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Exceptionally Well-Preserved Ammonites from the Upper Cretaceous (Turonian-Santonian) of North America: Implications for Ammonite Early Ontogeny

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ABSTRACT

Exceptionally well-preserved specimens of *Baculites* and *Scaphites* and closely related genera from the Upper Cretaceous (Turonian-Santonian) of North America provide clues to the early ontogenetic development of ammonites. The early whorls, known as the ammonitella, consist of the protoconch and first whorl terminating at the primary constriction and accompanying varix. The presence of a uniform tuberculate micro-ornamentation that ends abruptly at the end of the primary constriction suggests that the ammonitella is the embryonic ammonite shell. Internally, the ammonitella consisted of at least one septum, the proseptum, and the beginning of the siphuncle, known as the caecum. Prismatic deposits attached the caecum to the proseptum. The newly hatched ammonite was thus equipped to regulate buoyancy, necessary for further growth.

INTRODUCTION

Upper Cretaceous (Turonian-Santonian) strata from the Western Interior of North America are rich in ammonite species (see, for example, Meek and Hayden, 1862; Meek, 1876; Logan, 1898; Reeside, 1927a, 1927b, 1927c, 1931; Morrow, 1935, 1941; Fischer and Fay, 1953; Cobban, 1951a, 1951b, 1952, 1961, 1962, 1964, 1969, 1984, 1986, 1987; Cobban et al., 1958, 1962, 1976; Scott and Cobban, 1962, 1964; Scott et al., 1986; Gill and Cobban, 1966; Miller, 1968; Hattin, 1977, 1982; Kauffman and Powell, 1977;

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Fig. 1. A. Side view of the early whorls (ammonitella) of an ammonite showing the protoconch (PCH), first planispiral whorl, primary constriction (PC), and ammonitella edge (AE). B. Median cross section of the same specimen reveals the siphuncle (S), first septum or proseptum (1), second (2), third (3), fourth (4), and fifth (5) septa, flange (F), caecum (C), prosiphon (P), and primary varix (PV).

Landman, 1987, 1989). Specimens of many of these species are so well preserved that they retain their original shell structure. In this paper, we examine well-preserved specimens of *Baculites, Scaphites, S. (Pteroscaphites)*, and *Clioscaphites.* Some of these specimens are also free of any obscuring matrix inside their shells, permitting a close inspection of their internal elements. The early whorls of these species were studied to provide clues to the ontogenetic development of ammonites.

The early whorls of all ammonites are similar in morphology and are referred to as the ammonitella (Druschits and Khiami, 1970; Druschits et al., 1977; Tanabe et al., 1980). Descriptive terms are illustrated in figure 1. The ammonitella ranges in diameter from 0.5 to 1.5 mm and consists of a spheroidal or ellipsoidal initial chamber, the protoconch, followed by approximately one planispiral whorl. This whorl terminates in the primary constriction and accompanying varix, or thickening of the outer shell wall. Internally, septa subdivide the shell into chambers. The first septum, the proseptum, differs in shape and structure from all other septa. The inner lip of the protoconch is called the flange. The siphuncle originates in the protoconch as a swelling, known as the caecum, which is attached to the protoconch walls by means of prosiphonal sheets.

MATERIAL AND METHODS

The species studied, their geologic ages, and the localities at which they were collected are listed in table 1. Specimens were broken down and their early whorls were mounted on stubs, coated with gold, and viewed under scanning electron microscopy (SEM). Specimens were sometimes further broken down to expose new features and reexamined. All illustrated specimens are in the collections of the American Museum of Natural History (AMNH) and the Yale Peabody Museum (YPM).

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Fig. 2. A. Side view of the early whorls of an adult specimen of *Clioscaphites vermiformis* (AMNH 43033) showing the primary constriction (PC) and tuberculate micro-ornamentation on the ammonitella. Scale bar = 200 μ m. B. Close-up of the same specimen. The tuberculate micro-ornamentation extends to the adapical edge of the primary constriction. Scale bar = 40 μ m. C. Close-up of tubercles on the same specimen. Scale bar = 20 μ m. D. Close-up of tubercles on the ammonitella of an adult specimen of *Scaphites (Pteroscaphites) auriculatus* (AMNH 43034). Scale bar = 10 μ m.

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RESULTS

EXTERNAL APPEARANCE OF Ammonitella

The ammonitella is approximately $650 \ \mu m$ in diameter in *Scaphites* and its allied genera and approximately 750 $\ \mu m$ in diameter in *Baculites* (see Landman, 1987). The ammonitella terminates in the primary constriction and accompanying varix, which are illustrated in figures 2 and 3. The actual end of the ammonitella occurs at the end of the primary constriction. The angular distance between the end of the protoconch and the ammonitella edge is approximately 0.75 whorls in *Scaphites* and its allied genera and approximately 1.0 whorl in *Baculites*.

