AMERICAN MUSEUM Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3197, 15 pp., 8 figures, 1 table May 16, 1997

Foldlike Irregularities on the Shell Surface of Late Cretaceous Ammonoids

NEIL H. LANDMAN[1] AND JENNIFER A. LANE[2]

ABSTRACT

Small foldlike irregularities occur on the shell surface of well-preserved Mesozoic ammonoids. We describe such folds on the shell surface of two species of Late Cretaceous ammonoids, *Metoicoceras geslinianum* (d'Orbigny, 1850) (Acanthocerataceae) from the Cenomanian of Texas, and *Scaphites carlilensis* Morrow, 1935 (Scaphitaceae) from the Turonian of Kansas. Folds appear in the outer prismatic layer in *S. carlilensis* and in the nacreous layer in *M. geslinianum* (the outer prismatic layer is not preserved in the latter specimens). Folds observed included pinnate (= featherlike) folds consisting of longitudinal grooves with adorally divergent side branches and palmate folds diverging adorally from a single point. These features are common in the areas between ribs (= intercostal valleys), especially on the umbilical wall and shoulder.

One specimen of *S. carlilensis* in which the outer prismatic layer had flaked off in places reveals that the folds in the outer prismatic layer continue into the underlying nacreous layer. Thus, these folds may relate to "feather structure," which has generally been reported from the nacreous layer. However, feather structure is a much larger feature and usually covers much more of the shell surface.

SEM observations of the shell surface of *S. carlilensis* reveal that growth lines cross folds parallel to ribs. This serves to differentiate these folds from repaired shell injuries, in which growth lines curve backward. Instead, folds probably formed in the periostracum prior to calcification of the shell as the result of normal stresses during growth. Subsequently, these folds were "imprinted" on the outer prismatic, and then, the nacreous layer. More research is needed, especially in extant molluscs in which folds in the periostracum can be directly observed.

[1] Chairman and Curator, Department of Invertebrates, American Museum of Natural History.

[2] Intern (Research Experiences for Undergraduates Program), Department of Invertebrates, American Museum of Natural History: Undergraduate, New York University, College of Arts and Sciences, Department of Biology, 100 Washington Square East, New York, NY 10003-6688.

ISSN 0003-0082 / Price $2.00

INTRODUCTION

In general, it is rare to find specimens of ammonoids in which the original shell material is well preserved. The probability diminishes with increasing geological age, and the best preservation occurs in Mesozoic forms. Studies of well-preserved specimens reveal that the shell wall is subdivided into three layers: outer prismatic, nacreous, and inner prismatic (Birkelund, 1981). These layers are mainly composed of aragonite. In addition, there is an organic periostracum coating the surface of the shell. This layer is sometimes visible in cross sections through the shell wall (see, for example, Landman, 1987: fig. 55B; 1994: fig. 5). Ammonoids probably inherited this characteristic four-layered microstructure from the earliest ancestor of externally shelled cephalopods, known as HASC (= hypothetical ancestral siphonopodean cephalopod, Engeser, 1996: 14).

The actual process of shell growth in ammonoids was probably similar, in many respects, to that in present-day *Nautilus* (Lehmann, 1981; Ward, 1987; Bucher et al., 1996). In *Nautilus* (as well as in other molluscs), the periostracum is secreted by the mantle. The adoral portion of the mantle is subdivided into three plicae: outer, middle, and inner (Mutvei, 1964). The area between the outer and middle plicae, the periostracal groove, secretes the periostracum, which is composed of the protein conchiolin. The periostracum protects the calcareous shell from dissolution and acts as a matrix for the deposition of aragonitic crystals (Saleuddin and Petit, 1983: 199; Mutvei, 1964).

The periostracum is secreted by epithelial cells that line the periostracal groove. As the periostracum leaves the periostracal groove, it is strengthened by enzymes secreted by the mantle epithelium. Growth lines develop in the periostracum in response to variations in the rate of growth. When the periostracum reaches the outer surface of the mantle, the shell begins to calcify. Prior to this, the periostracum is known as the "free periostracum" (Checa, 1995: 870).

In *Nautilus,* the cells in the most adoral portion of the outer mantle surface secrete the first layer of shell, the spherulitic prismatic layer, which consists of vertical prisms of aragonite (Mutvei, 1964). This layer displays growth lines, presumably the same as those in the periostracum. The nacreous layer is secreted next, by the middle portion of the outer mantle surface. This layer is composed of aragonitic crystals in the form of horizontal layers of hexagonal tablets. The innermost shell layer is known as the inner prismatic layer and resembles the spherulitic prismatic layer in structure. It is secreted by the most adapical portion of the outer mantle surface, toward the posterior end of the animal.

In most species of *Nautilus,* the shell surface is smooth and is only covered with growth lines. In contrast, in many ammonoids, there are well-defined ornamental features such as ribs, spines, nodes, and tubercles. In addition, some well-preserved ammonoids show small foldlike irregularities on the shell surface. These folds, although developed only locally, can cover large areas of the shell. Checa (1995) called such features "microsculptures" and argued that they may be of considerable importance in understanding the process of ammonoid shell growth. His carefully documented study provided the inspiration for this paper.

In this study, we describe foldlike irregularities on the shell surface of two ammonoid species, *Scaphites carlilensis* Morrow, 1935 (Scaphitaceae) and *Metoicoceras geslinianum* (d'Orbigny, 1850) (Acanthocerataceae). We discuss how these folds relate to other shell features such as growth lines and ornament, and explore the causes and significance of these features. All specimens are reposited in the American Museum of Natural History, New York (AMNH), the Academy of Natural Sciences, Philadelphia (ANSP), the United States Geological Survey, Denver, Colorado (USGS), and the Black Hills Museum of Natural History, Hill City, South Dakota (BHI).

ACKNOWLEDGMENTS

We thank Dr. Antonio Checa (University of Granada) for reviewing an earlier draft of this paper and for providing us with valuable data. We also thank Dr. Roger Hewitt (McMaster University), Dr. Kazushige Tanabe

(University of Tokyo), and Dr. Cameron Tsujita (University of Western Ontario) for reviewing an earlier draft of the text. We thank Susan Klofak (AMNH) for assistance in preparing specimens, locating references, and translating some references from German; Andrew Modell, Kathleen Sarg, Barbara Worcester, Peling Fong-Melville, Portia Rollings, and Stephanie Crooms (all AMNH), and Peter Kaplan (Yale University) for help in preparing the manuscript and/or figures; and the AMNH library staff for assistance in locating references. Dr. William A. Cobban (USGS) and Elana Benamy (ANSP) loaned us well-preserved specimens of *Metoicoceras geslinianum* and *Scaphites carlilensis.* This work was funded in part by the Norman D. Newell Fund for Invertebrate Paleontology, the AMNH REU program, and the New York University Rudin Scholarship Grant for research in science.

MATERIAL AND METHODS

We studied six specimens of *Scaphites carlilensis* from the Upper Cretaceous (Turonian) of Kansas (AMNH 45348–45350, 45375, and ANSP 33677 (two specimens bear the same number)). These specimens consist of fragments of phragmocones and body chambers and are exceptionally well-preserved, with the outer prismatic layer intact. This species is approximately 40 mm in maximum length in macroconchs and approximately 25 mm in maximum length in microconchs; it is characterized by a hook-like adult body chamber (Cobban, 1951). Ribs are coarse and prorsiradiate on the flanks of the body chamber and increase by branching and intercalation at the ventrolateral margin. Ribs cross the venter straight or with a slight adoral or adapical projection, depending on their location on the body chamber (Cobban, 1951). All specimens were examined with light microscopy and four were examined with SEM (AMNH 45348–45350, 45375).

