Early Ontogeny of Mesozoic Ammonites and Nautilids

(Frühontogenese mesozoischer Ammoniten und Nautiliden)

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With 8 Text Figures and 3 Tables

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Abstract: Ammonites and nautilids display wide differences in their early ontogeny. Ammonites hatch with small embryonic shells approximately 1 mm in diameter, which may have spent some time in the plankton. Nautilids hatch with embryonic shells 10-25 mm in diameter, which are active swimmers. These and other differences suggest that ammonites may represent r-strategists and nautilids K-strategists.

Kurzfassung: Ammoniten und Nautiliden weisen große Unterschiede in ihrer Frühentwicklung auf. Ammoniten verlassen die Eikapseln mit kleinen embryonalen Gehäusen von ungefähr 1 mm Durchmesser und verbringen vermutlich einige Zeit im Plankton. Nautiliden schlüpfen mit embryonalen Gehäusen von 10-25 mm Durchmesser und sind aktive Schwimmer. Diese und weitere Unterschiede legen es nahe anzunehmen, daß Ammoniten "r-strategists" und Nautiliden "K-strategists" sind.

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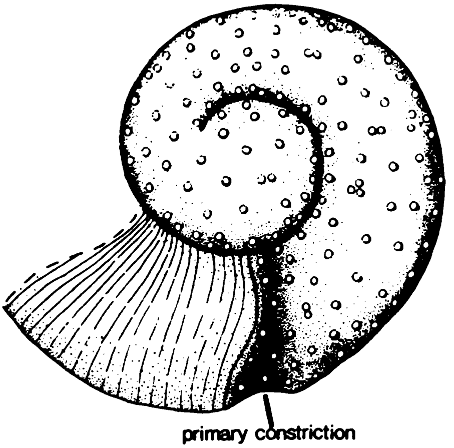
1. Introduction

The two groups of shelled cephalopods in the Mesozoic were the ammonites and the nautilids. The ammonites became extinct at the end of the Mesozoic, but the nautilids have survived into the Recent. Although both groups secrete a chambered external shell, numerous differences in their early ontogeny suggest the evolution of divergent developmental strategies. In this paper the shape and size of their embryonic shells are described and their respective life history patterns are discussed.

2. Observations

2.1 Ammonites

In all Mesozoic ammonites, including heteromorphs, the embryonic shell or "ammonitella" has a well defined morphology. It consists of a relatively large bulbous protoconch or initial chamber followed by approximately one planispiral



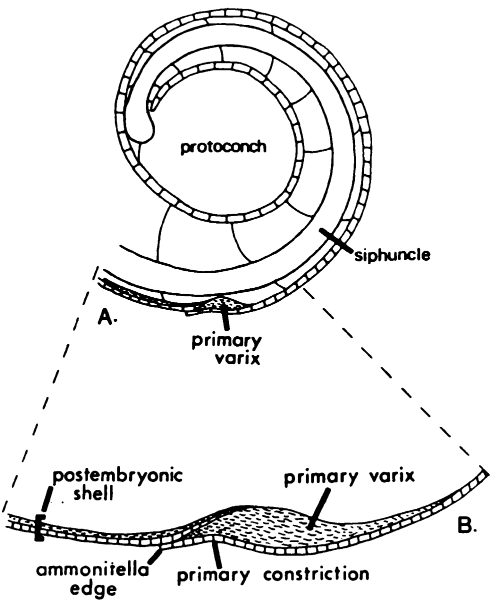
Text Fig. 1. The embryonic shell of ammonites consists of a bulbous protoconch followed by approximately one planispiral whorl. It ends at the primary constriction and displays tuberculate micro-ornamentation.

whorl (Text Fig. 1; Ruzhentsev 1962, Drushchits & Khiami 1970, Drushchits et al. 1977, Kulicki 1979, Bandel 1982, Landman 1982, 1985). The diameter of the embryonic shell ranges from 0.6-1.6 mm and attains its greatest size in the suborder Lytoceratina (Drushchits & Khiami 1970, Tanabe et al. 1979). The ratio of the diameter of the embryonic shell to that of the adult is low, approximately 10^{-2} to 10^{-3}.

