

Chapter 11

Ammonoid Embryonic Development

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1. Introduction

Ammonoids retain a record of growth in their shells, and, therefore, material is readily available for studies of early ontogeny. Such studies were performed first in the mid-19th century and have been pursued with vigor ever since. Using optical and scanning electron microscopy, ammonoid workers have described the morphology of the early whorls and have attempted to reconstruct the sequence of early ontogenetic development and to identify the embryonic shell.

Studies of early ontogeny are obviously crucial in understanding the ecology and mode of life of adults. Such factors as population structure and biogeographic distribution grow out of the constraints of early ontogeny. For example, differences in early life history may explain why some ammonoid species are more restricted in their biogeographic distribution than are others. These relationships may bear, in turn, on broader evolutionary issues such as species longevity and extinction.

Studies of early ontogeny are also helpful in trying to reconstruct phylogeny. In the studies of Hyatt (1866, 1883, 1889, 1894), Smith (1898, 1914), and Buckman (1887–1907, 1909, 1918), ontogeny and phylogeny were closely linked together in a theory of recapitulation. According to these authors, the early ontogenetic stages of an individual represented a recapitulation of the adult stages of its ancestors. Although this view no longer is considered valid, there are, nevertheless, numerous characters in early ontogeny that are useful in reconstructing phylogeny.

Much of the information presented in this chapter, especially with respect to the size of the embryonic shell, is new. However, the morphological descriptions and interpretations of ontogenetic development rely heavily on previously published data. Many of these data are based on Mesozoic rather than Paleozoic ammonoids because the former are generally better preserved. Specimens cited in this chapter are deposited in the American Museum of Natural History (AMNH), the University of Iowa (SUI), the University Museum of the University of Tokyo (UMUT), the New York State Museum (NYSM), and the Yale Peabody Museum of Natural History (YPM).

2. Description of the Ammonitella

2.1. Terminology

Figure 1 illustrates the terms used to describe the morphological features of the early whorls. The illustrated specimen represents the early whorls of the Late Cretaceous species *Scaphites whitfieldi* (Ancyloceratina), but the same terms are used for all ammonoids. The ammonitella is defined as the shell up to the end of the primary constriction (Druschits and Khiami, 1970; Druschits *et al.*, 1977a,b; Tanabe *et al.*, 1980; Birkelund, 1981; Landman,

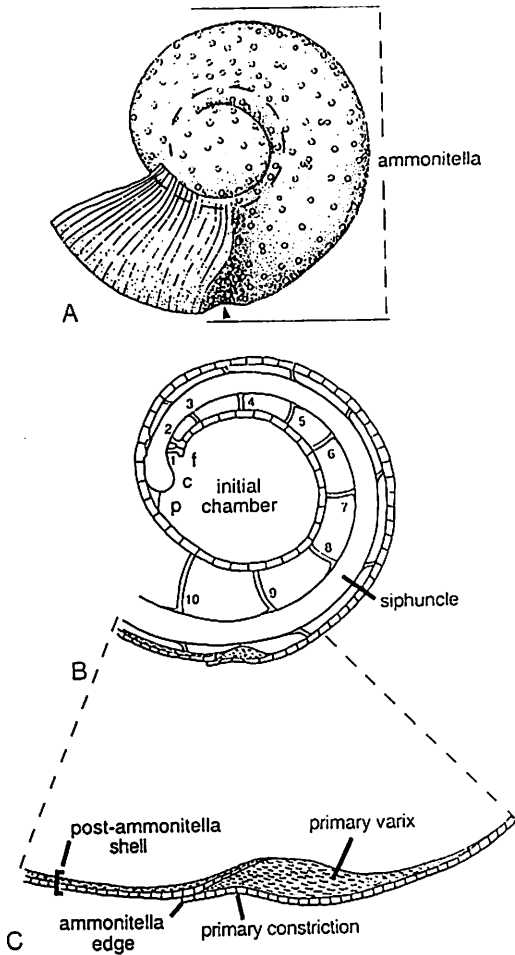


FIGURE 1. (A) Side view of the early whorls of an ammonoid based on a specimen of the Late Cretaceous species *Scaphites whitfieldi*. The ammonitella (about 0.7 mm in diameter) consists of the shell up to the primary constriction (arrow). The dashed line indicates the outline of the initial chamber in median cross section. (B) Median cross section through the same specimen showing the initial chamber (protoconch), flange (f), prosepium (1), primary septum (2), septa 3–10, cecum (c), prosiphon (p), and siphuncle. (C) Close-up of B showing the primary constriction, primary varix, ammonitella edge, and postammonitella shell.

1987). (This term originally was defined as the whole animal up to this point. It commonly is used in this sense as well as in the more restricted sense to mean only the shell of the animal.) The term “initial portion of the shell” (“*Gehäuse-Anfangsteile*,” Erben, 1960) refers in a general way to the beginning of the ammonitella. The term “initial chamber” (“*Anfangskammer*,” Branco, 1879, 1880; Schindewolf, 1933; Erben, 1960; “protoconch,” Owen, 1878;

Hyatt, 1883; "first whorl," Bandel, 1982) refers specifically to the portion of the ammonitella up to the proseptum.

2.2. Shape

The initial chamber ranges in shape from globular to spindle-like and has a circular to lenticular outline in transverse cross section (Fig. 2G–I; Branco, 1879, 1880; Bogoslovsky, 1969, Fig. 2; Erben, 1964, Fig. 1; Erben, 1966, Fig. 3). In median cross section, the initial chamber is U-shaped or, more commonly, forms the beginning of a spiral (Fig. 2D–F). A cicatrix, the scar-like feature on the early portion of the shell of many nautiloids (Arnold *et al.*, 1987), is absent. In ammonoids with a bulbous initial chamber, the succeeding whorls are loosely coiled or even straight. For example, in *Mimagoniatites*, the spherical initial chamber is loosely enveloped by the succeeding whorls, leaving an umbilical perforation (Fig. 2B). In ammonoids with a barrel- to spindle-shaped initial chamber, the succeeding whorls are closely coiled.

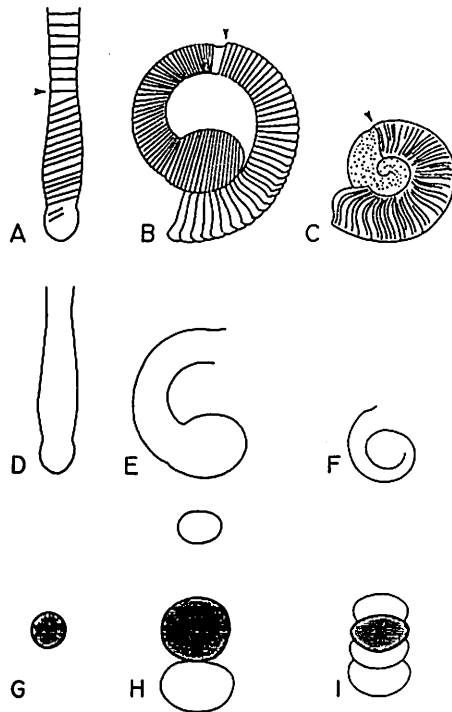


FIGURE 2. (A–C) Side views of the early whorls in *Pseudobactrites*, *Mimagoniatites*, and *Scaphites*. Arrows indicate the end of the ammonitella. (D–F) Median cross sections through the ammonitella in the same three genera. (G–I) Transverse cross-sections through the initial chamber (G) and initial chamber and first whorl (H, I) in the same three genera. The initial chamber is shaded. Scale bar, 1 mm.

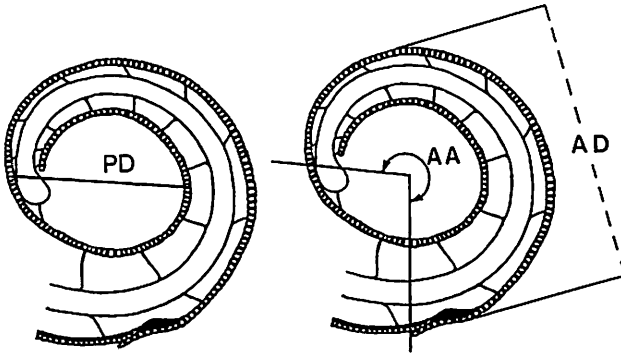


FIGURE 3. Median cross sections through the ammonitella showing measurements of the initial chamber diameter (PD), ammonitella diameter (AD), and ammonitella angle (AA).

They tightly envelop the initial chamber, leaving a shallow to deep dorsal impression in the whorl profile as seen in transverse cross section (Fig. 2I; Erben, 1964, Fig. 3).

The distal end of the initial chamber is marked by an abrupt narrowing of the shell in phylogenetically primitive ammonoids such as bacitrids (Fig. 2A; Mapes, 1979, Figs. 10–12), whereas there is only some flattening along the venter at this point in more advanced forms (Fig. 2F; Bandel, 1986). This change in shell shape was called the first growth change (“1. *Wachstums-Änderung*”) by Erben (1964), who interpreted it as indicating a major shift in ontogenetic development.

A second change in shell shape occurs at approximately one whorl from the end of the initial chamber in closely coiled ammonitellas; it appears as a groove in the shell wall, which is especially well expressed along the venter (Figs. 1, 2C). In bacitrids, this change in shape appears as a gradual narrowing of the shell, followed by a widening (Fig. 2A; Mapes, 1979, Figs. 10–12). This feature has been referred to as the primary constriction (Shul’ga-Nesterenko, 1926; Bogoslovskaya, 1959) or nepionic constriction (Erben *et al.*, 1968; Birkelund and Hansen, 1968), although a variety of other terms also have been used (“*Einschnürung*,” Branco, 1879, 1880; “*première varice*,” Grandjean, 1910; “*Anfangseinschnürung*,” Böhmers, 1936; “2. *Wachstumsänderung*,” Erben, 1964; Erben *et al.*, 1969; “primary varix,” Druschits and Khiami, 1970). Landman and Waage (1982) emphasized the importance of distinguishing the actual constriction in the shell wall (primary constriction) both from the shell thickening at this point (primary varix) and from the trace of this thickening on the steinkern (varix trace).

2.3. Size

Three measurements were made of the ammonitella in median cross section (Fig. 3). The diameter of the ammonitella (AD) is defined as the

distance from the adoral end of the primary constriction through the center of the initial chamber to the opposite side of the ammonitella. (In straight ammonitellas, for example, in bactritids, this dimension is more properly called length.) The diameter of the initial chamber (PD) is measured from the ventral edge of the proseptum through the center of the initial chamber to the opposite side. In closely coiled ammonitellas, the ammonitella angle (AA) is defined as the angle from the ventral edge of the proseptum to the adoral end of the primary constriction.

The diameter of the ammonitella ranges from a minimum of 0.5 mm to a maximum of 2.6 mm in all the suborders studied (Fig. 4; Table I). Most values occur between 0.5 and 1.5 mm (small to medium) except in the Agoniatitina (1.5–2.6 mm), Goniatitina (0.6–2.3 mm), and Lytoceratina (0.8–1.9 mm). In parabactritids, the ammonitella diameter (length) averages 1.4 mm (Hecht, 1991). In the Lytoceratina, ammonitella diameter appears to increase over geological time from the Middle Jurassic to the Late Cretaceous (Fig. 5).

The diameter of the initial chamber covaries with that of the ammonitella and ranges from 0.25 to 1.60 mm, with most values occurring between 0.25 and 0.75 mm (small to medium; Table I; House, 1985, Fig. 3; Lehmann, 1990, Fig. 4.69). The largest initial chambers occur in the Agoniatitina (0.80–1.6 mm). There is a strong positive correlation between initial chamber diameter and ammonitella diameter, both within and among species (Fig. 6; Tanabe *et al.*, 1979; Tanabe and Ohtsuka, 1985; Landman, 1987; Shigeta, 1993). A strong positive correlation also occurs between initial chamber volume and ammonitella volume (Fig. 7). However, the precise nature of this relationship may vary among suborders as, for example, between Goniatitina and Ammonitida, as illustrated in Fig. 7.

The ammonitella angle ranges from as little as 240° in some Ceratitina and Ammonitina to as much as 410° in some Goniatitina (e.g., *Peritrochia* and *Perrinites*; Fig. 8; Table I; Grandjean, 1910; Bogoslovskaya, 1959). The ammonitella angle in the Goniatitina is larger than those in all other suborders (Tanabe *et al.*, 1994). A plot of ammonitella angle versus ammonitella diameter in seven suborders reveals only a weak correlation (Fig. 9).

In closely coiled ammonitellas, the whorl width and radius of the spiral show no significant increase over the first whorl up to the end of the primary constriction. In contrast, after the primary constriction, there is an abrupt increase in both of these dimensions (Fig. 10; Currie, 1942, 1943; Palframan, 1967b; Tanabe, 1975, 1977a; Kulicki, 1974, 1979; Hirano, 1975; Obata *et al.*, 1979; Zell *et al.*, 1979; Landman, 1987, 1988). This change in whorl shape is dramatic in heteromorph ammonoids such as *Baculites*, in which the postammonitella shell becomes orthoconic (Brown, 1891; Bandel *et al.*, 1982, Fig. 1C), and *Eubostriyoceras*, in which the postammonitella shell becomes loosely coiled (Tanabe *et al.*, 1981, Pl. 35, Fig. 1e).

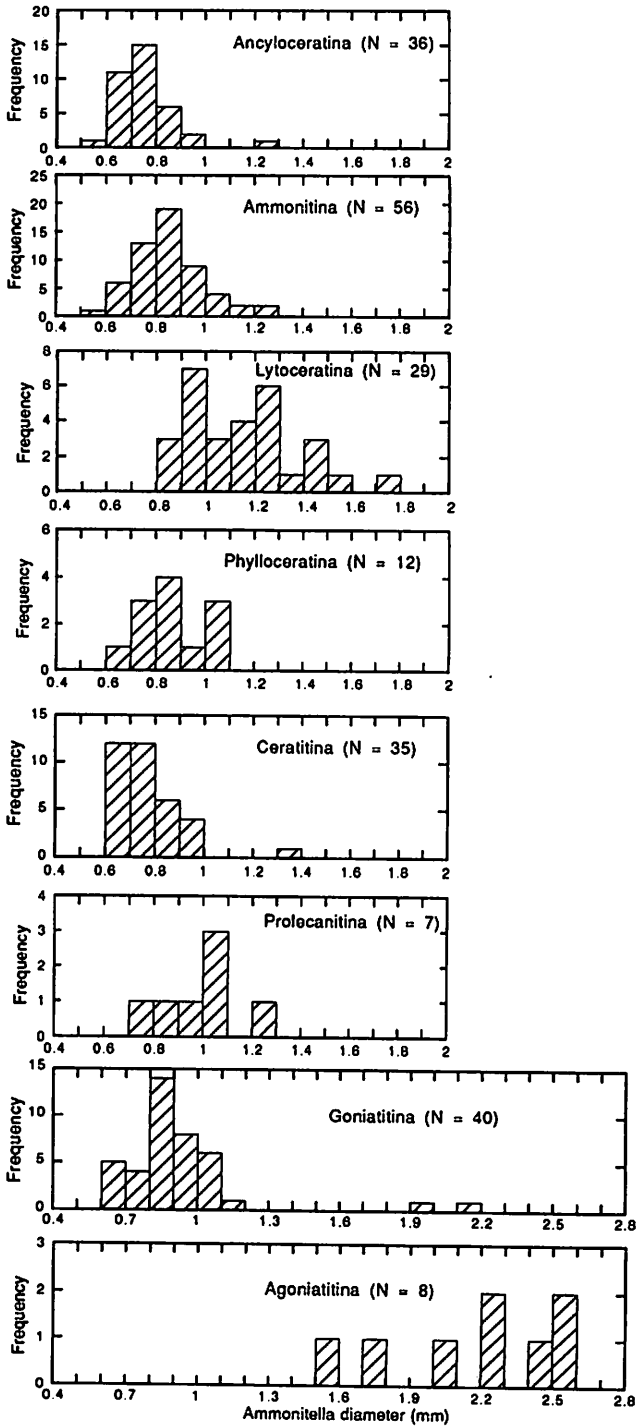


FIGURE 4. Size-frequency histograms of ammonitella diameter in eight ammonoid suborders. For species represented by more than two specimens, the mean was used. *N*, number of species. See Appendices for data sources.

Table I. Comparison of the Ammonitella in 11 Suborders of the Ammonoidea^a

Suborder	Initial chamber diameter (mm)*	Ammonitella diameter (mm)**	Ammonitella angle (degrees) [†]	Shape and length (mm) of prosiphon ^{††}	Shape of cecum	Initial position of siphuncle	Micro-ornamentation
Agoniatitina	Large to very large (0.80–1.60)	Large to very large (1.50–2.60)	—	—	—	—	Transverse lirae
Anarcestina	—	Medium (1.00)	—	—	—	—	Transverse lirae
Gephuroceratina	Medium to very large (0.65–1.10)	Medium (1.05–1.20)	—	—	—	—	Unknown
Tornoceratina	Medium to large (0.50–1.00)	Medium (1.40–1.50)	—	—	—	—	Transverse lirae
Goniatitina	Small to medium (0.30–0.70) but very large in <i>Perrinites</i> and <i>Gonioloboceras</i>	Small to medium (0.60–1.20) but very large in <i>Perrinites</i> and <i>Gonioloboceras</i>	Medium to large (345–410)	Short and curved (≤ 0.10)	Elliptical in median section	Mostly marginal but central in <i>Bisatoceras</i> and <i>Agathiceras</i>	Longitudinal lirae
Prolecanitina	Small to medium (0.35–0.60)	Small to medium (0.70–1.20)	Medium to large (310–355)	Short and curved (0.05–0.25)	Rectangular in median section	Marginal	Unknown
Ceratitina	Small to medium (0.30–0.65)	Small to medium (0.60–1.30)	Small to large (240–370)	Short and curved (≤ 0.20)	Elliptical in median section	Mostly marginal but central in the Ceratitaceae and Megaphylitaceae	Tubercles

Phylloceratina	Small to medium (0.40–0.65)	Small to medium (0.65–1.30)	Medium to large (260–380)	Short and curved (≤ 0.15)	Elliptical in median section	Central in the Phylloceratidae and marginal in the Ussuritidae	Tubercles
Lytoceratina	Small to very large (0.30–1.05)	Small to large (0.80–1.90)	Medium to large (270–365)	Short and curved (0.05–0.10)	Hemicircular in median section	Marginal	Tubercles
Ammonitina	Small to medium (0.30–0.70)	Small to medium (0.60–1.25)	Small to large (240–360)	Long and straight but short and curved in the Amaltheidae, Collignoni- ceratidae, and Placenti- ceratidae	Elliptical in median section	Central to subcentral	Tubercles
Ancyloceratina	Small to medium (0.25–0.70)	Small to medium (0.50–1.30)	Medium (255–330)	Long and straight (Ancylocera- taceae and Parahopli- taceae), short and curved (Scaphitaceae)	Elliptical in median section	Subcentral to marginal	Tubercles

^aSymbols: *small ($0.25 \leq PD < 0.5$), medium ($0.5 \leq PD < 0.75$), large ($0.75 \leq PD < 1.0$), very large ($PD \geq 1.0$); **small ($0.5 \leq AD < 1.0$), medium ($1.0 \leq AD < 1.5$), large ($1.5 \leq AD < 2.0$), very large ($AD \geq 2.0$); * small ($AA < 250$), medium ($250 \leq AA < 350$), large ($AA \geq 350$); ** short (≤ 0.3), long (> 0.3).