We also studied four specimens of *Metoicoceras geslinianum* from the Upper Cretaceous (Cenomanian) of Texas (USGS 14815, USGS 10174, and two specimens labeled USGS D9433), each consisting of part of an adult body chamber. This species ranges from approximately 195 to 245 mm in diameter in macroconchs and 135 to 210 mm in microconchs (Kennedy, 1988). Ribs in *M. geslinianum* are larger and more widely spaced than those in *S. carlilensis.* In addition, there are inner and outer ventrolateral tubercles in *M. geslinianum,* connected across the venter by a low, broad rib.

The specimens of *M. geslinianum* were selected for study because they appeared to be very well preserved. However, they are not as well-preserved as our specimens of *S. carlilensis,* and only the nacreous layer was present, not the outer prismatic layer. The nacreous layer was iridescent in appearance. Because the outer primatic layer was missing, growth lines were not preserved, and only a few observations based on these specimens are included in this paper. Only one specimen (USGS D9433) was studied with SEM; the others were examined with light microscopy.

In addition, a specimen of present-day *Nautilus scrobiculatus* (Lightfoot, 1786), AMNH 45386, from Papua New Guinea, was examined in order to investigate the pattern of growth lines associated with shell injuries. This specimen was selected because there was a conspicuous injury on the shell. We would have preferred to investigate the pattern of growth lines associated with a repaired injury in an ammonoid, but no specimens with the outer prismatic layer preserved showed any obvious injuries.

RESULTS

Scaphites carlilensis

We detected an outer prismatic layer on the four specimens studied with SEM. This layer is 2 μm thick (fig. 1B). This thickness represents a miniscule portion (1%) of the total thickness of the shell wall (200 μm). The nacreous layer is approximately 150 μm thick.

The surface of the outer prismatic layer is covered with striae spaced at intervals ranging from 1 to 10 μm (figs. 1B, D–F, 2C–F). The striae are approximately parallel to the ribs and to each other (figs. 1B, 2B). We interpret these features as growth lines.

Several types of folds are visible on the venter and umbilical wall. They occur partic-

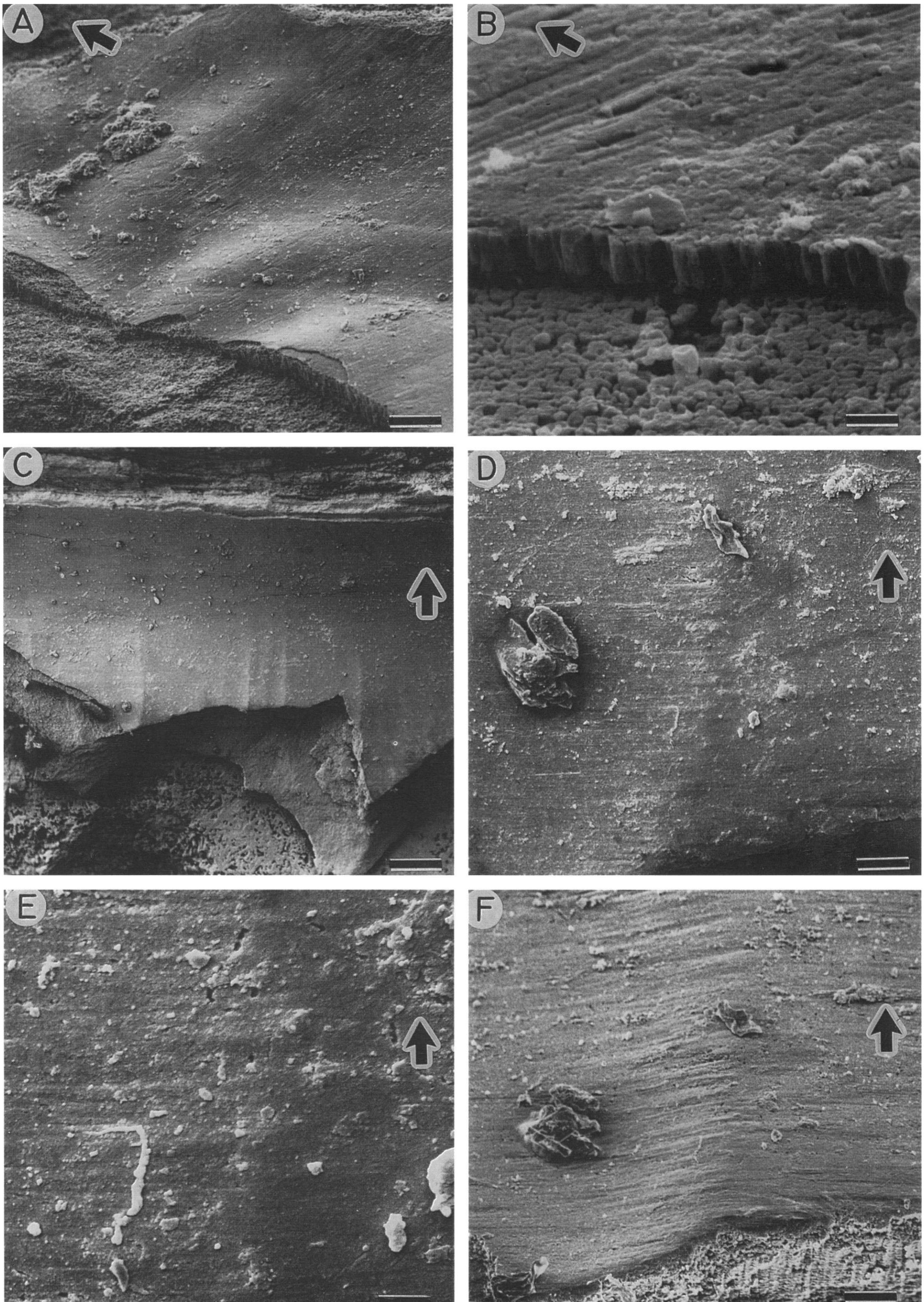


Fig. 1. *Scaphites carlilensis,* AMNH 45375, Upper Cretaceous (Turonian), Kansas. Arrows indicate adoral direction. **A.** View of part of adult phragmocone near umbilical margin showing random folds on shell surface. A piece of shell has broken off revealing a cross section through the outer prismatic and nacreous layers. Scale bar = 50 μm. **B.** Close-up of outer prismatic layer covered with growth

ularly in the area between ribs (= the intercostal valleys). One kind of fold consists of numerous side branches diverging from a long central axis, producing a featherlike or pinnate appearance (figs. 2A, B, 3B, 4A). The long, central axis forms a groove (the rachis), from which the folds diverge in an adoral direction. The rachis first appears on the adoral slope of a rib and the side branches begin to form in the middle of the intercostal valley (fig. 2A, B). This pattern persists onto the adapical slope of the next rib, but fades before reaching the rib crest.

In one specimen (fig. 2A), a set of pinnate folds on the venter continues across three successive intercostal valleys. These folds maintain the same relative position, forming a longitudinal pattern on the shell. Within each intercostal valley, the pinnate folds measure approximately 3.4 mm in length and range from 2.2 to 2.7 mm in maximum width. This pattern of persistent folds is visible only in the three intercostal valleys illustrated in the photo, and fades out adorally and adapically of this region.