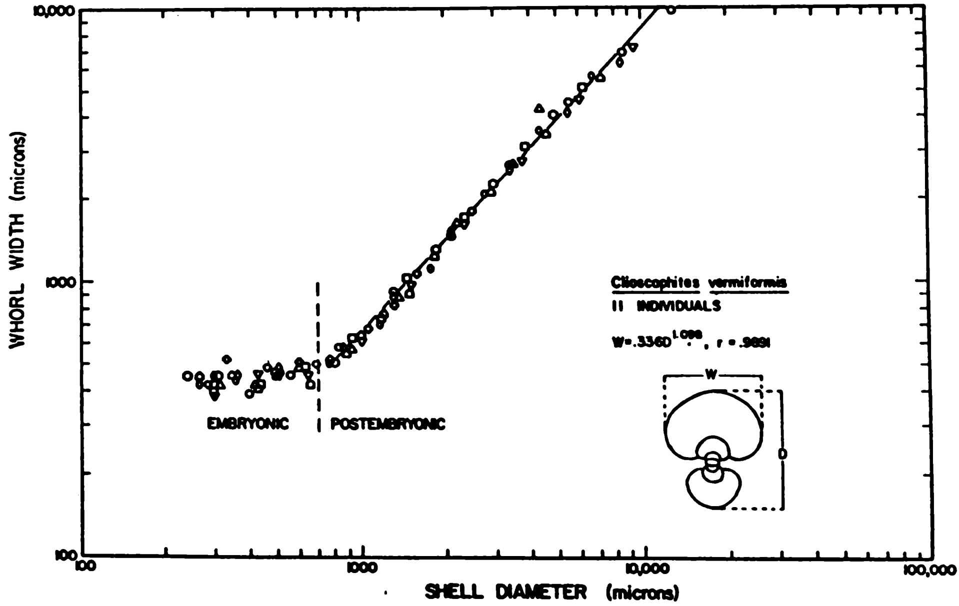
The embryonic shell terminates in a shallow groove known as the primary constriction (Text Fig. 1; Landman & Waage 1982). This feature was first observed in detail by Branco (1879, 1880) and later interpreted by Grandjean (1910) as the embryonic-postembryonic boundary. It is visible in the early whorls of well-preserved ammonites as a continuous groove in the actual shell of the ammonitella around the margin of the aperture. The term does not refer to the impression the constriction makes on the steinkern (see Landman & Waage 1982).

In many ammonites the embryonic-postembryonic boundary corresponds to a change in micro-ornamentation and the first appearance of growth lines (Text Fig. 1; Kulicki 1979, Bandel et al. 1982). In *Kosmoceras, Quenstedtoceras, Baculites, Lytoceras,* and *Scaphites* and related genera, this micro-ornamentation consists of minute tubercles uniformly distributed over the shell surface. The postembryonic shell is non-tuberculate and bears very fine transverse ridges which are probably growth lines. The embryonic shells of other ammonites are reported to be smooth, but an adult-like ornament develops after the constriction (Drushchits et al. 1977).

Coincident with the change in ornamentation is a change in the microstructure of the shell (Text Fig. 2; Drushchits et al. 1977, Kulicki 1979, Bandel et al. 1982). Up to the constriction, the shell is composed only of prismatic layers. However, at this developmental stage, the animal deposits nacre to form a swelling known as the



Text Fig. 2. A) Median cross section of the early whorls of an ammonite showing the siphuncle and septa. The embryonic shell is prismatic and ends in the primary constriction and accompanying varix, which is nacreous. B) Close-up of the varix reveals the ammonitella edge and postembryonic shell.



Text Fig. 3. Whorl width versus shell diameter for 11 specimens of *Clioscaphites vermiformis*.

primary varix (Drushchits & Khiami 1970, Birkelund & Hansen 1974, Kulicki 1979, Landman & Waage 1982). This swelling parallels the external constriction and lies close to its adapical side. The postembryonic shell which emerges from this point is characterized by both prismatic and nacreous layers (Birkelund 1981).

