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Ammonites

G E G Westermann, McMaster University, Hamilton, ON, Canada

Introduction

The term 'ammonite' (from genus *Ammonites*, Latin = lover/team of Ammon) was derived from *cornu Ammonis* (Latin = Horn of Ammon) because of its resemblance to the curved horns of the ram-headed sphinxes at the Roman temple of Jupiter Ammon in the Ammon oasis of Libya, a latinized form of the much older Egyptian temple Amun-Re at Thebes.

'Ammonites' is the popular name for the shells of the extinct Subclass Ammonoidea (Class Cephalopoda), which lived from Devonian to Cretaceous times. They are the most important fossils for Mesozoic biostratigraphy and biogeography. The animal that secreted the protective, external shell presumably had ten arms, two of which may have been modified into tentacles, but there is no direct evidence for the structure of the soft parts. The body chamber ('living chamber') housed the soft parts, whereas the chambered, essentially empty phragmocone provided the uplift of the neutrally buoyant organism. Some ammonites resemble the shell of the extant *Nautilus*, but all differ from the Subclass Nautiloidea by their internal structure, i.e., folded septa and a marginal, thin siphuncle. *Nautilus* shell is structurally very similar to ammonite shell.

This article treats, in sequence, ammonite shape and architecture, phylogeny, growth and sexual dimorphism, buoyancy and poise, functional morphology, and ecology.

Shape and Architecture

Shell size is usually from 5 to 30 cm, but ranges from 1 to 150 cm. The most common shape is ammonitocone, a closed planar spiral with involute to evolute coiling and varying whorl section (**Figures 1A–C**). Later ammonoids included a great variety of heteromorphs (= other shapes), including orthocones (straight), ancylocone (hooked), gyrocones and cyrtocones (open-curved), and helicones (snail-like). All may be smooth or ornamented with ribs (costae/plicae), tubercles, or spines, often changing with growth. Prominence of ornament tended to be higher in inflated than in compressed forms and increased during ammonoid evolution. Ribs may be single, branching, intercalating, or fasciculating (bundled). Nodes are rounded and spines prominent. Constrictions are periodic, deep folds.

The shell consists of high-strength nacre (mother-of-pearl), a bicomponent material of aragonite platelets separated by organic sheets. Fully grown, adult shells are recognized by the shape of body chamber and peristome. The former is often modified by partial uncoiling and inflation, both lowering the centre of mass; the peristome usually thickens with age, and may carry lateral lappets or a ventral rostrum. Other ammonoids grew until death.

Internally, the shell is divided into the phragmocone providing buoyancy and the body chamber protecting the animal. The phragmocone has transverse
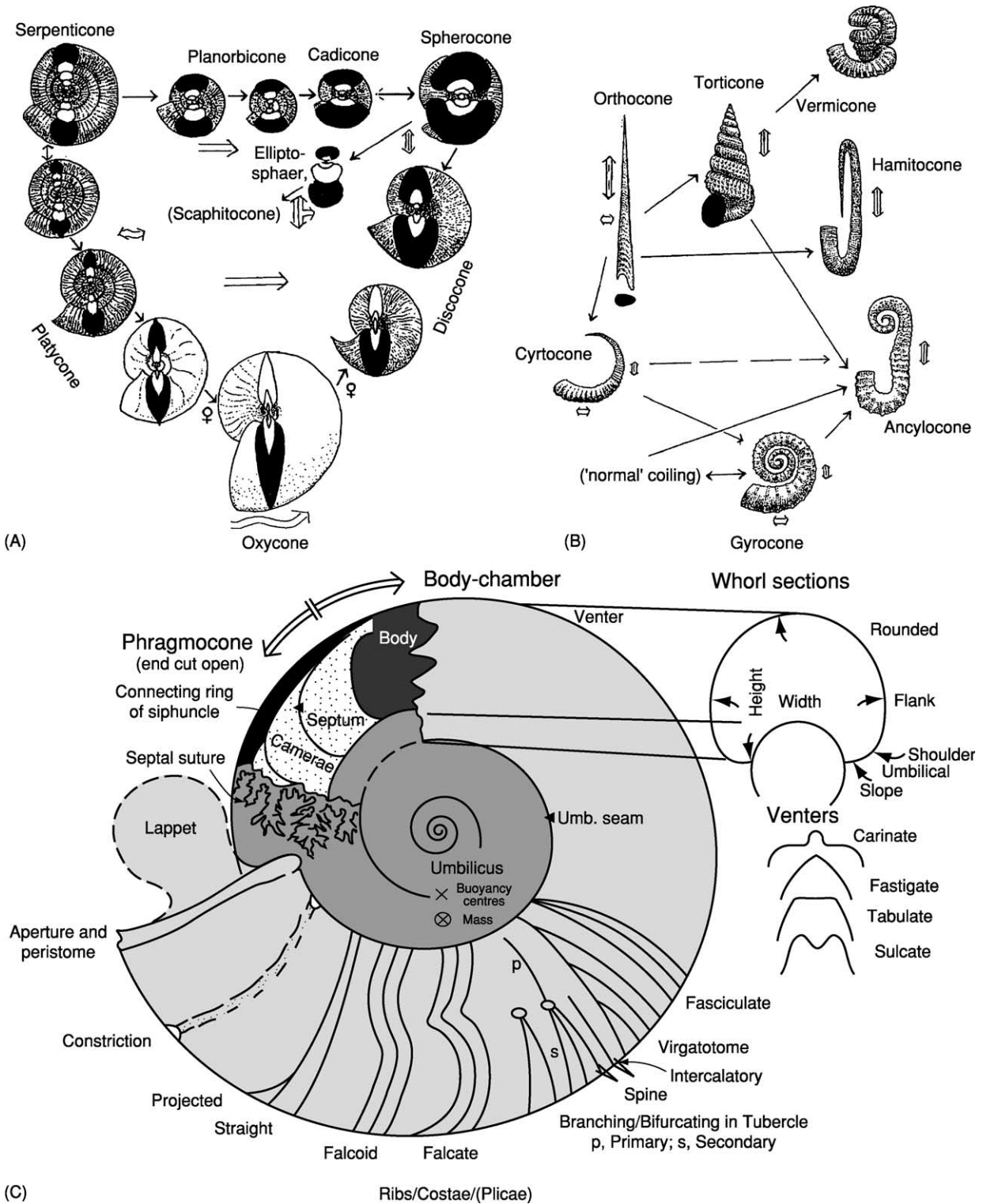
Figure 1 Ammonite morphology. (A) Planispiral shell shapes, illustrating the morphologic continuum (adapted from Westermann (1996)). (B) Major types of heteromorphs (adapted from Westermann (1996)). (C) Terminology of the ammonite shell; cut open at upper left to show interior of phragmocone.
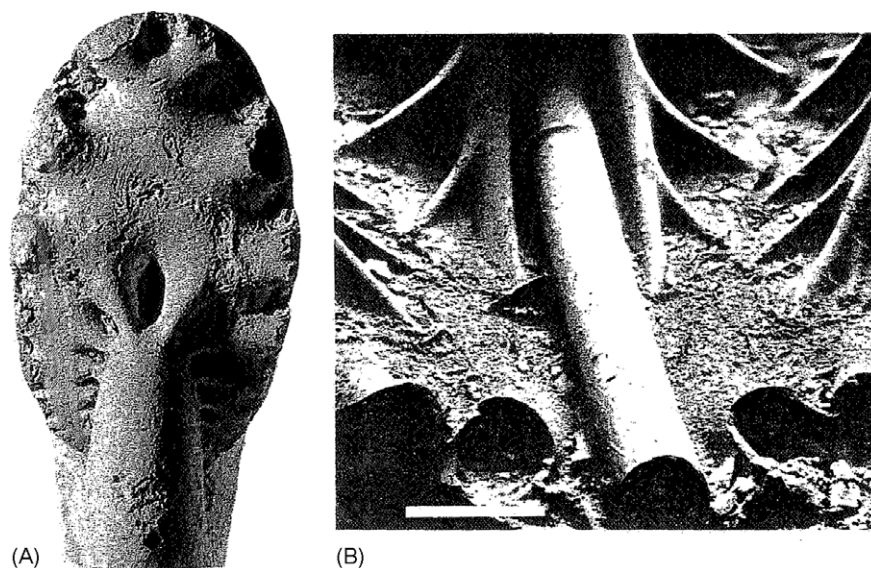
Figure 2 Ammonite septum and siphuncle. (A) Anterior view of the last septum of a Jurassic phylloceratid at natural size; from the central, flat region the flutes increase in prominence towards the margin but decrease on the narrow whorl overlaps; the positive flutes are the saddles, the negative ones the lobes. (B) Frontal view into an empty chamber of another Jurassic phylloceratid, scale bar 1 mm; shown are the siphuncle and 3rd and 4th-order 'frills' of two septa that attach to the wall, forming the medium part of the external lobe. (Adapted from Westermann and Tjujita (1999).)

