

Fossils explained 63



Ammonites

Ammonites were amongst the most successful marine animals during the Mesozoic. They evolved to fill a large variety of ecological niches across a wide spectrum of open-ocean and marine shelf environments. Despite the fact that hundreds of thousands have been collected in the last 200 years and are available for study in museum collections, the biology of ammonites—how they lived—is very difficult to understand. They lived such exotic and strange lives comparable with no group alive today, and seemed to break all the rules of Darwinian biology. Their importance in stratigraphy is due to their rapid evolution, which gave rise to a more refined zonal scheme than is possible with any other group of fossil, making the need to understand ammonite biology of more than academic interest.

If there's one fossil a collector visiting marine Mesozoic rocks expects to find, it's an ammonite—most people interested in natural history can recognize one. Not only do they look nice in the display cabinet or on the mantelpiece, they're also of vital use in stratigraphy—at the last count, the Jurassic was divided into over 150 ammonite subzones. Yet, in contrast with the vast majority of fossil groups discussed in these columns over the last 30 years, ammonites are extinct, and as such, we may never be able to offer a completely satisfactory explanation of how they lived.

Yet, we have a living, chambered cephalopod in the seas today—the *Nautilus*, about which we know quite a lot. How much of a guide to us is *Nautilus*—were ammonites simply a more elaborate version of a *Nautilus*—or were they very different in life style?

Biology of *Nautilus*

Modern *Nautilus* has a hollow, chambered portion of its shell, known as the phragmocone, with the chambered body suspended beneath it. Septal plates divide the chambers (Fig. 1). In life, the chambers or camerae are partially filled with fluid, and are connected through the centres of the septal plates by a tube of living tissue, the siphuncle. When arterial blood rich in salt flows along the siphuncle, osmotic pressure draws the low-salt cameral fluid into the siphuncle, leaving a partial vacuum. Gas diffuses from the body fluids into the chambers, and the animal becomes

more buoyant and rises. Contracting the blood vessels causes it to sink. This takes time—hours, some people would insist days—to make any significant change in its buoyancy. To travel any distance the main means of propulsion is by jet, squirted from the siphon. Videos of *Nautilus* swimming show that it is quite agile, if a little hampered by the fact that it has to swim backwards, with the frequent hazard of bumping into things.

Differences in the shell between ammonites and *Nautilus*

The coiling in *Nautilus* is described as involute, the enveloping whorl hiding almost all of the previous whorl. Ammonites varied from similarly involute to markedly evolute (Figs 3–5), the enveloping whorl barely touching the previous one. The external line where the enveloping whorl joins the preceding whorl is known as the umbilical seam, the area of inner whorl exposed being referred to as the umbilicus.

In *Nautilus*, the septal plates join the outer shell along a gently curved line, known as the suture. This can only be seen in fossils in the internal mould, when all the shell has been removed (Fig. 2). Ammonites differed in two important aspects—the siphuncle lay just beneath the outer margin of the shell, known as the venter, and the junction of the septal plate and the outer shell was complex and frilly, with the characteristic saddles and lobes (Fig. 3).

The septal plates of *Nautilus* are clearly there to

John K. Wright

Department of Earth Sciences, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK