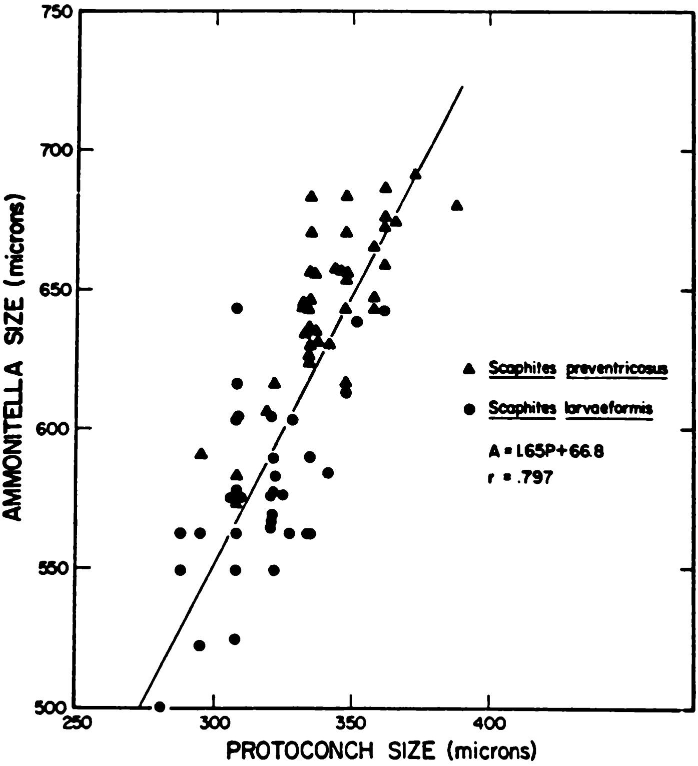
The onset of postembryonic growth also produces a change in whorl shape. For example, Text Fig. 3 is a plot of whorl width versus shell diameter in *Clioscaphites vermiformis* (Meek & Hayden). A break in the slope of the graph from 0.0 to approximately 1.0 occurs at the embryonic-postembryonic boundary. Similar changes have been observed in the genera *Kosmoceras* (Kulicki 1979), *Promicroceras* (Currie 1942), *Otoscaphites* (Tanabe 1975), *Gaudryceras* (Hirano 1975), and *Subprionocyclus* (Obata et al. 1979). This change in whorl shape is even more dramatically shown in heteromorph genera such as *Baculites,* in which the postembryonic shell forms an orthocone (Bandel et al. 1982, fig. 1C), and *Eubostrychoceras,* in which the postembryonic shell becomes loosely uncoiled (Tanabe et al. 1981, pl. 35, fig. 1e).

Internally, how many septa are formed by the end of the embryonic stage? The septa in ammonites consist of the proseptum and all succeeding septa (Text Fig. 2A). The proseptum, which is prismatic, differs in shape and structure from all succeeding septa, which are nacreous (Landman & Bandel 1985). The proseptum is also thicker than the next successive septum (Birkelund & Hansen 1974).

Study of preserved embryonic shells suggests that hatching may occur after formation of as few as one septum, the proseptum, and therefore only one buoyancy chamber, the protoconch. Landman (1982, 1985) described embryonic shells belonging to the genera *Baculites* and *Scaphites* from the Upper Cretaceous of Montana and Colorado that displayed only one septum, the proseptum. In postembryonic shells, the outer shell extended beyond the primary constriction and additional septa of nacreous microstructure developed. A broken embryonic shell of *B. chicoensis* (Trask) was illustrated by Smith (1901) from the Upper Cretaceous of California that also displayed only a proseptum. Similarly, Drushchits & Khiami (1970) reported preserved embryonic shells with only a proseptum from the Lower Cretaceous of Ul'yanovsk.

However, preserved embryonic shells with more than one septum have also been reported, indicating that in some genera additional septa may have developed before the end of the embryonic stage. For example, Bandel (1982) described ammonitellas with five to seven septa belonging to the genus *Baculites* from the Upper Cretaceous of Jordan. Kulicki (1979) reported preserved ammonitellas with more than one septum from the Jurassic of Cuba. Similarly, Wetzel (1959) reported preserved ammonitellas with one to two septa from the Jurassic of Germany. However, Landman (1985) has cautioned that at least some embryonic shells with more than one septum may represent fragments of larger shells that have broken at the embryonic-postembryonic contact. This contact provides a natural point of weakness for postmortem breakage, producing shells that are embryonic in their external appearance but which display postembryonic septa.

The embryonic shell thus comprises at least one septum, the proseptum, and one buoyancy chamber, the protoconch. The ammonitellas from Ul'yanovsk also contain a preserved caecum and prosiphon, indicating that these features were also



Text Fig. 4. Ammonitella diameter versus protoconch diameter for *Scaphites preventricosus* Cobban and *Scaphites larvaeformis* Meek & Hayden.

developed at this stage of growth (Drushchits & Khiami 1970). The protoconch diameter represents a large fraction of that of the embryonic shell, approximately one-third to one-half. The two diameters co-vary and display a positive correlation within and between species. For example, in Text Fig. 4 of two species of *Scaphites*, the correlation between protoconch diameter and ammonitella diameter is 0.80. Similar correlations have been obtained for numerous other ammonites (Tanabe et al. 1979) and suggest a constant relationship between buoyancy chamber volume and the volume of the shell.