septa that separate the camerae. As in all living cephalopods, these contained gas at less than atmospheric pressure, together with small amounts of water (cameral liquid). The ventro-marginal siphuncle (but dorso-marginal in Clymeniida), with phosphatised organic connecting rings, connected all camerae to the body and once contained the siphon.

Ammonoid septa are folded into a series of anticlastic, concavo-convex arches or 'flutes' (**Figure 2**), which abut the wall in the sutures ('suture lines') consisting of a series of adorally concave lobes separated by convex saddles (**Figure 3**). Sutures with undivided lobes and saddles are called goniatitic and usually are of either Z type (for 'zigzag') or M type (for 'meander'). Both reduced the free (unsupported) wall space, the Z type by large, subtriangular lobes and saddles that telescope with neighbouring sutures; the M type by more numerous lobes and saddles with parallel sides, without overlap. Ammonitic sutures developed when the original (primary) flutes formed secondary flutes, called lobules and folioles, during evolution or ontogeny; further (3rd- and 4th-order) subdivision of lobules and folioles are typical of later ammonoids. This resulted in 'complex' sutures with fine 'frills'. Significantly, size and spacing of the sutural elements are highly organised, providing improved wall support compared with goniatitic sutures. Sutures have been used in classification for two centuries, and their function is much debated (see below).

The only commonly preserved structures not attached to the shell are the aptychi (**Figure 4**), which are strongly calcified lower jaws. Aptychi are found mainly in Late Mesozoic ammonites and consist of paired plates hinged together by the organic 'horny' layer forming the ancestral jaw. They more or less fitted the whorl cross-section near the aperture and acted as opercula or protective lids. During active periods they could be folded and withdrawn for possible duplicate use as lower jaws.

Phylogeny

The evolution of the Subclass Ammonoidea (**Figure 5**) began with slender orthocones and cyrtocones, the long-ranging (Silurian-Triassic) Bactritoidea, which evolved into Palaeozoic nautiloids and lived as plankton with a vertical poise. From them evolved the Devonian Anarcestida, which retained orthoconic innermost whorls before coiling and had sinuous to goniatitic-Z sutures. The Goniatitida were mostly smooth spherocones and discocones with goniatitic-Z sutures that became goniatitic-M and ammonitic near their Permian extinction. The short-lived, Late Devonian Clymeniida, with goniatitic-Z sutures and diverse shapes including subtriangular coiling, were unique in their dorso-marginal siphuncle. The Prolecanitida were commonly smooth, platyconic, and discoconic brevidomes, suggesting nektic habitats, with goniatitic-M or ceratitic sutures. They were ancestral
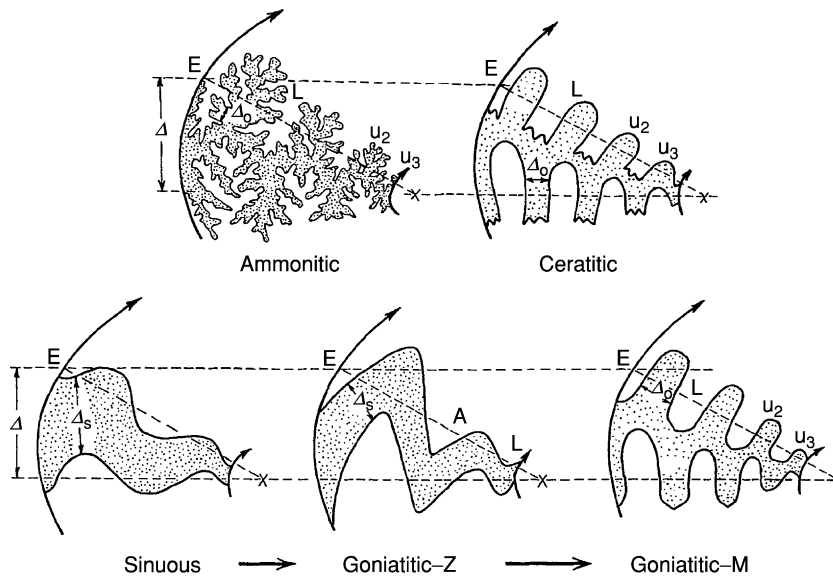
Figure 3 Schematic illustration of the major sutural types according to their function as wall supports, i.e., minimizing unsupported shell wall (between sutures $= \Delta_s$; between parts of same suture $= \Delta_o$), with septal spacing ($\Delta (\Delta)$) constant. Arrows indicate evolutionary trends. The lobes from venter to umbilical seam are: E, external; L, lateral; U, umbilical; A, adventive. Saddles are named after the lobes forming them, e.g., E/L saddle. (Adapted from Westermann (1975).)
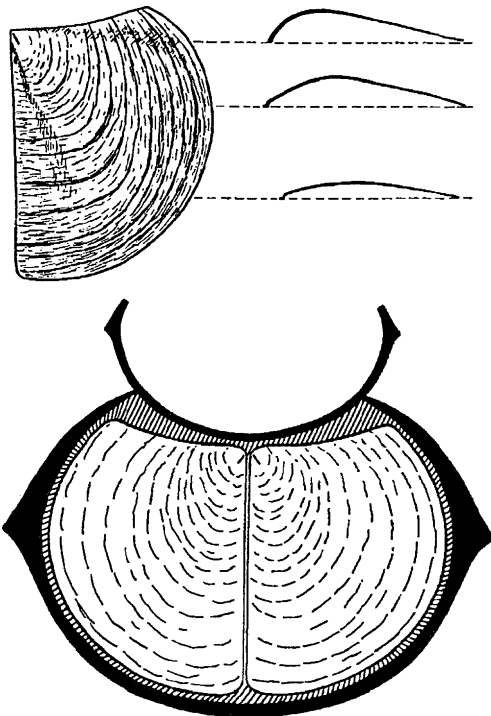

