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Fossil Focus — Coleoid cephalopods: the squid, cuttlefish and octopus

by Thomas Clements[*1]

What are coleoids?

The coleoid cephalopods (Fig. 1), squids, cuttlefish and octopuses[2], are an extremely diverse group of molluscs that inhabits every ocean on the planet. Ranging from the tiny but highly venomous blue-ringed octopus (*Hapalochlaena*) to the largest invertebrates on the planet, the giant and colossal squids (*Architeuthis* and *Mesonychoteuthis* respectively), coleoids are the dominant cephalopods in modern oceans. For humans, they are a vital dietary and economic resource and have an important role in our culture. Cephalopods have intrigued and been revered by humans from ancient times and, more recently, during the nineteenth and twentieth centuries, they became part of pop-culture. Stories of gargantuan *poulpes* attacking the submarine 'Nautilus' in Jules Vernes's 1870 book *Twenty Thousand Leagues Under the Sea* captivated Victorian audiences; these cephalopods are often mistakenly thought of as the vilified giant squid (or kraken), however, the French original translates as giant octopuses! Cephalopods are easy to cast as monsters; their 'alien'-like appearance and unique characteristics such as their wonderful ability to change the colour and texture of their skin, jet-like locomotion, capacity to squirt ink, and their remarkable mimicry, intelligence and problem-solving skills may contribute to the perception of dreadfulness. When coupled with reinforcement by films and books that stereotype cephalopods as slimey and terrifying monsters from the deep (I'm looking at you Davy Jones from the *Pirates of the Caribbean* films), it is easy to understand why these animals have such a frightful reputation. However, these wonderful creatures are a crucial component of marine ecosystems as both predators and prey, and as ocean temperatures rise, cephalopod populations are booming. For biologists, understanding the relationships between living cephalopod groups has been challenging, but thanks to the surprisingly rich fossil record, palaeontologists have driven our understanding of coleoid evolution with many recent discoveries. Here I will highlight some of the key findings that are revealing the evolutionary history of this fascinating group.

The coleoid fossil record

The cephalopod fossil record is dominated by animals that have external shells (an ectochoclear shell) like the famous ammonites, however, *Nautilus* is the only representative of this group still living. Extant cephalopods are dominated by the coleoids: cephalopods that have internal shells (an endocochlear shell). Historically, biologists have divided extant coleoids into two main groups based on the number and type of limbs they have. Squid and cuttlefish have ten limbs - eight arms and two tentacles (arms have suckers from the base to the tip whereas tentacles generally have suckers only at the end, on a 'club') - and are collectively grouped into the Decabrachia (Fig. 1). Octopuses have eight arms (and no tentacles) and sit within the order Octobrachia. Coleoid arms are paired for ease of identification, and the pair lost in the Octobrachia (the second dorsolateral arm pair) are not the same arm pair modified into tentacles in decabrachians (the fourth ventrolateral arm pair). This difference has caused considerable issues in understanding coleoid evolution.