The mode of life of the newly hatched ammonite could have been benthic (Wetzel 1959) but was more probably nektic or planktic (Kulicki 1974, 1979, Birkelund & Hansen 1974, Drushchits et al. 1977, Landman 1985). The protoconch, after removal of cameral liquid, would have acted as a float and permitted the newly hatched animal to spend some days or weeks in the plankton. The duration of this stage may have depended on the size of the embryonic shell and the mode of life of the adult. During this time, the animal could have been passive or capable of weak swimming. In fact, this mode of life is common among the young of many modern coleoids including planktic and nektic squids, sepioids, and benthic octopods with relatively small eggs (Boletzky 1974, 1977).

One association of young postembryonic shells that supports this hypothesis occurs in black shales of the Upper Cretaceous Sharon Springs Member of the Pierre Shale at Red Bird, Wyoming (see Gill & Cobban 1966). The shells, baculitids approximately 5 mm in length, are sparsely preserved in small grey limestone concretions without any other fossils. The environment of the Sharon Springs is interpreted as an anaerobic bottom with oxygenated water above, about 300 km from shore (Gill & Cobban 1966, Byers 1979). The young baculitids would have had to have been planktic or at least nektic soon after hatching to have lived in this environment.

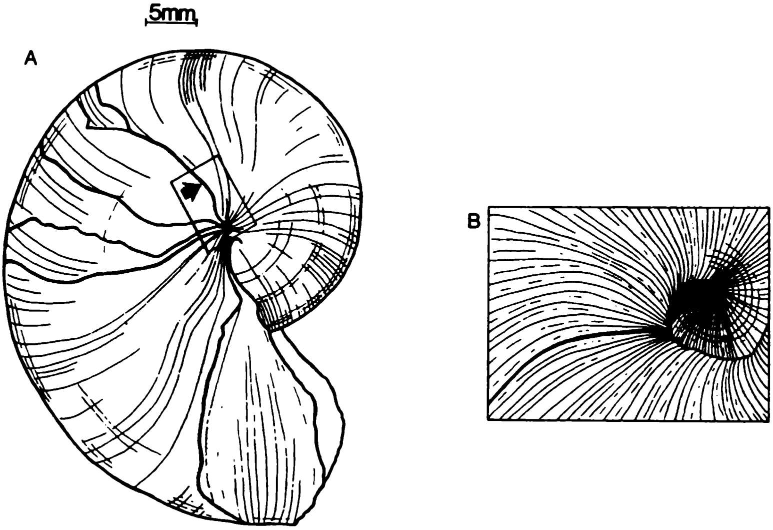
Other associations with preserved embryonic shells include both benthic and nektic species (Wetzel 1959, Landman 1982, 1985) and therefore provide no clearcut evidence about the mode of life of the newly hatched ammonite. The two documented finds of preserved ammonitellas in North America (Landman 1982, 1985) occur in relatively offshore habitats several hundred kilometers from the strandline (see also Kennedy & Cobban 1976). Like other accumulations of preserved embryonic shells (Wetzel 1959, Drushchits & Khiami 1970, Kulicki 1979, Birkelund 1979), they consist of large concentrations of several hundred to several thousand individuals. Such concentrations suggest the high fecundity of ammonites, but may also imply a limited dispersal capability for some time after hatching associated with adjusting to new environmental conditions. Alternatively, they may indicate the vulnerability associated with the critical transition from embryonic to postembryonic growth. These animals could easily be killed by large deposits of sediment or abrupt changes in the temperature and salinity of the water.

2.2 Nautilids

The embryonic shells of nautilids, called nautas, are commonly much larger than those of ammonites. The embryonic shell of modern *Nautilus* species (Text Fig. 5A) measures approximately 25-30 mm in diameter (Willey 1897a, Bandel 1982, Cochran et al. 1983). It hatches from an egg capsule that measures approximately 45 mm in maximum length (Willey 1897b). The size of the embryonic shell varies only slightly among species (Table 1), although very large samples may reveal significant differences. The diameter of the embryonic shell represents about one-tenth that of the adult. In *Eutrephoceras dekayi* (Morton), a widespread Upper Cretaceous nautilid species from North America, the embryonic shell commonly averages 10 mm in diameter (Text Fig. 6A; Table 1). However, in other species of this genus tentatively referred to *E. dekayi,* the embryonic shell may exceed 14 mm in diameter.