Figure 4 Jurassic aptychus (*Praestriaptychus*) and its reconstruction as a hinged pair in the aperture of the associated ammonite (*Stephanoceras*, Ammonitida); note excellent fit. Space at dorsal overlap presumably enabled water intake (3X).

to all Mesozoic ammonoids, beginning with the mainly Triassic Ceratitida, which had ceratitic to ammonitic sutures, closely followed by the long-ranging Phylloceratida, with broadly rounded saddles or folioles. In the earliest Jurassic, the Prolecanitida gave rise to the Lytoceratida and Ammonitida; the former distinguished by bipartite (not tripartite) saddles and lobes; the latter being the most common, coiled and often ornamented ammonites with complex sutures. Near the end of the Jurassic arose the last ammonoid order, the Ancyloceratida, probably also from the Lytoceratida. They included a host of heteromorphs and, remarkably, began with uncoiled forms. All four orders became extinct at the great end-Cretaceous mass-extinction.

Growth, Longevity, and Sexual Dimorphism

Growth of the shell began with the ammonitella in the minute egg (1–2 mm). After hatching, the shell grew by terminal secretion at the persistome, so that all growth stages are preserved in the fully grown shell. During periodic growth, the posterior mantle secreted cameral liquid in front of the last septum, followed firstly by a membrane and secondly by the nacreous septum. On completion, the (incompressible) liquid, possibly a gel as in the cuttlefish *Sepia*, was withdrawn through the siphuncle into the body. Salinity differences in the epithelium of the vascular siphon generated sufficient osmotic pressure to transport the fluid through the porous connecting rings into the body cavity, against the hydrostatic pressure of the ambient seawater. The new camera was at first
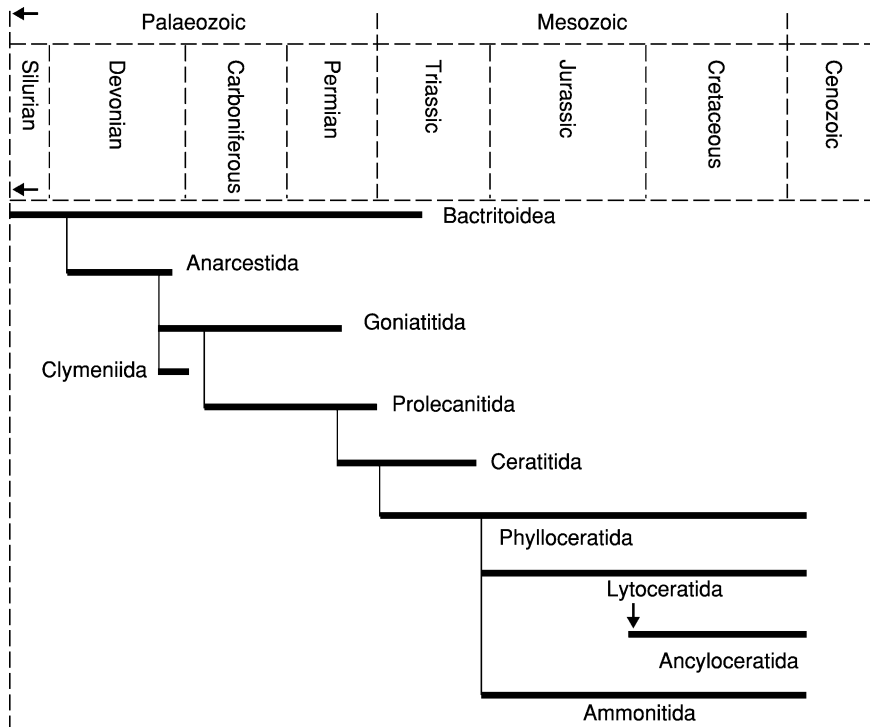
Figure 5 Phylogeny of the Ammonoidea orders.

under vacuum which was later partially replaced by gas at up to 1 atmosphere. Thus, the entire ambient pressure acted (directly) on the outer phragmocone wall and (indirectly through the soft body) on the latest/adoral septum risking its implosion, as well as on the organic connecting rings risking their explosion.