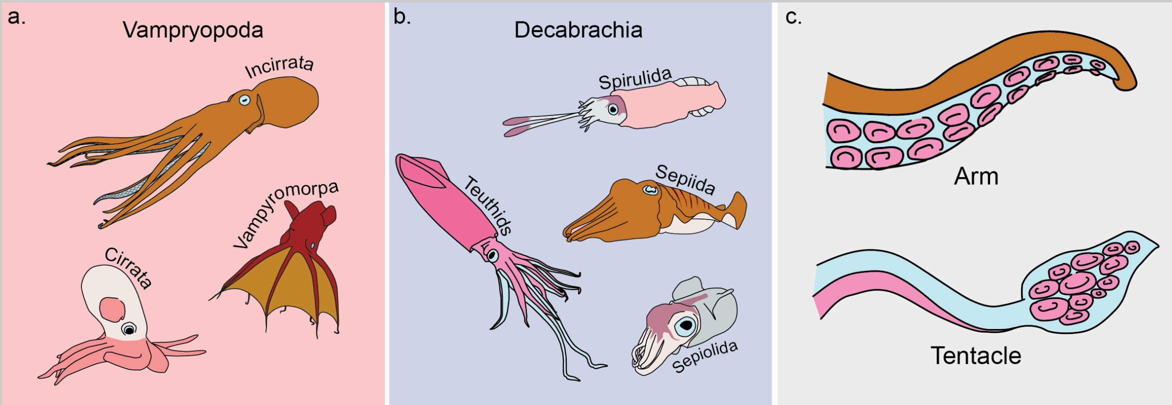

Figure 1 — Extant coleoids. A) The Vampyropoda: The incirrata octopus lack cirri, paired fins and have a greatly reduced or absent internal shell. These animals tend to be benthic and use jet proposition for rapid movement. The cirrata have cirri, paired fins and shells, however, lack ink sacs and generally cannot use jet propulsion, instead relying on their fins for active swimming. The extant Vampyromorpha consist of just one species, *Vampyroteuthis infernalis* (the vampire squid from hell). Similar to the cirrate octopus they have an internal shell, paired fins and cirri. They have two specialised reduced arms known as retractable filaments. Often longer than the animal's body length, they are thought to be sensory and used to catch nutrients in the marine snow. *Vampyroteuthis* also has photophores all over its body, used for signalling in the dark depths it inhabits. B) The Decabrachia. Consisting of squid (teuthids), Ram's Horn squid (Spirulida), Bobtail squid (Sepiolida), and cuttlefish (Sepiida). These animals all have eight arms and two tentacles. There are some decabracians which are exception to this rule, i.e. the squid groups *Lepidoteuthidae* and *Octopoteuthidae*, however, these species lose their tentacles during ontogeny. Tentacles are normally kept in a pouch while the animal is swimming but are then shot out during prey acquisition. The arms are then used to manipulate the prey for feasting. C) A cartoon to demonstrate the difference between an arm (suckers from base to tip) and a tentacle (sucker only found at the end, often on a 'club'). Illustrations are not to scale.

Coleoids are assigned into their different groups on the basis of the anatomy of body parts made of soft-tissue. This has some drawbacks when working on fossil material. Coleoid soft-tissues rarely preserve, so using limbs to determine the taxonomy of fossils is extremely limited. However, coleoids do have several body parts that fossilise regularly, such as mouthparts (the buccal mass), arm hooks, and statoliths (the mineralized part of the sensory receptor that helps them balance in the water), however, these isolated structures are often unhelpful for determining group relationships. The internal shell of coleoids is quite robust and has the highest preservation potential of any coleoid body-tissue. Most people have seen a cuttlefish shell, known as a cuttlebone, washed up on a beach or used as a calcium supplement for birds and other pets. Squid also have an internal chitinous shell, known as a gladius, because of its resemblance to the Roman legionnaire's sword of the same name. Most Octopuses have drastically reduced gladii, some species have completely lost theirs.

This has had an interesting impact on the understanding of coleoid evolution. Since the nineteenth century, palaeontologists have used fossilised gladii to determine the taxonomy of extinct coleoids. The distinctive shape of cuttlebones means that they are easily identified in the fossil record, and although extremely rare, the oldest unequivocal cuttlefish is known from Cretaceous rocks in the Netherlands (72 – 66 mya). The vast majority of fossil coleoids were assigned to the squid family because of the similarity of the fossils to modern squid gladii and it was thought that only decabrachians had well-developed internal shells.