In nautilids, hatching is commonly marked on the outer shell by a constriction known as the nepionic constriction (Willey 1897a). This feature is conspicuous on small shells of *Nautilus* and *Eutrephoceras* (Text Fig. 5A, 6A; Willey 1897a, Landman et al. 1983). In both these genera, it occurs at approximately 1.25 whorls from the apex of the shell (Stenzel 1964, Landman et al. 1983). The constriction is best developed on the flanks near the umbilicus and is accentuated by a subsequent expansion in whorl width of the postembryonic shell.

Sometimes, instead of a single distinct constriction, the shell is marked by several radial furrows. Usually, but not always, one of these furrows is more prominent and



Text Fig. 5. A) Specimen of *Nautilus pompilius* showing the nepionic constriction (arrow), which marks the end of the embryonic shell. The constriction continues as a line of repaired shell breakage across the venter. Additional shell breaks occur after the constriction. B) Close-up of the constriction near the umbilicus reveals no sharp change in ornamentation at this point.

Table 1. Size of the embryonic shell for selected species of *Nautilus* and *Eutrephoceras*. N = number of specimens; $\bar{x}$ = mean; s.d. = standard deviation. Specimens are in the collections of the Museum of Comparative Zoology, Harvard University; the Delaware Museum of Natural History; the Yale Peabody Museum; the Department of Geology, University of Iowa; the Department of Geology, Ohio University; the Department of Invertebrates, American Museum of Natural History; the Department of Geology, Bryn Mawr College; and the Black Hills Institute of Geological Research.

Species	Age	Locality	N	Embryonic	size (mm)
				$\bar{x}$	s.d.
N. belauensis	Recent	Palau	2	31.4	.65
N. macromphalus	"	New Caledonia	4	26.1	.78
N. scrobiculatus	"	Papua New Guinea	4	25.8	.78
N. pompilius	"	"	2	24.5	.71
"	"	Fiji	1	27.3	
"	"	Philippines	9	26.5	.75
N. pompilius?	"	Philippines?	45	26.0	1.25
E. dekayi	Late Cretaceous	Western Interior U.S.A.	20	10.0	.61
E. cf. *dekayi*	"	"	2	14.2	.14

represents the actual constriction. Areas of deformed shell may also occur just adapical of the constriction as illustrated in Eichler & Ristedt (1966, figs. 1, 2, 6). Formation of both the radial furrows and deformed shell are attendant on the end of embryonic development and emergence into the postembryonic environment.

Unlike the constriction in ammonites which consists of a broad, shallow depression, the constriction in nautilids is, in close-up, a narrow, angular indentation (Text Fig. 5B, 6B). The deepest point in the constriction marks the position of the aperture at hatching. The constriction may continue as a line of repaired shell breakage across the venter (Text Fig. 5A). Sometimes the constriction is present on one side of the shell, but is replaced on the other by a repaired shell break. Evidently, the aperture on that side broke soon after hatching and the injury extended adapical of the original position of the constriction. The shell break, therefore, only marks the approximate point of hatching.

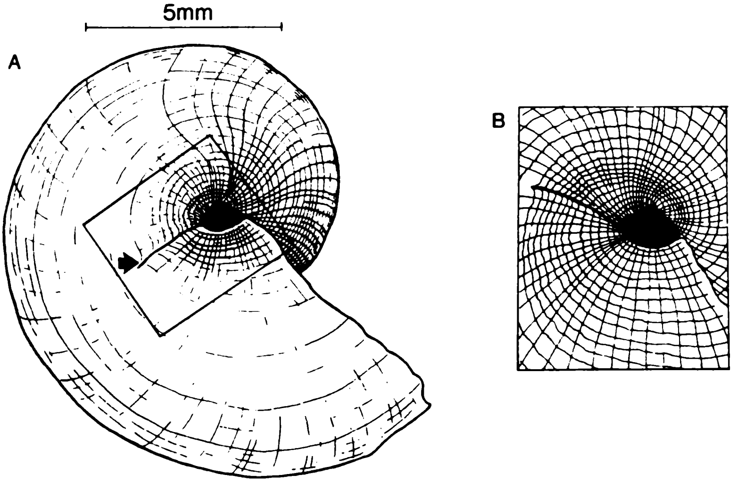
The constriction in *Nautilus* and *Eutrephoceras* does not demarcate a sharp change in ornamentation as it does in ammonites (Text Fig. 5B, 6B). For example, in *Nautilus pompilius* (Linné), the reticulate ornamentation developed on the early part of the embryonic shell, illustrated in Hyatt (1894) and Stenzel (1964), has already disappeared by the time the constriction forms. However, the growth increments after the constriction are more irregular than those before and impart an overall rough texture to the surface of the shell. Repaired shell breaks also commonly appear at or after the constriction (Stenzel 1964).