Growth of the pre-adult shell was mainly exponential (secretion time of each whorl increasing with the expansion rate W), followed by a slowing down, as indicated by the more closely spaced (approximated) last several septa. The total duration of growth depended on: (i) size; (ii) shell thickness, especially of the septa; (iii) diameter and wall thickness of the connecting rings: liquid transport depends on surface area and permeability; (iv) habitat depth: ambient pressure slowed cameral emptying; and (v) temperature: shell secretion is more rapid in warm than in cold water. The oceanic *Nautilus*, living at 200–400 m depth, is useful for comparison: at 20–25 cm adult diameter, the thickness of wall and septa are about 1 mm, and the connecting rings are narrow and thick-walled (i.e., strong); growth takes 10–15 years; adult/gerontic life is several more years. Most ammonoids were smaller or similar in size, had thinner septa and shell, broader and thinner-walled (i.e., weaker) connecting rings, and lived in mostly warm epeiric seas or as oceanic epiplankton at 30–150 m; growth took from 2 to 7 years. At the

other extreme, some oceanic ammonoids of similar size lived at 250–500 m depth (e.g., mesopelagic lytoceratids, phylloceratids, desmoceratids), resembled *Nautilus* in shell and siphuncle properties, and presumably grew at similar slow rates. Some ammonoids, however, were much larger and became proportionally older, perhaps 50 years or more. Several more years of adult/gerontic life are indicated for ammonites with strongly modified peristomes. But in some ammonoids, especially among oceanic forms, growth was indeterminate up to death and their size became gigantic ('megaconchs').

For a century and a half, consistently associated pairs of distinctly modified shells have been observed in many Jurassic and Cretaceous Ammonitida and interpreted as sexual dismorphism. In extreme cases, the two forms, called antidimorphs, differed so strongly that they have been placed in different families. The most obvious distinction is in adult size, with the larger shell or macroconch usually two to three times larger than the smaller shell or microconch (Figure 6). Because in living animals with size ratios between the sexes of at least 2, the larger one is always the female; the macroconch is considered the female shell and the microconch the male shell. Furthermore, egg capsules have been found in macroconchs only. In the classic sexual dimorphism of Ammonitida, the peristomes differ in that only the
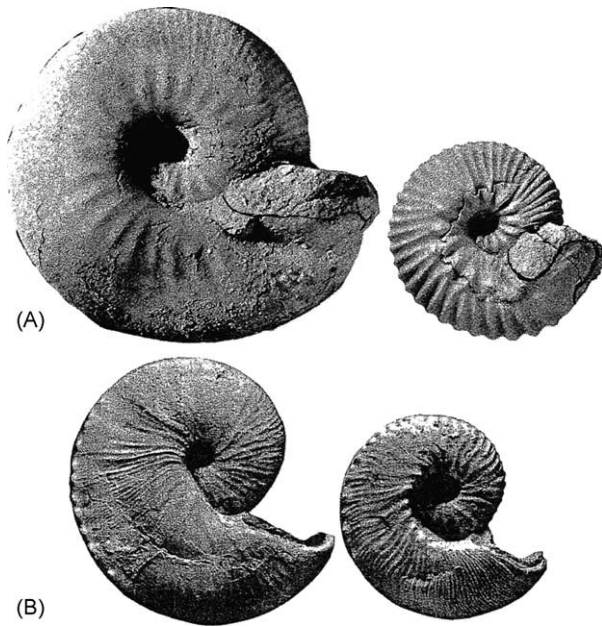
Figure 6 Sexual dimorphism. (A) Difference in size, body-chamber and aperture in Jurassic Ammonitida (*Emileia giebeli* ♂ and ♀, peristomes traced). (B) Difference in size and body-chamber in Cretaceous Ancyloceratida (*Hoploscaphites nicolletii*). (Adapted from Davis *et al.* (1996).)

microconchs or males have lateral extensions called lappets. In other Mesozoic ammonoids (e.g., Ancyloceratida), dimorphism is developed only in size and major to minor body-chamber modification, whereas dimorphism was rare in Palaeozoic ammonites and less clearly developed. Antidimorphs are recognized as conspecific because the inner whorls are identical and the animals have the same stratigraphic and geographic distributions. However, their numbers are often grossly mismatched; in many cases, the males are 10 (and up to 100) times more frequent, in others the females. The most probable causes for the mismatches are sexual segregation except during mating periods, and differences in postmortem drift (see below). Although the existence of sexual dimorphism is now universally acknowledged, at least for the Ammonitida, disagreement remains in classification; some ammonitologists still place all antidimorphs in different genera, even naming new ones; most place them in the same genus when specific pairing is impossible, and in the same species when pairing is highly probable. In the latter case, the sex symbols or 'macroconch (M)' and 'microconch (m)' are appended. The choice of classification is obviously of great consequence to phylogenetic reconstruction, biogeography, etc.

Disputed Functions of Ammonitic Septa and Complex Sutures

The main function of complex ammonitic sutures remains the most controversial topic among ammonitologist. The oldest ('orthodox') and still prevalent hypothesis resembles that of the Oxford professor William Buckland, who in 1827 concluded that this structure strengthened the shell (phragmocone) against implosion by ambient water pressure. *Nautilus*, which lives deeper than most ammonites did, has only simple, sub-hemispherical septa, but these are placed within well rounded, ovoid whorls with thick walls. Many typical ammonites, on the other hand, had flattened thin-shelled flanks with little (membrane) strength of their own, for example, platycones, oxycones, and compressed discocones. Their sutures were a functional improvement over goniatitic sutures by providing more closely spaced and somewhat elastic support for the weak, flat parts of the phragmocone wall (Figure 3), as well as some protection against predators. This prevented the shell from bending and fracturing (under tension) over stiff, distant sutures and from fracturing from tooth bites. Whorl section (e.g., laterally compressed for 'streamlining') was, therefore, the dominating factor, rather than habitat depth. Among related taxa with similar whorl shape, however, epeiric species often had simpler sutures (and weaker septa) than their oceanic relatives. Computer modelling and analysis (Finite-Elements) have shown that, with increasing complexity, the septa became stronger against the hydrostatic pressure transmitted through the body (as earlier theory had predicted). Recent claims to the contrary were based on faulty modelling.

Other hypotheses attempting to explain sutural complexity, include: (i) improved muscle attachment in the lobules and 'frills' for (a) better attachment of the mantle and/or muscle fibres, or (b) for a pre-septal gas bladder that could change overall buoyancy by expansion and contraction; (ii) improved liquid transport out of and/or into the chambers; and (iii) the retention of cameral liquid in the microcavities created by the lobules, folioles, and 'frills'. Hypotheses (i) and (ii) are not feasible because: (ia) The principal muscles were attached elsewhere; (ib) a preseptal gas bladder was inoperable because of basic gas laws and limitation of muscular forces; (ii) improved liquid transport would be ill served by marginal fluting because of difficult transport to the siphuncle, creating a 'bottleneck'; (iii) liquid storage was probably a *secondary* function of marginal fluting, keeping ballast water safe from swishing around.

