae (Lindgren et al. 2012).

Relationships within some of the four most diverse families are better understood than others. Cranchiidae is divided into two subfamilies: Cranchiinae and Taoniinae. While there have been no dedicated molecular studies on Cranchiidae, Lindgren et al. (2012) included three cranchiins and seven taoniins and found the family and both subfamilies to be monophyletic.

In contrast, a molecular study of Gonatidae, using three mitochondrial genes and including 14 species representing all four genera, found all genera, except *Eogonatus* which is monospecific, to be polyphyletic (Lindgren et al. 2005).

Similar issues have been found within Onychoteuthidae. Early molecular work (Bonnaud et al. 1998) suggested that the genera *Onychoteuthis* and *Moroteuthis* were in need of taxonomic revision. Subsequently Wakabayshi et al. (2007) used DNA barcoding to show that adults identified as belonging to the genus *Moroteuthis* fell in a clade with paralarvae known as *Onykia* (a genus where adults were unknown). However, to complicate matters further, *Onykia* does not appear to be monophyletic, since *Onykia carriboea* Lesueur, 1821, has fallen outside the main *Onykia* clade in molecular studies (Lindgren 2010; Lindgren et al. 2012) and resolved as sister taxon to *Ancistroteuthis lichtensteini* (Férussac [in Férussac and d'Orbigny], 1835).

Ommastrephidae has been divided into three subfamilies, Illicinae, Ommastrephinae, and Todarodinae which can be diagnosed on a few simple characters such as the sucker seriation on the dactylus of the tentacular club and whether or not photophores are present (Young et al. 2012b). A study using two mitochondrial genes and including 15 species in ten genera provided support for these divisions, recovering all the subfamilies as monophyletic in nearly all analyses (Wakabayashi et al. 2012). However, within Todarodinae, two genera (*Todarodes* and *Nototodarus*) were found to be polyphyletic, casting doubt on the characters used to separate them.

Bathyteuthida

This small group of deep-water squids currently comprises six species: three in the genus *Chtenopteryx* (family Chtenopterygidae) and three in the genus *Bathyteuthis* (family Bathyteuthidae). A molecular study including two *Chtenopteryx* species and three *Bathyteuthis* species recovered both genera as monophyletic and also as sister taxa (Lindgren et al. 2012).

Coleoidea: Octopodiformes

Octopodiformes comprises approximately 300 species in two orders, with all but one species within Octopoda. The order Vampyromorphida is represented by the single species *Vampyroteuthis infernalis* Chun, 1903 – the enigmatic vampire squid, widely recognized as a living fossil. It inhabits mesopelagic depths in the temperate to tropical zones of the world's oceans. Until recently, there was much debate as to whether the vampire squid was a representative of Decapodiformes or

Octopodiformes. However, its placement in Octopodiformes is confirmed by morphological evidence from hatchlings (Young and Vecchione 1999) and from embryological evidence of octopods (Boletzky 1978–1979, 2006). Molecular evidence has given conflicting results, but an increasing body of molecular evidence also supports the placement of Vampyromorphida in Octopodiformes (see, e.g., Yokobori et al. 2007; Strugnell and Nishiguchi 2007; Allcock et al. 2011). Kröger et al. (2011) place the earliest vampyromorph fossils in the late Triassic/early Jurassic, suggesting that this lineage has been evolving independently for about 200 million years.

The order Octopoda comprises two suborders, Cirrata (or Cirrina) and Incirrata (or Incirrina), and molecular evidence provides strong support for monophyly of these groups and for a sister-taxon relationship between them (Carlini et al. 2000; Strugnell et al. 2004, 2005, 2014; Lindgren et al. 2012). The earliest evidence of these taxa in the fossil record is found from Late Cretaceous deposits (Tanabe et al. 2008; Fuchs et al. 2009), although divergence time estimates (Kröger et al. 2011) place their separation in the Late Jurassic.

Cirrata comprises the finned octopods, which tend to have a gelatinous body and a deep web. The name Cirrata derives from the cirri that extend down the arms alongside the suckers. The fins are supported by an internal cartilaginous shell and the animals use these to swim, and while some finned octopods are primarily benthic, they may also be demersal or entirely pelagic.