However, these identifications have come under considerable scrutiny owing to a combination of biological and palaeontological discoveries. Although it was believed that most octopuses have no internal shell, the discovery of deep water-dwelling octopuses in the suborder Cirrata (characterised by large fins attached to the mantle above the eyes like the Dumbo octopus, *Grimpoteuthis*) found that these animals have vestigial internal shells. Some of the more recognisable Incirrata octopuses (which don't have external fins), such as the Giant Pacific Octopus, *Enteroctopus dofleini,* were also found to have small paired vestigial shells known as stylets. When biologists realised that the vampire squid, *Vampyroteuthis infernalis*, was actually a primitive form of octopus, it has a significant impact on understanding coleoid evolution. *Vampyroteuthis* has several 'primitive' morphological characters such as ten limbs (two of them are modified as retractable filaments used for feeding), cirri instead of suckers on certain parts of their arms but most importantly, a well-developed internal shell. Palaeontologists soon realised that many species of fossil 'squid' had shells similar to *Vampyroteuthis* and the octopuses. In 1986, German palaeontologists, Klaus Von Bandel and Helmut Leich, re-examined several soft-bodied fossil palaeo-squids and based on the shell similarities and the fact that none of the fossils had more than eight limbs, they reclassified them all as belonging to the same group as *Vampyroteuthis*; the Vampyropoda (stem, or primitive, octopuses). Subsequent work investigating modern squid revealed that squid gladii are notoriously variable in shape even within a single animal's lifetime, adding further evidence that many of the similarities used to identify palaeo-squids by the shell were, in fact, superficial. Reinvestigation of fossil material has not yielded a single soft-bodied, ten-armed fossil coleoid. The mass reclassification of fossil squid-like animals has been termed the 'Vampyropoda hypothesis' and was hotly debated by coleoid workers. However, since 2000, several large scale morphological investigations combining both extinct and extant coleoid shell data have corroborated the Vampyropoda hypothesis. Currently there are no known squid in the fossil record.

What do we know about coeloid evolution?

Over the past decade, studies have combined morphological and molecular data to form a picture of coleoid evolution (Fig. 2), despite the shortcomings of the fossil record. Molecular clock data indicates that Vampyropoda and Decabrachia diverged during the Permian (~276 ±75 Ma). The evolution of octopuses are fairly well understood. Recognisable soft-bodied fossil stem octopuses have been described from Jurassic Lagerstätten in France (165 Mya; Fig. 3), but the most spectacular soft-bodied octopus fossils are from the Cretaceous deposits of Lebanon (Fig. 3C,D). In 1896, the oldest fossil Cirrate octopus, *Palaeoctopus newboldi* (Fig. 3C), was described from the Hâkel and Hâdjoula fossil beds, Lebanon (Cenomanian, 100 Ma). Since then several other species, such as *Keuppia* (Fig. 3A) and *Styletoctopus,* have also been described from this area, preserving exquisite soft-tissue anatomical characters in calcium phosphate minerals. These fossils, coupled with the discovery of several isolated stem-octopus internal shells have allowed a nearly complete picture of shell reduction in octopuses from their belemnoid ancestors. This process is thought to have occurred because octopuses were evolving new methods of locomotion. Internal shells acts as the support for fins - in deep water dwelling *Vampyroteuthis* and Cirrate octopuses, these fins act to aid locomotion because the organisms rely on actively swimming. Incirrate octopus tend to live on the seafloor, so a reduced internal shell allows octopuses to change their body shape easily, ideal for squeezing into small crevices in reefs while hunting or avoiding predators.