Hydrostatics and Hydrodynamics: Reconstructing the Living Organism

Buoyancy, poise, stability, and bathymetry can be calculated for the shell and approximated for the living ammonoid, although the soft parts remain essentially unknown. The arms, which were presumably 10 in number, could not have been very muscular as in extinct coleoids (squid, belemnites, sepiids) which are well known from bituminous shales, and they must have been small to fit into the bodychamber (e.g., behind the aptychi). The head, arms, and hyponomes of ammonoids can therefore only be conjectured. They are here shown adapted to diverse feeding strategies (Figure 7).

The neutral buoyancy necessary for a free-floating organism, and which is present in all living cephalopods, requires strict correlations between shell thickness and the volumes of phragmocone and body chamber. The shell may be envisaged as a coiled cone: assuming similar shell thickness, the relative volumes and, hence, the relative lengths of phragmocone and body chamber must remain constant, whether the cone is slender or thick. When coiled into a logarithmic spiral, the slender cone (longicone) is a multiwhorled 'serpenticone' with long, thin body chamber (longidome; low expansion rate W *ca*. 1.5); the thick cone (brevicone) expands more rapidly (W *ca*. 2.5), and phragmocone and body-chamber become shorter (brevidome). In the longidomes, the body chamber was 1 to 2 whorls long; about 3/4 whorls in the abundant mesodomes (W *ca*. 2, i.e., shell diameter doubles with each whorl); and only about 1/2 of a whorl in the brevidomes, which resemble *Nautilus* (W 3–3.5).

Poise, i.e., the orientation of the aperture, and stability were obviously of great importance to the animal. Both were controlled by the positions of the centres of buoyancy and mass. The centre of buoyancy is the three-dimensional centre of the seawater displaced by the entire organism; the centre of mass is that of *all masses* within the same volume, with the principal variable being body-chamber length (measured in whorls). The buoyancy centre lies above the mass centre, and the distance between them determines the degree of stability, i.e., against the torque produced by the hyponome that threatens to rotate the organism. Stability limits the force of jet propulsion, depending on jet direction (vector force) relative to the centre of rotation (Figure 7). The densities of the phragmocone (*ca*. 0.2 kg/l) and body chamber with body (*ca*. 1.2 kg/l) differed greatly, so that brevidomes, with their body chamber mainly below the phragmocone, were more stable than mesodomes,

and longidomes, with the body chamber completely surrounding the phragmocones, were highly unstable. Stability sufficient for jet propulsion existed only in brevidomes and mesodomes. But torque could be prevented only in mesodomes, when the jet force would pass through the centre of rotation – but the animal was limited to swimming backward, as well as up- and downward. Forward swimming explains the apparently wasteful 'rocking' of *Nautilus*. Its extremely brevidomic shell places the hyponome so low that it can curve backward below the shell, although this creates a torque; *Nautilus* is able to swim forward as well as backward and upward simply by curving the hyponome. 'Rocking' results from jet pulsation: the power phase rotates the animal backward and the inherently high static stability makes its return to rest position.

Backward swimming, however, required good steerage for maneouvrability; spherocones could, at most, have used long, trailing tentacles as rudders, whereas in oxycones and keeled platycones the shell allowed good steerage.

Hydrodynamic potential varied greatly among ammonoids. Involute, compressed shells (oxycones, platycones, discocones), more or less smooth, are obviously 'streamlined', i.e., they produce relatively little drag and friction during locomotion; brevidomes, sometimes with their body chambers slightly uncoiled and inflated to lower the centre of mass, were among the best swimmers among ammonoids. Surface roughness provided by fine riblets (the golf-ball effect) may have further reduced drag in some cases. Like *Nautilus*, brevidomes could swim forward and backward. Velocity increased with size, but swimming was sluggish in all externally shelled (ecto-cochliate) cephalopods because the body-chamber limited contraction of the mantle cavity for pumping. Only some oxyconic brevidomes among the Ammonitida (e.g., *Aconeceras*, *Quenstedtoceras*) show large muscle scars that indicate the presence of effective head retractors as in *Nautilus*. These were either nektic hunters or demersal ('bentho-pelagic'), feeding from the seafloor. At the other extreme were the serpenticones and longidomic sphaerocones, ribbed or smooth, which were unable to swim because the slightest jet force would have rotated the unstable, high-drag shells. They belonged to the mega-plankton and, according to their shell strength, were either limited to drifting near the surface or able to dive into deep water, presumably diurnally. The many intermediate forms, i.e., the abundant planorbicones and cadicones, usually mesodomic and with prominent ornamention, also tended to increase stability at maturity. They were probably very sluggish
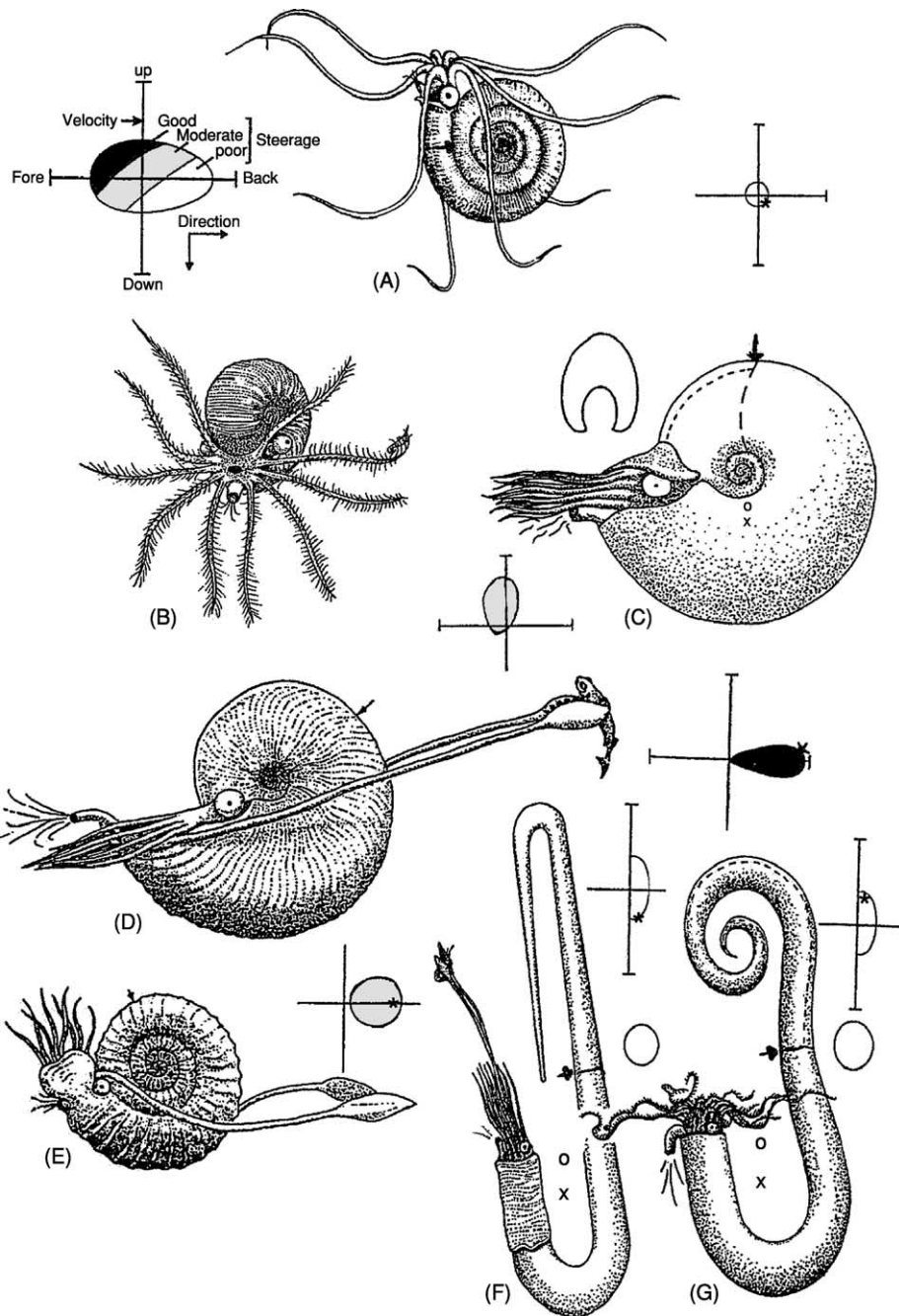
Figure 7 Reconstructions of poise and swimming potential according to shell form, body-chamber length, and stability based on estimated centres of mass (x) and buoyancy (o); head, arms, and hyponome conjectured for various feeding strategies. (A) serpenticone; (B) longidomic spherocone; (C) mesodomic discocone; (D) brevidomic oxycone; (E) mesodomic platycone, microconch; (F) hamitocone, with mantle overlap; (G) ancylocone. Small arrows indicate end of body-chamber. (Adapted from Westermann (1996) and Westermann and Tsujita (1999).)

