The monster nautiluses of the Palaeozoic

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The handful of nautilus species found in seas today are small, retiring animals that scavenge about at night, foraging for carrion and crustacean moults. However, nautiluses were not always so insignificant and during the first half of the Palaeozoic Era especially, nautiluses were major predators, occupying the same niches in Ordovician and Silurian seas as sharks do today.

The first nautiluses

Compared to their cousins, the ammonites, the Palaeozoic nautiluses are relatively unfamiliar animals. That is a shame, because they are truly remarkable, in all likelihood being the first really big predators to evolve on Earth. But, to understand how they reached the top so quickly, we need to look back at their ancestors, the floating 'snails' of the Cambrian.

Nautiluses are the most primitive of all the cephalopods, the group of molluscs that also includes squids, octopuses, cuttlefishes, ammonites and belemnites. Nautiluses appeared during the Late Cambrian, about 500mya, but what their ancestors might have been remains uncertain.

The traditional explanation is that the first nautiluses, such as *Plectronoceras exile*, were derived from monoplacophorans. These are snail-like molluscs today, limited to a few species only found in relatively deep water, but in the past they were quite diverse. Although they look a lot like a limpet, their internal anatomy is distinctive, with unusual features such as serial repetition of the gills, kidneys and reproductive organs along the body.

At least some monoplacophorans had chambered shells. The Late Cambrian species, *Knightoconus antarcticus* was one such species, but, unlike cephalopods, the chambers were all sealed off from one another. Only cephalopods have a siphuncle, a tube-like structure that runs through the chambers, allowing them to be connected to the living body of the animal. The siphuncle is important because it allows cephalopods to replace water inside the shell chambers with gas. By filling the chambers in this way, the cephalopod reduces its overall density and, once it acquires the same density as seawater, it neither floats to the top nor sinks to the bottom. Rather wonderfully, it simply hangs in midwater and can swim off in any direction it wants. Compare this to other molluscs, which have to drag their heavy shells around with them. Nautiluses and cuttlefishes continue to operate this way today, and ammonites and belemnites did so in the past.

Monoplacophorans, like *Plectronoceras exile*, had shells with chambers, but no siphuncle. Were the walls that formed the chambers for some other purpose? Did they work like bulkheads, so that the monoplacophoran could build shell that was thin and economical to construct, but just as strong as a thicker, unchambered shell? Perhaps, but recent work on the genetics of the molluscs suggests that cephalopods are more closely related to scaphopods (tusk shells) than they are to monoplacophorans. Modern scaphopods are small, specialised animals that live buried in the seafloor catching microscopic prey. While their genes might tell us they are closely related to the cephalopods, there are no obvious anatomical or ecological similarities.

Early success

Having become buoyant, nautiluses found themselves able to explore midwater habitats free from serious competition. As the Cambrian yielded to the Ordovician, most animals were stuck on the seafloor. The other molluscs crawled about on the bottom, as did worms and echinoderms, and most of the trilobites and crustaceans. While there were certainly fish

Dideroceras wahlenbergi **(formerly *Endoceras wahlenbergi*) is an example of one of the larger orthocone nautiluses. Complete shells are rare, but fragments 30 to 45cm long are common at certain horizons. Photo by Jens Rydell.**

around at the time, they were still armour plated and lacked a swim bladder, so these were also mostly confined to the sea bottom. The only large animals commonly found in midwater were drifting animals that fed on plankton - things like jellyfish and graptolites.

Therefore, Early Ordovician nautiluses found themselves with a unique combination of large size and mobility. They quickly became quite diverse and seemingly occupied a variety of different ecological niches. Of course, such assumptions are based purely on the shapes of their shells - as with ammonites, we know virtually nothing about the soft body parts of Palaeozoic nautiluses. In any case, what we do know of Ordovician nautiluses is that their shells came in lots of different shapes and sizes. One of the earlier types had coiled shells like those of *Plectronoceras exile*, but larger and more elongate, so that they looked a bit like elephant tusks. *Cyrtoceras ellipticum* is a well-known example of this type and, consequently, these nautiluses are referred to as having 'cyrtocone shells'. Because such shells would have rocked forwards and backwards if the nautilus tried to swim quickly, the assumption here is that these nautiluses swam slowly above the seafloor, picking off sessile (that is, non-mobile) prey such as clams and brachiopods. These nautiluses were usually rather small, with shells no more than 10 to 15cm in length.