E-mail: j.wright@es.rhul.ac.uk

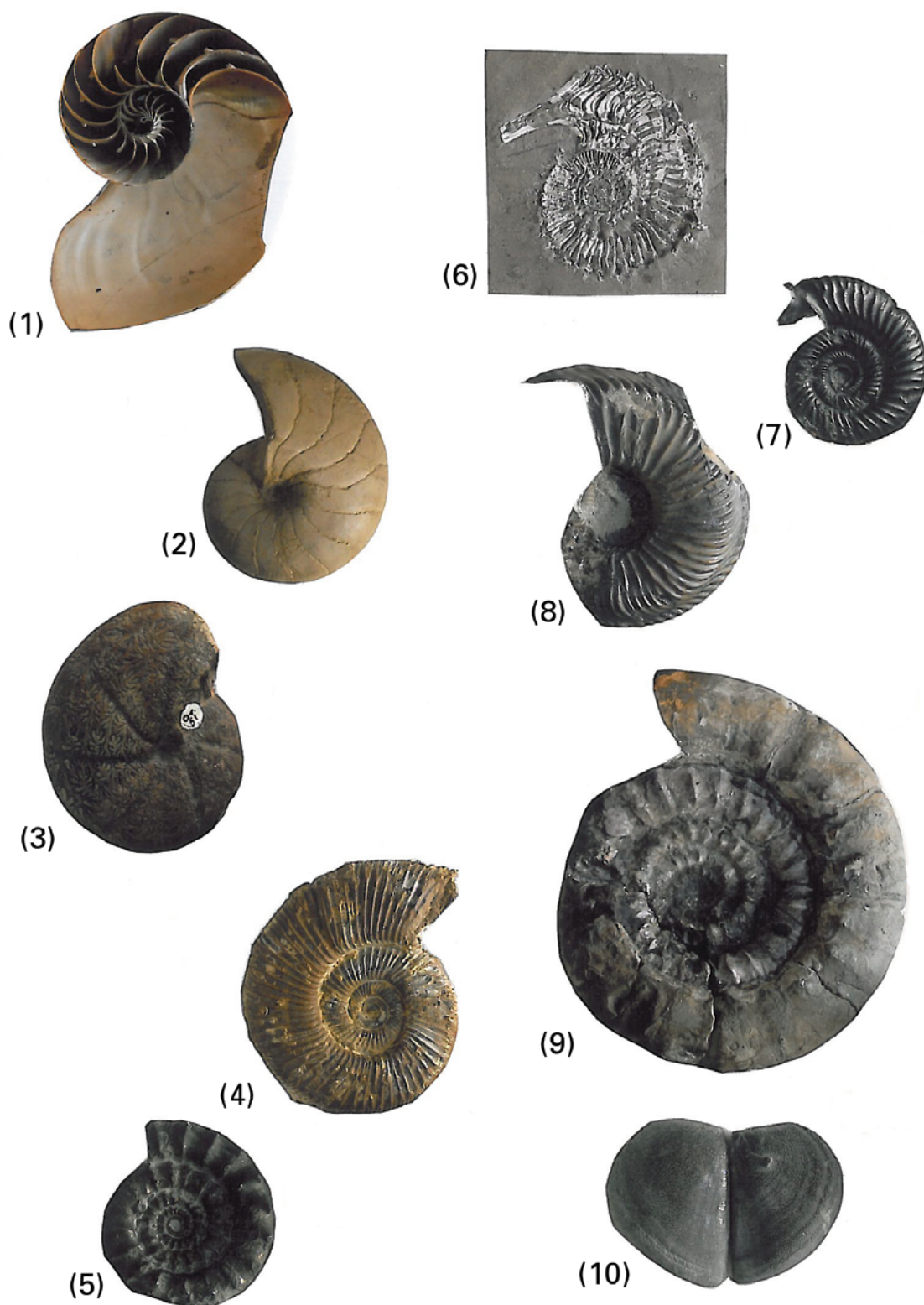


Fig. 1. Sectioned recent *Nautilus* showing the camerae, with connecting siphuncle, and body chamber, $\times 0.3$.

Fig. 2. Internal mould of *Nautilus* sp. from the London Clay showing curving sutures, $\times 0.5$.

Fig. 3. *Phylloceras* sp., Upper Lias, Lower Jurassic, showing complex suture, $\times 0.6$.

Fig. 4. *Perisphinctes* sp., Oxfordian, Frontenay, France, showing a common style of ribbing adopted by many genera through the Jurassic and Cretaceous, $\times 0.6$.

Fig. 5. *Microderoceras* sp., Lower Lias, Lower Jurassic, Lyme Regis Dorset, showing tubercles which were the bases of long, sharp spines, $\times 0.6$.

Fig. 6. *Kosmoceras* sp., Oxford Clay, Middle Jurassic, Peterborough, a microconch adult with lappet, $\times 0.7$.