The surface of the ammonitella in all species studied is covered with a uniform tuberculate micro-ornamentation (figs. 2, 3). The tubercles are irregularly distributed and



Fig. 3. A. Side view of the early whorls of a juvenile of *Scaphites whitfieldi* (AMNH 44833) showing the primary constriction (arrow) and accompanying varix and the ammonitella edge. The protoconch region is poorly preserved. Scale bar = $200 \,\mu m$. B. Close-up of the primary constriction and accompanying

List of Species Studied		
Species	Age (formation)	AMNH locality ^a
Clioscaphites vermiformis (Meek and Hayden)	Middle Santonian (Marias River Shale)	3175
Scaphites (Pteroscaphites) auriculatus (Cobban)	Lower Coniacian (Marias River Shale)	3173
Scaphites preventricosus Cobban	Lower Coniacian (Marias River Shale)	3173
Scaphites whitfieldi Cobban	Upper Turonian (Carlile Shale)	3179

TABLE 1 List of Species Studied

^a **3164**. SW¹/₄ sec. 26 and NW¹/₄NW¹/₄ sec. 35, T. 58N, R. 103W, Park County, Wyoming, Cody Shale. **3173**. Center sec. 20, T. 31N, R. 2W, Toole County, Montana, Kevin Member, Marias River Shale. **3175**. NW¹/₄ sec. 13, T. 31N, R. 4W, Toole County, Montana, Kevin Member, Marias River Shale. **3179**. NE¹/₄ sec. 18, T. 9N, R. 4E, Butte County, South Dakota, Turner Sandy Member, Carile Shale.

Lower Coniacian-Middle Santonian

Lower Coniacian-Middle Santonian

(Cody Shale, Marias River Shale)

(Cody Shale, Marias River Shale)

cover all exposed portions of the ammonitella. They are approximately 6 μ m in diameter and 2 μ m high (fig. 3E). The tubercless of the protoconch are sometimes more subdued than those on the rest of the ammonitella and may, in fact, coalesce into a single prismatic layer (fig. 2A). A similar phenomenon has been observed by Tanabe (1989) in species of *Anapachydiscus*. In most specimens studied, however, the tubercles on the protoconch are as distinct as those on the rest of the ammonitella (Bandel et al., 1982).

Bandel et al. (1982) noted that, in general, the tubercles may extend to the adapical end of the primary constriction, into its shallow depression, or onto the narrow extension of the shell adoral of the constriction. In species of *Baculites* and *Scaphites* and its allied genera, in which the ammonitella edge is well preserved, the tubercles stop at the adapical end of the primary constriction (fig. 3D). In contrast, in *Sphenodiscus*, in which the tubercles are approximately $2 \mu m$ in diameter, the micro-ornamentation persists into the primary constriction (Bandel et al., 1982: fig. 2A).

The end of the ammonitella coincides with an abrupt change in the appearance of the shell (figs. 1A, B, 2A, B, 3A, B, 4). The postammonitella shell that emerges from beneath the ammonitella edge is covered with fine striae interpreted as growth lines. These growth lines develop at an angle to the straight ammonitella edge and record the shape of the apertural margin. These lines become further modified during later ontogeny. For example, growth lines are initially the same in *S. whitfieldi* and *C. vermiformis* but diverge by the end of the first postammonitella whorl (fig. 4).

The change in the microstructure of the shell, which occurs at the ammonitella-post-

Baculites asper

Baculites codvensis

Morton

Reeside

3164, 3175

3164, 3175

[←]

varix in the same specimen. The tuberculate micro-ornamentation extends to the adapical end of the primary constriction. Scale bar = 50 μ m. C. Ventral view of the same specimen. Scale bar = 200 μ m. D. Close-up of the ventral edge of the ammonitella in the same specimen. Scale bar = 20 μ m. E. Side view of tubercles on a broken fragment of an ammonitella of S. whitfieldi (AMNH 44835). Scale bar = 10 μ m. F. Juvenile of *Baculites asper* or B. codyensis (AMNH 44836) showing its planispiral ammonitella and straight postammonitella shell. Scale bar = 200 μ m.

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Fig. 4. Illustrations of the early whorls of S. whitfieldi (A) based on AMNH 44833 and C. vermiformis (B) based on AMNH 43033. The postammonitella shell is covered with growth lines that develop at an angle to the straight ammonitella edge. The growth lines of C. vermiformis eventually become more flexuous than those of S. whitfieldi. Scale bar = $200 \ \mu m$.