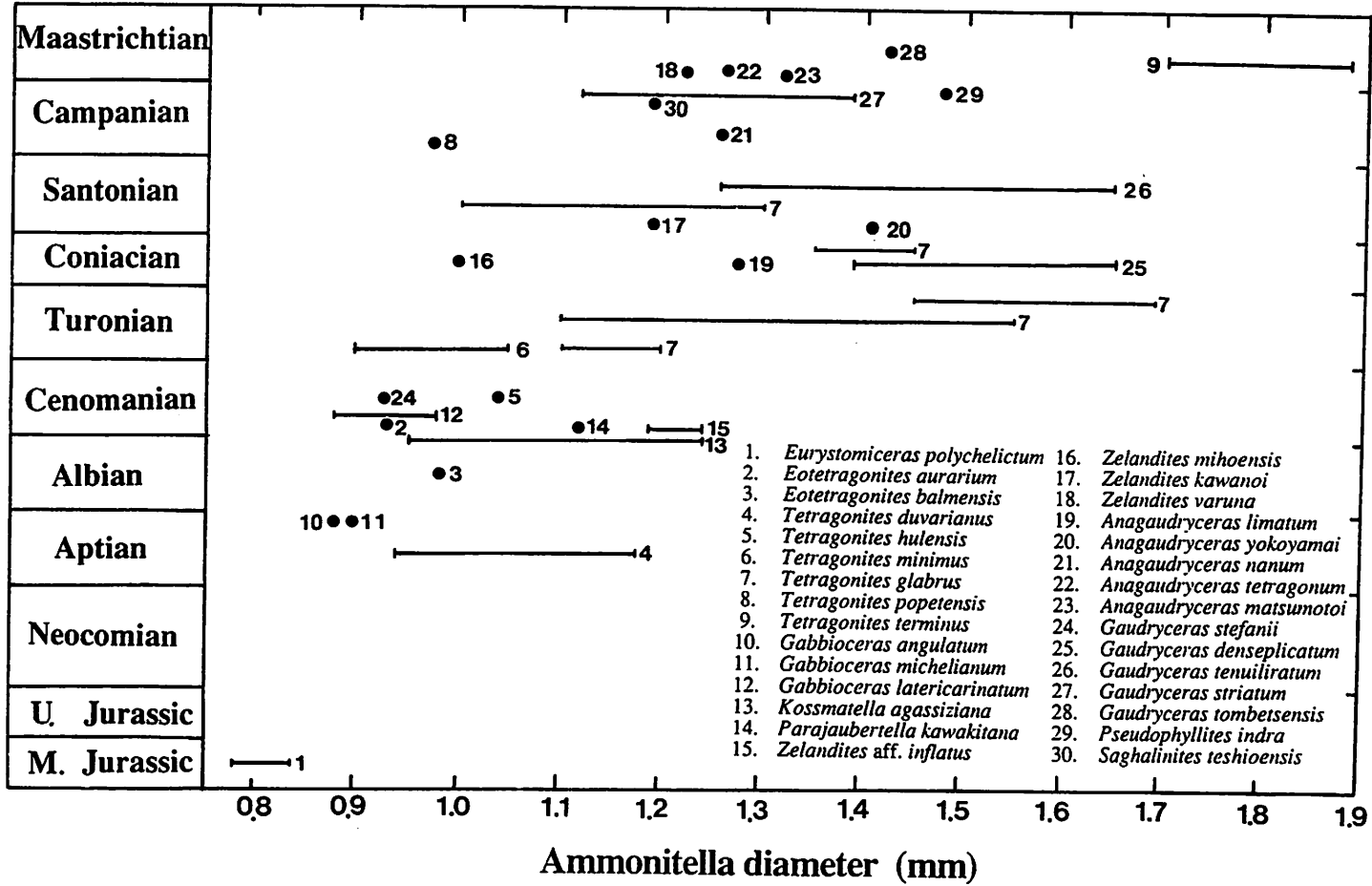


FIGURE 5. Change in ammonitella diameter in the Lytoceratina with respect to geological time. Horizontal bars indicate the range of variation within a single species.

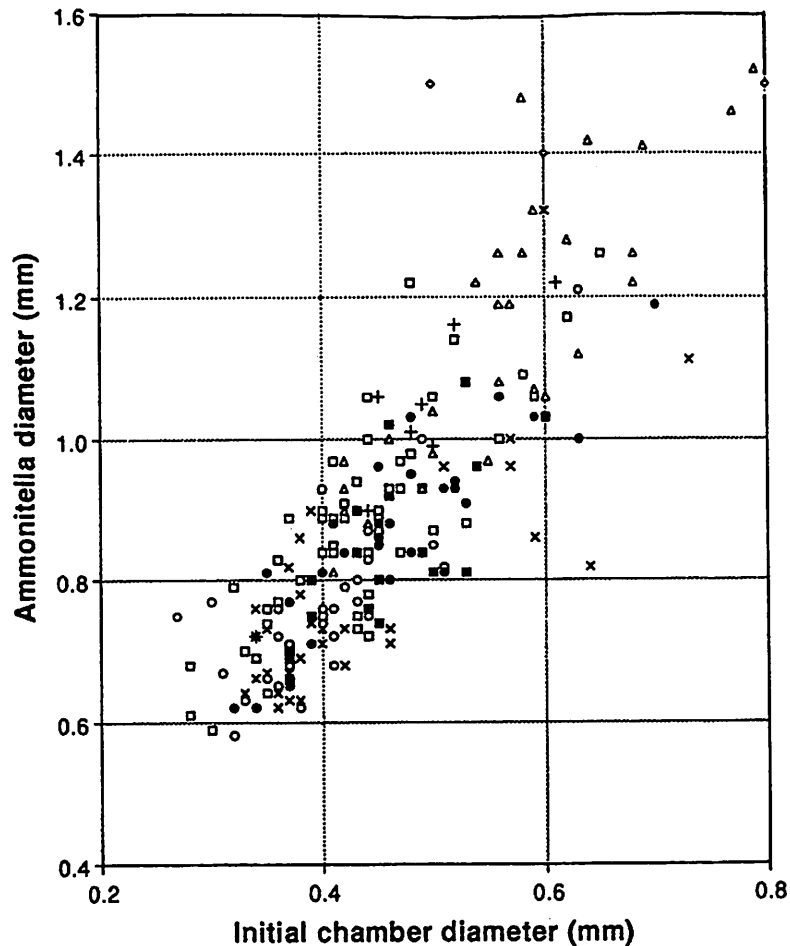
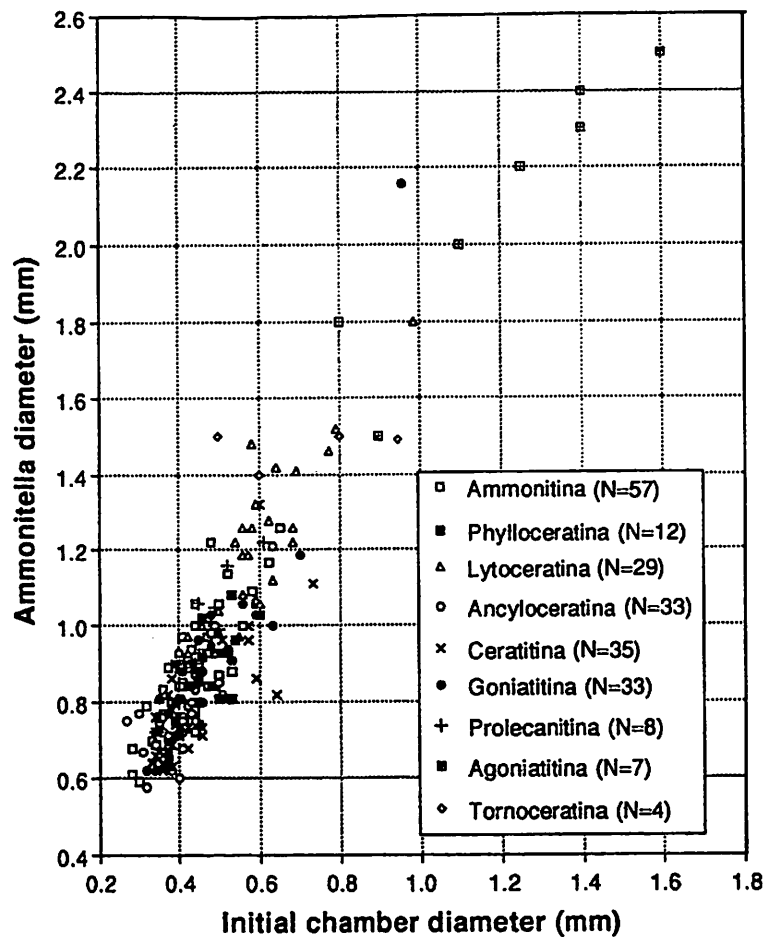


FIGURE 6. Ammonitella diameter versus initial chamber diameter in 223 species of the Ammonoidea. The right plot is a close-up of the lower left portion of the left plot. For species represented by more than two specimens, the mean was plotted. *N*, number of species. See Appendices for data sources.

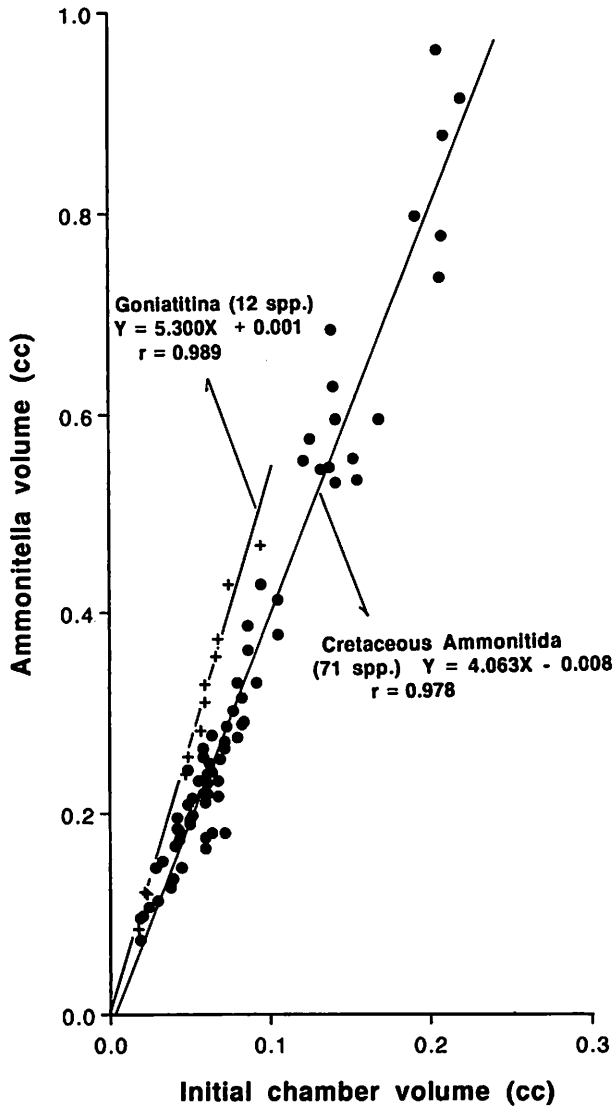


FIGURE 7. Ammonitella volume versus initial chamber volume in 12 species of Carboniferous Goniatitina and 71 species of Cretaceous Ammonitida. (Data from Shigeta, 1993, and Tanabe *et al.*, 1995).

2.4. Ornamentation

The ammonitella is commonly covered with a microornamentation that occurs on the exposed portions of the initial chamber and succeeding whorls and terminates at the end of the primary constriction. Growth lines are absent on the ammonitellas of Mesozoic ammonoids. As pointed out by Bandel

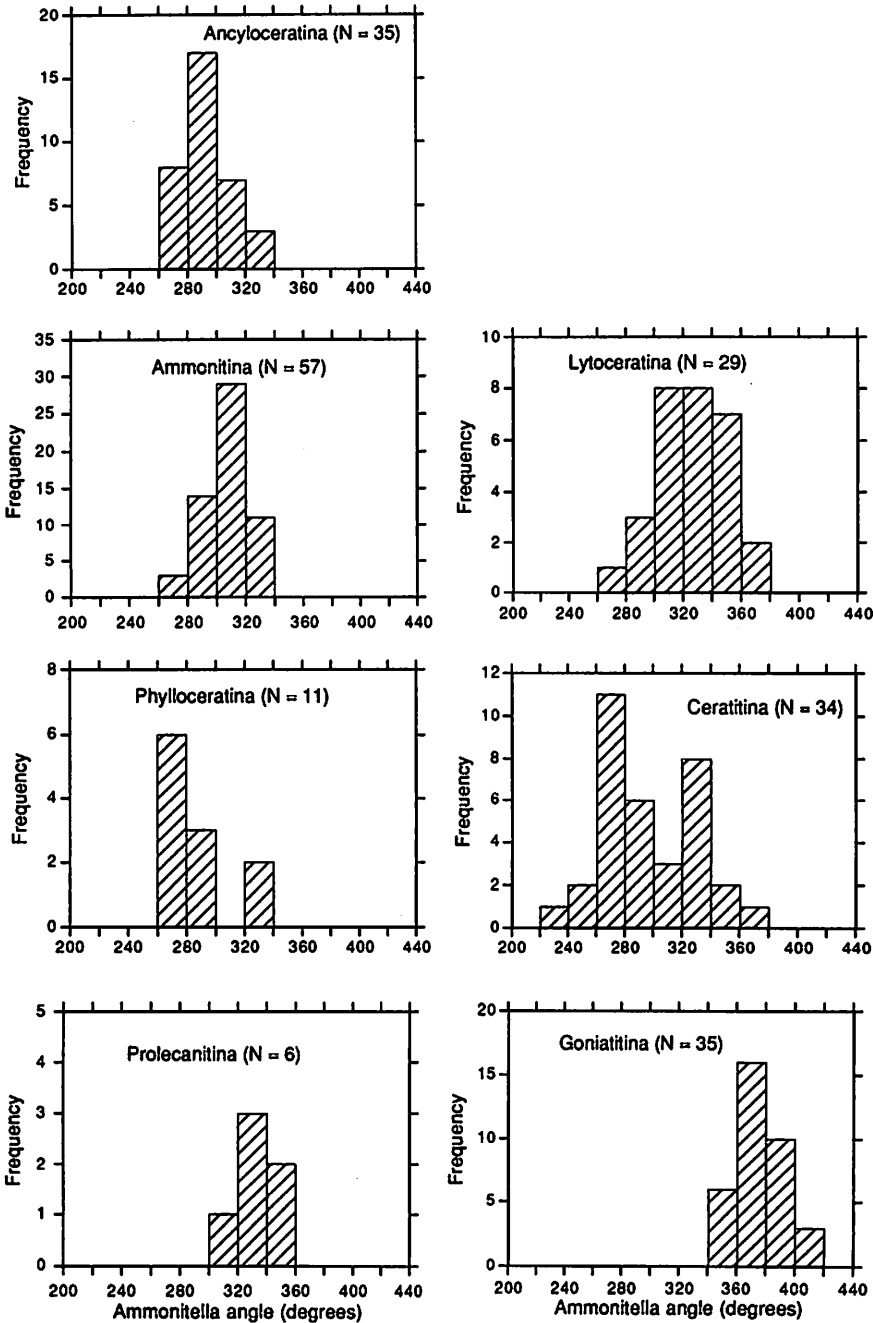


FIGURE 8. Size-frequency histograms of ammonitella angle in seven suborders of the Ammonoidea. For species represented by more than two specimens, the mean was used. *N*, number of species. See Appendices for data sources.

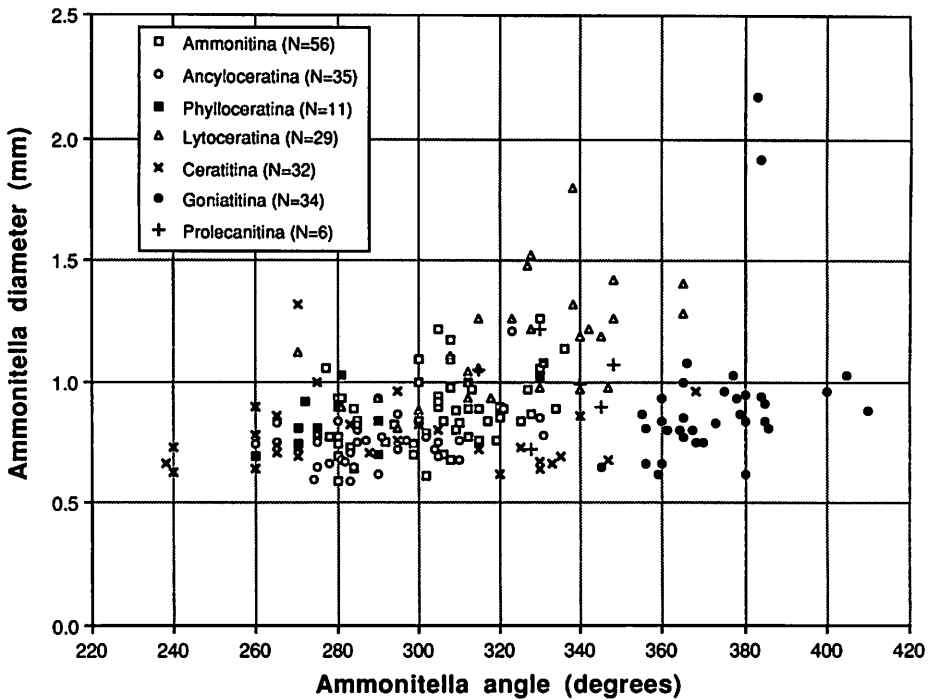


FIGURE 9. Ammonitella diameter versus ammonitella angle in 203 species of the Ammonoidea. For species represented by more than two specimens, the mean was plotted. *N*, number of species. See Appendices for data sources.

(1986), what has sometimes been mistaken for growth lines on steinkerns represents instead the impression of the inside surface of the shell wall on the internal mold. Growth lines have been reported from the ammonitellas of some Paleozoic ammonoids (“*Anwachsstreifen*,” Erben *et al.*, 1969), but these features probably are lirae rather than growth lines (see Chapter 12, this volume, for the distinction between growth lines and lirae).

Several kinds of ornamentation have been documented on ammonitellas (Table I). Lirae are present on the ammonitellas of many Paleozoic forms. In the Agoniatitina, the ammonitella is covered with fine transverse lirae parallel to the aperture (Fig. 11C; Babin, 1989, Pl. 1, Fig. 2; Wissner and Norris, 1991, Pl. 3.1, Fig. 1; Erben, 1964, Pl. 7, Figs. 6, 7, Pl. 8, Figs. 1, 2, 6, 7, Pl. 9, Fig. 1; Göddertz, 1989, Pl. 2, Fig. 2). In *Mimagoniatites*, these lirae develop a slight backward projection along the venter at the end of the initial chamber (Erben, 1964, Pl. 8, Figs. 3–5). In the Tornoceratina, the ammonitella also is covered with fine transverse lirae (Fig. 11E,F; Beecher, 1890; House, 1965, Fig. 2). Transverse lirae also have been reported in the Anarcestina (see Miller, 1938, Fig. 8). In the Goniatitina, in contrast, the ammonitella is ornamented with evenly spaced, longitudinal lirae; these disappear just before the end of the primary constriction (Fig. 11D; Tanabe *et al.*, 1993).