backward swimmers and/or vertical migrants, mostly in shallow water, where their coarse ribs and/or spines would have provided some protection from predators and, perhaps, camouflage. Ellipto-spherocones possessed an unstable immature stage followed by a stable adult stage. Extension of this trend led to the heteromorph scaphitocones. The result was greatly improved stability, with the aperture turned upward, i.e., an adaptation for vertical migration (Figure 7). Whereas the open coils of gyrocones lie in one plane,

the wider coils of cyrtocones are irregularly helicoidal. The former grew large and may have been demersal; the latter were small and perhaps lived as pseudoplankton coiled around floating seaweed (e.g., *Sargasso* Community). Hamitocones, with a series of parallel segments, must have rotated during growth. The adults had stable near-vertical poise with upward directed apertures, implying diving habits as megaplankton. Orthocones also had stable near-vertical poise, but with the aperture downward, implying that they were sluggish benthos feeders with rapid escape potential. The torticones were also (diurnal) vertical migrants, whereas the rare vermicones, with a complex growth programme, were planktic. Buoyancy calculations have shown that all heteromorphs were neutrally buoyant.

Habitat depth limits can be calculated from the strength of septa, phragmocone wall, and connecting rings, because cameral gas pressure was maximally that of the atmosphere. Physical properties of ammonoid shell (test) are calibrated on *Nautilus*. Ammonoid connecting rings resemble the chitinous inner tubes of *Nautilus*, but ammonoid septa differ greatly in their architecture, being folded and not basically hemispheres. Stresses in ammonite septa are therefore calculated using curvature and thickness of lobes or lobules. Wall strength between sutures has also been calculated (Figure 8). The resulting depth limits range from 50 to over 1000 m. Actual habitat depth was at about one-third to two-thirds of the limit.

Ecology: Food, Predators, and Habitat

Feeding habits are known only for a few ammonoids, but were presumably as diverse as their shells. The general presence of weak jaws and radulae and the apparent absence of muscular arms suggest a number of possibilities, such as: (i) filter-feeding in mid-water on passing microplankton and detritus; (ii) predation on macroplankton and/or sluggish nekton, including smaller or young ammonoids, by pursuit or ambush; and (iii) preying on benthos while hovering. The radula aided in swallowing soft organisms whole. The known rare records of crop or stomach contents are of pelagic ostracods, microcrinoids, larger crustacean appendices, and juvenile aptychi indicating cannibalism.

Many ammonite shells suffered broken body chambers and some of these injuries were healed by the mantle before embedding. The predators are usually not identified, but large crustaceans, fish, and marine reptiles are strongly suspect. The best evidence comes from large, shallow-water oxycones (*Placenticeras*) that lived in the murky surface waters of the Cretaceous Western Interior Seaway of North America.

These shells are perforated by numerous round holes that sometimes have the exact spacing and jaw angle of mosasaurs, large marine reptiles with conical teeth that are known from the same formation. Some authors believe that the holes are the diagenetically collapsed home scars (resting places) of limpets grazing on the empty shell, but this is improbable because of the shape and orientation of the holes.