Quite early on, some nautiluses evolved tightly coiled shells similar to those of ammonites and, indeed, modern nautilus species. For example, the Middle Ordovician species, *Estonioceras imperfectum*, has a coiled shell with successive whorls almost touching. Interestingly, these coiled nautiluses were not the ancestors of the ammonites, which instead seem to have evolved from a peculiar group of straight-shelled cephalopods known as the Bactritida, which appeared during the Early Devonian.

Because of their straight shells, members of the Bactritida, such as *Bactrites gracilis*, seem to have lived a head-downwards life. This is because the shell was less dense than the head, and so, when floating in the water, the animal would pivot around the centre of the shell, the apex pointing upwards and the living chamber pointing downwards. Perhaps these cephalopods drifted across the seafloor, picking off prey much like cyrtocone nautiluses. Or, perhaps, they were plankton feeders, moving up and down the water column, as many deep sea squid do today.

The Bactritida were not the only straight-shelled cephalopods though. Indeed, the Bactritida were rather an unimportant group, so far as we can tell, and it was other straight-shelled nautiluses that were ecologically much more significant. Known as 'orthocone nautiluses', their remains are very common in Ordovician and Silurian deposits, to the degree that certain limestones are known as 'orthoceratite limestones', precisely because of their abundance.

Among the best-known genera are *Orthoceras*, *Michelinoceras* and *Endoceras*. Instead of hanging head-downwards, they were oriented along the horizontal plane, like most modern squid. They solved the orientation problem by weighing down the apex of the shell with mineral deposits. Just as the tissue running through the siphuncle provided a mechanism for removing water from the chambers, so too was the siphuncle used for secreting these counterweights. The shell now operated like a see-saw, with the counterweight at the 'tail end' of the shell, balancing the body at the 'head end'. Therefore, orthocone nautiluses were able to swim - backwards at least - as quickly and easily as its jet propulsion would allow.

Why couldn't they use their jet propulsion to swim forwards? All cephalopods are limited in this regard, because the outlet from their jet is below the head, usually through a muscular tube of some sort. On modern nautiluses, this structure is called the hyponome. While this tube works very well at directing the jet away from shell, bending the tube backwards under the shell reduces the flow of water, in much the same way as tight bends in hose pipes slow down the flow of water. Therefore, modern cephalopods can swim quickly in reverse, but only slowly going forwards - orthocone nautiluses were presumably no different.

Ordovician giants!

Most *Orthoceras* and *Michelinoceras* were of moderate size, up to 30cm being typical, though exceptional species reached lengths of around a metre. However, there were much larger orthocone nautiluses swimming around the Ordovician seas. Some species of *Endoceras* got to over three metres in length, and fragments of some *Cameroceras* suggest they were even larger, perhaps as much as nine metres in length.

Were such giants active midwater swimmers or did they mostly drift above the seafloor, only jetting away when harassed? Did they swim after large prey, or were they slow grazers that fed on sessile animals or plankton? These are difficult questions to answer and, to be honest, the fossils do not tell us very much either way.

Dideroceras wahlenbergi **is a common constituent of what geologists often call 'orthoceratite limestone'. Photo by Jens Rydell.**

One problem with assuming they were active predators is that they could only swim rapidly in reverse. As we have seen already, cephalopod jet propulsion is great for swimming away from predators, but not so good for swimming forwards towards prey. Squid and cuttlefish solve this problem by using their fins to swim forwards, while octopuses prefer to crawl about when hunting. Modern nautiluses mostly use their tentacles to pull themselves along and, in all probability, Palaeozoic nautiluses were no different.

On the other hand, their large size would have made them formidable predators, even if they were not swimming particularly fast. Like other cephalopods, they were equipped with muscular tentacles and a strong beak, and it is hard to imagine a three metre *Endoceras* having any problems at all tackling a slow-moving animal like a trilobite or, for that matter, sessile prey like brachiopods. It is also important to remember that they were not competing with very much in terms of midwater predators of equivalent size. Midwater fish were few and generally small. So, as clumsy as it might have been by modern standards, a large, jet-propelled *Endoceras* looking for food was a pretty dangerous animal by the standards of the Ordovician!

So, were they the sharks of the Ordovician seas? Perhaps, but more like bottom-dwelling nurse sharks than midwater mackerel sharks. Top predators, yes, but not necessarily agile or fast-moving ones.

Distribution

Ordovician and Silurian nautiluses often have a very wide distribution. One of the most familiar species to fossil collectors will be *Michelinoceras michelini*, an orthocone nautiloid found in Central Europe and North Africa. Polished specimens from Morocco are staples of the fossil trade, being sold in gift shops, museums and at geological shows of all types. *Orthoceras regulare* can be found across a broad region of Europe, from Sweden to the Ukraine. *Dideroceras wahlenbergi* (formerly *Endoceras wahlenbergi*) has been collected from sites as far apart as Estonia and China.