In AMNH 45349, a portion of the outer prismatic layer showing a pinnate fold flaked off prior to our examination and exposed the underlying nacreous layer (fig. 3B, C). The pinnate pattern in the outer prismatic layer extends into the nacreous layer. All of the components of the fold appear in the nacreous layer, including the rachis, although it is possible that they are not as sharply defined as in the outer prismatic layer.

Growth lines are visible on the pinnate folds. The growth lines are parallel to the ribs and perpendicular to the rachis (fig. 2A–F). They cross the side branches of the folds obliquely.

Another type of fold we observed consists of small, linear ridges perpendicular to ribs (figs. 1C–F, 4B). These ridges are closely spaced next to each other and are confined to the middle of intercostal valleys; they do not extend to the rib slopes. In some specimens, these ridges are very abundant and form a pleated band around the shell (fig. 4B). The ridges illustrated in figure 1C–F range from approximately 60 to 400 μm in length and are approximately 40 μm wide. In other specimens, such ridges range from 150 to 300 μm in length and are approximately 50 μm wide.

Observations of these ridges in cross section reveal that these features do not represent thickenings of the outer prismatic layer (fig. 1F). Growth lines cross these ridges at right angles parallel to the ribs (fig. 1D–F).

Other folds on the shell surface of *S. carlilensis* include wedge-shaped folds on the adapical slopes of ribs near the rib crests; folds resembling pinchings-in of the shell surface on the adapical slopes of ribs; small indentations in the shell; and random folds that do not fit into any of the other categories (figs. 1A, 4C).

Metoicoceras geslinianum

The four specimens of *Metoicoceras geslinianum* lack an outer prismatic layer but retain an iridescent nacreous layer (fig. 5). Because the outer prismatic layer was missing, we could not observe the relationship between growth lines and folds.

In *M. geslinianum,* the shell surface is folded in a number of places. There appear to be several different kinds of folds corresponding to different parts of the shell, with some folds resembling those observed on the outer prismatic layer of *S. carlilensis.* One kind consists of longitudinal grooves on the venter (figs. 5B, 6E, F), which occur in the intercostal valleys, perpendicular to the ribs. In some places, these grooves develop adorally divergent side branches and resemble the pinnate folds observed in *S. carlilensis.* As in *S. carlilensis,* a groove first appears on the adoral slope of a rib and side branches de-

←

lines. Scale bar = 2 μm. **C.** View of intercostal valley on venter of adult phragmocone showing small, linear ridges perpendicular to ribs. Scale bar = 200 μm. **D.** Close-up of one of these ridges. Scale bar = 20 μm. **E.** Same ridge at a higher magnification. Growth lines cross ridge at right angles. Scale bar = 5 μm. **F.** Oblique cross-sectional view of same ridge. There is no thickening of the outer prismatic layer at this point. Scale bar = 20 μm.

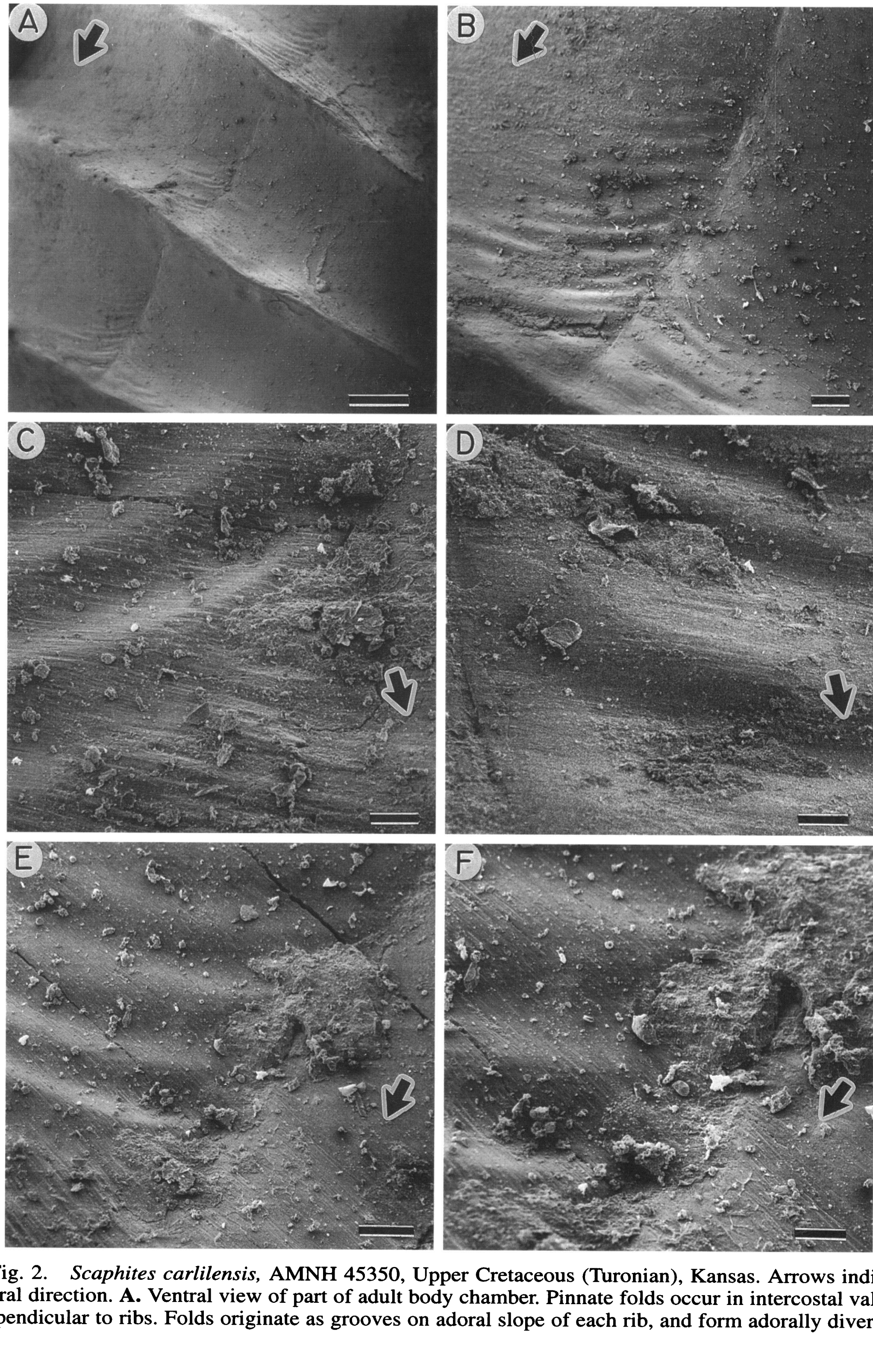


Fig. 2. *Scaphites carlilensis,* AMNH 45350, Upper Cretaceous (Turonian), Kansas. Arrows indicate adoral direction. **A.** Ventral view of part of adult body chamber. Pinnate folds occur in intercostal valleys perpendicular to ribs. Folds originate as grooves on adoral slope of each rib, and form adorally divergent