Fig. 7. *Perisphinctes* sp., Corallian, Upper Jurassic, North Yorkshire, a microconch adult with lappet, $\times 0.9$.

Fig. 8. *Cardioceras bukowskii* Maire, Corallian, Upper Jurassic, North Yorkshire, a microconch adult showing rostrum, $\times 0.7$.

Fig. 9. *Xenostephanus* sp. Kimmeridge Clay, Lincolnshire, a macroconch adult with simple aperture, $\times 0.3$.

Fig. 10. Pair of ammonite aptychi (not from the same individual), Kimmeridgian, $\times 0.7$.

strengthen the shell and prevent it imploding under pressure. *Nautilus* can go down quite deep, several hundred metres, and the septae clearly work very well. The reason why such a markedly more complex suture was vital for ammonites has never been satis-

factorily explained. Many times during its life cycle, the ammonite had to detach the frilly back margin of its mantle from the last septum; a very elaborate process considering the complex nature of the suture in, say, *Phylloceras* (Fig. 3), move the whole body

forwards, and then secrete a new septal plate. The advantages over the *Nautilus* system may be that a thin, frilly septum could be secreted quickly, and the ammonite was out of action, probably resting on the sea floor, for a much shorter time than *Nautilus*. The thin septum was a much more efficient use of aragonite, being stronger, and weighing less, making the ammonite more agile. Also, there is the possibility that as the area of septal plate was much greater in ammonites, if the plate were covered in tissue secreting/absorbing fluid, then the ammonite could change its buoyancy much more rapidly than *Nautilus*.

The young stage

Modern *Nautilus* hatch from their egg at a diameter of nearly 30 mm. Cretaceous nautiloids were smaller, hatching at about 9 mm diameter—still quite large. So, *Nautilus* produces only a few young, all free swimming on hatching, and capable of foraging for food at once. In contrast, Mesozoic ammonites produced numerous offspring 0.5–1.5 mm in diameter, which must have spent some time in the plankton being carried around by ocean currents. Therefore, very young ammonites had very different life styles from young nautiloids. This may explain the pattern seen at the Cretaceous–Tertiary (K/T) extinction, where ammonites with their planktonic stage suffered badly, as did other animals with planktonic stages.

Ornament

Nautilus today only has colour bands on its smooth shell, almost certainly because its main means of propulsion is by jet, and it needs a smooth shell to take full advantage of its means of propulsion. Ribs or spines would slow it down considerably. However, early nautiloids—late Palaeozoic to early Mesozoic, were quite strongly ribbed. These forms became extinct, possibly due to competition from ammonites.

Ammonites may be smooth like *Nautilus*, but often had quite complex ornament—either ribs or spines (Figs 4, 5). Recent studies have shown how complicated ornament formed. In the growing ammonite, the soft body advanced beyond the last-formed aperture, continuously secreting a smooth flexible chitinous periostracum. When the periostracum was extended to the length of a new rib, retraction of the soft tissue took place, folding the periostracum into a characteristic pattern. Calcification of the folded periostracum then took place, and the ammonite was ready to advance forwards again with a new rib-

