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External features of embryonic and early postembryonic shells of a Carboniferous goniatite *Vidrioceras* from Kansas

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Abstract. The ornamentation and dorsal wall structure of *Vidrioceras* (Cycloloboidea, Goniatitina) in the early ontogenetic stage are described on the basis of specimens from the Upper Pennsylvanian in Kansas, USA. The exposed surface of the embryonic shell is smooth, without any trace of ornamentation or growth lines. Regularly spaced lirae abruptly appear on the early postembryonic shell just adoral of the primary constriction. The inner surface of the dorsal wall in the embryonic and early postembryonic stages exhibits a distinct ornament consisting of evenly spaced, longitudinal ridges, which are replaced adorally by the typical wrinkled ornament in the subsequent stage. Our observations are in accord with those of goniatites from the Upper Carboniferous Buckhorn Asphalt of Oklahoma, suggesting that in the Goniatitina, the outer surface of the embryonic shell is smooth. Comparison with the embryonic shell formation of extant *Nautilus* suggests that in the Goniatitina, the embryonic shell was uniformly secreted by the shell gland on the posterior side of the embryo.

Key words: Ammonoidea, Carboniferous, development, embryonic shell, Goniatitina, Kansas, *Vidrioceras*

Introduction

The embryonic shell of ammonoids (termed the ammonitella by Druschits and Khiami, 1970) consists of a spherical initial chamber and approximately one subsequent whorl with a thick nacreous swelling (primary varix) at the aperture (for references see Landman *et al.*, 1996). The boundary between embryonic and postembryonic stages is marked by the primary constriction. Most previous studies on the external morphology and microstructure of embryonic shells of the Ammonoidea have been based on Mesozoic material with aragonitic preservation (Druschits and Doguzhaeva, 1981; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman, 1982, 1985, 1987; Landman and Bandel, 1985; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press, among others). In Paleozoic ammonoids, the microstructure of the embryonic shell is rarely preserved in most fossils due to diagenesis, except for aragonitic goniatites studied by Kulicki *et al.* (in press) from the Carboniferous Buckhorn Asphalt in Oklahoma, USA. Previous authors have indicated that the embryonic shells of Paleozoic ammonoids display ornamentation and features of several internal shell characters different from those of Mesozoic ammonoids (Beecher, 1890; Miller, 1938; House, 1965; Mapes, 1979; Tanabe *et al.*, 1993, 1994; Doguzhaeva, 1996; Landman *et al.*, 1996; Landman *et al.*, 1999; Klofak *et al.*, 1999; Kulicki *et al.*, in press). These studies have revealed a variety in the embryonic shell features in the Ammonoidea that can be used for higher-level phylogenetic analysis.

In this paper, we describe the ornamentation and the dorsal wall structure of goniatites at the embryonic and early postembryonic stages based on specimens from the Upper Pennsylvanian of Kansas, USA. Furthermore, the result of our observations is compared with data on other ammonoids and extant *Nautilus* and discussed for its implications for systematics and embryonic shell formation. Some of the specimens utilized have been studied by Tanabe *et al.* (1993), but those observations are partly reevaluated in this paper.

Material and methods

Tanabe *et al.* (1993) discovered an embryonic ammonoid assemblage in a carbonate concretion recovered from the Virgilian (Upper Pennsylvanian) offshore shale in Pomona, Kansas, USA. These authors classified the embryonic ammonoids into two morphotypes by the difference in the size and shape of their initial chambers, namely into a large and globular and a small and ellipsoidal one. They further assigned these large and small morphotypes to *Vidrioceras* (Vidrioceratidae, Cycloloboidea) and *Aristoceras* (Thalassoceratidae, Thalassoceratoidea) respectively, on the basis of comparison with their initial chambers with those of larger specimens of these two genera from the same concretion.

About one hundred well preserved specimens of the two genera at embryonic and early postembryonic stages were removed without etching from the weathered portion of the concretion by the wet-sieving method. They were coated with platinum and observed by scanning electron microscopy. Although the embryonic shells of *Aristoceras* occur more abundantly than those of *Vidrioceras*, we did not observe early shell features of the former genus because of poor preservation of the dorsal wall sculpture in the available specimens. As already pointed out by Tanabe *et al.* (1993), the goniatite specimens from Pomona preserve calcified shell material, and the recrystalized condition of their shell wall prevents study of the shell ultrastructure. Our observations are, therefore, mainly restricted to the external features of these specimens. All of the specimens utilized are housed in the University Museum, the University of Tokyo (UMUT).