Similarly in *Eutrephoceras dekayi,* no marked change in ornamentation takes place at the constriction (Text Fig. 6B). Here, the shell right up to the constriction displays reticulate ornamentation, which is present on the shells of *Nautilus* species at a similar size but well before the constriction. After the constriction, the reticulate ornamentation in *E. dekayi* becomes, at most, slightly weaker or more diluted, especially toward the venter. Repaired shell breaks also become common at or after the constriction.

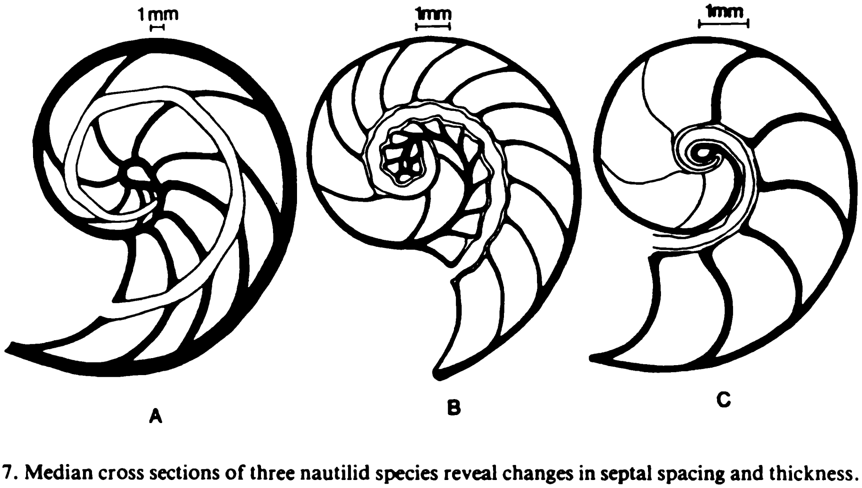
Internally, hatching is marked in nautilids by changes in the spacing and thickness of the septa and in their oxygen isotopic composition. In *Nautilus pompilius,* for example, septa 7 and 8 are commonly more closely spaced or "approximated" (Text Fig. 7A). This approximation coincides with the formation of the nepionic constriction on the outer shell one-third whorl forward (Naef 1923, Davis & Mohorter 1973). The first postembryonic septum is slightly thicker than the preceding septum but displays the same microstructure (Westermann 1973, Blind 1976).

The ratio of oxygen isotopes changes dramatically between these two septa (Text Fig. 8A; Eichler & Ristedt 1966, Cochran et al. 1981, Taylor & Ward 1983). Analyses of 11 specimens of *Nautilus pompilius* and *Nautilus macromphalus* Sowerby reveal a shift in $\delta^{18}O$ from light values characteristic of the first seven septa to heavier values for septum 8 forward. The light values are due to fractionation within the egg capsule (Cochran et al. 1981, Taylor & Ward 1983). The shift toward heavier values reflects the hatching event and first open contact with sea water.

In *Eutrephoceras dekayi,* the septal approximation occurs between septa 4 and 5 and probably corresponds in time of formation with the nepionic constriction on the outer shell one-third whorl forward (Text Fig. 7B; Landman et al. 1983). The