Fig. 5. Median cross section of the shell wall at the primary constriction (PC) and accompanying varix (PV) of a specimen of *Scaphites preventricosus* (AMNH 43036). The shell wall adoral of the constriction consists of an outer prismatic (OP) and inner nacreous layer (NA). Scale bar = $40 \ \mu m$.

ammonitella boundary, is illustrated in median cross section (fig. 5). The prismatic layer of the ammonitella thins out and a wedge of nacre, the primary varix, develops. This feature generally lies just adapical of the primary constriction. The postammonitella shell that emerges from beneath the primary varix is of uniform thickness and consists of an outer prismatic and an inner nacreous layer.

INTERNAL STRUCTURES

The internal structures of the ammonitella are illustrated in figures 6–8. These basically consist of the septa and siphuncle. The beginning of the siphuncle is the caecum. In specimens of *S. whitfieldi* free of matrix, the caecum appears as an oblate ellipsoid, approximately 150 μ m in width and 75 μ m in diameter (fig. 6). It is devoid of micro-ornamentation. Its microstructure on fractured surfaces appears to be homogeneous and it was probably originally composed of the same organic material as the siphuncle.

The caecum is attached to the protoconch wall by means of prosiphonal sheets, which extend as a nearly continuous apron along the convex wall of the caecum adapical of the proseptum. There are several prominent bands that extend out from the sheets in an adapical direction (fig. 6D). The sheets and their bandlike extensions create minute interspaces between the caecum and protoconch wall.

The shape of the caecum is the same in all the scaphite species studied. Tanabe and Ohtsuka (1985) have reported similar shapes in the scaphite species they examined from Japan. The shape of the prosiphonal sheets is also the same among all these species. According to Tanabe et al. (1979) and Tanabe and Ohtsuka (1985) short, adorally convex prosiphons are common in *Scaphites* as well as in many other genera within the order Ancyloceratina.

The caecum rests in the median saddle of the proseptum (fig. 7A), which is prismatic in microstructure (Landman and Bandel, 1985). The proseptum develops at the transition from the cuplike protoconch to the planispiral first whorl (Erben et al., 1969). It closes off the spheroidal to ellipsoidal protoconch and appears to form a continuation of the flange. A prismatic ridge occurs at the base of the proseptum in all the species studied (figs. 7D, 8C). The proseptum in species of *Baculites* also shows wrinkles, especially on the portion just below the flange (figs. 8C, F).



Fig. 6. A. Caecum (C) and prosiphonal attachment sheets (p) in a juvenile of *Scaphites whitfieldi* (YPM 6239). Scale bar = 100 μ m. B. View of the fractured surface of the caecum (C) in the same specimen. Scale bar = 10 μ m. C. Another view of the caecum (C) and prosiphonal attachment sheets (p) in the same specimen. Scale bar = 10 μ m. D. Close-up of the prosiphonal attachment sheets (p). Scale bar = 10 μ m.

The median portion of the proseptum consists of a circular opening whose diameter equals the whorl height. It is especially visible if the caecum is removed or absent due to diagenesis (figs. 7B, 8A). This opening is oriented in a nearly vertical position between the flange and outer shell wall. A groove appears around the opening of the proseptum in all the scaphite species studied (fig. 7C).

In species of Baculites and Scaphites and

its allied genera, a necklike attachment of the proseptum develops near the median plane (figs. 7C, D, 8B, D, E). Like the proseptum, it is prismatic in microstructure. It rides ventrally on the inside surface of the wall of the first whorl and precedes the second septum. It curves adorally from the proseptum and surrounds the adoral end of the caecum. Its opening is smaller than that of the proseptum.



Fig. 7. A. Fragment of a protoconch dissected from a juvenile of *Scaphites whitfieldi* free of matrix (AMNH 42899). The proseptum (1), caecum (C), and flange (F) are visible. Scale bar = 100 μ m. B. Interior of the protoconch and part of the first whorl of a juvenile of *S. whitfieldi* (AMNH 43037) showing the proseptum (1), flange (F), proseptal opening, second (2) and third septa (3), and the prochoanitic septal neck of the second septum. Scale bar = 100 μ m. C. Interior of the protoconch and part of the first whorl of a juvenile of *S. whitfieldi* (AMNH 42900) showing the proseptum (1), flange (F), opening of the proseptum with its necklike attachment (middle white arrow), and the second septum (2). A groove (right black arrow) occurs around the opening of the proseptum. Prismatic attachment deposits (left black arrow) of the siphuncle occur on the necklike attachment of the proseptum. Scale bar = 100 μ m. D. View into the interior of the protoconch and part of the first whorl of a juvenile of *S. whitfieldi* (YPM 6240) reveals the proseptum (1), part of its necklike attachment (upper arrow), and the ventral traces of the second (2) and third (3) septa. Note that the second septum only intersects the proseptum at the extreme lateral margins (middle arrow). A prismatic ridge occurs at the base of the proseptum (lower arrow). Scale bar = 10 μ m.