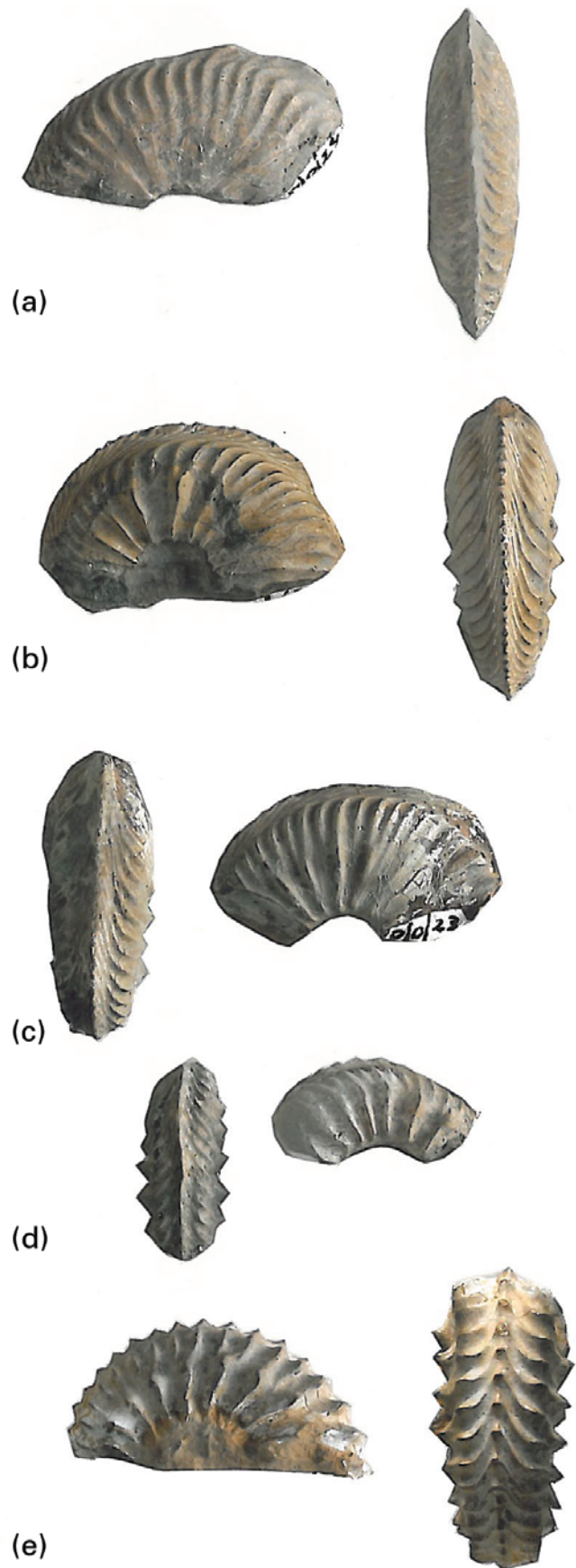


Fig. 11. Variation within *Cardioceras costicardia* Buckman biosp. All specimens are body chambers of microconchs, and come from the Red Nodule Bed of the Oxford Clay, Upper Jurassic, of Furzy Cliff, Dorset. **a.** A slim, nearly smooth variety, **b.** a form close to the holotype, **c.** *C. costicardia* var. *costellatum*, **d.** *C. costicardia* var. *studleyensis*, **e.** *C. costicardia* var. *quadrarium*. a–c, $\times 0.7$; d, e, $\times 0.8$

forming cycle. A similar but more complex operation was needed to form a spine. Because there are a very limited number of possibilities for folding the periostracum, the same rib patterns or spine patterns occur again and again throughout the Mesozoic, giving rise to frequent homeomorphy, and difficulty in identification of ammonites. The first thing an ammonite specialist may say on being given a specimen to identify is 'where did you collect it'. W.J. Arkell admitted that if given plaster casts of some Middle and Upper Jurassic perisphinctids, he would be unable to distinguish the separate forms.

Having a ribbed, corrugated shell strengthened it, protecting against predators and accidental damage. Prominent ribbing occurs typically in ammonites that lived in relatively shallow water sublittoral habitats. Spines were almost certainly protective, but very long ones may have been open at the end with sensors at the tips, enabling the animal to sense what was going on behind it—food or the approach of predators. When the animal advanced forwards in growing, the bases of the spines had to be sealed off.