The minute eggs and early juvenile (neanic) growth stages are rare in bituminous shales, which were deposited in lethal, oxygen-starved environments. This suggests that eggs (in gel?) and hatchlings floated in mid-water, where they were protected from active predators by the slight oxygen deficiency; they died and sank to the floor when dysoxic bottom waters rose periodically (Figure 9A). As in living cephalopods, some ammonoids may have spawned on oxygenated seafloors, but their minute aragonitic shells would have dissolved. Juvenile and immature ammonites are much scarcer than expected and the adults tend to range through a variety of lithofacies of epeiric seas upto 150–300 m deep. Most ammonoids did not depend on the seafloor and were pelagic: only a few species were demersal bottom feeders. A single case of brackish habitat has been documented by stable isotopes for the Late Cretaceous *Placenticeras*. Deep-water, oceanic sediments did not preserve ammonites, although epipelagic and some mesopelagic ammonoids lived in most oceans (Figure 9B). Most Jurassic-Cretaceous Phylloceratida and Lytoceratida have long been recognized as mostly deep-water ocean dwellers; planktic Ammonitida drifted and heteromorphic Ancyloceratida dived in the upper waters, and were dispersed far and wide by surface and subsurface currents.

Life Versus Death Assemblages: Migration and Post-Mortem Drift

There are two main reasons for numerical mismatches between sexual partners and for the common scarcity or even absence of immature shells from most fossiliferous deposits; spawning migrations and post-mortem transport. Most living cephalopods feed in open, deeper waters, but breed and die in shallow, warm waters. This often involves segregation of the sexes before and/or after mating, causing frequent mismatches (see Dimorphism above). The second reason for uneven sex ratios, as well as for the scarcity of immature shells, is selective surface drift of the empty shells. A strong natural bias for large shells of deep-water ammonoids over small, shallow-water species was caused by size and ambient pressure. Reflooding of the phragmocone causing sinking was much slower in large shells than in small ones,
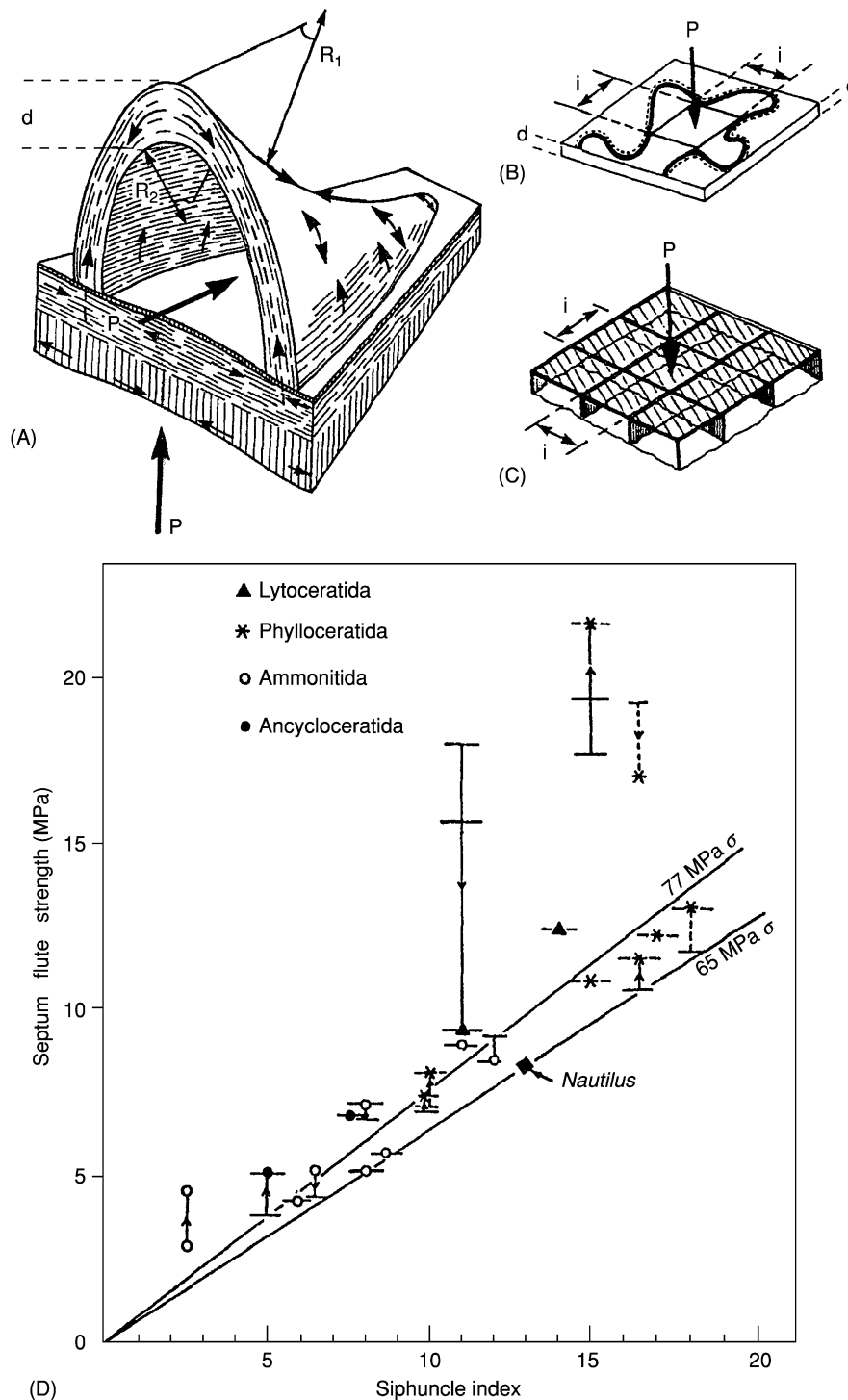
Figure 8 The shell parameters used for bathymetry, based on the ammonitic septum, phragmocone wall, and siphuncle. (A) Lobule of last septum with anticlastic curvature used to calculate Septum Flute Strength; R_1 and R_2, orthogonal radii; P, hydrostatic pressure; d, septum thickness; arrows, compressive and tensile stresses. (B) Wall with lobule to calculate wall strength, the implosion depth based on the unsupported wall distance; i, length of largest unsupported square; d, wall thickness. (C) Connecting ring of siphuncle, cross-section (Siphuncle Strength Index $= 100 \times d_s/r_i$). (D) Habitat limits based on septum and siphuncle of adult ammonoids and *Nautilus* (ontogenies indicated): correlation is good except for some compressed, deep-water Phylloceratida, which have thicker septa that functioned significantly as lateral braces; depth limit calibrated on *Nautilus*. (Adapted from Hewitt (1996).)
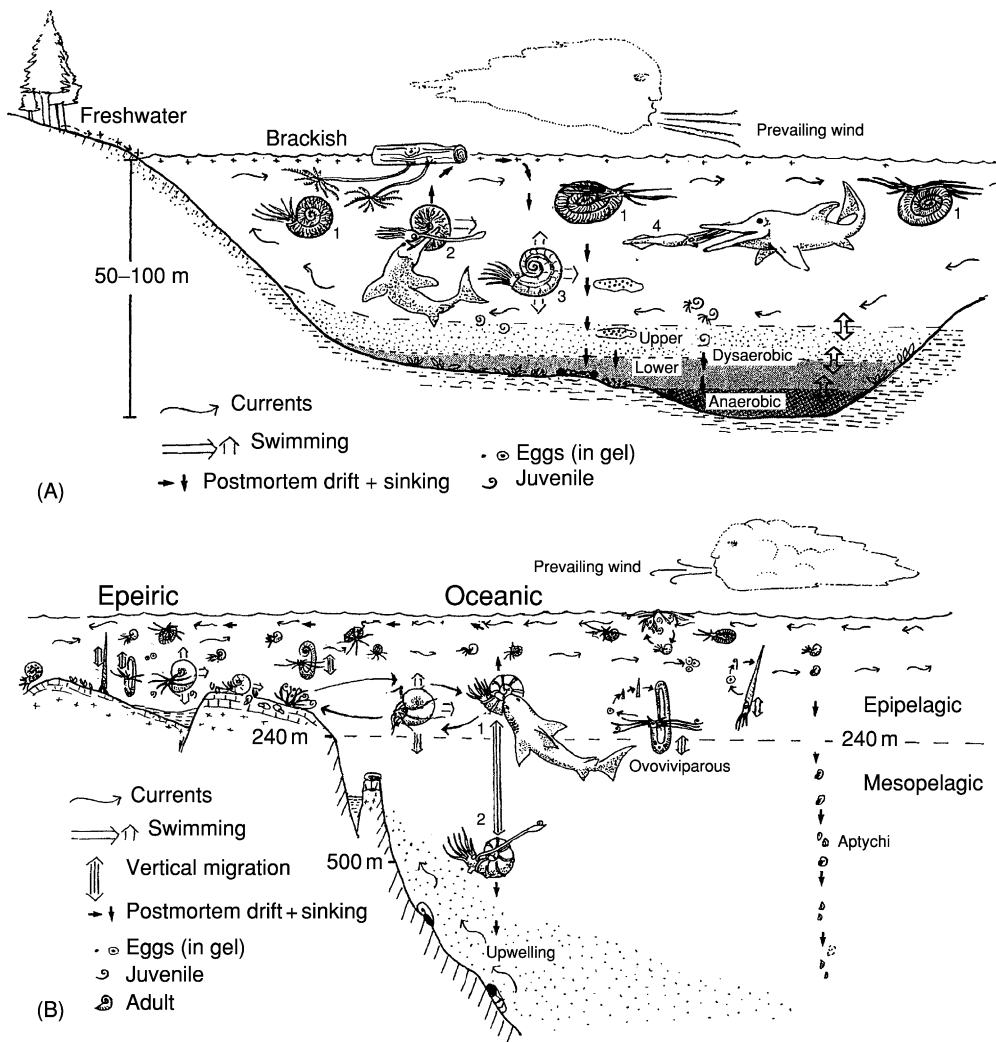
Figure 9 Possible scenarios for Jurassic-Cretaceous ammonoid habitats, with life-cycles and post-mortem drift. (A) Epeiric basin, black-shale facies, e.g., Early Jurassic *Posidonia* Shale or Jet Rock; 1, serpenticonic, epiplanktic drifters (*Dactylioceras*); 2 and 3, discoconic predators (*Harpoceras, Hildoceras*), prey of ichthyosaurs; 4, belemnite animal. (B) Ocean, slope, shelf, and epeiric sea; serpenticonic Ammonitida drift and heteromorphic Ancyloceratida dive in both biomes; most Ammonitida are restricted to epeiric seas; typical Phylloceratida (1) were deep-water swimmers and typical Lytoceratida (2) among the deepest vertical migrants; only calcitic aptychi reach the deep-sea floor. (Adapted from Westermann (1996).)