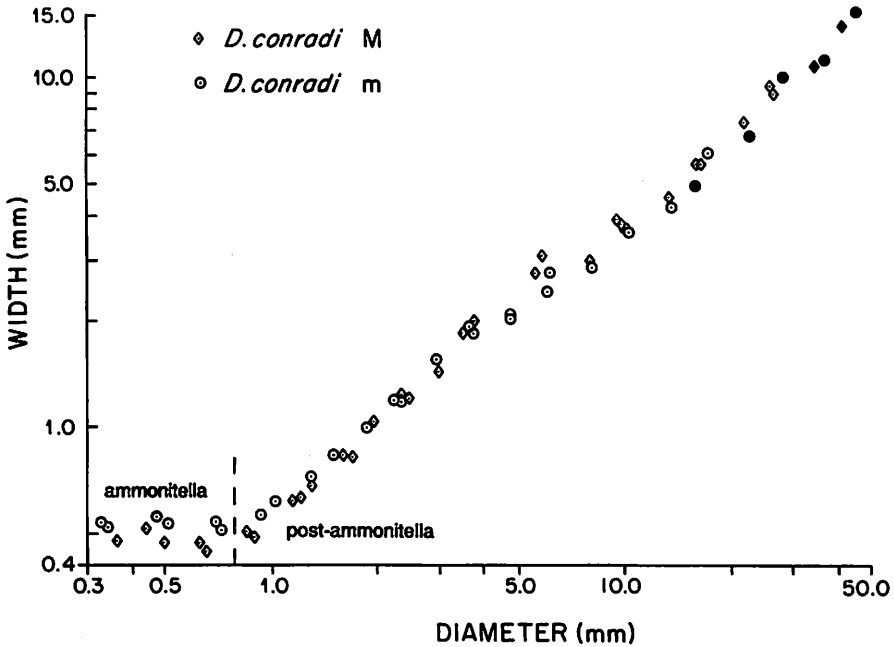


FIGURE 10. Whorl width versus shell diameter through the ontogeny of six adults [three macroconchs (M) and three microconchs (m)] of *Discoscaphites conradi* showing the abrupt change in whorl width at the end of the ammonitella. Black symbols indicate measurements near the base of or in the mature body chamber. (After Landman and Waage, 1993, Fig. 162)

In the Ceratitina, Lytoceratina, Phylloceratina, Ammonitina, and Ancyloceratina, the ammonitella is covered with a tuberculate microornamentation rather than with lirae (Figs. 12 and 13; Kulicki, 1974, 1979; Bandel, 1982; Bandel *et al.*, 1982; Landman, 1985, 1987; Landman and Waage, 1993; Tanabe, 1989; for data on the Ceratitina, W. Weitschat, personal communication, 1993). The tubercles range in diameter from 2 to 10 μm and, in general, are irregularly distributed over the exposed surface of the ammonitella. They die out at the end of the primary constriction. In some ammonoids, the tubercles coalesce into a single layer covering part of the initial chamber (Fig. 13E; Tanabe, 1989; Chapter 4, this volume).

In other ammonoids, the surface of the ammonitella appears smooth (Fig. 11A,B). For example, Miller (1938) described smooth ammonitellas in some Gephuroceratina, although this smoothness may simply reflect poor preservation (see also Clausen, 1969). In the Bactritina, the shaft after the initial chamber is ornamented with transverse lirae, but it is unclear whether these are also present on the initial chamber (Erben, 1964; Mapes, 1979).

There is an abrupt change in ornamentation at the end of the primary constriction (Figs. 11A, 12C-F, and 13F). For example, at this point in *Tornoceras*, the lirae abruptly become biconvex, with a forward projection

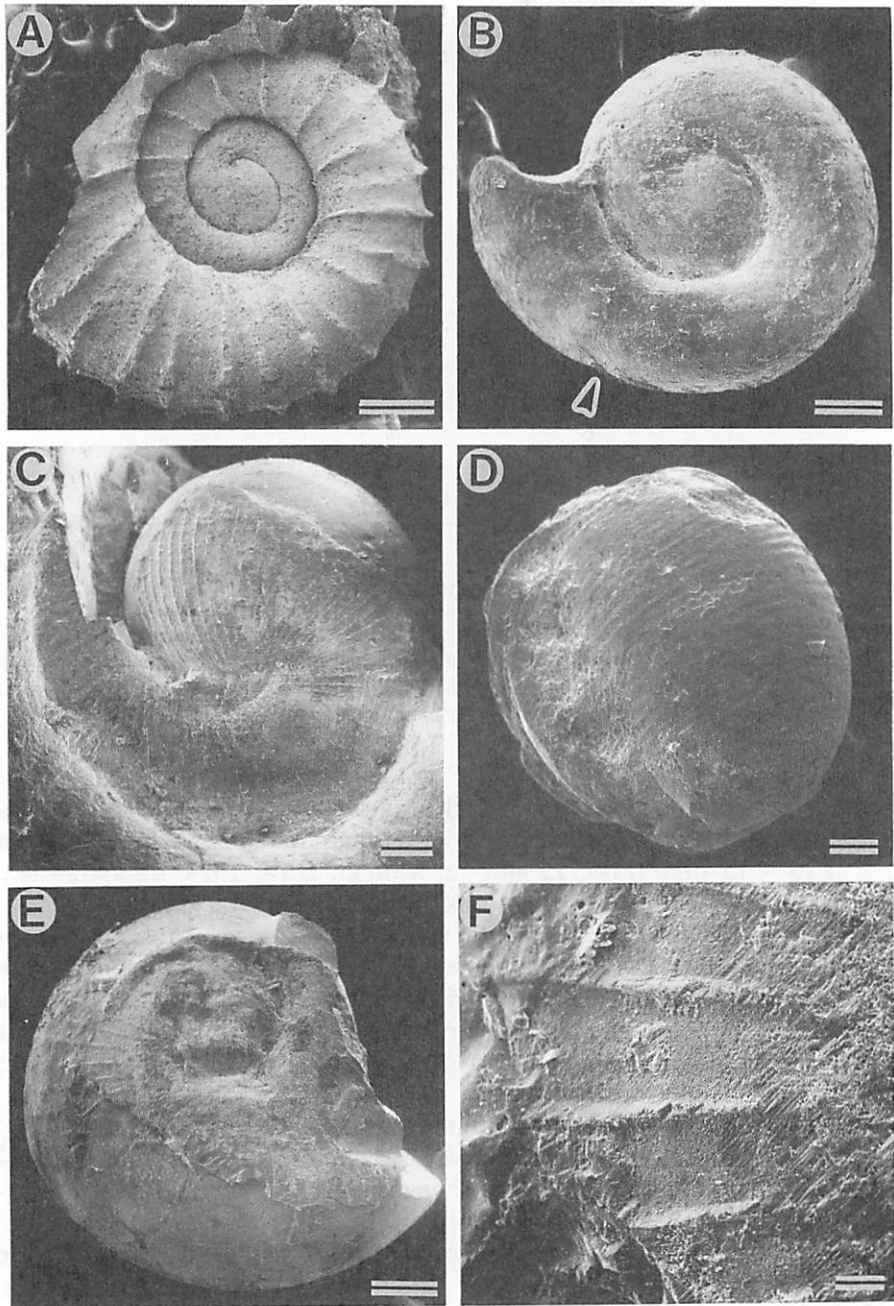


FIGURE 11. Early whorls of Paleozoic ammonoids. (A) *Manticoceras sinuosum* (Gephuroceratina), Upper Devonian, New York State, NYSM 3755 (12306/7). No ornamentation is visible on the ammonitella, possibly because of poor preservation, but prominent subcostae appear immediately afterward. Scale bar, 500 μm . (B) *Probeloceras lutheri* (Gephuroceratina), Upper Devonian, New York State, NYSM 12726. The specimen is a steinkern and shows the varix trace (arrow). Scale bar, 200 μm . (C) *Agoniatites vanuxemi* (Agoniatitina), Middle Devonian, New York State, NYSM 3545 (12000/6). The ammonitella is covered with fine transverse lirae. Scale bar, 200 μm . (D) *Vidrioceras* sp. (Goniatitina), Upper Pennsylvanian, Kansas, UMUT PM 19014. The ammonitella is covered with evenly spaced longitudinal lirae. Scale bar, 100 μm . (E,F) *Tornoceras (Tornoceras) uniangularis aldenense* (Tornoceratina), Middle Devonian, New York State, NYSM 12553. (E) The ammonitella is covered with fine transverse lirae. Scale bar, 200 μm . (F) Close-up of lirae. Scale bar, 20 μm .

along the ventrolateral margin and a backward projection along the venter (Beecher, 1890; House, 1965, Fig. 2). In *Scaphites*, the shell just adoral of the primary constriction is covered with fine ribs and growth lines (Fig. 12C–F), but in *Gaudryceras*, this part of the shell is covered with evenly spaced subcostae (Fig. 13F; Tanabe, 1989).

2.5. Microstructure of the Shell Wall

The microstructure of the shell wall of the ammonitella has been documented in the Ammonitina, Phylloceratina, Lytoceratina, and Ancyloceratina (Erben *et al.*, 1969; Kulicki, 1974, 1979; Birkelund and Hansen, 1974; Birkelund, 1981; Druschits and Khiami, 1970; Druschits and Doguzhaeva, 1974, 1981; Druschits *et al.*, 1977a,b; Chapter 4, this volume).

The shell wall of the ammonitella is thin. For example, in the Late Cretaceous heteromorph *Baculites*, it is approximately 2 μm thick at the proximal end of the initial chamber and increases to a thickness of approximately 4 μm at the distal end of the initial chamber. It reaches a thickness of approximately 8 μm just adapical of the primary varix.

The shell wall is constructed of several prismatic layers, but the number and the position of these layers are subject to debate (Fig. 14). Erben *et al.* (1968, Fig. 1; 1969, Fig. 5) reported five layers (Fig. 14A, p_1 – p_5) in the wall of the initial chamber, all but one of which (Fig. 14A, p_4) wedge out on the outer side before or at the distal end of the initial chamber (Fig. 14A, arrow). According to these authors, a new layer (Fig. 14A, p_6) appears on the inner side at this point and eventually forms most of the wall of the first whorl. Birkelund and Hansen (1968; 1974, Fig. 2) reported only two layers in the wall of the initial chamber, both of which wedge out on the outer side at the distal end of the initial chamber (Fig. 14B, arrow; see also Druschits *et al.*, 1977a, Fig. 6; Tanabe *et al.*, 1980, Fig. 4, for slight variations). According to these authors, two new layers appear on the inner side at this point and form the wall of the first whorl. Kulicki (1979, Figs. 6, 7) confirmed that there are two principal layers in the wall of the initial chamber, but he identified the outer

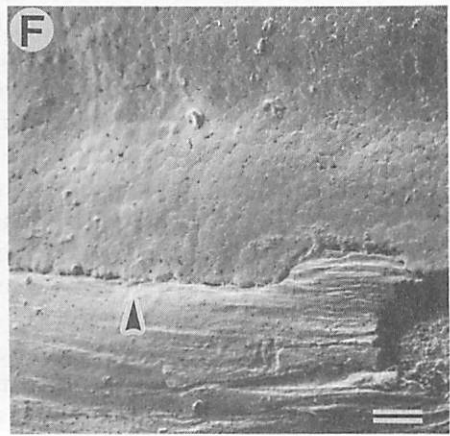
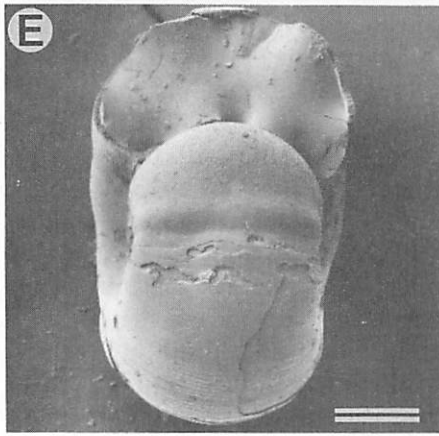
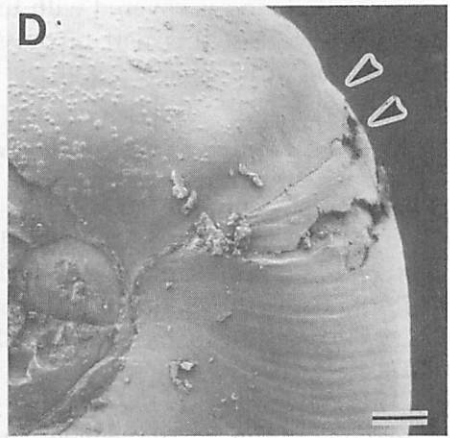
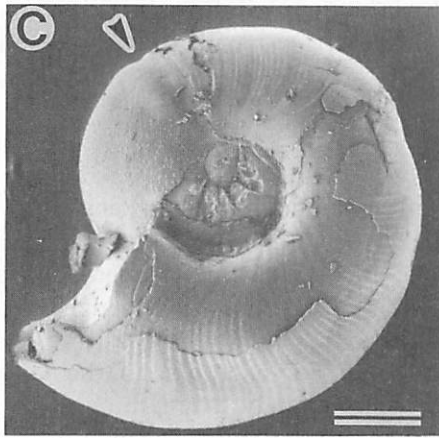
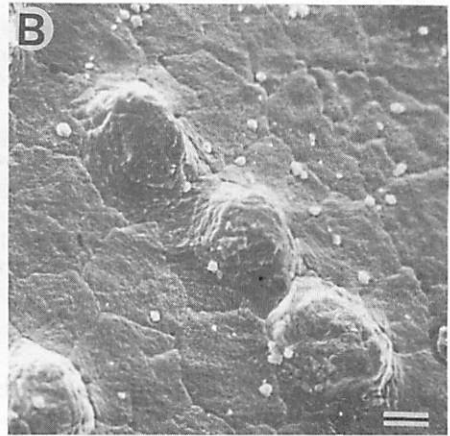
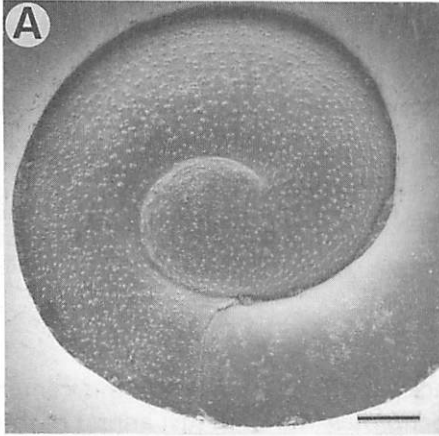


FIGURE 12. Early whorls of Mesozoic ammonoids. (A,B) Species of *Hoploscaphites* or *Jeletzkytes* (Ancyloceratina), Upper Cretaceous, South Dakota, YPM 34113. (A) View of the ammonitella showing the tuberculate ornamentation. Scale bar, 100 μm . (B) Close-up of tubercles. Scale bar, 2 μm . (C–F) *Scaphites whitfieldi* (Ancyloceratina), Upper Cretaceous, South Dakota, AMNH 44833. (C) View of part of the ammonitella and first whorl showing the primary constriction (arrow). The region of the initial chamber is poorly preserved. Scale bar, 200 μm . (D) Close-up of the primary constriction (upper arrow) and ammonitella edge (lower arrow). Scale bar, 50 μm . (E) Ventral view of the primary constriction. Scale bar, 200 μm . (F) Close-up of the ammonitella edge (arrow) and postammonitella shell covered with fine ribs and growth lines. Scale bar, 10 μm .

one as the dorsal wall of the first whorl (Fig. 14C, dp) and the inner one as the actual wall of the initial chamber (Fig. 14C, pi; he also recognized two other layers of more limited extent, ip and ml). According to him, the actual wall of the initial chamber does not wedge out but forms the external layer of the wall of the first whorl (Fig. 14C, op). This wall also includes two additional layers (Fig. 14C, ip, mp), which first appear on the inner side at the distal end of the initial chamber. In contrast, Bandel (1982, Figs. 41, 43, 46–48) and Tanabe (1989, Fig. 7) argued that the wall of the initial chamber wedges out, but on the inner side, and that the external layer of the wall of the first whorl (Fig. 14D, op) first appears on the outer side near the distal end of the initial chamber (Fig. 14D, arrow).

The most marked change in microstructure in all ammonoids whose microstructure has been studied occurs at the primary constriction (Erben *et al.*, 1968, 1969; Birkelund and Hansen, 1968, 1974; Birkelund, 1981; Kulicki, 1974, 1979; Druschits *et al.*, 1977a). The prismatic layer of the first whorl decreases in thickness, and a large pad of nacre develops on the inside of the shell. This pad of nacre is known as the primary varix (Druschits and Khiami, 1970; Druschits and Doguzhaeva, 1974; Landman and Waage, 1982; also called “*première varice*,” Grandjean, 1910; Dauphin, 1975, 1977; “*nepionic ridge*,” Druschits *et al.*, 1977a,b, 1980; and “*nepionic swelling*,” Kulicki, 1979; we include the primary varix as part of the ammonitella, although this feature was excluded in the original definition of this term by Druschits and Khiami, 1970, p. 30). It parallels the primary constriction and lies close to its adapical end (first illustrated in Hyatt, 1872, Pl. 4, Fig. 11). In some specimens the outer prismatic layer doubles back along the inside edge of the primary varix (Kulicki, 1974, 1979). The postammonitella shell emerges from below the primary varix and consists of both an outer prismatic and an inner nacreous layer (Figs. 1, 12C–F and 14).

2.6. Septa

Schindewolf (1928, 1929, 1951, 1954) called the first septum the proseptum to emphasize its uniqueness relative to all other septa. The proseptum develops at the distal end of the initial chamber (Fig. 15A,C; Erben *et al.*, 1969).

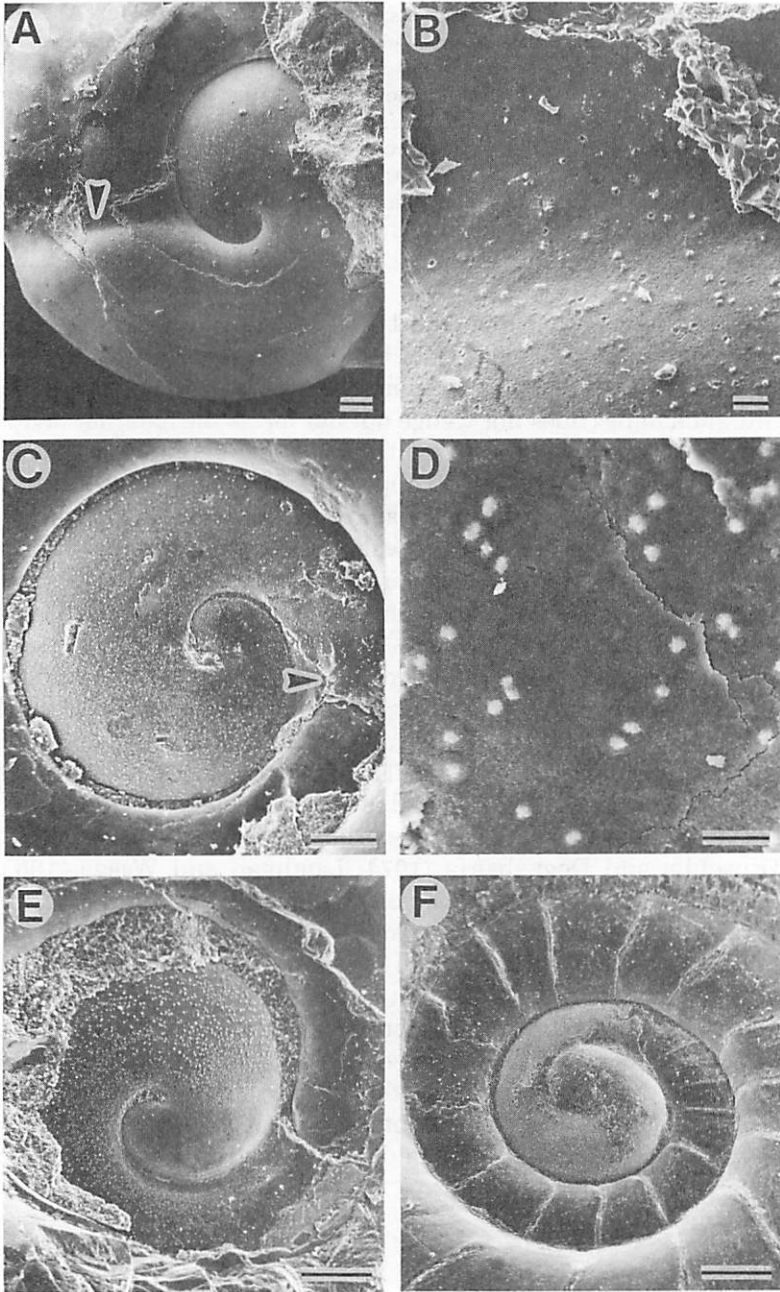


FIGURE 13. Early whorls of Mesozoic ammonoids. (A,B) *Sphenodiscus lenticularis* (Ammonitina), Upper Cretaceous, South Dakota, YPM 34985. (A) View of the ammonitella and primary constriction (arrow). Scale bar, 100 μm . (B) Close-up of tubercles on the ammonitella. Scale bar, 10 μm . (C,D) *Metaplaticeras subtilistriatum* (Ammonitina), Upper Cretaceous, Hokkaido, UMUT MM 18328. (C) View of the ammonitella and primary constriction (arrow). Scale bar, 130 μm . (D) Close-up of tubercles on the ammonitella. Scale bar, 13 μm . (E) *Anapachydiscus* sp. (Ammonitina), Upper Cretaceous, Hokkaido, UMUT MM 18327. The tubercles have coalesced into a single layer covering part of the initial chamber. Scale bar, 90 μm . (F) *Gaudryceras denseplicatum* (Lytoceratina), Upper Cretaceous, Hokkaido, UMUT MM 18322. The postammonitella shell is ornamented with prominent subcostae. Scale bar, 330 μm .