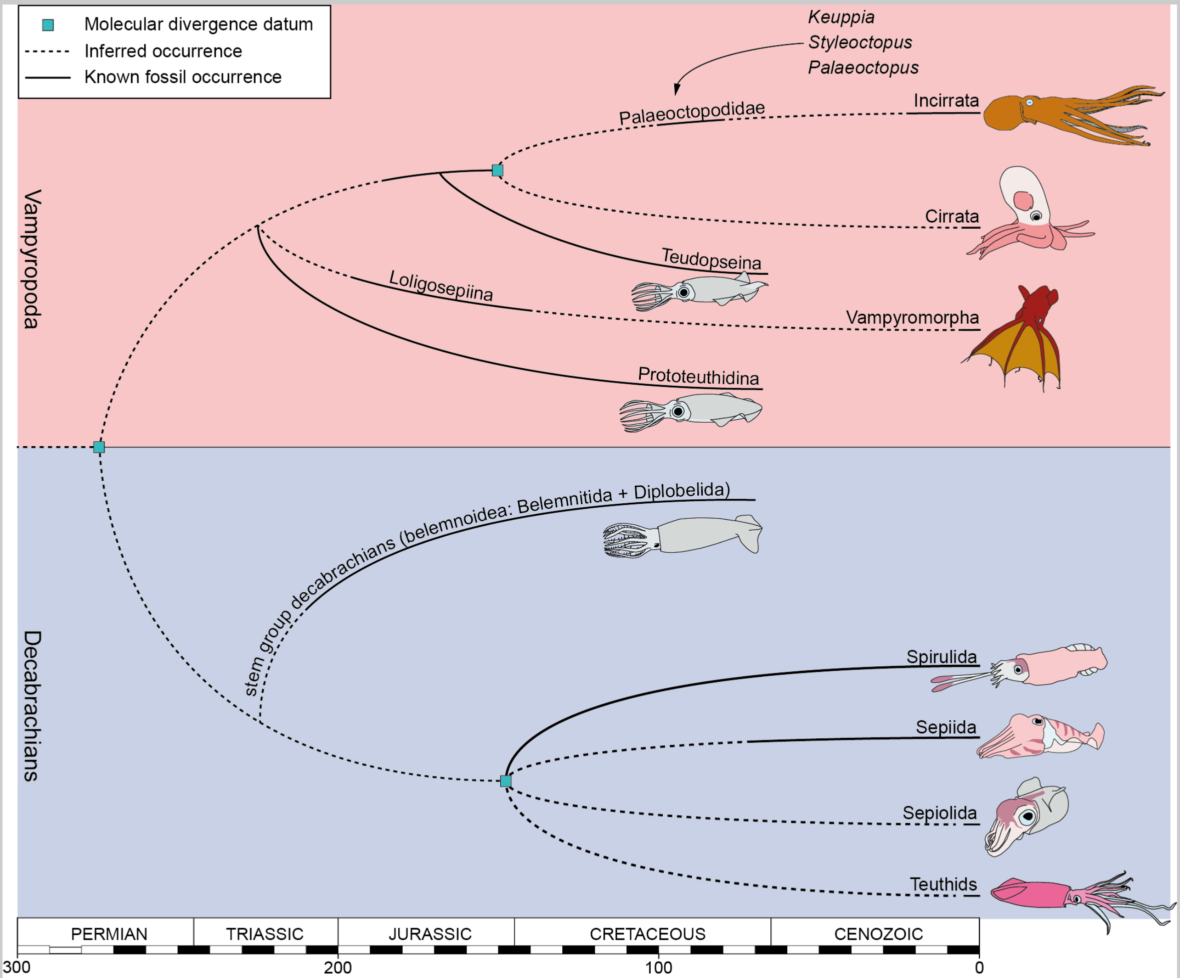

Figure 2 — The evolutionary relationships of major extant and fossil coleoid groups. Solid lines indicate fossil occurrences. Squares indicate molecular divergence dates (taken from Kröger et al. 2011). Image edited from Clements *et al.* (2016).

The almost non-existent decabrachian fossil record means that untangling the evolution of crown-group squid is very difficult. Molecular-clock data suggests that the squids and cuttlefish diverged from their belemnoid ancestor later than the vampyropods diverged, but around the same time as the two main octopus groups (the Incirrata and Cirrata) diverged, during the late Jurassic, around ~150 (± 30) Ma. The discovery of cuttlebones, isolated decabrachian jaws and fossilised internal shell of a type of deep water squid (*Spirula spirula* – the rams horn squid) in Cretaceous rocks also indicates that decabrachians had evolved around the time *Palaeoctopus* was swimming in the oceans, but no fossil squids are known. Investigations into this bias have indicated that the mode of life may have contributed to the lack of squids in the fossil record. Because swimming uses a lot of energy, squids commonly use chemicals that are less dense than water, such as ammonia, as a buoyancy aid. Ammonia is generated during their metabolism and squid store this waste chemical throughout their body to preserve energy, maintaining their position in the water column rather than constantly swimming. By contrast, octopuses, which live on the seafloor, excrete all their ammonia. During fossilisation, these buoyancy chemicals act to inhibit the replacement of soft-tissues by authigenic minerals (especially calcium phosphate) preventing the preservation of squid. The lack of these buoyancy chemicals allows phosphate minerals to replace octopus soft-tissues.