especially those with thick-walled, narrow connecting rings (siphuncle surface grows with the square of diameter, chamber volume with the cube) – just as cameral emptying rates in growing shells. Similarly, the reflooding rate depended on the depth at death: it was rapid only under high ambient pressure, so that the shell sank immediately; during slower refilling in shallower water the shell would rise to the surface (Figure 9) before sinking after weeks or months of drifting. Drifting distance has been much debated, but it was probably rarely more than a few tens of kilometres in epicontinental seas. An exceptional case, however, was observed in the Andes at the edge of the palaeo-Pacific: several gigantic lytoceratids of almost certainly meso-pelagic habitat were found in a nearshore assemblage. The sinking aragonitic shells of dead oceanic ammonoids were dissolved below compensation depth, but their calcitic aptychi have been found in red deepsea clay.

Summary

Most ammonoids were pelagic and a few demersal between 30 and 150 m depth in epeiric seas; others were epi- to mesopelagic in the oceans; and some lived in epeiric seas as well as oceans, for example,

cosmopolitan longidomes. Their principal food was micro- and mesoplankton, including young ammonoids, presumably caught with weak arms or tentacles, and sinking organic detritus netted with an umbrella-like arm crown, as well as benthos. Their predators were fish, reptiles, and larger ammonoids. The most diverse ammonoid assemblages are found in sediments of warm tropical and subtropical seas and typically include mainly adults. Gray and black shales that originated in temperate or basinal waters, on the other hand, tend to have low-diversity faunas that may include ammonitellas and juveniles; single, highly variable species dominate, sometimes ranging from ribbed spherocones to smooth oxycones or platycones. Their contrasting hydrodynamic properties did not apparently function; these ammonoids were mega-plankton without significant locomotion.

Ocean currents, rather than swimming, were the main means of wide dispersal, because planktic species tend to be more cosmopolitan than nektic species. Prime examples are longidomic spherocones (e.g., arcestid Ceratitida) and serpenticones (e.g., dactylioceratid and psiloceratid Ammonitida) as well as many heteromorphs (Ancyloceratida), which lived in the shallow waters of all seas. The mainly oceanic Phylloceratida and Lytoceratida evolved much more slowly, which may account for their wide species distributions. The importance of most ammonites in biostratigraphy (*see* **Biozones**) and biogeography resulted from rapid evolution combined with high potential for planktic dispersal.

See Also

Biozones. **Fossil Invertebrates:** Molluscs Overview; Cephalopods (Other Than Ammonites).

Further Reading

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