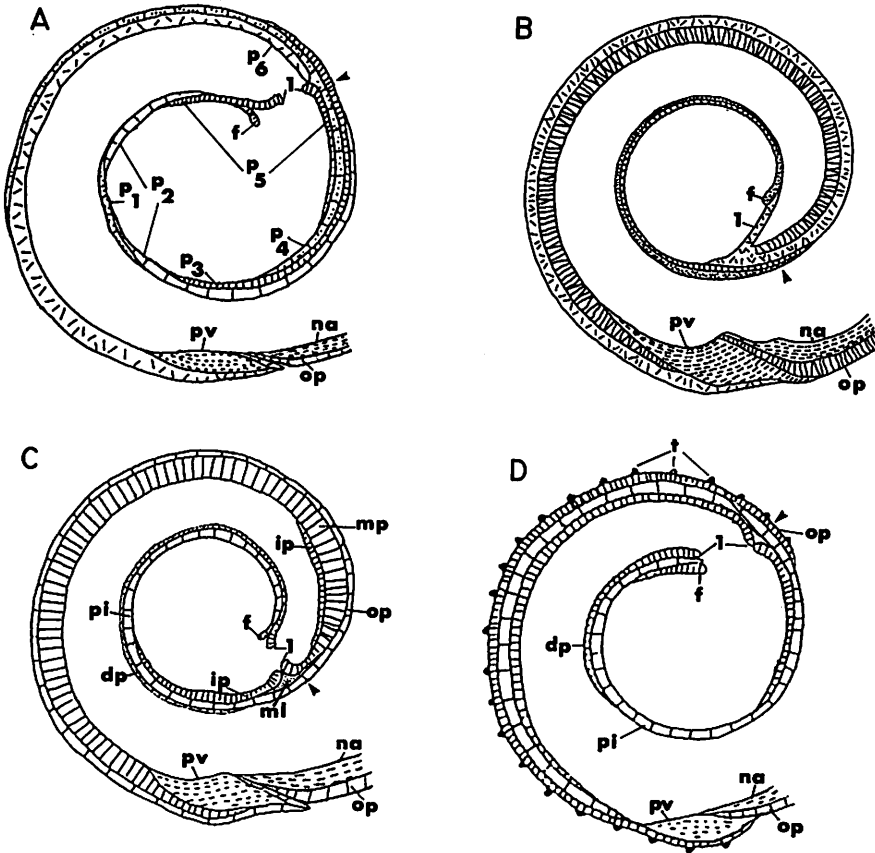


FIGURE 14. Microstructure of the shell wall of the ammonitella as reported by (A) Erben *et al.* (1968, 1969), (B) Birkelund and Hansen (1968, 1974), (C) Kulicki (1979), and (D) Bandel (1982). Abbreviations: 1, proseptum; dp, dorsal prismatic layer of the first whorl; f, flange; ip, inner prismatic layer of the initial chamber or of the first whorl; ml, middle prismatic layer of the initial chamber; mp, middle prismatic layer of the first whorl; na, nacreous layer of the postammonitella shell; op, outer prismatic layer of the first whorl or of the postammonitella shell; pi, prismatic layer of the initial chamber; pv, primary varix; t, tubercles. Arrows indicate the distal end of the initial chamber. See text for explanation.

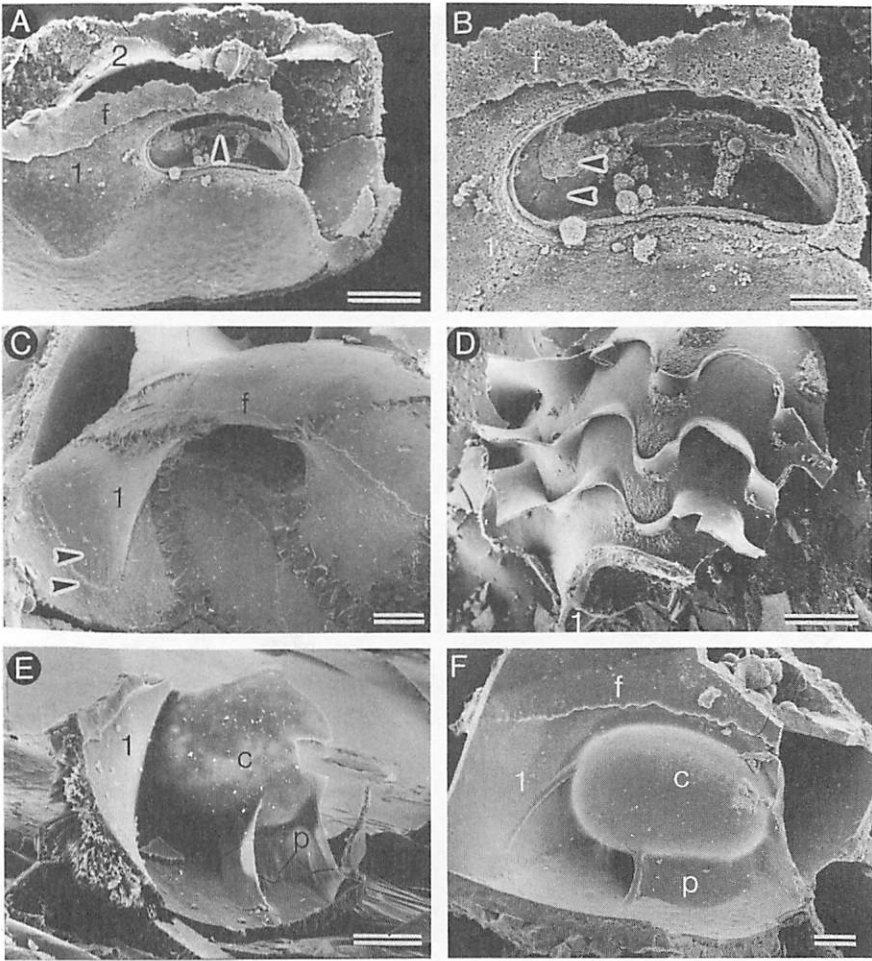


FIGURE 15. Internal features of the ammonitella observed in specimens free of matrix. (A,B) *Scaphites* sp. cf. *S. whitfieldi* (Ancyloceratina), Upper Cretaceous, South Dakota, AMNH 42900. (A) Interior of the initial chamber and first whorl showing the proseptum (1), its neck-like attachment (arrow), flange (f), and second septum (2). Scale bar, 50 μm . (B) Close-up of the proseptum (1), its neck-like attachment (lower arrow), and flange (f). Prismatic attachment deposits (upper arrow) of the siphuncle occur on the neck-like attachment of the proseptum. Scale bar, 20 μm . (C) *Baculites* sp. (Ancyloceratina), Upper Cretaceous, Wyoming, AMNH 42905. Interior of the initial chamber showing the proseptum (1) and flange (f). A prismatic ridge (lower arrow) occurs at the base of the proseptum, and the surface of the proseptum is marked by wrinkles (upper arrow). Scale bar, 40 μm . (D) *Euhoplites* sp. (Ammonitina), Lower Cretaceous, England, AMNH 27261a. Muscle scars are visible on the inside surface of the dorsal wall adoral of the proseptum (1) and the lobes of the next few septa. The first scar actually consists of two separate but connecting scars. Scale bar, 100 μm . (E) *Quenstedtoceras* sp. (Ammonitina), Middle Jurassic, Poland, AMNH 42911. Close-up of the proseptum (1), cecum (c), and prosiphon (p). Note the wrinkles in the prosiphon. Scale bar, 40 μm . (F) *Hypacanthoplites* sp. (Ammonitina), Lower Cretaceous, Germany, AMNH 20952a. Close-up of the proseptum (1), flange (f), cecum (c), and prosiphon (p). Scale bar, 40 μm .

It closes off the initial chamber and appears to form a continuation of the flange, i.e., the inner lip of the initial chamber (Bandel, 1982). There is an opening in the middle of the proseptum that approximately equals the whorl height.

The shape of the proseptum is different from that of all subsequent septa (Schindewolf, 1954; Erben *et al.*, 1969). Variation in the shape of the proseptum and its corresponding suture, the prosuture, was documented first by Branco (1879, 1880) and later by Schindewolf (1928, 1929). Branco described three character states of the prosuture: asellate, latisellate, and angustisellate, depending on the size of the dorsal and ventral saddles. However, this categorization probably needs to be expanded because it does not accommodate the full range of variation observed within the Ammonoidea (see, e.g., House, 1965; Bensaïd, 1974).

The proseptum is prismatic in microstructure (Erben *et al.*, 1969; Birkelund and Hansen, 1974; Druschits *et al.*, 1977a,b). In median cross section, it shows a complex relationship with the shell wall (Erben *et al.*, 1969; Birkelund and Hansen, 1974; Kulicki, 1979). For example, in median cross sections of *Quenstedtoceras*, the ventral portion of the proseptum forms a continuation of the middle prismatic layer of the initial chamber (Fig. 14C, ml; Kulicki, 1979, Figs. 7, 10). In well-preserved specimens free of interior matrix, a prismatic ridge appears at the base of the proseptum, and the surface of the proseptum is marked by wrinkles along the lateral lobes (Fig. 15A,C; Landman and Bandel, 1985).

In some ammonoids, an adorally directed neck-like attachment develops around the proseptal opening (Fig. 15A,B; Landman, 1985, 1987; Landman and Bandel, 1985; Bandel, 1986). This neck-like attachment forms a suture where it joins the shell wall and can easily be mistaken for a second proseptum. Two proseptra have been reported in the Prolecanitina and Goniatitina by Böhmers (1936). This author noted that the first two septa in these forms differ from subsequent septa in having short amphichoanitic necks (necks directed both adapically and adorally). Based on this evidence, he called both septa proseptra, a terminology later adopted by Miller and Unklesbay (1943), Miller *et al.* (1957), and Arkell (1957, p. L101). However, other studies have suggested that these two septa represent the proseptum and second septum with an amphichoanitic neck and a retrochoanitic neck, respectively (Schindewolf, 1954; Tanabe *et al.*, 1994).

The second septum, sometimes called the primary septum, has a shape completely different from that of the proseptum (Fig. 15A; Schindewolf, 1928, 1929, 1951, 1954; Erben *et al.*, 1969). It is characterized by ventral and dorsal lobes and as many as three lateral and umbilical lobes, depending on the suborder (Schindewolf, 1954; Wiedmann and Kullmann, 1981). The second septum is the developmental basis in ontogeny for all subsequent septa.

The distance between the proseptum and second septum varies markedly among suborders. The second septum may be separated from the proseptum and form its own suture. In other ammonoids, such as *Quenstedtoceras*, the

second septum rides dorsally on the proseptum, although the two septa are distinct ventrally (Druschits and Khiami, 1970; Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985). As a result, the second septum in this genus forms an incomplete internal suture (Bandel, 1986).

The microstructure of the second septum, like that of all subsequent septa, differs from that of the proseptum. In all ammonoids in which septal microstructure has been studied (Ammonitina, Lytoceratina, Phylloceratina, and Ancyloceratina), the second and all later septa are composed mainly of nacre (Birkelund and Hansen, 1974; Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985). The observation of a prismatic second septum by Erben *et al.* (1969) has not been substantiated (Bandel, 1986).

2.7. Siphuncle

The bulb-like beginning of the siphuncle, called the cecum, is located in the initial chamber (Fig. 15E,F). Like the rest of the siphuncle, presumably the cecum was originally organic (Bandel, 1982; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986) and, in well-preserved specimens, retains traces of fine wrinkles (Kulicki, 1979).

The shape of the cecum in median cross section is elliptical, hemicircular, or rectangular (Table I). It is elliptical in the Bactritina, Goniatitina (Fig. 16A), Ceratitina (Fig. 16B), Phylloceratina (Fig. 17A), Ancyloceratina (Fig. 17B), and Ammonitina (Fig. 17C,D); this shape probably is the phylogenetically primitive condition. In contrast, the cecum is rectangular in the Prolecanitina (Fig. 16C,D) and hemicircular in the Lytoceratina (Fig. 16E,F).

The cecum is attached to the inside surface of the initial chamber by means of the prosiphon, which consists of one or more bands (Figs. 15E,F, 16, and 17; Munier-Chalmas, 1873; Crickmay, 1925; Zakharov, 1972; Druschits and Doguzhaeva, 1981; this feature was called the "fixator" by Druschits *et al.*, 1977b, 1980). The prosiphon was originally organic, and wrinkles are commonly present along its length (Fig. 15E; Kulicki, 1979). Although there is variation in the morphology of the prosiphon within a single species (Kulicki, 1979; Bandel, 1982, 1986; Landman and Bandel, 1985), it is possible to distinguish two main types in the Ammonoidea as a whole (Grandjean, 1910; Zakharov, 1972, 1974, 1989; Druschits and Doguzhaeva, 1974, 1981; Vavilov and Alekseyev, 1979; Tanabe *et al.*, 1979, 1980; Birkelund, 1981; Landman, 1987; Blind, 1988; Table I). In most Ammonitina, excluding the Amaltheidae, Collignoniceratidae (Fig. 17F), and Placenticeratidae, the prosiphon is long and nearly straight (Fig. 17C-E). In contrast, it is short and curved in the Bactritina, Goniatitina (Fig. 16A), Prolecanitina (Fig. 16C,D), Lytoceratina (Fig. 16E,F), Phylloceratina (Fig. 17A), and some Ancyloceratina (Fig. 17B). In the Ceratitina, the shape and size of the prosiphon are highly variable (Fig. 16B; Weitschat and Bandel, 1991).

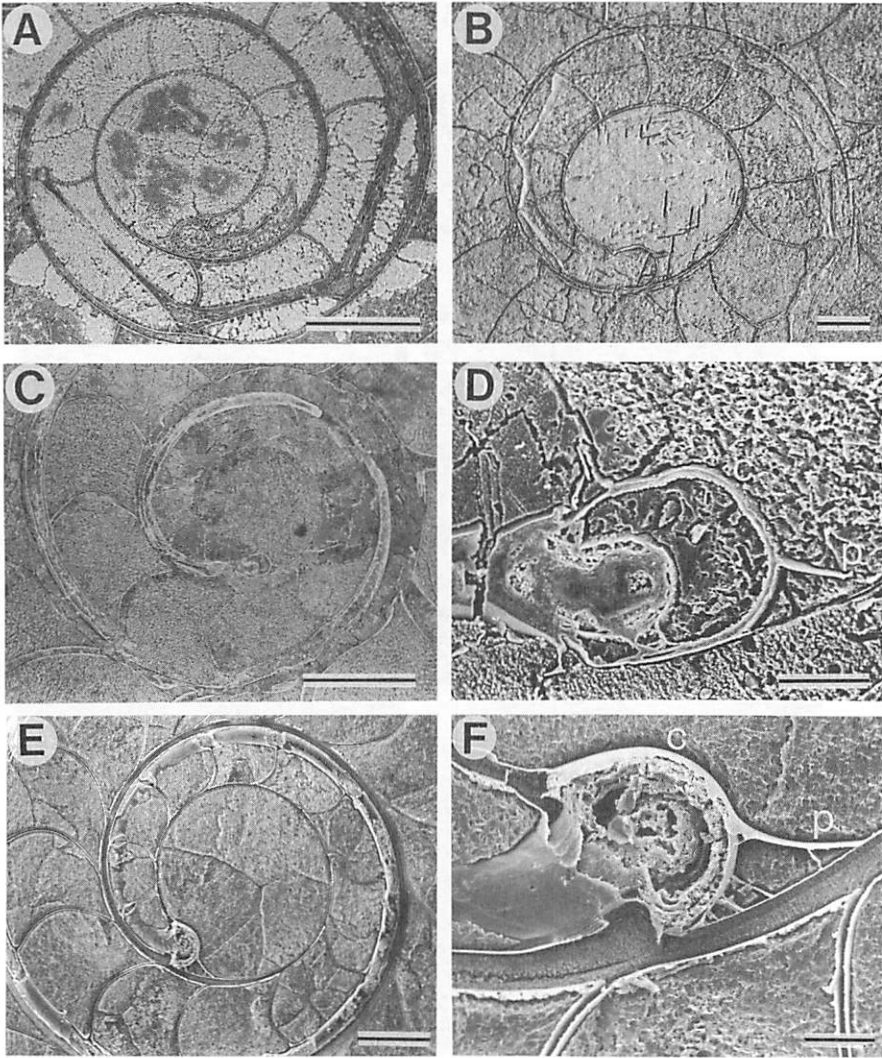


FIGURE 16. Median cross sections through the early whorls of Paleozoic and Mesozoic ammonoids showing the shape of the cecum and prosiphon. (A) *Glaphyrites warei* (Goniatitina), Middle Pennsylvanian, Oklahoma, UMUT PM 19026-1. Scale bar, 250 μm . (B) *Indigirites tozeri* (Ceratitina), Middle Triassic, Spitsbergen, AMNH 44353. Scale bar, 100 μm . (C,D) *Artinskia electraensis* (Prolecanitina), Middle Permian, Nevada, UMUT PM 19040-2. (C) Overall view. Scale bar, 500 μm . (D) Close-up of cecum (c) and prosiphon (p). Scale bar, 50 μm . (E,F) *Gaudryceras striatum* (Lytoceratina), Upper Cretaceous, Hokkaido, UMUT MM (= EES 11). (E) Overall view. Scale bar, 230 μm . (F) Close-up of cecum (c) and prosiphon (p). Scale bar, 42 μm .

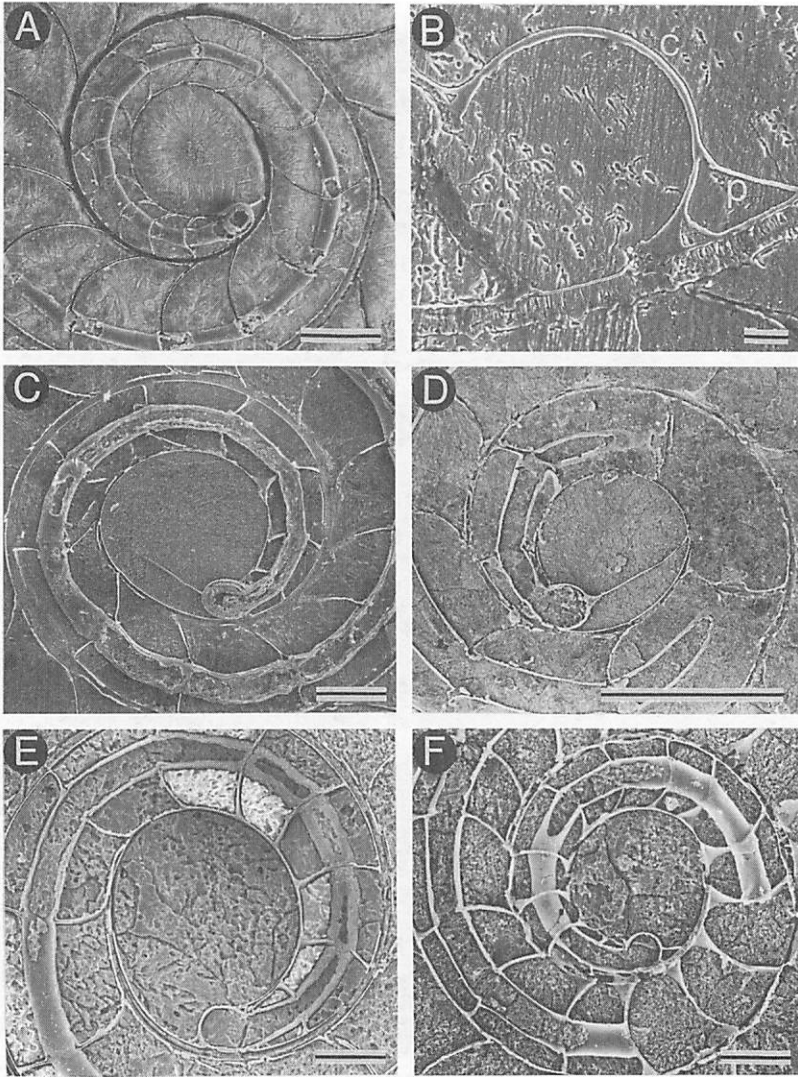


FIGURE 17. Median cross sections through the early whorls of Paleozoic and Mesozoic ammonoids showing the shape of the cecum and prosiphon. (A) *Hypophylloceras subramosum* (Phylloceratina), Upper Cretaceous, Hokkaido, UMUT MM 19683 (= EES 19). Scale bar, 300 μm . (B) *Scaphites preventricosus* (Ancyloceratina), Upper Cretaceous, Montana, AMNH 43035. Close-up of the cecum (c) and prosiphon (p). Scale bar, 10 μm . (C) *Damesites sugata* (Ammonitina), Upper Cretaceous, Hokkaido, UMUT MM 18326 (= EES 37). Scale bar, 160 μm . (D) *Eleganticeras elegantulum* (Ammonitina), Lower Jurassic, England, UMUT MM 19066-1. Scale bar, 500 μm . (E) *Promicroceras* sp. (Ammonitina), Lower Jurassic, England, UMUT MM 19069-1. Scale bar, 124 μm . (F) *Subprionocyclus neptuni* (Ammonitina), Upper Cretaceous, Hokkaido, UMUT MM 19075. Scale bar, 160 μm .