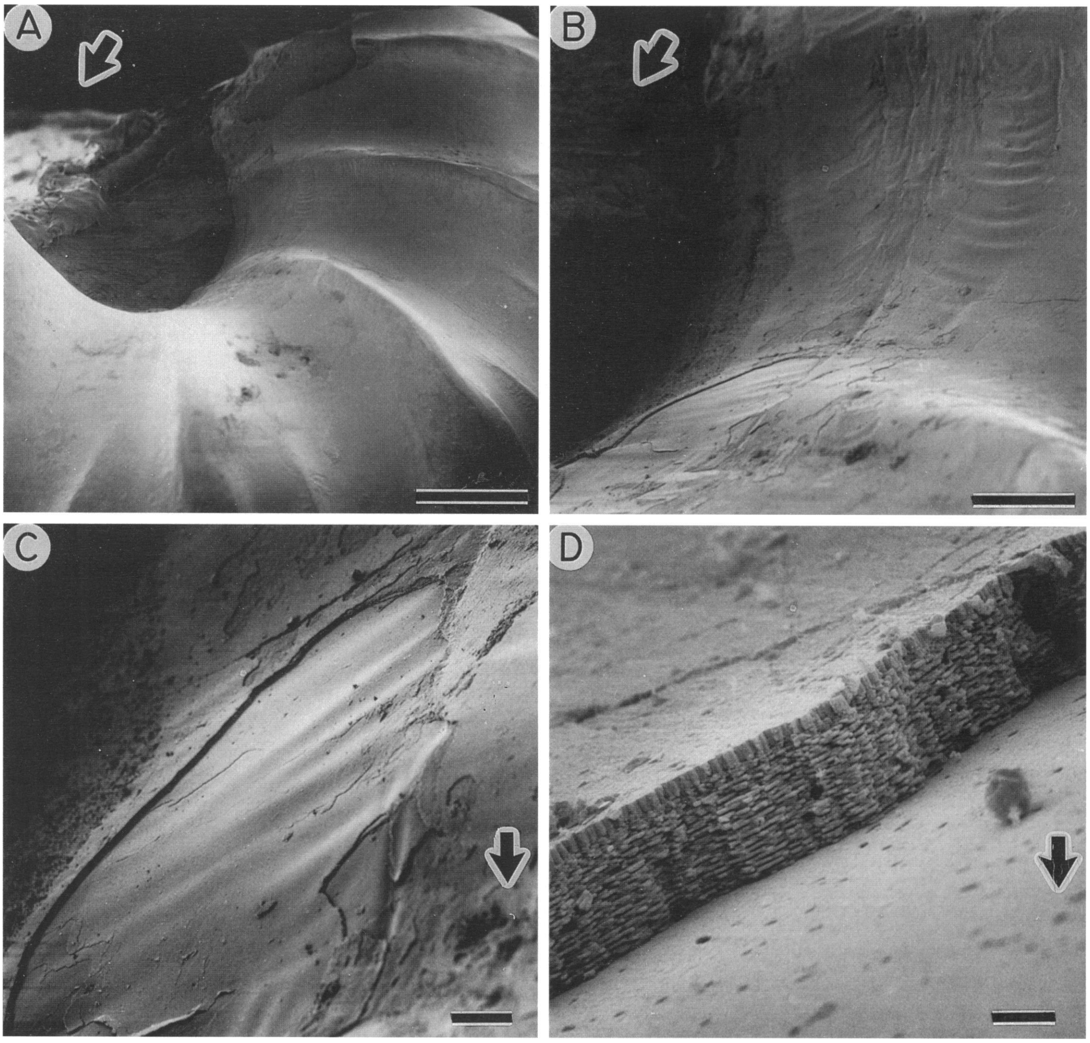


Fig. 3. *Scaphites carlilensis.* AMNH 45349, Upper Cretaceous (Turonian), Kansas. Arrows indicate adoral direction. **A.** Lateral view of part of adult body chamber. Small pinnate folds are visible on umbilical wall (in the middle of the photo). Scale bar = 2 mm. **B.** Close-up showing folds on umbilical wall. Part of the outer prismatic layer has broken off, revealing the underlying nacreous layer. Scale bar = 500 μm. **C.** Close-up of broken area of shell showing that the folds in the outer prismatic layer extend into the underlying nacreous layer. Scale bar = 100 μm. **D.** Close-up of same area, showing a cross section of outer prismatic and nacreous layers. Outer prismatic layer is 2 μm thick. Scale bar = 5 μm.

←

side branches when they reach the middle of the intercostal valley. The folds fade before reaching the crest of the next rib. Scale bar = 1 mm. **B.** Close-up of bottom pinnate fold in A. Side branches diverge adorally from central groove. Scale bar = 200 μm. **C.** Left side of same pinnate fold. Growth lines cross side branches obliquely. Scale bar = 50 μm. **D.** Right side of same pinnate fold. Scale bar = 50 μm. **E.** Close-up of middle pinnate fold in A. Growth lines are parallel to ribs and cross side branches obliquely. Scale bar = 100 μm. **F.** Close-up of central groove of same pinnate fold. Scale bar = 50 μm.

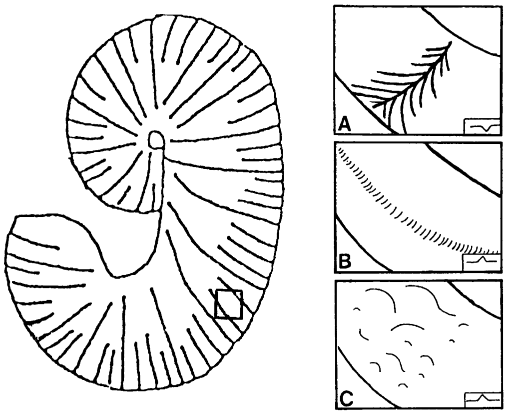


Fig. 4. Close-ups (right) of *S. carlilensis* (25 mm maximum length), illustrating three kinds of folds on shell surface. Adoral direction is toward lower left in A–C. Boxes on lower right in A–C represent cross sections through the folds. **A.** An adorally divergent pinnate fold. **B.** Small linear ridges in the middle of an intercostal valley, forming a pleated band around the shell. **C.** Random folds.

velop in the middle of the intercostal valley. These folds fade out before reaching the rib crest.

Another variation observed in intercostal valleys on the flanks of some specimens consists of small, adorally divergent branches superficially similar to pinnate folds (figs. 5D, E, 6C, D). However, these branches radiate from a single point rather than from a rachis, creating a palmate rather than pinnate pattern. In one specimen, these palmate folds appear in the same relative position in several successive intercostal valleys, creating a longitudinally continuous pattern, before eventually fading out.

Additional types of folds in *M. geslinianum* include small grooves that converge toward the apices of nodes (fig. 6A, B); small pits in the shell surface resembling the pits in a golf ball, which also occur on the nodes; small dents on the shell flanks (fig. 5C); and random folds that do not fit into any of the previously described categories (fig. 5C).

Nautilus scrobiculatus

The growth lines in *Nautilus scrobiculatus* are similar to those in other species of *Nautilus* even though the periostracum is unusually thick in this species (Ward, 1987). There is a crescent-shaped area in AMNH 45386 marking a point at which the shell was broken (fig. 7A–C). Adapical of the injury, growth lines cross the shell in a radial direction parallel to each other and to the shell aperture (fig. 7A). Adoral of the injury, however, growth lines bend backward toward the injured area (fig. 7A–D). The point at which these growth lines converge corresponds to the center of the injured area (fig. 7A, B).