Unfortunately for palaeontologists, some scientific names have been used rather loosely and, because orthocone nautiluses are quite difficult to identify to species level, reports of things described as *Orthoceras* sp. or *Endoceras* sp. are very common. Fossil collectors with specimens sold under such names should treat these identifications as strictly provisional.

***Estonioceras imperfectum* was one of the coiled nautiluses of the Ordovician, superficially similar to the much later ammonites. Photo by Jens Rydell.**

How they appeared and saw the world

One of the interesting things about Palaeozoic nautiluses is that the shells of some specimens have revealed traces of colour markings, typically concentric or zigzag bands. What were these colour markings for? Most likely, they acted as some sort of camouflage, breaking up the outline of the shell and making the animal less easily seen by its predators or its prey.

It is assumed the Palaeozoic nautiluses had simple pinhole camera eyes like those of modern nautiluses, in which case, their eyesight was relatively poor compared to the superb eyes possessed by squids and octopuses. Whatever else the colours on their shells were for, they were not for communication between individuals, unlike the bright colour patterns that octopuses, squids and especially cuttlefish now use to interact with each other.

Modern nautiluses hunt primarily by smell rather than sight. Did Palaeozoic nautiluses operate in the same way? Perhaps they swam across the seafloor, using their tentacles to search for suitable prey. Nautilus tentacles are both sensors and grapplers, so as soon as they detected anything edible, it would be quickly entangled and dragged up to the mouth.

Regardless of how they sensed their environment, one thing the Ordovician nautiluses did bring to the world was something approaching intelligence. Modern cephalopods are famously ‘brainy’ animals, being adept at solving man-made puzzles in labs as well as performing all sorts of sophisticated behaviours in the wild.

Modern nautiluses are not quite so smart as cuttlefish or octopuses, but, by the standards of most other invertebrates, they have large brains and complex nervous systems. Handling food with their tentacles, while processing visual and taste data at the same time, requires a fair amount of brain power. If we could go back in time and take a swim in an Ordovician sea, the big orthocone nautiluses would very likely be the only animals that would be curious enough to approach and, in their own way, look back at us.

Extinction

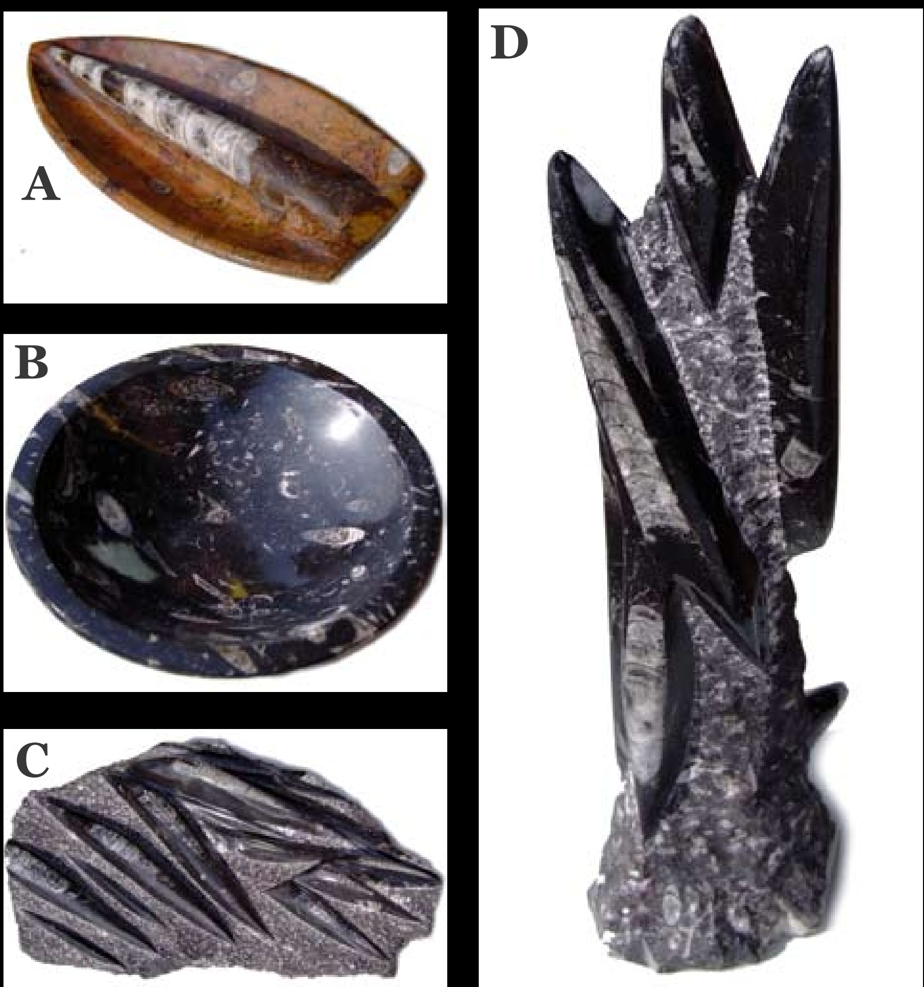
The Ordovician–Silurian extinction event set the orthocone nautiluses back significantly. To be fair, the really big species in the genera *Endoceras* and *Cameroceras* belonged to the order Endocerida, a group that went into decline from the middle part of the Ordovician onwards. However, the order Orthocerida included most of the small and medium-sized species, including *Orthoceras* and *Michelinoceras*. For whatever reason, these straight-shelled nautiluses managed to pass through the Ordovician–Silurian extinctions relatively unscathed and were quite diverse in the Silurian.