The cecum and siphuncle are attached to the septa by means of prismatic attachment deposits; these have been referred to as "auxiliary deposits" (Fig. 15B; Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985; Chapters 4 and 6, this volume). The initial position of the siphuncle ranges from marginal to central, depending on the suborder (Figs. 16 and 17; Table 1; Druschits and Doguzhaeva, 1974, 1981; Tanabe and Ohtsuka, 1985).

2.8. Muscle Scars

Muscle scars are rarely preserved in the ammonitella, although they have been detected in a few genera of Ceratitina and Ammonitina (see Chapter 3, this volume). Bandel (1982) documented the ontogenetic progression of muscle scars in *Quenstedtoceras*. He identified a muscle scar on the inside surface of the flange, a pair of muscle scars on the adoral face of the proseptum on either side of the proseptal opening, and another pair of muscle scars on the inside surface of the dorsal wall adoral of the second septum. He noted that, adoral of the third septum, these two muscle scars united into a single muscle field. A similar sequence has been reported in *Euhoplites* (Fig. 15D; Landman and Bandel, 1985) and in several genera of Triassic Ceratitina (Weitschat and Bandel, 1991).

3. Sequence of Embryonic Development

Information about the embryonic development of ammonoids comes from two sources: examination of specimens actually preserved at early ontogenetic stages and study of the morphology and microstructure of the early whorls of larger specimens. In order to reconstruct early ontogenetic stages using the second method, it usually is necessary to break down specimens to expose the inner whorls. These two approaches are complementary and provide the best evidence available for determining the sequence of embryonic development.

3.1. Reconstructions Based on the Early Whorls of Larger Specimens

Reconstructions based on the morphology of the early whorls of larger specimens have been suggested by numerous workers (Branco, 1879, 1880; Hyatt, 1894; Smith, 1901; Grandjean, 1910; Shul'ga-Nesterenko, 1926; Schindewolf, 1929; Spath, 1933; Böhmers, 1936; Trueman, 1941; Currie, 1944; Shimansky, 1954; Arkell, 1957; Erben, 1962, 1964, 1966; Erben *et al.*, 1969; Palframan, 1967a; Druschits and Khiami, 1970; Druschits *et al.*, 1977a; Druschits and Doguzhaeva, 1981; Makowski, 1971; Zakharov, 1972; Birkelund and Hansen, 1974; Birkelund, 1981; Kulicki, 1974, 1979; Tanabe *et al.*, 1980;

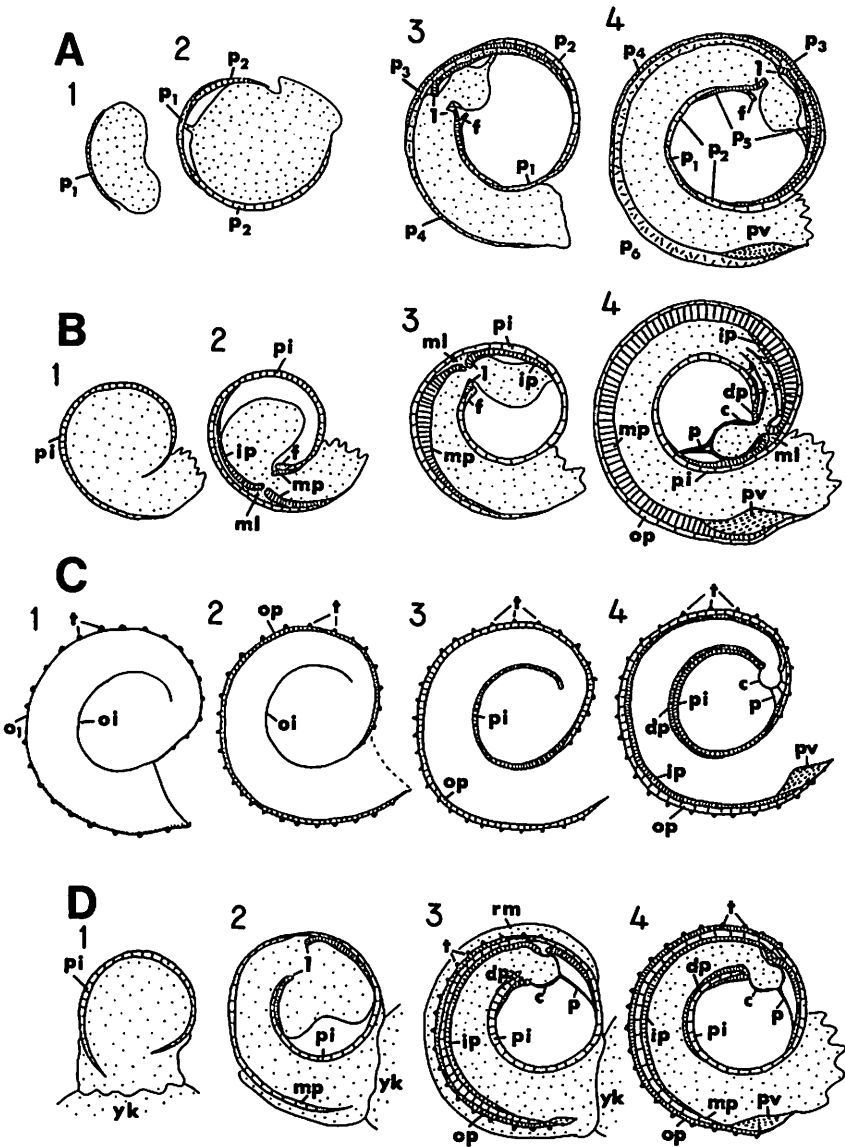


FIGURE 18. Four different models (A–D) depicting the sequence of ammonoid embryonic development (1–4). Animals are represented in median cross section with soft tissues shaded. (A) Erben *et al.* (1969, Fig. 5) described three stages in early ontogeny: an embryonic stage (1,2), a larval stage (3), which was followed by metamorphosis (4), and a postlarval stage (not shown). Six prismatic layers (p₁–p₆) comprise the wall of the initial chamber and first whorl and were secreted sequentially. (B) Kulicki (1979, Fig. 7) emphasized a *Nautilus*-like mode of embryonic shell development. (C) Bandel (1982, Figs. 40, 46, 47) argued that the ammonitella originally consisted of an organic, unmineralized shell. (D) Tanabe (1989, Fig. 7) proposed that the ammonitella was temporarily enveloped by the outer mantle late in embryonic development.

Tanabe, 1989; Lehmann, 1981; Bandel, 1982, 1986; Landman, 1982, 1987; Blind, 1988). We review several of these reconstructions in the next few pages.

The first detailed reconstruction based on SEM data was that of Erben (1962, 1964, 1966) and Erben *et al.* (1968, 1969), who recognized three phases in early ontogeny (Fig. 18A). According to them, in the first phase, the initial chamber was secreted inside the egg capsule. The animal then hatched as a veliger larva with a ciliated velum. During this larval stage, the first whorl, prosepium, flange, cecum, and prosiphon formed. The primary constriction and accompanying varix were thought to have developed during metamorphosis. Following metamorphosis, additional septa were secreted, and a nacreous layer was added to the shell wall.

This reconstruction was based primarily on four lines of evidence:

1. Microstructure of the shell wall. Erben *et al.* (1968, 1969) observed that several of the layers comprising the wall of the initial chamber wedged out on the outer side at the distal end of the initial chamber and were replaced by a new layer that formed most of the wall of the first whorl. They related this change to hatching. However, Kulicki (1979) has suggested that the wall of the initial chamber does not, in fact, wedge out but forms the external layer of the wall of the first whorl (but see also Bandel, 1982). In addition, there is no evidence of a discontinuity on the shell surface at the transition from the initial chamber to the first whorl; if there had been a break in secretion at this point, a discontinuity would be present (Kulicki, 1979, p. 128).
2. Ornamentation. Erben (1962, 1964, 1966) noted a change in the pattern of growth lines ("*Anwachsstreifen*") in phylogenetically primitive ammonoids at the distal end of the initial chamber. For example, he reported that the growth lines in *Mimagoniatites* developed a slight backward projection along the venter at this point; this projection became more pronounced over the course of the first whorl (Erben, 1964, Fig. 4, Pl. 8, Figs. 3–5). Erben (1966, p. 651) interpreted this change as indicating the development of a locomotor organ such as a velum. Bogoslovsky (1969, p. 66) argued that this change reflected instead the development of a funnel in the embryonic stage. Close

FIGURE 18. (Continued) According to his model, the prismatic layer of the initial chamber (pi) and the middle (mp) and inner (ip) prismatic layers of the first whorl were formed by the interior epithelium, whereas the outer prismatic layer of the first whorl (op) with tubercles (t) was secreted by the exterior epithelium of the reflected mantle (rm). Abbreviations: 1, prosepium; c, cecum; dp, dorsal prismatic layer of the first whorl; f, flange; ip, inner prismatic layer of the initial chamber or of the first whorl; ml, middle prismatic layer of the initial chamber; mp, middle prismatic layer of the first whorl; oi, organic wall of the initial chamber; o₁, organic wall of the first whorl; op, outer prismatic layer of the first whorl; p, prosiphon; pi, prismatic layer of the initial chamber; pv, primary varix; rm, reflected mantle; t, tubercles; yk, yolk mass. See text for more details.

inspection of the shell surface reveals that the features in question are not, in fact, growth lines but lirae (see Chapter 12, this volume, for the distinction between growth lines and lirae). The changes in the lirae are gradual, and such gradual changes in ornamentation have been documented in the embryonic development of other molluscs, for example, modern *Nautilus* (see Arnold *et al.*, 1987). In any event, the most marked change in ornamentation in all ammonoids occurs at the primary constriction, not before.

3. Primary varix. Erben *et al.* (1969) interpreted the appearance of nacre late in shell development, in the form of the primary varix, as an indication of metamorphosis because, in contrast, nacre appears early on in the ontogenetic development of *Nautilus*, where metamorphosis is absent. But even in the embryonic development of *Nautilus*, the initial shell material at the cicatrix is not nacreous but prismatic (Arnold *et al.*, 1987). Nacre appears only later, lining the interior of the cap-shaped initial shell.
4. The shape of the proseptum. According to Erben *et al.* (1969; see also Schindewolf, 1954, pp. 230–231), the change in shape from the proseptum to the second septum implies a complete metamorphosis of the ammonoid soft body. However, Bandel (1982, p. 68) has argued that, because the proseptum formed before the formation of the siphuncle, the proseptum has a shape different from that of all later septa. Hewitt (1985) has also pointed out that the shape of the proseptum in Mesozoic ammonoids is an adaptation to “resist circumferential stresses imposed by subsequent whorls.”

The alternative model of early ontogeny is that of direct development in which there are only two phases, embryonic and postembryonic. This model has been suggested by many workers and is widely accepted today (Grandjean, 1910; Böhmers, 1936; Druschits and Khiami, 1970; Druschits *et al.*, 1977a; Druschits and Doguzhaeva, 1981; Zakharov, 1972; Kulicki, 1974, 1979; Birkelund and Hansen, 1974; Tanabe *et al.*, 1980; Tanabe, 1989; Bandel, 1982, 1986; Landman, 1982, 1987).

In the model of direct development, the ammonitella is the embryonic shell. In many species, therefore, the newly hatched ammonoid more or less resembles a miniature adult. The most compelling pieces of evidence for this model are (1) the uniform surface of the ammonitella, without any indication of a discontinuity in secretion, and (2) the abrupt changes in ornamentation, shell shape, and microstructure at the end of the primary constriction. Similarly abrupt changes coincide with hatching in many other molluscs (Bandel, 1975, 1982; Jablonski and Lutz, 1980).

This model is also consistent with the fact that development is direct, without a larval phase, in all living cephalopods whose early development has been studied (Arnold and Williams-Arnold, 1977; Arnold *et al.*, 1987; Wells and Wells, 1977; Bandel and Boletzky, 1979; Boletzky, 1988). Although

the term "larva" sometimes is used in cephalopods to refer to individuals immediately after hatching, these individuals do not undergo any metamorphosis (Ruzhentsev and Shimansky, 1954; Boletzky, 1974, 1993; Wells and Wells, 1977). Hence, such an animal is not a "larva" in the strict sense of the term.

Within the framework of direct development, it is difficult to reconstruct the exact sequence in which the ammonitella formed. We review three models that cover most of the possible variations.

Based on his study of *Quenstedtoceras*, Kulicki (1979) suggested that the ammonitella formed by accretionary growth (Fig. 18B). According to him, the initial chamber was secreted by a cap-like secretory zone. Subsequently, this zone differentiated into two subzones, an anterior one, which formed the outer layer of the wall of the first whorl, and a posterior one, which formed the inner layers of the walls of the initial chamber and first whorl. Kulicki inferred that, during formation of the prosepium, the soft body withdrew from the initial chamber, after which the cecum and prosiphon developed. The primary varix was thought to have formed right before hatching during a temporary withdrawal of the mantle margin, at which time secretion of nacreous material occurred.

Bandel (1982, 1986, 1989, 1991) introduced a new concept in his model of embryonic development (Fig. 18C). He argued that in the early stages of embryonic development, the ammonitella consisted of an organic, unmineralized shell. He based this argument on studies of well preserved specimens of *Quenstedtoceras* and the observation that in living cephalopods with small embryonic shells (<2 mm in size), e.g., *Spirula*, the embryonic shell is initially entirely organic. According to Bandel, the organic ammonitella was secreted in uninterrupted contact with the gland cells of the mantle. The surface of this organic shell was devoid of growth lines and, in Mesozoic ammonoids, was covered with a tuberculate microornamentation. This shell was thought to have been mineralized rapidly by prismatic needles from the inside; this formed an outer layer of uniform thickness, preserving the original ornamentation of the organic shell. A similar process of rapid mineralization has been reported in modern archaeogastropods (Bandel, 1986). It is important to note that this outer layer was inferred to have formed only on the exposed portions of the ammonitella. In closely coiled ammonitellas, the portion of the initial chamber covered by the first whorl still would have been unmineralized at this stage. Subsequently, several prismatic layers supposedly were secreted from the inside, starting backward from the aperture; this served to thicken the original, outer layer and complete the rest of the wall of the initial chamber.

Bandel (1982) also reconstructed the developmental sequence of the internal features. According to his model, a portion of the visceral mass first differentiated to form the cells of the siphuncle. Subsequently, the rest of the visceral mass withdrew from the initial chamber, remaining attached to it only by retractor muscles, thought to have been located on the inside surface of the flange, and by siphuncular tissue, thought to have been located on the inside

surface of the initial chamber. The visceral mass then formed the organic precursor of the proseptum, which assumed the shape of the apical end of the visceral sac. Thus, according to Bandel, the proseptum formed before the formation of the actual siphuncle, explaining the unique shape of the proseptum relative to all other septa. After mineralization of the proseptum, the retractor muscles reattached in two bundles onto the adoral face of the proseptum. Finally, the cecum and prosiphon developed, which would have permitted the removal of cameral liquid from the initial chamber.

Tanabe (1989) presented an alternative model to explain the presence of tubercles and absence of growth lines on the ammonitellas of Mesozoic ammonoids (Fig. 18D). He proposed that the ammonitella was enveloped temporarily by the outer mantle late in embryonic development, a process similar to that which occurs in modern *Spirula*. According to this model, the outer mantle secreted a thin prismatic layer with tuberculate ornamentation on the exposed portions of the shell. Tanabe based this hypothesis on his observation that tubercles commonly cover several contiguous prisms on the outer layer, suggesting that the tubercles developed after the completion of the underlying prisms. Following the secretion of this outer layer, the mantle was thought to have migrated back toward the aperture, resuming its earlier position.

3.2. Evidence from Specimens Preserved at Early Ontogenetic Stages

Several fossils interpreted as ammonoid eggs have been reported from the Mesozoic (Dreyfuss, 1933; Wetzel, 1959; Lehmann, 1966, 1981; Müller, 1969). These structures appear as hollow spheres approximately 0.5 mm in diameter. They are filled with calcite or the same material as the surrounding matrix and show no evidence of embryonic shells inside. They occur either scattered in the rock associated with ammonitellas and small juveniles (Dreyfuss, 1933; Wetzel, 1959) or clustered as a mass within the body chambers of adults (Lehmann, 1966, 1981; Müller, 1969). With their small size and lack of embryonic shells inside, these small spheres may represent eggs at an early stage of development (Kulicki, 1979). This interpretation is consistent with the fact that the eggs of many modern cephalopods grow in size during embryogenesis (Zuev and Nesis, 1971).

These ammonoid eggs, if truly that, would shed some light on mode of development (e.g., possible brooding within the body chamber in some ammonoids) but provide no information about the embryonic development of the shell. The best source of such information comes from accumulations of embryonic shells preserved at different developmental stages. These accumulations may represent egg masses in which the individual embryos developed at different rates (asynchronous development). These eggs may have been deposited on the sea floor (Mapes *et al.*, in prep.) or, alternatively, may

have been laid originally as gelatinous masses in midwater, settling to the bottom only afterward, a phenomenon similar to that observed in the midwater squid *Illex illecebrosus* (see O'Dor, 1983; Mangold, 1987; Hewitt, 1993; Chapter 16, this volume).