DISCUSSION

The specimens of *Scaphites carlilensis* provide important information on the thickness of the outer prismatic layer and the pattern of growth lines associated with the folds. The outer prismatic layer on the venter of the adult body chamber is only 2 μm thick; it is uncertain whether this is the original thickness or represents the result of some dissolution during the fossilization process. However, the presence of what we interpret as growth lines tends to support the conclusion that the outer prismatic layer is unaltered. In contrast, none of the specimens of *Metoicoceras geslinianum* preserves the outer prismatic layer.

The growth lines on the surface of the outer prismatic layer in *S. carlilensis* consist of striae spaced at intervals from 1 to 10 μm. The fact that these lines are parallel to the aperture and perpendicular to the presumed direction of growth suggests that these are, in fact, growth lines, and not the product of diagenesis. As such, these lines presumably formed in the periostracum in response to variations in the rate of growth and were then "imprinted" on the outer prismatic layer during shell secretion.

We observed several kinds of folds in *S. carlilensis* and *M. geslinianum.* The main kinds are pinnate folds, palmate folds, and small ridges and grooves perpendicular to the ribs. In summary, pinnate folds are featherlike, originating as grooves on the adoral slopes of ribs and forming adorally divergent side branches as they reach the middle of the intercostal valleys. They then fade out on the adapical slope of the next rib. These folds appear on the umbilical wall and venter in *S. carlilensis* and on the venter in *M. geslinian-*

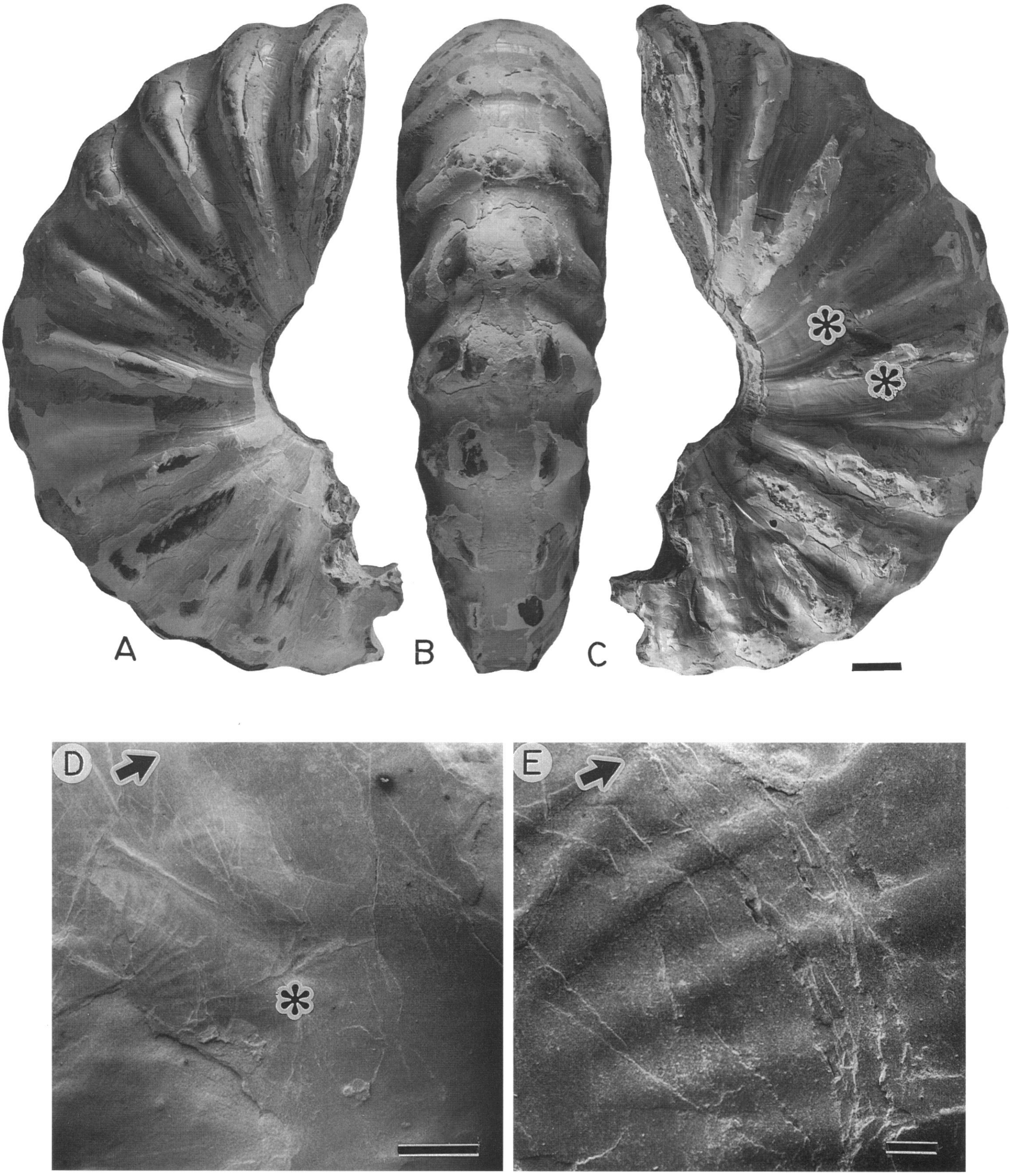


Fig. 5. *Metoicoceras geslinianum,* USGS D9433, Upper Cretaceous (Cenomanian), Texas. Arrows indicate adoral direction. **A.** Left lateral view of part of adult body chamber showing small foldlike irregularities on shell surface. Same scale as C. **B.** Ventral view of same specimen showing small longitudinal grooves and pinnate folds in intercostal valleys. Same scale as C. **C.** Right lateral view of same specimen. Note dent (upper asterisk) and random folds (lower asterisk). Scale bar = 1 cm. **D.** Close-up of adapical portion of C showing a palmate fold (asterisk). Scale bar = 2 mm. **E.** Close-up of same palmate fold, which consists of adorally divergent side branches radiating from a single point. Scale bar = 200 μm.

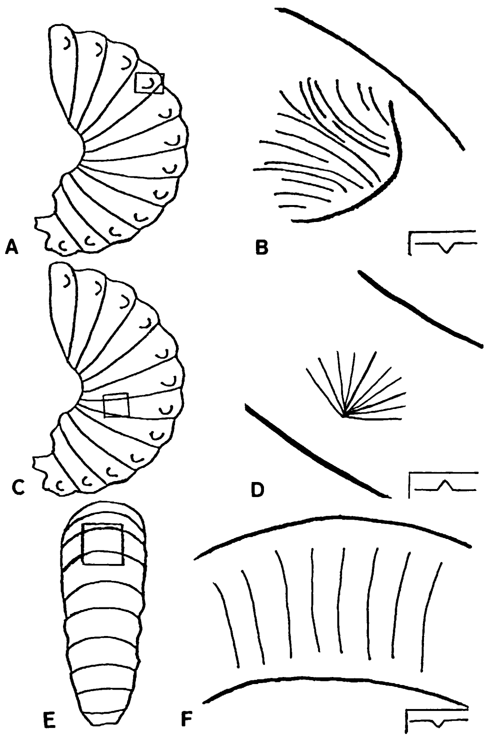


Fig. 6. Schematic drawings of *Metoicoceras geslinianum* in figure 5 illustrating three kinds of folds on the shell surface. Boxes on lower right in B, D, and F represent cross sections through the folds. **A.** Right lateral view. **B.** Close-up of ventrolateral node covered with small grooves. Adoral direction is to the left. **C.** Right lateral view. **D.** Close-up of palmate fold in an intercostal valley. Adoral direction is to the upper right. **E.** Ventral view. **F.** Close-up of small grooves in an intercostal valley. Adoral direction is toward the top.

um. Palmate folds consist of adorally divergent branches originating from a single point. They only appear along the flanks in *M. geslinianum.* Both pinnate and palmate folds sometimes traverse several successive intercostal valleys, fading out and reappearing in the same longitudinal position on the shell. Small ridges only appear in the middle of intercostal valleys in *S. carlilensis.* Lastly, grooves appear in the middle of intercostal valleys and on the nodes. These might be a variety of pinnate fold that lacks side branches.