Adult stage

When ammonites approached maturity, the last few septae were laid down close together and the detail in the suture was often approximated. The umbilical seam began to uncoil, and the ammonite had reached its maximum size. Adult male and female *Nautilus* are very similar in size. However, when adult ammonites are compared, ammonites which clearly had the same rib pattern in the early whorls, and which were apparently the same species, became adult either quite small—*c.* 30 to 100 mm, or quite large—*c.* 100–500 mm. The small forms, known as microconchs (Figs 6, 7), often have elaborate apertures, with marked constrictions and lappets (Figs 6, 8), or the venter may project to form a rostrum (Fig. 9). The larger forms, known as macroconchs, have only a simple aperture (Fig. 9). The general consensus is that microconchs were the males and the macroconchs the females, having space in the larger shell for the ovaries containing thousands of eggs to be released on spawning. The marked difference in size means that for most of the year the two forms must have lived in completely different environments, and only came together periodically for spawning. The earliest microconch/macroconch pairs have been recognized in faunas from Liassic rocks in the Lower Jurassic. The phenomenon reached its peak in the Middle and Upper Jurassic, when the ratio in sizes may reach 1 : 10, and is less marked in Cretaceous faunas.

The recognition of macroconchs and microconchs has serious implications for ammonite taxonomy, as members of the same biological species have in the past, because of their very different sizes, been given different specific, and often different subgeneric,

names. Only rarely, with exceptionally preserved faunas, is it possible to be certain of which macroconch went with which microconch, and to allocate one biospecies name. In most cases, due to poor preservation and to the difficulty of matching up microconch rib patterns in the inner whorls of macroconchs, the old names are still used as 'morpho-species' and 'morpho-subgenera', with the recognition that these are probably macroconchs and microconchs of one biological species.

Jaws and opercula

Most ammonites seem to have been scavengers or predators, and their jaws are quite like those of *Nautilus*. Thus, ammonites had calcified jaws; as in *Nautilus* the front portion of the upper jaw was strongly projecting like a parrot's beak, serving for biting and cutting up food with strong jaw muscles. Rows of serrated ridges in the lower jaw and grooves in the upper jaw served for cutting up food into smaller pieces.

The two plates forming the lower jaw are called aptychi (Fig. 10), and for a very long time were considered to be solely an operculum or plate which closed the aperture when danger threatened. It was only in the 1970s that specimens were found with the aptychi opposing the upper jaw, forming a lower jaw. But we're still stuck with the problem that in many ammonites, the paired aptychi would admirably fit the aperture to form a protective operculum. *Nautilus* itself has a protective chitinous hood, and signs of this are seen in some Triassic ammonites. Jurassic and Cretaceous ammonites evolved a better protection, for ammonite specialists now recognize that the aptychi formed both the lower jaw and the operculum. The aptychi normally sat horizontally opposing the upper jaw, but when danger threatened could be rotated through 90° to close the aperture.

Food

Most modern cephalopods are highly skilled carnivores taking a wide variety of prey. Modern *Nautilus* is an opportunist feeder, feeding on a wide variety of crustaceans. Very well preserved Upper Lias ammonites from Germany found recently have yielded new data on ammonite feeding habits. Though flattened, the specimens are very well preserved, often with jaw apparatus, and stomach contents. Ball-shaped inclusions of fragments of a small crustacean are common. These include claws and body segments. This is probably food held in the animal's crop ready to be digested.

Intra-specific variation

Modern *Nautilus* is divided into 6 or 7 species, all of which show very little intraspecific variation. How-

ever, one of the most puzzling things about ammonites is that it is very clear that there was a great range in variation within species. All the specimens in Fig. 11a–e came from the same horizon in the Oxford Clay of Dorset, and clearly lived together. Conventionally, they are subdivided into different species and even subgenera. Yet, when you plot the dimensions of hundreds of examples of similar cardioceratid ammonites as histograms, the smooth forms or the ribbed forms, the slim forms or the squat forms do not cluster—you just get one smooth Gaussian curve—showing that we are dealing with one highly variable species. Obviously, this again causes problems for taxonomy. Current papers are uniting dozens of specific names under one species, with the old specific names often being regarded as just varieties.

It's almost as though ammonites had life styles such that selection pressures on the anatomy of the shells were very limited. There does not seem to have been the degree of predation which would have compelled them to adopt particular shapes and rib patterns as being more effective in enabling them to escape predators than others. It's probable that they had very good defensive mechanisms similar to the octopuses' ink sac, and if damaged they could often repair their shells. Damaged but repaired shells are very common. However, we can't deny that ammonites often formed a meal for large predators (Fig. 15).