Kulicki (1989) and Kulicki and Doguzhaeva (1994) documented the development of the embryonic shell in the Early Cretaceous genus *Aconeceras* based on actual specimens from the Symbirsk area, Russia (see Chapter 4, this

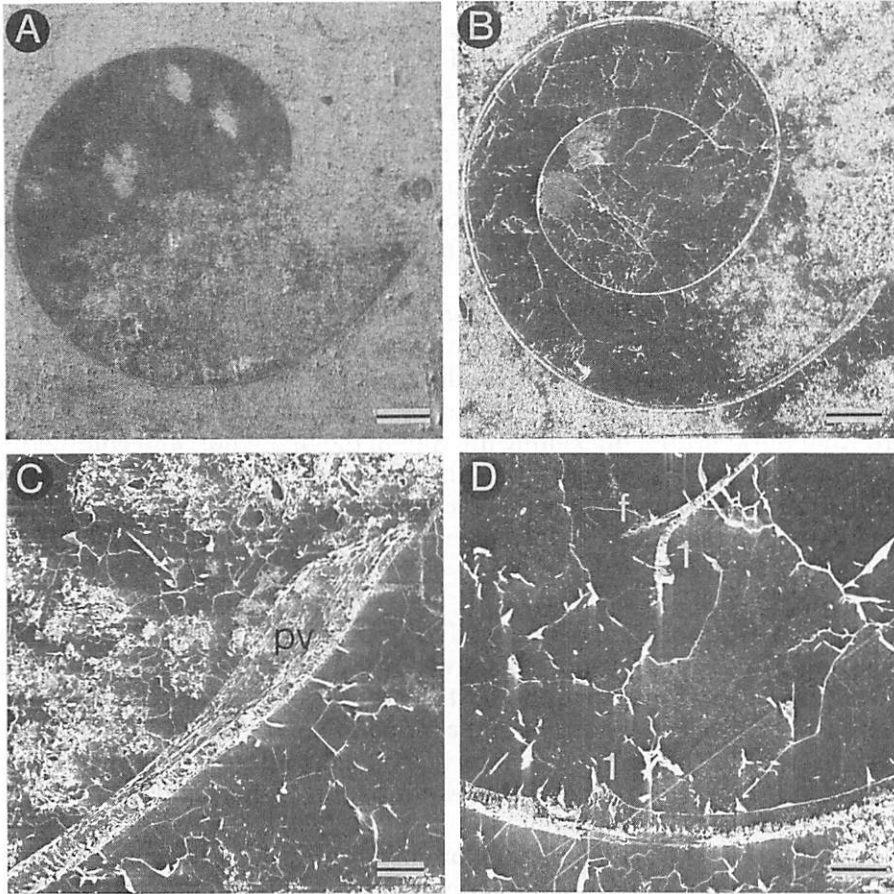


FIGURE 19. Median cross sections through embryonic shells of *Baculites* (Ancyloceratina) showing two developmental stages. (A) Embryonic shell of *Baculites* sp. cf. *B. asper* or *B. codyensis*, Upper Cretaceous, Montana, AMNH 44834. This specimen is at an early stage of development; the portion of the initial chamber covered by the first whorl is still unmineralized. Scale bar, 100 μ m. (B–D) Embryonic shell of *Baculites* sp. cf. *B. mariasensis* or *B. sweetgrassensis*, Upper Cretaceous, Montana, AMNH 43203. This specimen is at a much later stage of development; both the initial chamber and first whorl are now completely mineralized. (B) Overall view showing the proseptum and primary varix. Scale bar, 100 μ m. (C) Close-up of the primary varix (pv). Scale bar, 20 μ m. (D) Close-up of the proseptum (1) and flange (f). Scale bar, 20 μ m.

volume; see also Ruzhentsev, 1974, Pl. 1, Fig. 1; Druschits and Khiami, 1970). They described three successive stages in embryonic development: (1) mineralization of the exposed portions of the initial chamber and first whorl ending at the primary constriction, (2) mineralization of the wall of the initial chamber near the site of the future proseptum, and (3) mineralization of the rest of the wall of the initial chamber and formation of the primary varix and proseptum.

Similar developmental stages have been observed in specimens of Late Cretaceous *Baculites* from North America (Fig. 19; see Landman, 1982). In specimens corresponding in their degree of development to the first stage described by Kulicki and Doguzhaeva (1994), the portion of the initial chamber covered by the first whorl is not preserved and is presumed to have been still organic (Fig. 19A). Alternatively, it is possible that this part of the initial chamber was mineralized but simply broke off. However, these specimens are so similar to those described by Kulicki (1989) and Kulicki and Doguzhaeva (1994, Fig. 6A) that a more likely hypothesis is that all of these specimens represent the same stage in the embryonic development of the shell.

Both of these studies strongly support Bandel's (1982, 1986) model according to which the ammonitella of Mesozoic ammonoids initially consisted only of an organic shell. As Bandel hypothesized, the exposed portions of the ammonitella mineralized first. Thereafter, mineralization proceeded backward from the aperture, thickening the wall of the first whorl and completing the rest of the wall of the initial chamber. However, it is unclear from these studies whether the tuberculate ornamentation of the ammonitella was originally present on the surface of the organic shell as suggested by Bandel (1982) or whether it developed later as proposed by Tanabe (1989).

In contrast to these data supporting the existence of an originally organic ammonitella in Mesozoic ammonoids, Tanabe *et al.* (1993) presented evidence suggesting an accretionary mode of growth in Carboniferous *Goniatitina* (Fig. 20). Based on actual specimens of *Aristoceras* and *Vidrioceras*, these authors identified three successive stages in the formation of the embryonic shell: (1) mineralization of the initial chamber, (2) mineralization of part of the first whorl, and (3) mineralization of the rest of the first whorl and formation of the primary varix and proseptum.

In addition to the accumulations of embryonic shells referred to in the previous paragraphs, there are numerous reports of intact ammonitellas that provide further information about shell development [as listed in geological order: Mississippian *Goniatitidae* from Alberta (Schindewolf, 1959); Carboniferous *Goniatitidae* from Britain and Ireland (Ramsbottom, 1981; Tanabe *et al.*, 1995); Pennsylvanian *Bactritoidea* from Texas and Kansas (Hecht and Mapes, 1990); Early Permian ammonoids from the Aktyubinsk area, Russia (Ruzhentsev, 1974, Pl. 1, Fig. 2); Middle Triassic *Ceratitidae* from Nevada (H. Bucher, personal communication, 1993); Late Triassic ammonoids from Austria (Wiedmann, 1973); Early Jurassic ammonoids from France (Dreyfuss,

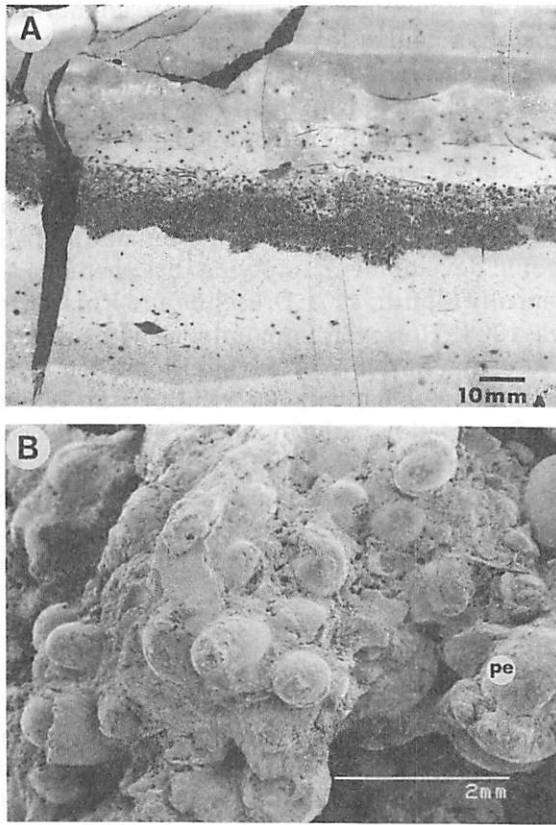


FIGURE 20. (A) Cross section through a mass of preserved ammonitellas of *Vidrioceras* sp. and *Aristoceras* sp. (both Goniatitina) in a carbonate concretion from the Upper Pennsylvanian of Kansas. (B) Close-up of a weathered portion of the concretion showing densely packed ammonitellas and small postembryonic shells (pe). (After Tanabe *et al.*, 1993, Fig 1.)

1933); Early Jurassic *Arnioceras* from England (Trueman, 1941); Early Jurassic *Harpoceras elegans* from Germany (Wetzels, 1959); Middle Jurassic *Quenstedtoceras* from Poland (Blind, 1979; Chapter 4. this volume); Late Jurassic Perisphinctidae from Cuba (Kulicki and Wierzbowski, 1983); Late Cretaceous *Baculites* from North America (Smith, 1901) and Jordan (Bandel, 1982); Late Cretaceous *Scaphites* from North America (Landman, 1985); and Late Cretaceous *Baculites* or *Hoploscaphites* from Denmark (Birkelund, 1979, 1981)]. These ammonitellas all terminate at the primary constriction and accompanying varix, suggesting that hatching occurred after formation of these features. The primary varix probably developed just prior to hatching during a temporary withdrawal of the mantle margin (Kulicki, 1979).

Internal features are sometimes present in these ammonitellas and consist of the cecum, prosiphon, and at least one septum. However, the cecum and prosiphon are rarely preserved, probably because these structures were originally organic (see Wetzel, 1959; Landman, 1982). [Alternatively, the absence of a prosiphon may indicate that this feature had not formed yet. According to R.A. Hewitt (personal communication, 1993), the prosiphon formed by shrinkage of cameral membranes as the fluid (or gel) was pumped out of the initial chamber.] The proseptum is always present and probably formed near the end of embryonic development, implying that nacreous septa developed only postembryonically (Smith, 1901; Druschits and Khiami, 1970; Landman, 1982; Tanabe *et al.*, 1993). However, ammonitellas with more than one septum also occur, indicating that in some species additional septa may have formed before hatching (Blind, 1979; Bandel, 1982; Kulicki and Wierzbowski, 1983). Such species-specific variation in the number of embryonic septa has, in fact, been reported in modern sepioids (Bandel and Boletzky, 1979). However, Landman (1985) has cautioned that some supposedly embryonic shells with more than one septum may actually represent fragments of larger specimens that have broken at the embryonic–postembryonic shell boundary.

4. Posthatching Mode of Life

Like the adults of most ammonoids, ammonitellas were probably neutrally buoyant at or soon after hatching and, consequently, could have lived in the water column rather than on the bottom (Zakharov, 1972; Kulicki, 1974, 1979; Druschits *et al.*, 1977a; Tanabe *et al.*, 1980; Tanabe and Ohtsuka, 1985; Bandel, 1982, 1986; Landman, 1985; Ward and Bandel, 1987; Westermann, 1990; Weitschat and Bandel, 1991; Kakabadzé and Sharikadzé, 1993; Chapter 16, this volume; but compare Wetzel, 1959). The initial chamber represents a relatively large float that originally was filled with liquid (or gel; R.A. Hewitt, personal communication, 1993); this liquid (or gel) subsequently was removed via the cecum and prosiphon (Trueman, 1941; Zakharov, 1972, 1989; Tanabe *et al.*, 1980; Landman, 1987; Hewitt, 1988). This event probably occurred just prior to or immediately after hatching; in the latter case, it would have resulted in a slight delay before entry into the water column.

The size relationships among the component parts of the ammonitella provide additional support for the hypothesis of neutral buoyancy. As noted previously, there is a strong positive correlation between the volume of the initial chamber (phragmocone) and the volume of the ammonitella (phragmocone plus body chamber) both within and among species (Fig. 7; Shigeta, 1993). In contrast, there is a negative correlation between ammonitella angle and the whorl expansion rate of the ammonitella so that larger ammonitella angles are associated with more closely coiled ammonitellas (Tanabe and Ohtsuka, 1985, Fig. 6). Both of these correlations probably reflect volumetric relationships necessary to maintain neutral buoyancy.

Density calculations performed on actual ammonitellas are also consistent with the hypothesis of neutral buoyancy. Shigeta (1993) reported measurements on ammonitellas of several Cretaceous ammonoids, assuming that animals hatched with a single septum and without any cameral liquid in the initial chamber. According to his measurements, the density of these ammonitellas was less than that of sea water. However, such measurements are subject to error because of the difficulty of estimating the volume of shell material and cameral liquid and the weight of the soft body (Westermann, 1993; Chapter 16, this volume). Allowing for the limitations of this methodology, the values calculated fall within the range of neutral buoyancy.

With the possible exception of the Agoniatitina and Bacritina, most ammonoids probably followed a planktic mode of life at hatching (Zakharov, 1972; Kulicki, 1974; "pseudolarval stage" of Kulicki, 1979; Druschits *et al.*, 1977a; Landman, 1982, 1985; Tanabe and Ohtsuka, 1985; Morton, 1988; Westermann, 1990; Shigeta, 1993; see Chapter 16, this volume). This hypothesis is based on two functional arguments: the small size of the ammonitella and its nearly spherical shape, both of which are presumably adaptations to life in the plankton (Kulicki, 1979). A planktic mode of life is common among many modern coleoids including nektic squids and sepioids and benthic octopods with relatively small eggs (Boletzky, 1974, 1977, 1987b; Vecchione, 1987). Among octopods, this mode of life is considered the phylogenetically primitive condition, whereas a benthic mode of life at hatching is considered derived (Boletzky, 1987b, 1992).

In the plankton newly hatched ammonoids may have been active swimmers or more probably, passive vertical migrators, drifting with surface currents (Birklund and Hansen, 1974; Kulicki, 1974; Ward and Bandel, 1987; Westermann, 1990; Weitschat and Bandel, 1991; Chapter 16, this volume; see Sturani, 1971, p. 46, for a description of another mode of life in algal meadows, especially for *Lytoceratina* and *Phylloceratina*). This planktic stage may have lasted several weeks or months, depending on the size of the ammonitella (Kulicki, 1979), its rate of growth (Westermann, 1990; Shigeta, 1993), and the mode of life of the adult (see Boletzky, 1974, 1977, 1987b). In addition, Shigeta (1993) suggested that the duration of the planktic stage was dependent on the rate of increase in the density of the newly hatched ammonoid (but see Westermann, 1993). In the plankton, ammonoids may have secreted as many as two whorls, reaching shell diameters of 3–5 mm (Westermann, 1954, 1990; "neanoconch" of Westermann, Chapter 16, this volume; Kulicki, 1974; Landman, 1987).

A planktic mode of life at hatching is consistent with a number of observations on the mode of occurrence of specimens preserved at this stage. There are several occurrences of ammonitellas and very small juveniles with older juveniles and adults and mostly nektic and planktic organisms in environments in which the bottom was anaerobic with oxygenated water above (Upper Jurassic Jagua Formation in Cuba, Kulicki and Wierzbowski, 1983; Middle Triassic Fossil Hill Member of the Favret Formation in Nevada, H.

Bucher, personal communication, 1993; Silberling and Nichols, 1982; Upper Cretaceous Sharon Springs Member of the Pierre Shale in Wyoming, Landman, 1988). These assemblages are “quasiautochthonous” and strongly suggest that the newly hatched ammonoids were planktic or at least nektic. In addition, there are numerous examples of mixed assemblages of juvenile and adult ammonoids from presumably well-oxygenated environments in which very small juveniles (<3–4 mm shell diameter) are rare or absent (Middle Jurassic Bearraig Sandstone Formation in northwest Scotland, Morton, 1988; Upper Cretaceous Yezo Group in Hokkaido, Japan, Shigeta, 1993; Upper Cretaceous Fox Hills Formation in South Dakota, Landman and Waage, 1993; Landman and Klofak, in prep.). These data suggest that newly hatched ammonoids may have lived in a different environment from that of older juveniles and adults, although their absence may also result from taphonomic processes. A planktic mode of life at hatching is also consistent with the fact that some Mesozoic ammonoids such as the Late Cretaceous heteromorph *Turrilites costatus* have broad biogeographic distributions despite the fact that the adults of these species are presumed to have been poor swimmers (Ward and Bandel, 1987; but see Chapter 16, this volume, for an alternative explanation).

5. Reproductive Strategy

The embryos of cephalopods are generally larger than those of other molluscs (Naef, 1922; Berthold and Engeser, 1987; Engeser, 1990). Two size classes can be distinguished within the cephalopods as a whole: embryos less than about 2 mm in size versus embryos greater than about 2 mm in size (Bandel and Boletzky, 1979; Bandel, 1991; Engeser, 1990). The embryos of ammonoids, to judge from their embryonic shells, fall into the first category. In marked contrast, the quintessential example of the second category is the embryo of *Nautilus*, which measures approximately 30 mm in size (Arnold *et al.*, 1987; Landman, 1988).

The reproductive strategy of ammonoids was similar to that of many coleoids (Engeser, 1990; Tanabe *et al.*, 1993). The common occurrence of ammonitellas in dense concentrations suggests that ammonoids produced a large number of offspring, probably thousands of embryos per female (Ward and Bandel, 1987; Landman, 1988; see Mangold, 1987, pp. 172–178, for a comparison of the number of offspring in coleoids). The ammonoid embryonic shell is small relative to that of the adult, implying little parental investment per egg. As a corollary, many ammonoids, like the majority of coleoids, were probably semelparous, reproducing once and then dying. The length of embryonic development probably also was similar to that in many coleoids, which lasts several tens of days depending on temperature conditions (Boletzky, 1974, 1977, 1987a; Hewitt, 1988; Weitschat and Bandel, 1991). The occurrence of large numbers of preserved ammonitellas further suggests that

many species experienced a high degree of mortality at hatching (Kulicki, 1979; Kulicki and Wierzbowski, 1983; Bandel, 1982; Landman, 1987). Juveniles also are abundant in some ammonoid assemblages (Ziegler, 1962; Callomon, 1963; Lehmann, 1966; Kennedy and Cobban, 1976; Kulicki and Wierzbowski, 1983; Morton, 1988; Shigeta, 1993; Landman and Waage, 1993), implying that this age group comprised a large portion of the population.

Several authors have characterized the reproductive strategy of ammonoids relative to that of present-day *Nautilus* as r-selected versus K-selected (House, 1985; Landman, 1988; Hewitt, 1988; see also Vermeij, 1978). *Nautilus* is iteroparous, with females laying a few large eggs over several breeding seasons (Landman, 1988). The eggs are extremely yolk-rich, and the embryonic shell gradually forms by accretionary growth (Arnold *et al.*, 1987). The eggs develop very slowly, with hatching in aquaria taking more than 1 year after egg laying (Carlson, 1991). In addition, in *Nautilus*, as in other K-selected species, juveniles comprise a small portion of the population (Saunders and Ward, 1987).

Although ammonoids are clearly r-selected relative to *Nautilus*, within the ammonoids themselves, as in modern coleoids (Boletzky, 1977; Mangold, 1987), there is a wide range of variation. For example, the Agoniatitina, with ammonitellas nearly 3 mm in diameter, contrast with most other ammonoids with ammonitellas approximately 0.5–1.5 mm in diameter. Even among these more typical ammonoids, variation in ammonitella size may correlate with differences in number of offspring and length of embryonic development (e.g., deep-water Lytoceratina versus shallow-water Ammonitina). Moreover, differences in the embryonic size of species may correlate with differences in biogeographic distribution and population structure. For example, in Late Cretaceous ammonoids from Japan, Tanabe and Ohtsuka (1985) and Shigeta (1993) reported that species with smaller embryonic shells (e.g., collignoniceratids, whose embryonic shells are $\leq 700 \mu\text{m}$) were more restricted in their facies distribution and displayed more juveniles in their preserved assemblages than species with larger embryonic shells (e.g., Lytoceratina, Phylloceratina, and Desmoceratidae, whose embryonic shells are $\geq 1000 \mu\text{m}$). These correlations are probably part of a still larger picture that includes differences in environmental tolerance, ecological specialization, and adult mode of life.

6. Future Research

One of the most conspicuous gaps in any review of ammonoid embryonic development is the lack of studies on Paleozoic ammonoids. There are few or no recent data on the microstructure and internal features of such groups as the Anarcestina and Bactritina. There also is little information on the ornament of the embryonic shells in these groups. However, the hypothesis that there is more than one pattern of embryonic development within the Am-

monoidea (Tanabe *et al.*, 1993) requires further testing using additional data from as many ammonoid groups as possible.

In addition, the reproductive strategy of ammonoids clearly links them more closely to coleoids than to nautiloids (Engeser, 1990; Tanabe *et al.*, 1993; Jacobs and Landman, 1993). This relationship between ammonoids and coleoids needs to be more fully explored by explicit studies comparing embryonic development and posthatching mode of life in both these groups. Within the Ammonoidea, the diversity, albeit limited, in the size and shape of embryonic shells also suggests that more attention must be given to studies linking early ontogeny with other species-specific traits such as biogeographic distribution, population structure, and evolutionary longevity.