Growth lines in *S. carlilensis* cross all folds parallel to the aperture. Specifically, in pinnate folds, growth lines are perpendicular to the rachis and oblique to the side branches.

It is uncertain whether folds in the nacreous layer of *M. geslinianum* actually correspond to similar structures in the outer prismatic layer of *S. carlilensis,* because no specimens of *M. geslinianum* with the outer prismatic layer intact were available for study. However, in *S. carlilensis,* some of the folds in the outer prismatic layer clearly continue into the nacreous layer, suggesting that within the same specimen, at least, the folds appear in both layers. By implication, therefore, the folds in the two species, albeit from different layers, are homologous.

There are several references in the literature to foldlike structures in ammonoid shells. One is the "wrinkle layer" (also called "Runzelschicht," "Ritzstreifen," and "stries creuses"), which is associated with the dorsal shell layer (Walliser, 1970; Birkelund, 1981; Doguzhaeva and Mutvei, 1986; Kulicki, 1996). The "wrinkle layer" consists of a series of ridges and grooves, forming a fingerprintlike pattern.

The folds we observed are clearly unrelated to the "wrinkle layer" because our folds occur in the outer layers of the shell, specifically, in the outer prismatic and nacreous layers. In addition, our folds do not form a fingerprintlike pattern.

A variety of foldlike structures have been documented in ammonoids by Checa (1995). All of his specimens were examined with light microscopy and one specimen was also examined with SEM (Late Jurassic *Pavlovia*). Checa identified eight different kinds of folds, many of which correspond to the ones we observed. Our pinnate folds correspond to his category 8 microsculpture, which he described as "low-relief longitudinal lines or smooth longitudinal strips, and associated arcuate wrinkles" (ibid.: 868). These folds appear and disappear across several successive intercostal valleys, forming a longitudinal pattern on the shell. Similarly, the grooves we observed in intercostal valleys may also correspond to his category 8 microsculpture but differ in lacking side branches. On the other hand, the grooves on the nodes in *M. geslinianum* may be a variation of Checa's category 3 microsculpture, which he described as "wrinkles associated with concave primary ribs" (ibid.: 866). Linear ridges in the middle of intercostal valleys in *S. carlilensis* may correspond to Checa's category 1 microsculpture ("tiny, closely spaced, low-relief wrinkles at the intercostal valleys . . . perpendicular to ribs," ibid.: 866). Dents on the ribs and in the intercostal valleys appear to correspond to his category 4 microsculpture.

Palmate folds are more difficult to classify. They occur across several successive intercostal valleys, suggesting that they are related to Checa's category 8 microsculpture. However, they differ from it in having side branches that originate from a single point, rather than from a central axis. They may correspond instead to his category 3 microsculpture ("wrinkles associated with concave primary ribs"), although palmate folds appear in intercostal valleys.

None of the folds we observed corresponds to what is classically known as feather structure (fig. 8). Feather structure was first described by Petitclerc (1918) as "weak ornament in the form of little feathers" (authors' translation from the French). It consists of a band of adorally convergent chevron folds that covers all or only the outer portion of the flanks (Arkell et al., 1957). Feather structure is more common in smooth-shelled ammonoids and has been reported in a number of Jurassic and Cretaceous genera including *Baculites, Placenticeras, Protoecotraustes, Beudanticeras, Brewiceras, Taramelliceras, Tragophylloceras,* and *Oxynoticeras* (see Checa, 1995, for references).

Feather structure is closest to palmate folds. However, the chevron folds in feather structure converge adorally, whereas those in palmate folds diverge adorally. Feather structure, despite its name, does not resemble pinnate folds because there is no central groove. Feather structure is also a much larger feature than any of the folds we described. We measured the maximum width of the band of feather structure (as a percentage of whorl height) in five specimens of *Placenticeras meeki* Böhm and one specimen of *Sphenodiscus lobatus* (Tuomey). As shown in table 1, the band of feather structure represents approximately one-third to nearly one-half of the whorl height and is located on the outer flanks. In contrast, pinnate folds and palmate folds represent approximately 15 and 10 percent, respectively, of whorl height.

In addition, feather structure generally has been reported from "the inner shell layer" (Arkell et al., 1957: L92; but see Checa, 1995: 885). In contrast, the pinnate folds in *S. carlilensis* occur in the outer prismatic layer. However, our data suggest that folds in the outer prismatic layer continue into the nacreous layer. The nacreous layer formed after the secretion of the outer prismatic layer, and evidently conformed to the shape of the overlying layer. Thus, we suspect that feather structure in the nacreous layer reflects a similar pattern in the outer prismatic layer.

There are many possible explanations for the small foldlike irregularities we observed on the shell surface of ammonoids. Pinnate folds superficially resemble the "forma verticata" described by Hengsbach (1996), which is generally interpreted as a repaired shell injury (Holder, 1956). However, as shown in our example of a repaired shell injury in *Nautilus scrobiculatus,* the pattern of growth lines in an injury differs from that in a pinnate fold. In a repaired injury, the growth lines adoral of the shell break point backward in the direction of the injured area (fig. 7A–D). In contrast, in a pinnate fold, the growth lines remain parallel to the ribs and do not point backward along the central groove of the fold.

Another possible explanation is that the folds in ammonoids were caused by irritations in the underlying mantle. Keupp (1979) has attributed some examples of shell abnormalities to parasites. Although this interpretation is difficult to completely disprove, it is unlikely; the occurrence of different types of folds on different parts of the shell tends to refute it. For example, the small ridges in *S. carlilensis* tend to occur only in the middle of intercostal valleys; pinnate folds form longitudinal patterns on the shell, appearing and disappearing across a succession of intercostal valleys; and small folds of the type observed on the nodes of *M. geslinianum* do not occur elsewhere on the shell.