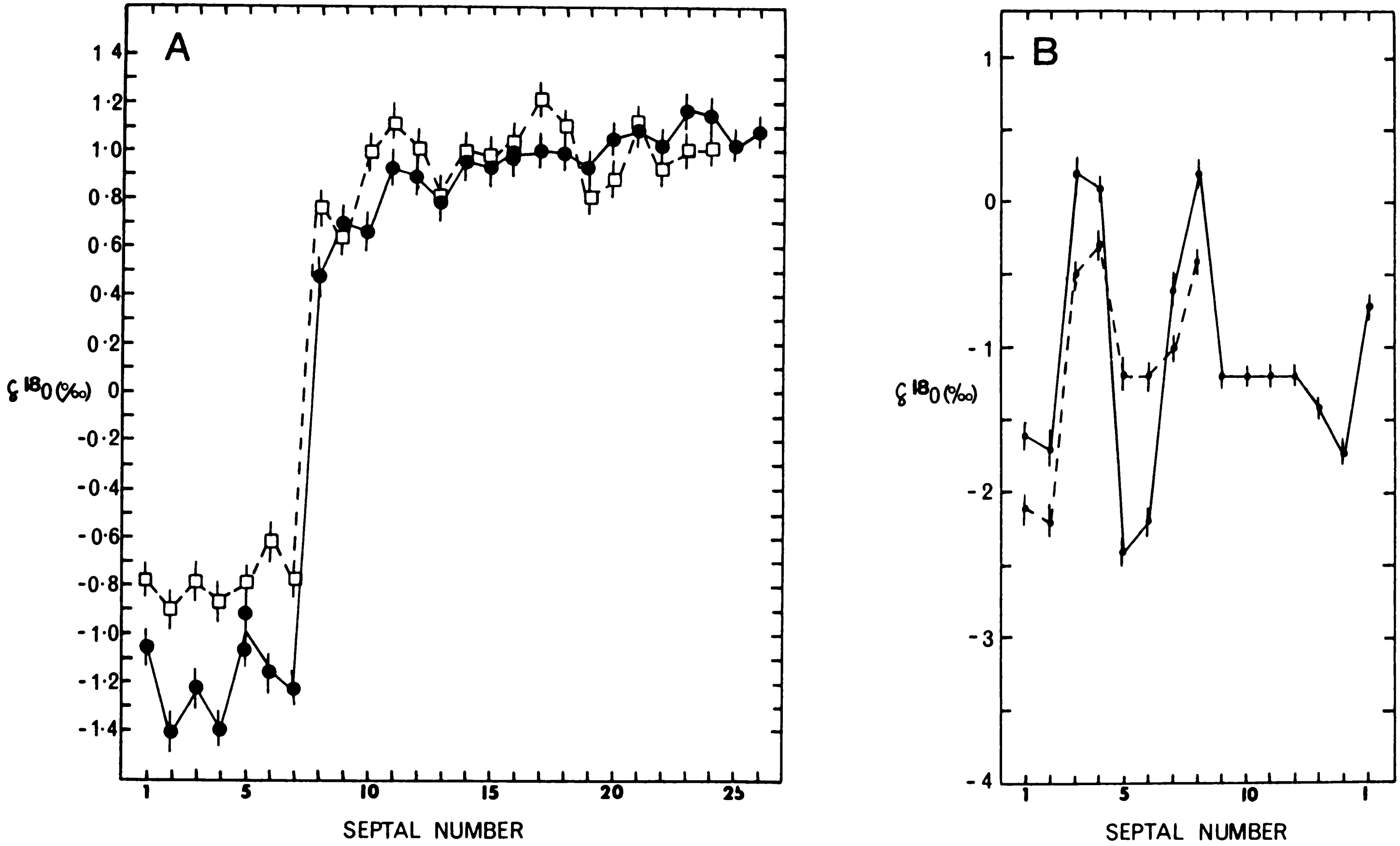


Text Fig. 6. A) Specimen of *Eutrephoceras dekayi* showing the nepionic constriction (arrow), which marks the end of the embryonic shell. B) Close-up of the constriction near the umbilicus reveals no sharp change in the ornamentation at this point.



Text Fig. 7. Median cross sections of three nautilid species reveal changes in septal spacing and thickness. A) In *Nautilus pompilius*, septa 7 and 8 are closely spaced. B) In *Eutrephoceras dekayi*, septa 4 and 5 are closely spaced. C) In *Aturia morrissi*, the early septa are evenly spaced but a four-fold increase in thickness occurs between septa 3 and 4.

septa before the approximation are slightly thinner and, therefore, weaker than the succeeding septa (Westermann, pers. comm., in Landman et al. 1983). Between septa 4 and 5, the ratio of oxygen isotopes shows a shift of variable magnitude from heavier to lighter values followed by a return to heavier values over the next one to three septa (Text Fig. 8B). This isotopic shift may also be due to the hatching event


A
1·4
1·2
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δ18O (‰)
0
-0·2
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1
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15
20
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SEPTAL NUMBER
B
1
0
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and may result from a combination of kinetic and equilibrium effects on emergence from the egg capsule (Landman et al. 1983).