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Appendix I. Dimensions of the Ammonitella in 11 Suborders of the Ammonoidea

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks
Anarcestina	Anarcestaceae	Anarcestidae	<i>Archoceras (A.) paeckelmanni</i> Schindewolf	—	1.0*				Bensaïd (1974)
			<i>Archoceras (A.) tataense</i> Bensaïd	—	1.0*				Bensaïd (1974)
Gephuroceratina	Gephurocerataceae	Gephuroceratidae	<i>Probeloceras lutheri</i> (Clarke)	—	1.06				NYSM 12726
			<i>Manticoceras (M.) bullatum</i> Wedekind	0.68–0.85	1.2*				Clausen (1969)
			<i>Manticoceras (M.) affine</i> (Stein.)	0.75–1.10	—				Clausen (1969)
			<i>Manticoceras (M.) orbiculum</i> (Beyr.)	0.68–0.88	—				Clausen (1969)
			<i>Manticoceras (M.) adorfense</i> Wedekind	0.65–0.83	—				Clausen (1969)
			<i>Manticoceras (M.) serratum</i> (Stein.)	0.63–0.70	—				Clausen (1969)
			<i>Manticoceras (M.) intumescens</i> (Beyr.)	0.65–0.80	—				Clausen (1969)
			<i>Manticoceras (M.) cordatum</i> (Sdgbr.)	0.68–0.83	—				Clausen (1969)
			<i>Manticoceras (M.) crassum</i> Wedekind	0.68–0.83	—				Clausen (1969)
			<i>Manticoceras (M.) drevermanni</i> Wedekind	0.68–0.78	—				Clausen (1969)
			<i>Manticoceras (M.) galeatum</i> Wedekind	0.70–0.90	—				Clausen (1969)
Agoniatitina	Agoniatitaceae	Agoniatitidae	<i>Agoniatites obliquus</i> (Whidborne)	1.4*	2.4*				Wissner and Norris (1991)
			<i>Agoniatites holzapfeli</i> Wedekind	1.4*	2.3*				Erben (1964)
			<i>Agoniatites fulguralis</i> (Whidborne)	1.6*	2.5*				Erben (1964)
			<i>Agoniatites</i> sp.	—	2.6*				Erben (1964)
		Mimagoniatitidae	<i>Mimagoniatites (M.) cf. zorgensis</i> (Roemer)	1.2–1.3*	2.2*				Erben (1964)

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks		
Tornoceratina	Mimocerataceae		<i>Mimagoniatites (M.) fecundus</i> (Barrande)	1.1*	1.9–2.1*				Erben (1964)		
			<i>Convoluticeras lardeuxi</i> Erben	0.8*	1.8*				Erben (1964)		
			<i>Cyroceratites gracilis</i> (Meyer)	0.9*	1.5*				Erben (1964)		
	Tornocerataceae		<i>Tornoceras (T.) arkonense</i> House	0.8	1.5*				House (1965)		
			<i>Tornoceras (T.) uniangulare widderi</i> House	—	1.5				House (1965)		
			<i>Tornoceras (T.) uniangulare aldenense</i> House	0.89–1.0	1.49				House (1965)		
			<i>Tornoceras (T.) uniangulare uniangulare</i> (Conrad)	0.8	—				House (1965)		
			<i>Tornoceras (T.) uniangulare obesum</i> Clarke	0.98	—				House (1965)		
			<i>Tornoceras (T.) concentricum</i> House	0.6	1.4				House (1965)		
			<i>Tornoceras (T.) arcuatum</i> House	0.71	—				House (1965)		
Goniatitina	Dimorphocerataceae	Dimorphoceratidae	<i>Aulatornoceras bicostatum</i> (Hall)	0.5	1.4–1.5*				House (1965)		
			<i>Dimorphoceras politum</i> (Shumard)	—	0.90	—	—	—	SUI 1755		
			Girtyoceratidae	<i>Girtyoceras meslerianum</i> (Girty)	0.45	0.96	400	—	—	UMUT PM 19023-1	
				<i>Eumorphoceras plummeri</i> (Miller and Youngquist)	—	1.04	—	—	—	UMUT PM 19030	
				<i>Gatherites morrowensis</i> (Miller and Moore)	0.42	0.84	385	—	—	UMUT PM 19032	
			Goniatitaceae	Goniatitidae	<i>Goniatites</i> sp. aff. <i>G. crenistria</i> Phillips	0.48	0.95	382	0.11	0.23	UMUT PM 19019-1
						0.60	1.10	372	0.08	0.13	UMUT PM 19019-2
					<i>Goniatites choctawensis</i> Shumard	0.56	1.06	345	—	—	UMUT PM 19020-1
						0.55	1.09	386	0.06	0.07	UMUT PM 19020-2
					<i>Goniatites multiliratus</i> Gordon	0.53	0.94	384	—	—	UMUT PM 19033
Agathiceratidae	<i>Agathiceras applini</i> Plummer and Scott	0.48	1.03	—	0.05	0.10	SUI 1766				

Neoglyphio- cerataceae	Neoglyphio- ceratidae	<i>Neoglyphioceras abramovi</i> Popow	0.49–0.52	0.92–0.94	360	0.05	0.10	Zakharov (1974)	
	Cravenocera- tidae	<i>Cravenoceras richardsonianum</i> (Girty)	0.46	0.80	367	—	—	UMUT PM 19021	
Gastriocera- cerataceae	Gastriocera- tidae	<i>Cravenoceras incisum</i> (Hyatt)	0.53	0.95	380	—	—	UMUT PM 19022-1	
		<i>Pseudogastrioceras simulator</i> (Girty)	0.40	0.80	364	0.04	0.17	SUI 1740	
	Reticulo- ceratidae	Glaphyritidae	<i>Pseudogastrioceras fedorowi</i> (Karpinsky)	0.38–0.40	0.74–0.76	370	—	—	Bogoslovskaya (1959)
			<i>Paragastrioceras</i> sp.	0.48	0.84	360	—	—	Bogoslovskaya (1959)
			<i>Owenoceras bellilineatum</i> (Miller and Owen)	—	0.87	355	—	—	SUI 1713
			<i>Arkanites relictus</i> (Quinn, McCaleb and Webb)	0.51	0.81	386	—	—	UMUT PM 19029
		Glaphyritidae	<i>Glaphyrites hyattianus</i> (Girty)	0.59	1.03	405	0.05	0.08	UMUT PM 19025-2
			<i>Glaphyrites warei</i> (Miller and Owen)	0.46	0.88	385	0.06	0.13	UMUT PM 19026-1
				0.45	0.86	372	0.05	0.12	UMUT PM 19026-2
			<i>Glaphyrites jonesi</i> (Miller and Owen)	0.54	0.96	375	—	—	UMUT PM 19027
Homoceratidae	Goniolobocera- tidae	<i>Glaphyrites clinei</i> (Miller and Owen)	0.39	0.71	382	—	—	UMUT PM 19028	
			0.52	0.94	364	—	—	SUI 1735	
		<i>Glaphyrites welleri</i> (Smith)	0.35	0.81	356	0.03	0.09	SUI 1726	
		<i>Homoceras subglobosum</i> (Bisat)	0.53	0.91	385	0.10	0.19	UMUT PM 19024-2	
		<i>Gonioloboceras welleri</i> Smith	—	1.92	384	—	—	SUI 1743	
		<i>Properrinites bakeri</i> (Plummer and Scott)	0.70	1.19	—	—	—	SUI 1790	
Shumardi- taceae	Perrinitidae	<i>Perrinites</i> sp.	1.03	2.31	383	—	—	AMNH 41183a	
			0.89	2.00	382	0.16	0.18	AMNH 41183b	
Adriani- taceae	Adrianitidae	<i>Texoceras</i> sp.	—	0.97	—	—	—	UMUT PM 19037-1	
		<i>Adrianites dunbari</i> Miller and Furnish	0.63	1.00	365	0.12	0.19	SUI 1764	

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks
			<i>Crimites elkoensis</i> Miller, Furnish and Clarke	0.37	0.65	345	—	—	UMUT PM 19038
			<i>Crimites krotowi</i> Karpinsky	0.34–0.39	0.73–0.81	365	—	—	Bogoslovskaya (1959)
	Popanocerataceae	Popanoceratidae	<i>Popanoceras annae</i> Ruzhencev	—	0.66	—	—	—	SUI 1777
			<i>Peritrochia erebus</i> Girty	0.45	0.88	410	—	—	UMUT PM 19039-1
			<i>Peritrochia typicus</i> Ruzhencev	0.40–0.42	0.88	340	—	—	Bogoslovskaya (1959)
			<i>Stacheoceras subinterruptum</i> (Krot.)	0.39–0.46	0.84	380	—	—	Bogoslovskaya (1959)
	Neiococerataceae	Metalegoceratidae	<i>Metalegoceras baylorense</i> White	0.45	0.85	365	0.02	0.05	UMUT PM 19035
	Cyclolobaceae	Cyclolobidae	<i>Mexioceras guadalupense</i> (Girty)	0.52	0.93	378	—	—	SUI 1782
		Vidrioceratidae	<i>Vidrioceras</i> sp.	0.44	0.80	361	—	—	UMUT PM 19329
	Thalassocerataceae	Thalassoceratidae	<i>Eothalassoceras inexpectans</i> (Miller and Owen)	0.37	0.66	356	0.03	0.08	UMUT PM 19036-1
				0.37	0.66	360	—	—	UMUT PM 19036-2
			<i>Thalassoceras gemmellaroi</i> Karpinsky	0.30–0.34	0.58–0.66	380	—	—	Bogoslovskaya (1959)
			<i>Aristoceras</i> sp.	0.36	0.75	368	—	—	UMUT PM 19010
		Bisatoceratidae	<i>Bisatoceras</i> n. sp.	0.34	0.62	354	0.11	0.31	UMUT PM 19033-1
Prolecanitina	Medlicottiaceae	Pronoritidae	<i>Pronorites praepermicus</i> Karpinsky	0.61	1.22	330	0.26	0.43	SUI 1686
			<i>Neopronorites vulgaris</i> (Karpinsky)	0.44–0.54	1.00–1.10	310–320	—	—	Bogoslovskaya (1959)
			<i>Neopronorites permicus</i> (Tschernow)	0.44–0.56	0.96–1.10	340	—	—	Bogoslovskaya (1959)
		Medlicottiidae	<i>Artinskia electraensis</i> (Plummer and Scott)	0.48	1.01	340	—	—	UMUT PM 19040-1
				0.52	1.16	355	0.05	0.10	UMUT PM 19040-2
			<i>Artinskia artiensis</i> (Grünewaldt)	0.43–0.44	0.90	345	—	—	Bogoslovskaya (1959)

		<i>Medlicottia orbignyana</i> (Verneuil)	0.34	0.72	326–330	—	—	Bogoslovskaya (1959)	
Prolecanitaceae	Daraelitidae	<i>Daraelites elegans</i> Tschernow	0.45	1.06	—	—	—	Bogoslovskaya (1959)	
Ceratitina	Noritaceae	Olenikitidae	<i>Olenikites spiniplicatus</i> (Mojsisovics)	0.35	0.73	325	0.05	0.14	AMNH 44347
			<i>Subolenekites altus</i> (Mojsisovics)	0.40	0.72	315	0.11	0.28	UMUT MM 19041
			<i>Svalbardiceras spitzbergensis</i> Frebold	0.37	0.70	290	—	—	AMNH 44349
			<i>Svalbardiceras sibiricum</i> (Mojsisovics)	0.39	0.89–0.91	260	—	—	Zakharov (1971)
		Ophiceratidae	<i>Nordophiceras schmidti</i> (Mojsisovics)	0.38	0.78	260	0.04	0.10	Zakharov (1971)
			<i>Ophiceras</i> sp.	0.39	0.74	—	—	—	Zakharov (1974)
		Meekoceratidae	<i>Arctoceras septentrionale</i> (Diener)	0.51	0.68	—	—	—	Zakharov (1974)
			<i>Kingites</i> sp.	0.42	0.68	347	0.28	0.67	Zakharov (1974)
			<i>Boreomeekoceras keyserlingi</i> (Mojsisovics)	0.35	0.73	325	—	—	UMUT MM 19045-1
			<i>Arctomeekoceras rotundatum</i> (Mojsisovics)	0.37	0.82	280–285	0.07	0.19	Zakharov (1971)
			<i>Wyomingites spathi</i> (Kummel)	0.29	—	—	—	—	Zakharov (1974)
			<i>Wyomingites chaoi</i> (Kiparisova)	0.29	—	—	—	—	Zakharov (1974)
		Paranannitidae	<i>Paranannites aspenensis</i> Hyatt and Smith	0.37	0.66	238	0.05	0.14	Zakharov (1974)
			<i>Paranannites spathi</i> (Frebold)	0.35	0.67	330	—	—	UMUT MM 19343
			<i>Prospingites grambergi</i> Popow	0.38–0.41	0.68–0.79	265	0.03–0.09	0.22	Zakharov (1971)
Megaphyllitaceae	Parapopano-ceratidae	<i>Parapopanoceras paniculatum</i> Popow	0.34	0.66	333	0.06	0.18	AMNH 44352	
		<i>Stenopopanoceras mirabile</i> Popow	0.38	0.72	270	—	—	UMUT MM 19054	
		<i>Amphipopanoceras asseretoi</i> Dagys and Konstantinov	0.38	0.69	335	—	—	UMUT MM 19055	
		Megaphyllitidae	<i>Megaphyllites prometheus</i> Shevyrev	0.53–0.60	0.94–1.05	270–280	—	—	Druschits and Doguzhaeva (1981)

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks
	Nathorsti- taceae	Nathorstitidae	<i>Indigirites tozeri</i> Weitschat and Lehmann	0.32–0.33	0.59–0.68	330	0.15	0.47	AMNH 44353, UMUT MM 19056
			<i>Stolleyites tenuis</i> (Stolley)	0.36	0.62	320	0.06	0.17	AMNH 44354
	Arcestaceae	Cladiscitidae	<i>Phyllocladiscites basarginensis</i> Zakharov	0.59	0.76–0.96	265	0.10	0.17	Zakharov (1974)
		Arcestidae	<i>Arcestes</i> sp.	0.37	0.63	—	—	—	Zakharov (1974)
	Ceratitaceae	Ceratitidae	<i>Frechites laqueatus</i> (Lindstroem)	0.46	0.71	288	0.05	0.11	AMNH 44357
			<i>Frechites humboldtensis</i> (Hyatt and Smith)	0.59	—	—	—	—	Arkad'yev and Vavilov (1984)
			<i>Frechites</i> sp.	0.60	1.32	270	—	—	Arkad'yev and Vavilov (1984)
			<i>Gymnotoceras falciforme</i> (Smith)	0.38	0.69	270	—	—	Arkad'yev and Vavilov (1984)
			<i>Gymnotoceras meeki</i> (Mojsisovics)	0.39–0.45	0.72–0.73	270	0.22	0.49	Arkad'yev and Vavilov (1984)
			<i>Gymnotoceras rotelliforme</i> (Meek)	0.45	—	—	—	—	Arkad'yev and Vavilov (1984)
			<i>Anagymnotoceras varium</i> (McLearn)	0.38	0.86	340	—	—	UMUT MM 19344
		Sibiritidae	<i>Sibirites eichwaldi</i> Mojsisovics	0.35–0.37	0.60–0.67	260	0.04	0.11	Zakharov (1971)
			<i>Parasibirites grambergi</i> Popow	0.40	0.71	265	0.02	0.05	Zakharov (1971)
		Keyser- lingitidae	<i>Keyserlingites</i> sp.	0.64	0.81–0.82	300	0.26	0.40	Zakharov (1971)
	Dinaritaceae	Columbitidae	<i>Columbites</i> sp.	0.46	0.73	240	0.02	0.04	Zakharov (1974)
			<i>Subcolumbites multiformis</i> Kiparisova	0.34–0.41	0.63	240	0.05	0.13	Zakharov (1971)
	Danubitaceae	Danubitidae	<i>Czekanowskites rieberi</i> Dagys and Weitschat	0.39	0.80	305	—	—	AMNH 44358
		Longobardi- tidae	<i>Grambergia taimyrensis</i> Popow	0.34	0.76	295	—	—	Zakharov (1971)
	Sagecera- taceae	Sageceratidae	<i>Pseudosageceras</i> sp.	0.57	0.96	295	0.07	0.07	Zakharov (1971)

		Hedenstroemiidae	<i>Hedenstroemia hedenstroemi</i> (Keyserling)	0.63	—	287–296	0.13	0.21	Zakharov (1974)
			<i>Hedenstroemia mojsisovicsi</i> Diener	0.45–0.53	—	—	—	—	Zakharov (1974)
	Pinacocerataceae	Ptychitidae	<i>Aristoptychites kolymensis</i> Kiparisova	0.54	0.96	368	0.12	0.22	AMNH 44360
		Gymnitidae	<i>Placites polydactylus oldhami</i> Mojsisovics	0.39	—	—	0.04	0.09	Zakharov (1974)
Phylloceratina	Phyllocerataceae	Ussuritidae	<i>Eophyllites</i> sp.	0.042–0.43	—	—	—	—	Zakharov (1971)
			<i>Indigiophyllites spitsbergensis</i> (Oeberg)	0.46	1.02	330	0.07	0.15	AMNH 44362
			<i>Calliphylloceras velledae</i> (Michelin)	0.43–0.56	0.80–0.88	280–300	0.08	0.19	Druschits and Doguzhaeva (1981)
			<i>Calliphylloceras subalpinum</i> (Anthula)	0.45	0.80	275	—	—	Druschits and Khiami (1970)
			<i>Ptychophylloceras ptychoicum</i> (Quenstedt)	0.38–0.41	0.69	260	—	—	Druschits and Doguzhaeva (1981)
			<i>Holcophylloceras</i> sp.	0.46–0.59	0.70–0.91	270	0.07–0.10	0.15–0.17	Druschits and Doguzhaeva (1981)
			<i>Holcophylloceras guettardi</i> (Rasp.)	0.45–0.55	0.70–0.91	270–280	0.04–0.07	0.18	Druschits and Doguzhaeva (1981)
			<i>Partschiceras</i> sp.	0.41–0.49	0.63–0.85	260–280	0.04–0.08	0.14	Druschits and Doguzhaeva (1981)
			<i>Partschiceras japonicum</i> (Matsumoto)	0.46	0.92	272	—	—	Shigeta (1993)
			<i>Hypophylloceras subramosum</i> (Shimizu)	0.53–0.66	0.90–1.15	270–292	0.06–0.12	0.10–0.12	Tanabe <i>et al.</i> (1979)
			<i>Hypophylloceras hetonaiensis</i> (Matsumoto)	0.43	0.90	280	—	—	Shigeta (1993)
			<i>Phyllopachyceras ezoense</i> (Yokoyama)	0.47–0.58	0.85–1.30	284–377	0.02–0.13	0.04–0.27	Tanabe <i>et al.</i> (1979)

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks	
			<i>Phyllopachyceras</i> sp.	0.44	0.76	—	—	—	Druschits and Khiami (1970)	
Lytocera- tina	Lytocera- taceae	Lytoceratidae	<i>Eurystomiceras polychelictum</i> Bockh	0.39–0.42	0.78–0.84	290– 300	0.03	0.08	Druschits and Doguzhaeva (1981)	
			<i>Biasaloceras subsequens</i> (Karakasch)	0.32–0.34	—	—	—	—	Druschits and Khiami (1970)	
			<i>Protetragonites tauricus</i> Kul.-Voron.	0.65	—	—	—	—	Druschits and Khiami (1970)	
		Tetrago- nitacae	Tetragonitidae	<i>Tetragonites duvalianus</i> d'Orbigny	0.50–0.70	0.94–1.18	300– 330	0.03– 0.07	0.06– 0.11	Druschits and Doguzhaeva (1981)
	<i>Tetragonites hulensis</i> Murphy			0.50	1.04	312	—	—	Shigeta (1993)	
				<i>Tetragonites glabrus</i> (Jimbo)	0.56	1.08	331	—	—	Shigeta (1993)
				<i>Tetragonites popetensis</i> Yabe	0.42	0.97	340	—	—	Shigeta (1993)
				<i>Tetragonites minimus</i> Shigeta	0.50–0.60	0.90–1.05	320– 340	0.06	0.10	Shigeta (1989)
				<i>Tetragonites terminus</i> Shigeta	0.93–1.05	1.7–1.90	330– 345	0.12	0.13	Shigeta (1989)
				<i>Gabbioceras latericarinatum</i> Anthula	0.49	0.88–0.98	280– 300	0.04	0.10	Druschits and Doguzhaeva (1981)
				<i>Gabbioceras angulatum</i> Anderson	0.44	0.88	300	0.09	0.20	AMNH 44370
				<i>Gabbioceras michelianum</i> (d'Orbigny)	0.42	0.90	281	—	—	Shigeta (1993)
				<i>Pseudophyllites indra</i> (Forbes)	0.58	1.48	327	—	—	Shigeta (1993)
				<i>Saghalinites teshioensis</i> Matsumoto	0.56	1.19	340	—	—	Shigeta (1993)
			Gaudry- ceratidae	<i>Eotetragonites aureum</i> (Anderson)	0.29	0.93	312	—	—	Druschits and Doguzhaeva (1981)
				<i>Eotetragonites balmensis</i> (Breistroffer)	0.50	0.98	347	0.09	0.18	AMNH 44368