From the middle of the Devonian onwards, even the Orthocerida started to decline in diversity. The evolution of fast, agile midwater fish, with strong jaws, was probably the key issue. Sharks and placoderms were more agile swimmers than orthocone nautiluses, and their jaws would have made short work of their shells.

Surprisingly perhaps, the Orthocerida managed to hang on for quite a long time, the last species being known from sediments of Triassic age (though some palaeontologists place these late species in a related, but distinct group of their own, the order Pseudorthocerida). However, through their descendants, the Orthocerida have continued to maintain their importance.

The Bactritida mentioned earlier were an offshoot of the Orthocerida and, while the Bactritida themselves are pretty obscure, two very important groups of cephalopods branched off from them. These were the ammonoids and the coleoids. The ammonoids include the ammonites and their relatives, and they were terrifically important from the later part of the Palaeozoic through to the very end of the Mesozoic. The coleoids are the belemnites and their modern day relatives, the cuttlefishes, octopuses and squids.

So, while the orthocone nautiluses of the Palaeozoic may be long gone, their descendants live with us still.



Michelinoceras michelini **is a familiar fossil, widely sold polished or sectioned. The famous black marble which, contain,** ***Orthoceras*** **specimens, is also worked into ornaments: A)** ***Orthoceras*** **carved into a boat, B) black marble bowl with polished** ***Orthoceras*****, C) large slab of published** ***Orthoceras*****, D) carved statue of** ***Orthoceras*****.**

Book review

Jon Trevelyan (UK)

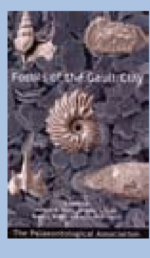
Fossils of the Gault Clay
Field guide to fossils no. 12.

It is always exciting when Palass publishes a new field guide to fossils. However, their last (Silurian Fossils of the Pentland Hills, Scotland, Field Guide to Fossils No. 11), despite being of the expected quality, suffered from being somewhat esoteric in its subject matter. This one, number 12 in the series, is back on form and, like their guide to the chalk (No. 2) is for 'cenomaniacs', this is likely to be the constant companion for anyone, who (like me) loves the Gault Clay.

Like others in the series, it has the usual excellent black and white photographs of beautifully prepared specimens. Each chapter is authored by a specialist in the relevant subject, containing an introduction, followed by detailed systematic descriptions of each specimen.

However, after the beautifully produced Ammonites & other Cephalopods of the Lower Cretaceous Albion of the South East of England (Fred Clouter, published by The Medway Fossil & Mineral Society) was published in 2007, is there a need for another guide to the Gault? The answer is that this publication (as always with the Palass guides) is a more academic piece. It covers the full range of fossils to be found in the Gault of the entire UK, whereas Fred's book is more populist and limited in range (to cephalopods and the southeast). Therefore, for the keen amateur as well as the professional, there are good reasons to have both publications on the shelf.

If I have one criticism, it is that geologists, including many of those who contributed to this excellent tome, use a private language that is unintelligible to anybody outside of the geological 'elite' or not in possession of a geological dictionary. I believe it is time to acknowledge that the academic language of geologists is often unnecessary and counterproductive. One contributor, who does not fall into this trap, is Deposits' own Neale Monks, who authors the chapter on heteromorph ammonites. I wonder if there is any connection!



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