The most likely explanation is that the folds on the shell surface initially formed in the periostracum before the shell was calcified. Checa (1995: 872) suggested that the

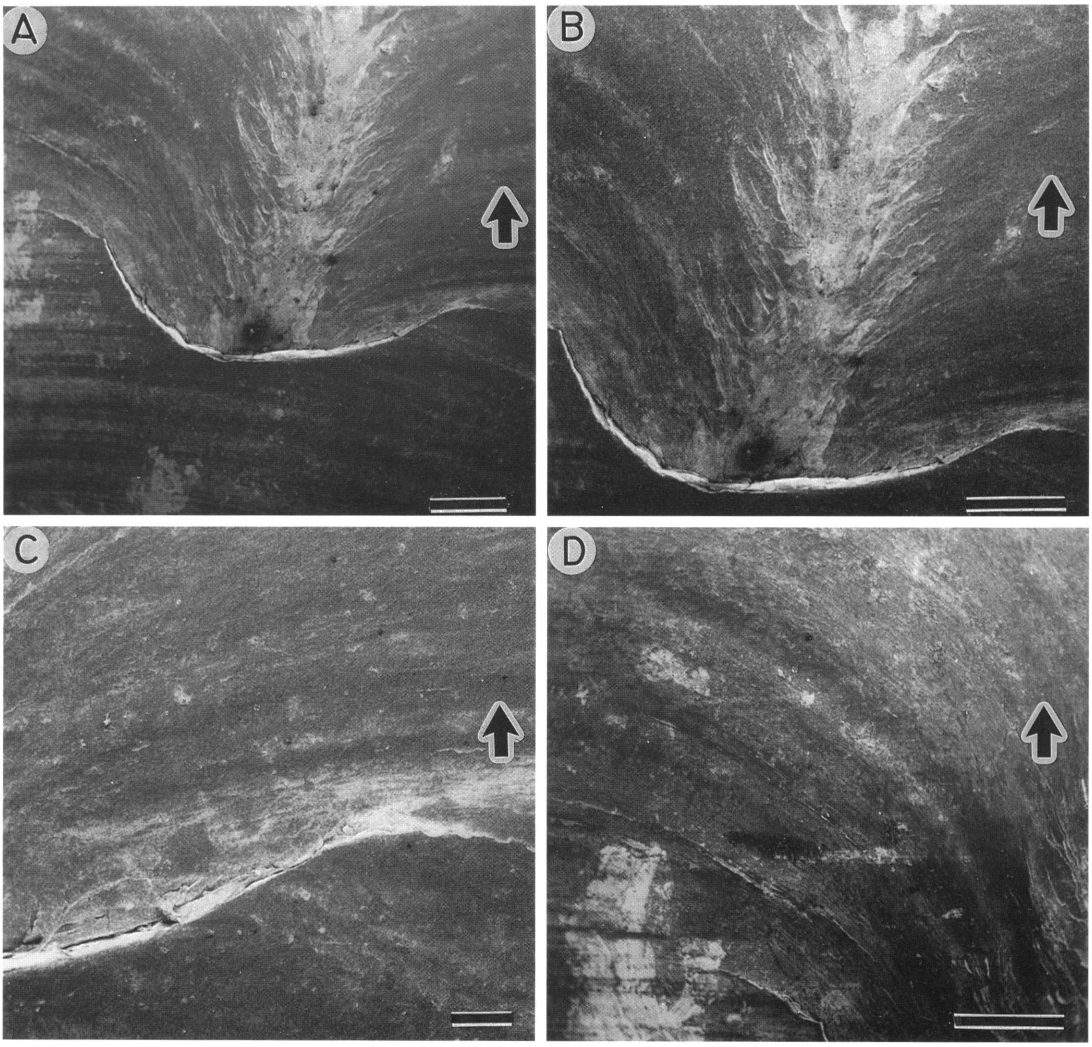
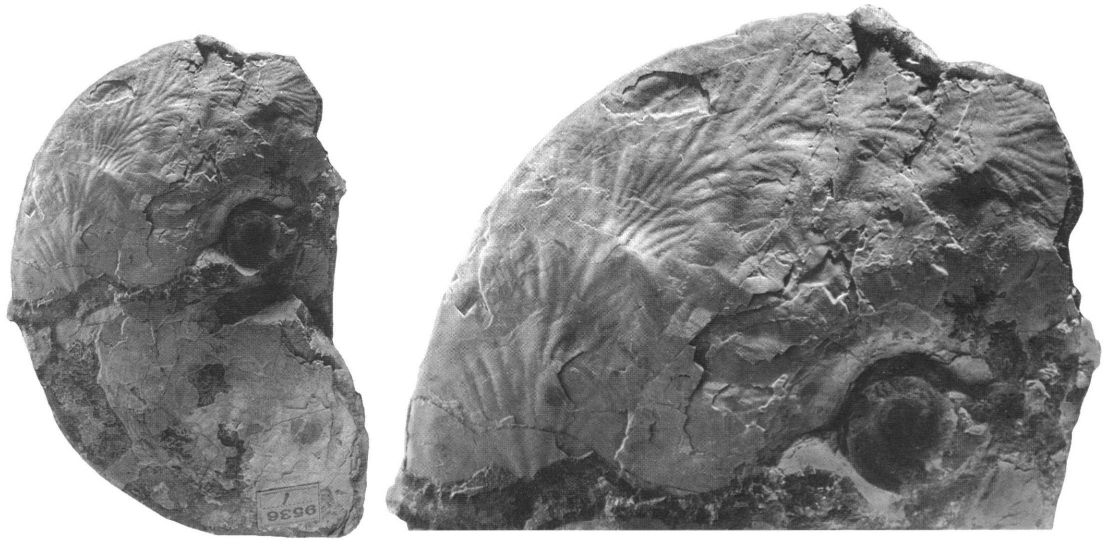


Fig. 7. A repaired injury in the shell of *Nautilus scrobiculatus,* AMNH 45386, Papua New Guinea. Arrows indicate adoral direction. **A.** Overview of injured area (crescent-shaped white area in middle of photo). The shell surface is covered with growth lines. Adapical of the injury (lower portion of photo), growth lines cross the shell in a radial direction whereas adoral of the injury, growth lines bend backward. Scale bar = 2 mm. **B.** Close-up of repaired area. The spherulitic prismatic layer has flaked away in some places exposing the underlying nacreous layer. Scale bar = 2 mm. **C.** Close-up of right ide of repaired area showing the contrast in the direction of growth lines adapical and adoral of the injury. Scale bar = 500 μm. **D.** Close-up of left side of repaired area. Growth lines curve sharply backward toward the injury. Scale bar = 2 mm.

folds resulted from stresses within the periostracum caused by changes in the local shape of the aperture. The circumference of the whorl cross section decreases as the shell passes from a rib crest into an adjacent intercostal valley. Therefore, the periostracum would have had to contract toward the middle of the intercostal valley to accommodate this change in shape. Folds would have developed in the periostracum as a consequence. They then would have disappeared in passing from the intercostal valley to the next rib crest. Such an explanation is consistent with the distribution of pinnate folds.

In addition, Checa (1995: 882–885) suggested that folds in the periostracum may



A B

Fig. 8. *Placenticeras meeki* Böhm, AMNH 9536/1, Upper Cretaceous (Campanian), South Dakota. **A.** Right lateral view showing a band of feather structure running along the outer third of the flanks. Adoral direction is toward the specimen label. Scale bar = 1 cm. **B.** Close-up of feather structure showing adorally convergent folds. Scale bar = 5 mm.

have been produced as the result of muscular contraction of the mantle. He maintained that ammonoids secreted a longer free periostracum than do other molluscs and this periostracum was connected to the mantle along longitudinal lines of attachment. Checa hypothesized that the mantle initially extended beyond the apertural margin to the position of the next rib. Subsequently, the mantle (and attached periostracum) retracted, forming a rib, as in an accordion, and, at the same time, generated small folds in the periostracum. During calcification, the outer prismatic layer conformed to the shape of the periostracum. Therefore, the folds in the periostracum were "imprinted" on this layer and subsequently, on the nacreous layer.