In the Miocene nautilid species *Aturia morrissi* Michelotti from Italy, the shell shape of the early whorls is compressed and the first few septa are all equally spaced (Text Fig. 7C). However, a four-fold increase in thickness occurs between septa 3 and 4. This increase from approximately 15 μm to 60 μm probably indicates the point of hatching.

The fecundity of nautilids is much lower than that of ammonites. Modern *Nautilus* species lay few eggs. In two studies of aquarium-maintained animals, approximately 10 eggs/female were laid over a spawning period of 5 months (Martin et al. 1978, Hamada et al. 1978). However, newly hatched nautilids have rarely been observed in the field. They may inhabit deep water (>300 m, Ward & Martin 1980), although the only live-caught animals, described as active swimmers, were collected in a shallow lagoon (Davis & Mohorter 1973). Reports of preserved embryonic shells of fossil nautilids are rare (Bandel, in press) and suggest a similarly low fecundity or absence of favorable environments for preservation.

3. Summary

The criteria for recognizing the embryonic-postembryonic boundary differ in ammonites and nautilids (Table 2). In ammonites, hatching is marked on the outer shell by a constriction, a change in ornamentation, the first appearance of growth

Table 2. Indicators of hatching in ammonites and nautilids.

		Ammonites	Nautilids
Outer Shell	Constriction	×	×
	Ornament/growth lines	×	
	Shape	×	×
	Structure	×	
	Shell repair	×	×
Septa	Spacing		×
	Shape	×	
	Structure	×	
	Thickness	×	×
	Isotopes		×

Text Fig. 8. $\delta^{18}O$ (0/00) versus septal number in two specimens of *Nautilus pompilius* (A) and two specimens of *Eutrephoceras dekayi* (B). The isotopic break between septa 7 and 8 in *Nautilus* and septa 4 and 5 in *Eutrephoceras* reflects hatching and first open contact with sea water (from Cochran et al. 1981 and Landman et al. 1983).

lines, a change in shape, and the appearance of a new calcareous microstructure. Internally, it may be denoted by a change in septal shape, structure, and thickness. In nautilids, hatching may be marked on the outer shell by a constriction, an increase in shell surface roughness, the first appearance of healed injuries, and an expansion in whorl width. Internally, it may be characterized by a change in septal spacing, thickness, and the ratio of oxygen isotopes.

Table 3. Comparison of the early development between ammonites and nautilids.

	Ammonites	Nautilids
Embryonic size (mm)	0.6-1.5	10-25
Number of embryonic septa	≥ 1	>1
Mode of life	Planktic?	Free swimming
Embryonic size/adult size	Low (10^{-2}-10^{-3})	High (10^{-1}-10^{-2})
Number of offspring/female	High ($\sim 10^3$)	Low (10^1-10^2)
Strategy	r	K

Table 3 summarizes the early development of the two groups. In ammonites, the diameter of the embryonic shell ranges from approximately 0.6 to 1.5 mm; in nautilids from approximately 10-25 mm. In ammonites, the embryonic shell may display as few as one septum and buoyancy chamber compared to several in nautilids. The mode of life in newly hatched ammonites may have been planktic, whereas it is probably free-swimming in nautilids. The ratio of the diameter of the embryonic shell to that of the adult shell is low in ammonites (10^{-2}-10^{-3}) but relatively higher in nautilids (10^{-1}-10^{-2}). The number of offspring per female is high in ammonites ($\sim 10^3$) but relatively lower in nautilids (10^1-10^2).

On the basis of these differences, we may describe the life history strategies of ammonites and nautilids as r-selected and K-selected, respectively (see MacArthur & Wilson 1967). These terms are relative and have been modified by Vermeij (1978) to include a third category of stress tolerant species. According to this ecological classification, ammonites represent r-strategists because they channel their reproductive energy into a large number of small offspring. Nautilids are closer to K-strategists or Vermeij's stress tolerant species because they produce a few large, well developed offspring.

These distinctions describe the extreme ends of the spectrum. In fact, the ecology of ammonites with relatively large embryonic shells may begin to approach that of nautilids with relatively small embryonic shells. Nevertheless, many other differences in life history, ecology, and evolution may ultimately correlate with these marked differences in early ontogeny.

Acknowledgments

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