Cirrata was reviewed by Collins and Villanueva (2006). In their systematic section, they followed the proposals made by Piertney et al. (2003), based on molecular work involving a single mitochondrial gene, that Cirrata comprises four families. Revising some of the existing taxonomy and clarifying the status of some difficult taxa, Collins and Villanuevea (2006) suggested the following families were valid: Cirroteuthidae for the pelagic genera *Stauroteuthis*, *Cirroteuthis*, and *Cirrothauma*; Grimpoteuthidae for the genera *Grimpoteuthis*, *Cryptoteuthis*, and *Luteuthis*; Opisthoteuthidae for the genus *Opisthoteuthis*; and Cirroctopodidae for the genus *Cirroctopus*. However, other arrangements are also followed. For example, Vecchione et al. (2014) place the genera in three families as follows: Opisthoteuthidae (*Cirroctopus*, *Grimpoteuthis*, *Luteuthis*, *Opisthoteuthis*, *Cryptoteuthis*), Cirroteuthidae (*Cirroteuthis*, *Cirrothauma*), and Stauroteuthidae (*Stauroteuthis*). They also note the morphological similarity between Cirroteuthidae and Stauroteuthidae (united as Cirroteuthidae by Collins and Villanueva), which have similar body shape, long cirri, and a secondary web, but which differ markedly in shell shape. Although these classifications are not widely different, further molecular work with additional markers would be extremely useful.

Incirrata comprises the benthic octopuses familiar from shallow waters, as well as some more unusual groups. Young et al. (1998) discussed the unusual "oral-end-down" habit of benthic octopuses, which mostly crawl on the seafloor using their arms. They noted that the brain of *Vampyroteuthis* indicates that it is capable of processing complex chemotactile signals from the arms and wondered whether the arms played some important role in *Vampyroteuthis* or its ancestors that might have facilitated oral exploratory behavior of the seafloor so as to lead to the evolution of benthic octopods. In fact, recent work (Hoving and Robison 2012) shows that

vampire squids are detritivores and use their retractile filaments to accumulate food in a sticky matrix which is then passed to the mouth, so oral exploration of the benthos in a hypothetical ancestor is not an unreasonable proposition. However, this mode of feeding also raises interesting questions as to the role of venom in vampyromorphs, and comparisons between vampyromorphs and octopods would be interesting from an evolutionary point of view.

Incirrata is divided into two superfamilies: Argonautoidea, comprising the genera *Haliphron*, *Argonauta*, *Ocythoe*, and *Tremoctopus*, each placed in their own family, and Octopodoidea, comprising all other genera of incirrate octopods. The argonautoid families are unusual and highly diverse but are united by an unusual feature: that males have a detachable hectocotylus. The only known species of *Haliphron* inhabits deep waters around the world. It shows exceptional sexual dimorphism, with females reaching a total length of 2 m versus about 30 cm in males. The four *Tremoctopus* species, known as blanket octopuses, have extensive but thin webs. They float in the upper layers of subtropical and tropical oceans. They are also sexually dimorphic, with males about 5 % the size of females, which can reach more than a meter in total length. The four *Argonauta* species are also found in the upper layers of subtropical and tropical oceans. They are unique in that the female secretes a calcareous shell, in which it lives and lays its eggs. It is from the delicate nature and shape of the shell that the animal gets its common name "paper nautilus." Males are also dwarf and have been reported associated with salps. The single known species of *Ocythoe* is also found in upper water layers but of temperate oceans. The males are also dwarf.

Several molecular studies confirm Argonautoidea as sister group to all other incirrate octopuses (Strugnell et al. 2004, 2014; Lindgren et al. 2012). Naef (1921/1923) suggested that Alloposidae and Tremoctopodidae were closely related to one another, as were Argonautidae and Ocythoidae, based on the structure of the hectocotylized arm. Bizikov (2004) supported this arrangement, but based on the structure, or absence, of the stylets (shell remnants). Subsequent molecular work (Strugnell and Allcock 2010), based on several mitochondrial genes, supported this arrangement.