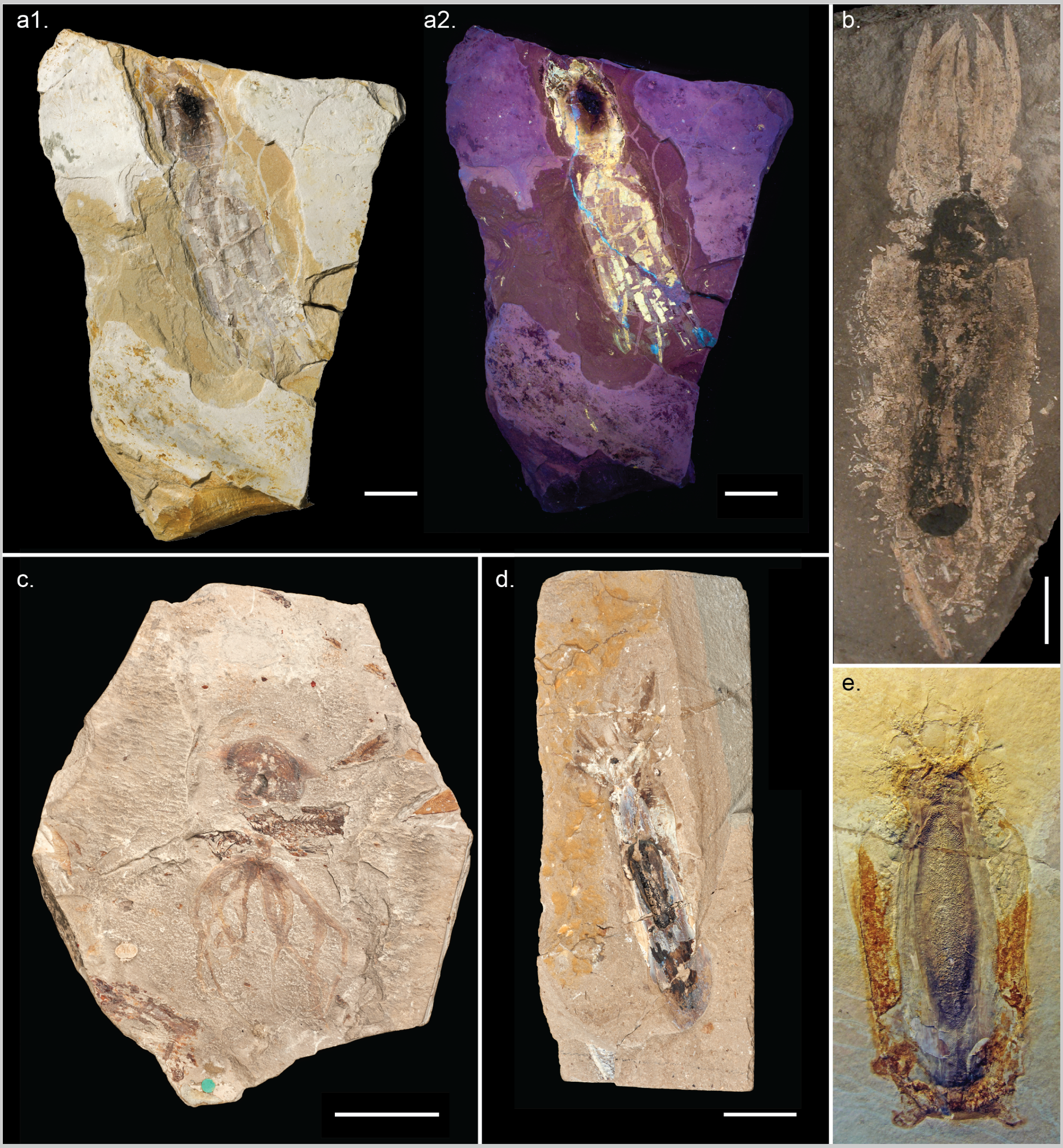

Figure 3 — A) Crown vampyropod *Keuppia* sp., Cretaceous, Lebanon, in both normal light and UV. The soft-tissues are preserved in calcium phosphate which fluoresces brightly against the rock matrix. B) stem vampyropod *Loligosepia aalensis*, lower Toarcian, Germany (Photo courtesy of Dirk Fuchs: LWL-Museum für Naturkunde). Named as a squid, both soft-tissue (note number of arms) and shell morphology indicates it is a stem vampyropod. C) *Palaeoctopus newboldi*, Cretaceous, Lebanon. The first soft-tissue octopus fossil ever described in 1896. The paired fins can be observed – currently it is the oldest known cirrate. A fish is preserved overlying the octopus. D) an unknown species gladii from Lebanon. The ink sac is preserved *insitu*. E) *Trachyteuthis* gladii, Tithonian, Germany (Photo courtesy of Christian Klug: Jura-Museum Eichstätt). This was originally described as a palaeo-cuttle fish due to the similarity of the gladii morphology, however, is a stem Vampyropod. Scales: a1, a2, c: 5 cm. b & d: 2 cm. Photos a1, a2, c and d courtesy of Jonathan Jackson, NHMUK. NHMUK Photos copyright belongs to The Trustees of the Natural History Museum.