This necklike attachment is especially conspicuous in the scaphites studied. This structure forms a strong adoral bend on the venter so that it is distinct from the proseptum, which it joins laterally and dorsally (figs. 7D, 8D). The angular distance, measured along the venter, between the proseptum and its necklike attachment is approximately 15°. In con-



Fig. 8. A. View into the protoconch of a juvenile of *Baculites asper* or *B. codyensis* (AMNH 42905) shows the proseptum (1), proseptal opening, and flange (F). The caecum and siphuncle are not preserved. Scale bar = $40 \ \mu m$. B. Close-up of the same specimen reveals the flange (F), proseptum (1), and opening of the proseptum. A short necklike attachment (arrow) occurs at the opening of the proseptum. Scale bar = $40 \ \mu m$. C. Close-up of the same specimen shows wrinkles (upper arrow) on the proseptum (1). A prismatic ridge occurs at the attachment of the proseptum to the wall of the protoconch (lower arrow). Scale bar = $40 \ \mu m$. D. Overview of the same specimen after most of the proseptum (1) has been removed reveals the short necklike attachment of the proseptum (arrow) adapical of the second septum (2). Scale bar = $40 \ \mu m$. E. The junction of the proseptum (1) and necklike attachment of the proseptum (arrow) magnified from figure 8D (white box). Scale bar = $40 \ \mu m$. F. Juvenile of *Baculites asper* or *B. codyensis* (AMNH 42906) showing wrinkles on part of the proseptum (1) just below the flange (F). Scale bar = $40 \ \mu m$.

trast, the necklike attachment of the proseptum in *Baculites* is smaller and forms only a slight adoral bend on the venter.

Prismatic structures also occur on the opening of the proseptum and its necklike attachment in both the scaphite and baculite species studied (fig. 7C). These deposits serve to attach the siphuncle and caecum to the septa. They have been termed false septal necks (Birkelund and Hansen, 1974), cuffs (Druschits et al., 1977), auxiliary deposits (Kulicki, 1979), and prismatic attachment deposits (Bandel, 1982; Landman and Bandel, 1985).

The second septum lies at a moderate distance from the proseptum in both the scaphite and baculite species studied. The angular distance, measured along the venter, between the proseptum and second septum is approximately 35° in scaphites and approximately 20° in baculites. In both groups, the first two septa intersect only at the extreme lateral margins (fig. 7D). The second septum is slightly convex toward the aperture in median cross section and exhibits a prochoanitic neck (fig. 7B). Unlike the proseptum, the second septum and all subsequent septa are nacreous in microstructure (Landman and Bandel, 1985).

DISCUSSION

The ammonitellas of the species studied are similar to those of other ammonites (Kulicki, 1974; Bandel, 1982, 1986; Bandel et al., 1982; Tanabe, 1989). Any deviation in structural plan during the course of ontogeny only occurs after the formation of the ammonitella (fig. 3F). The uniform appearance of the ammonitella suggests that the early ontogenetic development of ammonites was direct, without a larval phase (Grandjean, 1910; Druschits and Khiami, 1970; Druschits et al., 1977; Kulicki, 1974, 1979; Birkelund and Hansen, 1974; Bandel, 1982, 1986; Landman, 1987; Tanabe, 1989). According to this view, both the protoconch and first whorl terminating at the end of the primary constriction and accompanying varix formed during embryogenesis. The presence of a tuberculate micro-ornamentation that extends without interruption to the primary constriction argues against an intervening larval stage after formation of the protoconch. A scheme of direct development in ammonites is further supported by the fact that all cephalopods whose early ontogeny is known exhibit direct development (Arnold and Williams-Arnold, 1977; Wells and Wells, 1977; Bandel and Boletzky, 1979; Landman, 1987).