TABLE 1
Feather Structure in Two Species of Late Cretaceous Ammonoids

Specimen	WH[a]	FS[b]
Placenticeras meeki Böhm		
AMNH 9536/1	32.6	14.1 (43.2)
AMNH 45392	46.1	15.8 (34.3)
BHI 4746	15.4	6.3 (40.9)
BHI 4747	18.3	7.9 (43.2)
AMNH 45395[c]	75.3	23.0 (30.5)
Sphenodiscus lobatus (Tuomey)		
AMNH 9589/2	22.0	8.9 (40.4)

[a] Whorl height (mm).
[b] Maximum width of the band of feather structure (mm). Figures in parentheses are dimensions as a percentage of whorl height.
[c] Illustrated in Haas, 1961: 231.

The muscles responsible for contraction may have been located along the lines of attachment of the mantle to the periostracum. If this were true, however, the growth lines on the periostracum (presumably on both the outer and inner surfaces) would have been deformed during contraction. The analogy is pulling a drawstring through a piece of woven fabric. In this analogy, the drawstring represents the line of attachment and the threads of the fabric perpendicular to the drawstring represent the growth lines. When the drawstring is pulled backward, it creates a pinching-in of the fabric along the line of attachment, creating a pinnate fold. The "growth lines" are deformed so that they point backward along the central groove of the fold. However, in reality, growth lines cross the grooves of pinnate folds at right angles.

The degree of deformation of growth lines may have depended on the rigidity of the periostracum. Checa (1996, personal commun.) suggested another analogy using a more rigid material than fabric, namely, aluminum foil. In these experiments, parallel lines representing growth lines were drawn across a sheet of aluminum foil. The foil was then placed on a soft, spongy surface to simulate the soft mantle underneath the periostracum. A finger drawn along the aluminum foil simulating the contraction of a muscle produced folds very similar in appearance to pinnate folds. The "growth lines" were not deformed but crossed the central grooves of these folds at right angles. However, the "muscle" in this experiment was not actually attached to the "periostracum," but simply slid along it.

Another possibility, and the one favored by Checa (1995), is that the muscles responsible for mantle contraction were located in "an active oral muscular area" (ibid.: 882). The periostracum was connected to the mantle along longitudinal lines of attachment but these lines of attachment were "more or less inert" (ibid., p. 882). When the mantle retracted, the periostracum was passively pulled backward producing a variety of minor folds, especially in the intercostal valleys. The growth lines in the periostracum would not have been deformed in this process.

The exact mechanism of formation of the small foldlike irregularities on the shell surface of ammonoids is still unclear, and more observations are necessary to help resolve this issue. The relationship of these folds to feather structure also requires further study. Is feather structure simply a large-scale version of palmate folds, only in reverse? In a broader context, are the folds on the shell surface of ammonoids unique to these animals or do these features also occur in other molluscs? If folds are present in extant species, this would permit a better understanding of their formation.

REFERENCES

Arkell, W. J., B. Kummel, and C. W. Wright
1957. Mesozoic Ammonoidea. *In* R. C. Moore (ed.), Treatise on invertebrate paleontology, Pt. L, Mollusca 4: L80–L439. Boulder, CO, and Lawrence, KS: Geol. Soc. Amer. and Univ. Kansas Press.

Birkelund, T.
1981. Ammonoid shell structure. *In* M. R. House and J. P. Senior (eds.), The Ammonoidea, Syst. Assoc. Spec. Vol. 18: 177–214. London: Academic Press.

Bucher, H., N. H. Landman, S. M. Klofak, and J. Guex
1996. Mode and rate of growth in ammonoids. *In* N. H. Landman et al. (eds.), Ammonoid paleobiology, topics in geobiology 13: 407–461. New York: Plenum Press.

Checa, A.
1995. A model for the morphogenesis of ribs in ammonoids inferred from associated microsculptures. Palaeontology 37: 863–888 (1994 imprint).

Cobban, W. A.
1951. Scaphitoid cephalopods of the Colorado Group. U.S. Geol. Surv. Prof. Pap. 239: 36 pp.

Doguzhaeva, L. A., and H. Mutvei
1986. Functional interpretation of inner shell layers in Triassic ceratid ammonites. Lethaia 19: 195–209.

Engeser, T. S.
1996. The position of the Ammonoidea within the Cephalopoda. *In* N. H. Landman et al. (eds.), Ammonoid paleobiology, topics in geobiology 13: 3–19. New York: Plenum Press.

Grégoire, C.
1987. Ultrastructure of the *Nautilus* shell. *In* W. B. Saunders and N. H. Landman (eds.), *Nautilus*: The biology and paleobiology of a living fossil, pp. 463–486. New York: Plenum Press.

Haas, O.
1961. A *Placenticeras* with feather structure. J. Paleontol. 35: 230–231.

Hengsbach, R.
1996. Ammonoid pathology. *In* N. H. Landman et al. (eds.), Ammonoid paleobiology, topics in geobiology 13: 581–605. New York: Plenum Press.

Hölder, H.
1956. Über Anomalien an jurassischen Ammoniten. Paläontol. Z. 30(1/2): 95–107.
Hyatt, A.
1903. Pseudoceratites of the Cretaceous. U.S. Geol. Surv. Monogr. 44: 1–351.
Keupp, H.
1979. Nabelkanten-Präferenz der forma verticata Hölder 1956 bei Dactylioceraten (Ammonoidea, Toarcien). Paläontol. Z. 53(3/4): 214–219.
Kennedy, W. J.
1988. Late Cenomanian and Turonian ammonite faunas from north-east and central Texas. Spec. Pap. Palaeontol. 39: 1–31.
Landman, N. H.
1987. Ontogeny of Upper Cretaceous (Turonian-Santonian) scaphitid ammonites from the Western Interior of North America: systematics, developmental patterns, and life history. Bull. Am. Mus. Nat. Hist. 185: 117–241.
1994. Exceptionally well-preserved ammonites from the Upper Cretaceous (Turonian-Santonian) of North America: Implications for ammonite early ontogeny. Am. Mus. Novitates 3086: 15 pp.
Lehmann, U.
1981. The ammonites: their life and their world. Cambridge: Cambridge Univ. Press.
Morrow, A. L.
1935. Cephalopods from the Upper Cretaceous of Kansas. J. Paleontol. 9: 463–473.
Mutvei, H.
1964. On the shells of *Nautilus* and *Spirula* with notes on shell secretion in noncephalopod molluscs. Ark. Zool. 16: 221–278.
Orbigny, A. d'
1850. Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés. Vol. 2. Paris: Masson.
Okamoto, T.
1989. Changes in life orientation during the ontogeny of some heteromorph ammonoids. Palaeontology (London) 31(2): 281–294.
Petitclerc, P.
1918. Ornamentation peu connue chez certaines ammonites jurassiques. Bull. Soc. Géol. France, Sér. 4, 18: 233–234.
Saleuddin, A. S. M., and H. P. Petit
1983. The mode of formation and structure of the periostracum. *In* A. S. M. Saleuddin and K. M. Wilbur (eds.), The Mollusca, Vol. 4, Physiology, Pt. 1: 199–234. New York: Academic Press.
Vermeij, G.
1993. A natural history of shells. Princeton: Princeton Univ. Press.
Walliser, O. H.
1970. Über die Runzelschicht bei Ammonoidea. Göttinger Arb. Geol. Paläontol. 5: 115–126.
Ward, P. D.
1987. The natural history of *Nautilus*. Boston: Allen and Unwin.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://nimidi.amnh.org. Or address mail orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**