Way of life

Studies of oxygen isotopes of ammonite shells show that the shells formed in cooler waters at the same depth as sessile bivalves and gastropods. Ammonites thus had a whole variety of mainly benthic life styles living on or near the sea floor. These were the round-whorled, ribbed forms (Fig. 12), which must have been sedately mobile, while spiny forms (Fig. 13) and flat-ventered forms must have spent most of their time resting on the sea floor. Some ammonites clearly must have been much more mobile (Fig. 14), these oxycone forms clearly being designed for rapid movement. Such forms are rather exceptional, however, as the niche for rapidly-moving ambush-predators was largely occupied by squid and belemnites.

In the Cretaceous heteromorph forms became especially common (Figs 15–18). Uncoiling took many forms. In the simplest case, the body chamber hung suspended beneath the coiled phragmocone. Open spiral forms such as *Hamitella* (Fig. 16) clearly could not swim rapidly, and must have drifted with ocean currents. Forms with a long axis such as *Turitella* (Fig. 17) and *Baculites* (Fig. 18) probably lived on or near the sea floor and could swim speedily in the one direction away from danger if threatened. Hook-shaped forms and complex, intertwined forms had such a big difference between their centres of buoy-

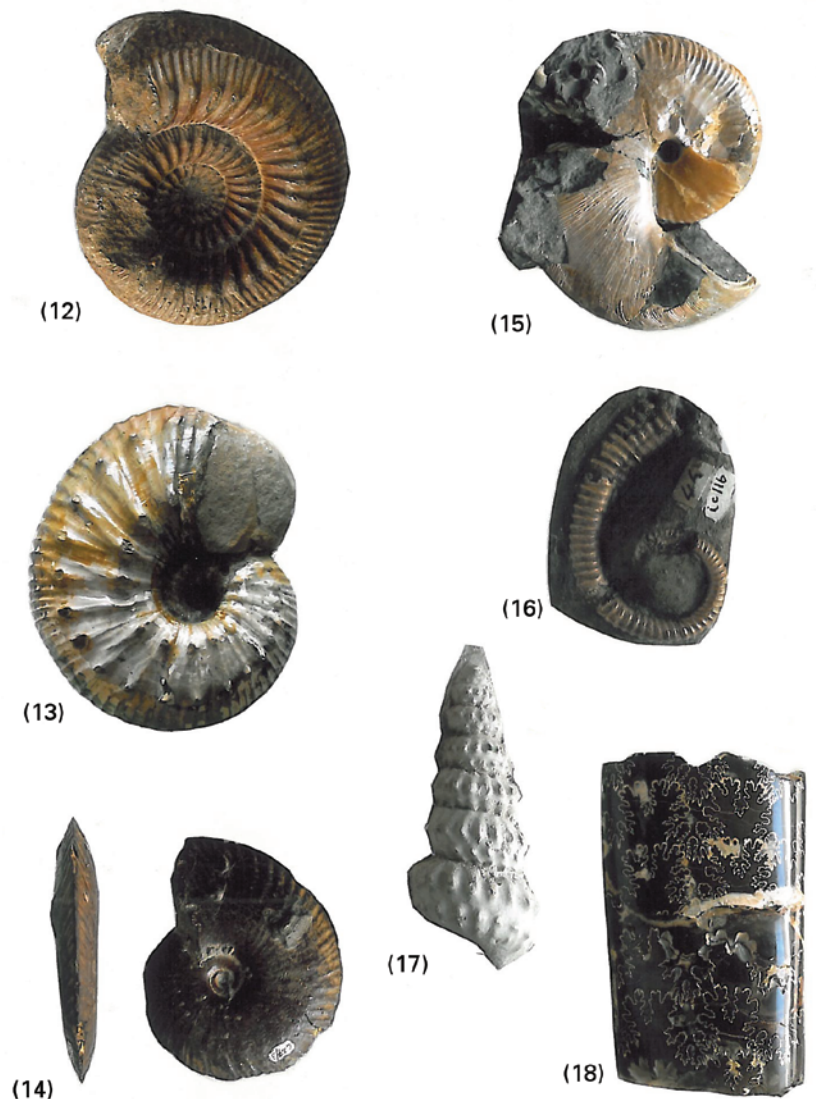


Fig. 12. *Stephanoceras humphriesianum* (J.de C. Sowerby), Inferior Oolite, Middle Jurassic, Dorset—a round-whorled form with trifurcating ribs—three secondary ribs arise from each primary, $\times 0.3$.