The estimated dates for divergence of the crown-group octopuses and decabrachians suggests that their evolution was driven by ecological shifts during the Mesozoic Marine Revolution (242 Mya to 62 Mya). Adaptations in free-swimming coleoid cephalopods, such as streamlining, shoaling, and high metabolic rates, may have been a response to increased competition from ray-finned fish, marine reptiles and sharks. The reduction and eventual loss of their complex chambered internal shell allowed decabrachians and finned octopuses to become faster swimmers than belemnoids as well as allowing them to colonise deeper water than their shelled ancestors (high water pressure would cause the external shells of cephalopods such as ammonites to implode). This direct competition from free-swimming coleoids may have marginalised the belemnites during the late Jurassic period, possibly contributing to their eventual extinction during the Cretaceous.

Much of the recent work describing fossil coleoids, especially stem coleoids, has been led by Dirk Fuchs, who has contributed greatly to the understanding of coleoid evolution. There are still gaps in the fossil record, but through ongoing work from Dirk and many others, the evolution of this fascinating group is become clearer and a lot less alien.

Ambiguous fossils

In the coleoid fossil record there are some outliers that do not seem to fit with the current understanding of coleoid evolution. The most obvious is the Cambrian oddity; *Nectocaris pteryx* known from the Emu Bay Shale in Australia, Chenjiang region of China and Burgess Shale in Canada. Other than superficially looking like some form of primitive cuttlefish, *Nectocaris* has many characteristics, such as camera-type eyes, paired tentacle appendages and a funnel-like structure that are superficially similar to those of crown coleoids and was originally described as such. Since then, studies have questioned this designation, because re-examination of the fossils disputed many of these characters, especially the taxonomically informative external siphon. It is unlikely that *Nectocaris* is a cephalopod or even a mollusc, rather it is probably an independent 'experimental' lineage of the Lophotrochozoa (invertebrates including molluscs, bivalves, and annelids but excluding arthropods).

Another notable contentious coleoid fossil is *Pohlsepia mazonensis*, from the Carboniferous Mazon Creek fossil bed in Illinois (300 mya). Described as the oldest octopus, it is preserved as a white stain within an iron carbonate concretion. *Pohlsepia* was interpreted as a Cirrate octopus and superficially looks remarkably similar to one, but there are several factors that make this interpretation unlikely. *Pohlsepia* has no internal shell, which would be expected in a stem lineage of Cirrate octopuses. It is unlikely that, if it had an internal shell, it rotted away before fossilisation, because shells are seen in other Mazon Creek cephalopods. The body outline of *Pohlsepia* is poorly defined and key vampyropod soft-tissue characteristics, such as suckers, are missing. One ambiguous specimen of *Pohlsepia* has ten distinct arms with no suckers, which counters our current understanding of octopus evolution. Another point of contention is that *Pohlsepia* appears in the Carboniferous period, long before the molecular clock suggests that the Vampyropoda and Decabrachia diverged (during the Permian period). The good fossil record of intermediate stem-octopus fossils throughout the Mesozoic era and the supposed presence of highly derived characters (i.e. the lack of internal shell) in *Pohlsepia*, makes it is highly unlikely that this organism can be definitively classified as a vampyropod. Further work is required to interpret this enigmatic fossil.

Suggestions for further reading

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[2]The correct plural of octopus is a source of constant debate. Although octopi and octopuses are widely used and acceptable plurals, the word octopus stems from ancient Greek and so the plural should be octopodes (pronounced oc-top-o-dees). Both ‘octopodes’ and ‘octopuses’ are commonly used in scientific literature, and I will use octopuses for clarity. But I personally think octopodes is cooler.