			<i>Gaudryceras stefaninii</i> Venzo	0.40	0.93	318	—	—	Shigeta (1993)
			<i>Gaudryceras denseplicatum</i> (Jimbo)	0.71–0.86	1.39–1.65	320–335	0.11	0.16	Tanabe <i>et al.</i> (1979)
			<i>Gaudryceras striatum</i> (Jimbo)	0.66–0.69	1.12–1.39	342–353	0.09	0.15	Ohtsuka (1986)
			<i>Gaudryceras tombetsense</i> Matsumoto	0.64	1.42	348	—	—	Shigeta (1993)
			<i>Anagaudryceras limatum</i> (Yabe)	0.62	1.28	365	0.07	0.11	AMNH 44373
			<i>Anagaudryceras yokoyamai</i> (Yabe)	0.69	1.41	365	—	—	Ohtsuka (1986)
			<i>Anagaudryceras nanum</i> Matsumoto	0.56	1.26	315	—	—	Shigeta (1993)
			<i>Anagaudryceras tetragonum</i> Matsumoto and Kanie	0.58	1.26	323	—	—	Shigeta (1993)
			<i>Anagaudryceras matsumotoi</i> Morozumi	0.59	1.32	338	—	—	Shigeta (1993)
			<i>Kossmatella agassiziana</i> Pictet	0.52–0.67	0.94–1.27	300–315	0.04–0.07	0.08–0.10	Druschits and Doguzhaeva (1981)
			<i>Parajaubertella kawakitana</i> Matsumoto	0.60–0.66	1.12	270	0.04–0.07	0.12	Druschits and Doguzhaeva (1981)
			<i>Zelandites</i> sp. aff. <i>Z. inflatus</i> Matsumoto	0.67–0.68	1.19–1.24	320–336	0.06	0.09	Tanabe <i>et al.</i> (1979)
			<i>Zelandites mihoensis</i> Matsumoto	0.46	1.00	312	—	—	Shigeta (1993)
			<i>Zelandites kawanoi</i> (Jimbo)	0.57	1.19	345	—	—	Shigeta (1993)
			<i>Zelandites varuna</i> (Forbes)	0.54	1.22	342	—	—	Shigeta (1993)
			<i>Karsteniceras obatai</i> Matsukawa	0.27	0.75	305	—	—	Shigeta (1993)
Ancylorceratina	Ancylorcerataceae	Ancylorceratidae	<i>Ptychoceras renngarteni</i> Egonin	0.50	0.85	330	0.33	0.66	Druschits and Doguzhaeva (1981)
		Ptychocerataidae	<i>Luppovia</i> sp.	0.37	0.70	290	—	—	Doguzhaeva and Mikhailova (1982)
	Douvillei-cerataceae	Douvillei-ceratidae	<i>Diadochoceras nodosocostatiforme</i> (Shimizu)	0.30	0.77	291	—	—	Shigeta (1993)

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks
			<i>Diadochoceras</i> sp.	0.38–0.45	0.70–0.80	260– 270	0.08	0.16	Druschits and Doghuzhaeva (1981)
	Deshaye- sitaceae	Deshaye- sitidae	<i>Deshayesites deshayesi</i> (d'Orbigny)	0.42–0.56	0.91–1.09	300	0.10– 0.21	0.24– 0.38	Druschits and Doghuzhaeva (1981)
		Parahoplitidae	<i>Acanthohoplites</i> sp.	0.33–0.45	0.62–0.88	270– 280	0.07– 0.13	0.21– 0.29	Druschits and Doguzhaeva (1981)
			<i>Colombiceras</i> sp.	0.35–0.41	0.60–0.63	280– 300	0.07	0.30	Druschits and Doguzhaeva (1981)
			<i>Nolaniceras</i> sp.	0.38–0.45	0.73–0.85	270– 280	0.08– 0.14	0.21– 0.35	Druschits and Doguzhaeva (1981)
			<i>Hypacanthoplites subcornuianus</i> (Shimizu)	0.40	0.93	290	—	—	Shigeta (1993)
			<i>Hypacanthoplites</i> sp.	0.38–0.49	0.73–0.92	260– 270	0.18	0.33	Druschits and Doguzhaeva (1981)
			<i>Nodosohoplites sinuosocostatus</i> Egoian	0.38–0.41	0.71–0.76	250– 270	0.10– 0.11	0.27	Druschits and Doguzhaeva (1981)
			<i>Parahoplites melchioris</i> Anthula	0.55–0.70	1.13–1.29	315– 330	0.25– 0.26	0.50– 0.59	Druschits and Doguzhaeva (1981)
	Scaphitaceae	Scaphitidae	<i>Scaphites planus</i> (Yabe)	0.40–0.55	0.73–0.95	280	0.08	0.15	Tanabe (1977a), Tanabe <i>et al.</i> (1979)
			<i>Scaphites yonekurai</i> Yabe	0.44	0.87	295	—	—	Shigeta (1993)
			<i>Scaphites pseudoaequalis</i> Yabe	0.35–0.46	0.64–0.80	295	0.12	0.27	Tanabe (1977b)
			<i>Scaphites larvaeformis</i> Meek and Hayden	0.28–0.36	0.52–0.65	266– 300	—	—	Landman (1987)

<i>Scaphites carlilensis</i> Moreman	—	0.59–0.60	274	—	—	Landman (1987)
<i>Scaphites warreni</i> Meek and Hayden	0.27–0.38	0.60–0.72	266– 290	—	—	Landman (1987)
<i>Scaphites whitfieldi</i> Cobban	0.25–0.40	0.55–0.74	260– 308	0.04	0.12	Landman (1987)
<i>Scaphites nigricollensis</i> Cobban	0.34–0.40	0.60–0.76	253– 308	—	—	Landman (1987)
<i>Scaphites corvensis</i> Cobban	0.31	0.67	282	—	—	Landman (1987)
<i>Scaphites preventricosus</i> Cobban	0.29–0.42	0.58–0.71	257– 292	0.03	0.09	Landman (1987)
<i>Scaphites depressus</i> Reeside	0.32–0.40	0.68–0.83	282– 292	—	—	Landman (1987)
<i>Clioscaphtes vermiformis</i> (Meek and Hayden)	0.29–0.44	0.60–0.82	259– 306	—	—	Landman (1987)
<i>Hoploscaphtes nicolletii</i> (Morton)	0.39–0.46	0.72–0.81	288– 316	—	—	Landman and Waage (1993)
<i>Hoploscaphtes comprimus</i> (Owen)	—	0.65–0.67	—	—	—	Landman and Waage (1993)
<i>Jeletzkytes spedeni</i> Landman and Waage	0.40–0.42	0.72–0.80	292– 302	—	—	Landman and Waage (1993)
<i>Jeletzkytes nebrascensis</i> (Owen)	0.41	0.68	310	—	—	Landman and Waage (1993)
<i>Discoscaphites conradi</i> (Morton)	0.37–0.43	0.72–0.80	299– 320	—	—	Landman and Waage (1993)
<i>Discoscaphites gulosus</i> (Morton)	0.34–0.38	0.67–0.77	294– 313	—	—	Landman and Waage (1993)
<i>Discoscaphites rossi</i> Landman and Waage	0.31–0.37	0.65–0.72	296– 314	—	—	Landman and Waage (1993)
<i>Otoscaphtes puerculus</i> (Jimbo)	0.43–0.58	0.71–0.92	285	—	—	Tanabe (1977a), Tanabe <i>et al.</i> (1979)
<i>Otocaphites klamathensis</i> (Anderson)	0.37–0.48	0.67–0.83	285	—	—	Tanabe (1977b)
<i>Otoscaphtes matsumotoi</i> Tanabe	0.43	0.80	285	—	—	Shigeta (1993)

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks	
Ammonitina	Turrilitaceae	Baculitidae	<i>Baculites</i> sp.	—	0.78	331	—	—	Landman (1982)	
	Hildocerataceae	Hildoceratidae	<i>Eleganticeras elegantulum</i> (Young and Bird)	0.40–0.42	0.80–0.88	277–292	0.28	0.71	Tanabe and Ohtsuka (1985)	
		Graphoceratidae	<i>Graphoceras opalinum</i> (Rein)	0.36	—	—	0.21	0.58	Grandjean (1910)	
	Psilocerataceae	Arietitidae	<i>Arietites</i> sp.	0.35	0.64	284	—	—	Tanabe and Ohtsuka (1985)	
			<i>Arietites kridion</i> Hehl.	0.37	—	—	0.05	0.14	Grandjean (1910)	
			<i>Coroniceras reynsei</i> (Spath)	0.30	0.59	280	0.04	0.13	UMUT MM 19684	
	Eoderocerataceae	Amaltheidae	<i>Amaltheus margaritatus</i> d'Orbigny	0.42	—	310	0.06	0.14	Grandjean (1910)	
			<i>Amauroceras ferrugineum</i> (Simpson)	0.56	1.00	300	0.05	0.09	Unregistered Hamburg Univ. specimen	
			<i>Pleuroceras</i> sp.	0.50	1.06	277	—	—	Tanabe and Ohtsuka (1985)	
			Eoderoceratidae	<i>Promicroceras</i> sp.	0.42–0.43	0.71–0.75	280–286	0.25	0.58	UMUT MM 19069-1-2
			Dactyloceratidae	<i>Peronoceras fibulatum</i> (Sowerby)	0.45	0.89	312	0.22	0.49	Ohtsuka (1986)
	Stephanicerataceae	Sphaeroceratidae	<i>Sphaeroceras brongniarti</i> (Sowerby)	0.34	—	—	0.25	0.73	Grandjean (1910)	
	Spirocerataceae	Spiroceratidae	<i>Spiroceras calloviense</i> Morris	0.47	0.84	325	0.25	0.53	YPM 01854	
Haplocerataceae	Oppeliidae	<i>Aconeceras trautscholdi</i> Sinzov	0.30–0.35	0.63	295	—	—	Druschits and Khiami (1970)		
			0.34–0.38	0.64–0.90	275–360	0.08–0.17	0.24–0.50	Druschits and Doguzhaeva (1981)		
		<i>Sanmartinoceras</i> sp.	0.42–0.45	0.84	300	0.14	0.31	Druschits and Doguzhaeva (1981)		

Perisphinctaceae	Craspiditidae	<i>Simbirskites coronatiformis</i> Pavlow	0.55–0.60	1.05–1.12	300–315	0.11–0.40	0.20–0.67	Druschits and Doguzhaeva (1981)
		<i>Simbirskites elatus</i> Pavlow	0.57–0.60	1.05–1.06	—	—	—	Druschits and Doguzhaeva (1981)
		<i>Simbirskites</i> sp.	0.48	0.98	308	0.23	0.48	Druschits and Doguzhaeva (1981)
		<i>Speetonicerias versicolor</i> (Trautschold)	0.53–0.63	1.02–1.15	300	0.21–0.38	0.39–0.60	Druschits and Doguzhaeva (1981)
		<i>Craspedodiscus discofalcatus</i> Lahusen	0.55–0.70	1.13–1.20	300–315	0.15–0.56	0.27–0.72	Druschits and Doguzhaeva (1981)
		<i>Craspedodiscus</i> sp.	0.65	1.26	330	0.40	0.62	Druschits and Doguzhaeva (1981)
Desmocera- taceae	Desmocera- tidae	<i>Beudanticeras laevigatum</i> Sowerby	0.51–0.55	0.99	310	—	—	Druschits and Khiami (1970)
			0.49–0.55	0.77–0.99	330	0.17	0.31–0.35	Druschits and Doguzhaeva (1981)
		<i>Beudanticeras beudanti</i> (Brongniart)	0.44	1.06	330	0.38	0.86	Dauphin (1975)
		<i>Zurcherella falcistriata</i> (Anthula)	0.38–0.42	0.76–0.80	282–290	—	—	Druschits and Khiami (1970)
			0.38–0.42	0.66–0.84	270–290	0.21–0.27	0.57–0.64	Druschits and Doguzhaeva (1981)
		<i>Desmoceras kossmati</i> Matsumoto	0.40	0.90	305	—	—	Shigeta (1993)
		<i>Desmoceras japonicum</i> (Yabe)	0.45–0.48	0.95–0.98	317–337	—	—	Ohtsuka (1986), Shigeta (1993)
<i>Desmoceras ezoanum</i> Matsumoto	0.48	1.22	305	—	—	Shigeta (1993)		
	<i>Damesites latidorsatus</i> (Michelin)	0.41	0.85	320	0.29	0.71	Dauphin (1975)	

Suborder	Superfamily	Family	Species	PD (mm)	AD (mm)	AA (deg)	PL (mm)	PL/PD	Remarks
			<i>Damesites ainuanus</i> Matsumoto	0.35–0.38	0.67–0.73	290– 308	0.15	0.40	Tanabe <i>et al.</i> (1979), Ohtsuka (1986)
			<i>Damesites damesi</i> (Jimbo)	0.36–0.46	0.83–0.95	307– 360	0.15– 0.26	0.32– 0.57	Tanabe <i>et al.</i> (1979), Shigeta (1993)
			<i>Damesites semicostatus</i> Matsumoto	0.34–0.47	0.77–0.91	313– 320	0.26	0.66	Tanabe <i>et al.</i> (1979), Shigeta (1993)
			<i>Tragodesmocerooides subcostatus</i> Matsumoto	0.36–0.47	0.83–0.92	304– 314	—	—	Tanabe <i>et al.</i> (1979), Tanabe and Ohtsuka (1985)
			<i>Desmophyllites diphylloides</i> (Forbes)	0.44–0.47	0.83–0.89	298– 320	—	—	Ohtsuka (1986)
			<i>Desmophyllites</i> sp.	0.43	0.84	317	0.27	0.62	Tanabe and Ohtsuka (1985), Ohtsuka (1986)
			<i>Microdesmoceras tetragonum</i> Matsumoto and Muramoto	0.43	0.94	305	—	—	Shigeta (1993)
			<i>Melchiorites</i> sp.	0.32–0.36	0.67–0.70	270– 290	0.17– 0.25	0.53– 0.71	Druschits and Doguzhaeva (1981)
			<i>Valdedorsella akuschaensis</i> (Anthula)	0.28	0.68	308	—	—	Shigeta (1993)
			<i>Pseudohaploceras nipponicus</i> (Shimizu)	0.32	0.79	302	—	—	Shigeta (1993)
			<i>Puzosia orientale</i> Matsumoto	0.36	0.83	310	—	—	Shigeta (1993)
			<i>Mesopuzosia pacifica</i> Matsumoto	0.37–0.43	0.83–0.84	302– 310	0.28	0.66	Tanabe <i>et al.</i> (1979), Shigeta (1993)
			<i>Mesopuzosia yubarensis</i> (Jimbo)	0.28	0.61	302	—	—	Shigeta (1993)
			<i>Bhimaites takahashii</i> Matsumoto	0.37	0.89	306	—	—	Shigeta (1993)
			<i>Hauericeras angustum</i> Yabe	0.33	0.70	312	—	—	Shigeta (1993)
			<i>Hauericeras gardeni</i> (Bailey)	0.38–0.50	0.70–0.73	315	0.15	0.30	Tanabe <i>et al.</i> (1979), Tanabe and Ohtsuka (1985)

	Pachydiscidae	<i>Anapachydiscus yezoensis</i> Matsumoto	0.35	0.76	315	—	—	Shigeta (1993)
		<i>Eupachydiscus haradai</i> (Jimbo)	0.37–0.53	0.73–1.07	306– 333	0.25	0.48	Tanabe <i>et al.</i> (1979), Tanabe and Ohtsuka (1985)
		<i>Menuites pusilus</i> Matsumoto	0.50	0.87	328	0.15	0.30	Tanabe <i>et al.</i> (1979)
		<i>Canadoceras kossmati</i> Matsumoto	0.41	0.89	315	—	—	Shigeta (1993)
		<i>Canadoceras mystricum</i> Matsumoto	0.44	1.00	312	—	—	Shigeta (1993)
		<i>Teshioites</i> sp.	0.46	0.92	305	—	—	Shigeta (1993)
	Kossmati- ceratidae	<i>Eogunnarites unicus</i> (Yabe)	0.35	0.76	319	—	—	Shigeta (1993)
		<i>Marshallites compressus</i> Matsumoto	0.41	0.97	313	—	—	Shigeta (1993)
		<i>Yokoyamaoceras ishikawai</i> (Jimbo)	0.39–0.61	0.80–0.97	297– 344	0.28	0.53	Tanabe <i>et al.</i> (1979), Shigeta (1993)
Acantho- cerataceae	Acantho- ceratidae	<i>Mantelliceras japonicum</i> Mat., Muramoto and Takahashi	0.40	0.89	284	—	—	Shigeta (1993)
		<i>Calycoceras orientale</i> Matsumoto, Saito and Fukada	0.46	0.93	281	—	—	Shigeta (1993)
	Collignoni- ceratidae	<i>Collignoniceras woolgari</i> (Mantell)	0.45	0.82	294	—	—	UMUT MM 19074
		<i>Subprionocyclus bakeri</i> (Anderson)	0.36–0.42	0.74–0.75	270– 313	—	—	Unregistered UMUT specimens
		<i>Subprionocyclus neptuni</i> (Geinitz)	0.37–0.50	0.70–0.85	242– 307	0.03– 0.09	0.08– 0.21	Unregistered UMUT specimens
		<i>Subprionocyclus minimum</i> (Hayasaka and Fukada)	0.35–0.50	0.59–0.89	250– 348	0.03– 0.15	0.09– 0.39	Unregistered UMUT specimens
		<i>Protexanites minimus</i> Matsumoto	0.35	0.74	280	—	—	Shigeta (1993)
		<i>Texanites kawasakii</i> (Kawada)	0.47	0.93	280	—	—	Shigeta (1993)
Hoplitaceae	Placenti- ceratidae	<i>Metaplacenticeras subtilistriatum</i> (Jimbo)	0.49–0.54	1.09–1.19	315– 356	0.12	0.22	Tanabe <i>et al.</i> (1979), unregistered UMUT sp.

*Estimate

**Appendix II. Age and Locality Data of Species Cited in the Text and Not Listed in Appendix I.
See Also Appendix, Chapter 6, this volume.**

Suborder	Species	Horizon	Locality	Sample
Goniatitina	<i>Gonioloboceras welleri</i> Smith	Pennsylvanian	Jacksboro, Texas	N=1 (SU1 1743)
	<i>Vidrioceras</i> sp.	U. Pennsylvanian	Pomona, Kansas	N=1 (UMUT PM 19329)
	<i>Aristoceras</i> sp.	U. Pennsylvanian	Pomona, Kansas	N=1 (UMUT PM 19010)
Prolecanitina	<i>Artinskia electraensis</i> (Plummer and Scott)	M Permian	Buck Mt., Nevada	N=2 (UMUT PM 19040-1,2)
Ceratitina	<i>Paranannites spathi</i> (Frebold)	Smithian	Spitsbergen	N=1 (UMUT MM 19343)
	<i>Anagymnotoceras varium</i> (McLean)	M. Anisian	Spitsbergen	N=1 (UMUT MM 19344)
Ammonitina	<i>Collignoniceras woolgari</i> (Mantell)	M. Turonian	Black Hills, S. Dakota	N=1 (UMUT MM 19074)
	<i>Subprionocyclus bakeri</i> (Anderson)	M. Turonian	Obira, Hokkaido	N=11
	<i>Subprionocyclus neptuni</i> (Geinitz)	U. Turonian	Manji, Hokkaido	N=66
	<i>Subprionocyclus minimus</i> (Hayasaka and Fukada)	U. Turonian	Manji, Hokkaido	N=44

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