Fig. 13. *Liparoceras cheltense* (Murchison), Lower Lias, Lower Jurassic, Cheltenham—a round-whorled form with two spiral rows of tubercles, $\times 0.5$.

Fig. 14. *Oxynoticeras oxynotum* (Quenstedt), Lower Lias, Lower Jurassic, Cheltenham, a smooth, very slim form, $\times 0.4$.

Fig. 15. *Hoploscaphites nicoletti* (Owen), Upper Cretaceous, South Dakota, USA. A moderately heteromorph form which has been predated and the body chamber eaten, possibly by a squid, $\times 0.6$.

Fig. 16. *Hamitella annulatum* (d'Orbigny), Gault Clay, Lower Cretaceous, Folkestone, $\times 0.6$.

Fig. 17. *Turitella* sp. (cast). Chalk, Upper Cretaceous, a heteromorph form mimicking a gastropod, but still mobile, $\times 0.6$.

Fig. 18. *Baculites compressus* (Say), Upper Cretaceous, South Dakota, USA—part of the phragmocone of a 1 m+ long straight heteromorph ammonite, $\times 0.5$.

ancy and mass that they were almost certainly stable floating platforms rising to the surface only at night, and feeding on plankton via frilly tentacles.

Conclusions

Nautilus, with its smooth, thick shell, is very unspecialized, and very similar forms have been in existence for millions of years. Ammonites, with their complex shells, suggest specialized, narrowly niched forms prone to high rates of speciation and extinction, making them ideal zone fossils. What ammonites did was to take the basic body plan of *Nautilus*, and improve it and refine it in very many ways, almost out of recognition in extreme cases.

Acknowledgements

All figured specimens are in the collection of the Department of Earth Sciences, Royal Holloway, excepting Figs 7, 8 and 11 (author's collection).

Suggestions for further reading

Andrew, C., Howe, P., Paul, C.R.C. & Donovan, S.K. 2010. Fatally bitten ammonites from the lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset. *Proceedings of the Yorkshire Geological Society*, v.58, pp.81–94.

Callomon, J.H. 1963. Sexual dimorphism in ammonites. *Transactions of the Leicester Literary and Philosophical Society*, v.57, pp.21–56.

Callomon, J.H. 1985. The evolution of the Jurassic ammonite family *Cardioceratidae*. In: *Special Papers in Palaeontology*, v.33. The Palaeontological Association, London.

Etches, S., Clarke, J. & Callomon, J.H. 2008. Ammonite eggs and ammonitellae from the Kimmeridge Clay Formation (Upper Jurassic) of Dorset, England. *Lethaia*, v.42, pp.204–217.

Kennedy, W.J. & Cobban, W.A. 1976. Aspects of ammonite biology, biogeography and biostratigraphy. In: *Special Papers in Palaeontology* v. 17. The Palaeontological Association, London.

Lehman, U. 1981. *The Ammonites—Their Life and Their World*. Cambridge University Press, Cambridge.

Wiedmann, J. & Killmann, J. (eds). 1985. *Cephalopods, Present and Past*. 2nd International Cephalopod Symposium, Tübingen, Germany.

Wright, J.K. 2012. Speciation in the cardioceratinid ammonites of the Costicardia Subzone (Cordatium Zone) of the Oxfordian of Skye. *Scottish Journal of Geology*, v.48, pp.61–72.

Young, J.R., Gale A.S., Knight, R.I. & Smith, A.B. 2010. *Fossils of the Gault Clay*. The Palaeontological Association, London.