The ammonitellas of the species studied as well as those of all other ammonites lack growth lines. Two hypotheses have been proposed to explain their absence during embryogenesis. Bandel (1982) suggested that their absence may be due to the rapid mineralization of an originally organic shell, which is similar to the process that occurs in archaeogastropods. According to this hypothesis, the originally organic shell was mineralized by prismatic needles of aragonite, forming an initial layer of uniform thickness that preserved the original ornamentation of the organic shell (Bandel, 1975, pp. 50-52). Subsequently, other mineral layers were deposited from the interior, increasing the thickness of the outer wall. This model has been supported by the discovery of intact ammonitellas from the Lower Cretaceous (Aptian) of Russia in which three successive developmental stages have been identified: 1) mineralization of the exposed portions of the protoconch and first whorl ending at the primary constriction, 2) mineralization of the wall of the protoconch near the site of the future proseptum, and 3) mineralization of the rest of the wall of the protoconch and formation of the primary varix and proseptum (Kulicki, 1989; Kulicki and Doguzhaeva, 1990).

In contrast, Tanabe (1989) has proposed an alternative model, based on analogy with coleoid cephalopods, to explain both the presence of tubercles and absence of growth lines on the ammonitella. According to his model, the embryonic shell was initially secreted by the interior shell gland. Subsequently, the mantle epithelium reflected and enclosed the embryonic shell, forming an endocochleate arrangement. During this stage, the mantle epithelium secreted a thin prismatic layer with tuberculate micro-ornamentation on the surface of the embryonic shell. Thereafter, the mantle epithelium withdrew toward the aperture restoring the ectocochleate condition.

The tuberculate micro-ornamentation of the ammonitella may have facilitated the process of hatching from the egg capsule. In many molluscs, hatching is the result not only of enzyme secretion but also of the mechanical action of the embryo against the wall of the capsule leading to its ejection. In contrast, the primary varix may have served a function immediately after hatching. According to Kulicki (1979), the weight of the primary varix may have helped orient the newly hatched shell in the water. Otherwise, the nearly spherical shape of the ammonitella with the protoconch near the center would have resulted in a coincidence between the centers of gravity and buoyancy, and a consequent loss in static equilibrium.

During embryogenesis, the ammonite formed at least one septum at the posterior end of the body, the proseptum, which closed off the protoconch from the body chamber. Examination of the species of *Baculites* and *Scaphites* provides clues to the formation of the proseptum. Both genera show a prismatic ridge at the base of the proseptum (figs. 7D, 8C), which represents the attachment site of the organic membrane that later mineralized to form the proseptum. In a specimen of *Baculites*, the proseptum also preserves the wrinkles of this organic membrane (fig. 8C).

Ammonites may have formed additional septa before hatching but the presence of a single septum would have been sufficient to permit buoyancy regulation. Indeed, the difference in shape and microstructure between the proseptum and all later septa suggests that the proseptum was the only septum that formed during embryogenesis (Druschits and Khiami, 1970; Druschits et al., 1977; Landman, 1987). This hypothesis has been further supported by the discovery of intact ammonitellas with only a single septum, the proseptum, from the Upper Cretaceous (Turonian-Campanian) of North America (Smith, 1901; Landman, 1982, 1985) and the Lower Cretaceous (Aptian) of Russia (Druschits and Khiami, 1970; Kulicki and Doguzhaeva, 1990). However, other intact ammonitellas have been reported with more than one septum preserved (Wetzel, 1959; Blind, 1979; Bandel, 1982; Kulicki and Wierzbowski, 1983).

The caecum and prosiphonal sheets also formed during embryogenesis. These features have been reported from preserved ammonitellas of at least two ammonite species (Druschits and Khiami, 1970; Landman, 1982). These structures were responsible for regulating the amount of liquid and gas in the protoconch in order to maintain the buoyancy of the newly hatched animal. As shown in figure 6, the caecum is an oblate ellipsoid, similar in shape to the protoconch, and presents a large surface area for the transfer of liquids.

The prosiphonal attachment sheets may also have facilitated the transfer of liquids. They may have acted as wicks to conduct liquid to the caecum or they may have provided a network of interstitial spaces for storage of liquid as it drained from the protoconch. The prismatic deposits on the openings of the proseptum, its necklike attachment, and later septa, which served to attach the caecum and siphuncle, may also have been involved in cameral liquid removal (Bandel and Boletzky, 1979; Bandel, 1982).

In summary, ammonites probably hatched at the end of the primary constriction and accompanying varix. The embryonic shell or ammonitella consisted of the body chamber and phragmocone, most of which was the large protoconch. Internally, there was at least one septum, the proseptum, and the caecum so that buoyancy regulation necessary for further growth was possible. The postembryonic shell differed in microstructure from the ammonitella and consisted of both prismatic and nacreous layers. In addition, the surface of the postembryonic shell was covered with growth lines. The onset of postembryonic growth also produced changes in whorl shape (Landman, 1987). Such changes were especially dramatic in heteromorph genera, such as Baculites, which formed a straight postembryonic shell.

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