Argonautoidea has been hypothesized to have a benthic ancestry, because of the morphological resemblance of species to benthic octopuses in Octopodoidea (Naef 1921–1923). Relevant characters include the absence of fins and cirri, and a well-developed frontal lobe system, and evidence of corneas (Young et al. 1998).

Octopodoidea is easily the most speciose group of Octopodiformes, and relationships within it are still not well understood, although some advances have been made in recent years. Until recently, all benthic Octopodoidea were placed in the family Octopodidae, with the four valid pelagic genera distributed in the families Amphitretidae (*Amphitretus*), Vitreledonellidae (*Vitreledonella*), and Bolitaenidae (*Bolitaena*, *Japatella*) and often combined into a suborder Ctenoglossa on the basis of the structure of their radulae. However, early molecular work (Carlini and Graves 1999; Carlini et al. 2001) had suggested that the family Octopodidae was not monophyletic, and further evidence for this was provided in a study showing that the pelagic genera were a derived branch within Octopodidae, leading the authors to

Table 2 Major lineages within Octopodiformes

Order	Suborder	Superfamily	Included families
Vampyromorphida			Vampyroteuthidae
Octopoda	Cirrata		Cirroctopodidae, Cirroteuthidae, Grimpoteuthidae, Opisthoteuthidae
	Incirrata	Argonautoidea	Alloposidae, Argonautidae, Ocythoidae, Tremoctopodidae
		Octopodoidea	Amphitretidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae, Octopodidae

suggest these genera had neotonous origins (Strugnell et al. 2004). This topology has since been recovered in multiple studies (Strugnell et al. 2008, 2014; Lindgren et al. 2012), which led Strugnell et al. (2014) to propose a revised taxonomy based on a molecular study utilizing three nuclear and four mitochondrial genes and including representatives of 25 Octopodoidea genera as well as *Vampyroteuthis* and representatives of the argonauts and cirrates. They combined the four pelagic genera into a single family Amphitretidae, with the genera placed within the subfamilies Amphitretinae, Vitreledonellinae, and Bolitaeninae. They placed the genus *Bathypolypus* in a family of its own, Bathypolypodidae. *Eledone* and *Aphrodoctopus*, two genera with uniserial suckers and heteromorphic arm tips in males, were combined in the family Eledonidae. Southern Ocean and deep-sea octopuses with uniserial suckers were combined in the family Megaleledonidae. The origins of this clade were explored by Strugnell et al. (2008), who showed that changing environmental conditions in the mid-Miocene led to strengthening of the thermohaline circulation and the consequent spreading of Antarctic bottom water northward, allowing radiation of a clade of octopuses out of Antarctica. *Muusoctopus*, *Enteroctopus*, *Sasakiopus*, and *Vulcanoctopus* were placed in a new family Enteroctopodidae. All other genera remained in the family Octopodidae.

A summary of octopod higher-level systematics is provided in Table 2. Although our understanding of octopus systematics has improved substantially in recent years, there are still many species whose generic affinities remain unclear. The tightening of the diagnosis of the genus *Octopus*, which for many years had contained a large number of widely divergent species, left many species without a generic placement. The work of Strugnell et al. (2014) shows that currently available molecular markers are well suited to solving such problems.

Conclusions

Cephalopoda is a particularly interesting class from an evolutionary point of view and therefore provides extensive opportunities for comparative studies. It is highly divergent, with widely differing body forms and species that inhabit widely differing environments. It is not particularly speciose, making comparative studies across the whole group a real possibility. Furthermore, it contains species on long branches,

which have been evolving independently for hundreds of millions of years such as the nautiluses, *Spirula* and *Vampyromorpha*, as well as groups that have undergone recent radiations such as the sepiids, possibly *Idiosepius*, and some myopsid genera. Our understanding of deep phylogenetic relationships is still poor and may only be solved by genomics, but suitable molecular markers do exist to solve many of the remaining taxonomic issues at more shallow nodes, and progress in these areas is likely to be rapid in the coming years, dependent only on sampling opportunities and resources.

Cross-References

► Toxicity in Cephalopods

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