Observations

Embryonic shells

General morphology and ornamentation.— The embryonic shells of *Vidrioceras* examined are all globular in overall shape and consist of a spindle-shaped initial chamber and approximately one subsequent planispiral whorl (Figure 1). In median section, a thick nacreous swelling (primary varix) appears on the inner side of the prismatic layer in the apertural region (see Tanabe *et al.*, 1995, figure 2A). The first whorl is much broader than high, covering the greater portion of the initial chamber (Figures 1, 2). The spiral length of the embryonic shell (=ammonitella angle of Landman *et al.*, 1996) is relatively long, measuring about 360° in median section. The embryonic shell diameter in the specimens examined ranges from approximately 720 μm (UMUT PM19872-1; Figure 1.1) to 780 μm (UMUT PM19872-3; Figure 1.3a). The exposed surface of the shell at the embryonic stage is smooth without any trace of ornamentation or growth lines (Figure 1).

Dorsal wall of the first whorl.— In several embryonic and early postembryonic specimens, part of the first whorl has been lost due to mechanical destruction during the taphonomic process or due to the wet-sieving procedure. In those specimens, evenly spaced longitudinal ridges are visible on the dorsal side of the missing whorl portion (Figures 2.1–2.3, 3.1, 3.2). They never occur on the lateral flanks of the initial chamber that are free from the first whorl. This fact indicates that the longitudinal ridges represent the sculpture on the inside surface of the dorsal wall of the first whorl. A weaker ridge is occasionally intercalated between the longitudinal ridges (Figure 2.3b).

Remarks.— Tanabe *et al.* (1993, fig. 3A) described evenly spaced longitudinal ridges on the ventrolateral side of several embryonic shells of *Vidrioceras* from the same locality and interpreted them as the surface ornamentation. However, our reexamination of these and additional specimens reveals that the longitudinal ridges are not the surface ornamentation but the microornamentation on the inner side of the dorsal wall, and that the exposed surface of the embryonic shell of *Vidrioceras* is in fact smooth.

Early postembryonic shells

The embryonic shell margin is easily visible from outside by the presence of the slightly depressed primary constriction followed by the sharp apertural edge (see arrows, Figure 1.1, 1.3a). Fine transverse lirae abruptly appear on the adoral side of the primary constriction. They are initially rectiradiate in the early postembryonic stage (Figure 1.1, 1.3a, b), but become prorsiradiate and gently convex at the venter in a later stage. Each lira is asymmetric in cross section with a steep edge on the adoral side and is gently inclined adapically (Figure 1.3b).

The change of the inner surface sculpture of the dorsal wall is visible in several early postembryonic shells whose body whorl is partly lost secondarily (Figure 2.1–2.3). In one of these specimens, shown in Figure 2.2, the longitudinally ridged ornament disappears on the dorsal side of the embryonic shell aperture and a wrinkled ornament similar to a human fingerprint pattern begins to appear on the adoral side of the primary constriction. In the embryonic or early embryonic specimen shown in Figure 2.4, the wrinkled ornament already exists on the dorsal side near the shell margin. In another two specimens, shown in Figure 2.1 and 2.3, the longitudinally ridged ornament extends for a half whorl beyond the primary constriction. These observations clearly indicate that *Vidrioceras* exhibits some variation in the ontogenetic change of the dorsal wall ornament.

Comparison with other ammonoids

On the basis of observations on excellently preserved material from the Pennsylvanian (Desmoinesean) Buckhorn Asphalt in Oklahoma, Kulicki *et al.* (in press) reported that the outer surface of the embryonic shells of goniatites is smooth without any trace of ornamentation or growth lines, as is the case of *Vidrioceras* described herein. These observations strongly suggest that in the Goniatitina the embryonic shell is smooth.

Ornamentation on embryonic shells of the Goniatitina differs from those of other ammonoid suborders. In the Devonian Agoniatitina, Anarcestina and Tornoceratina, the

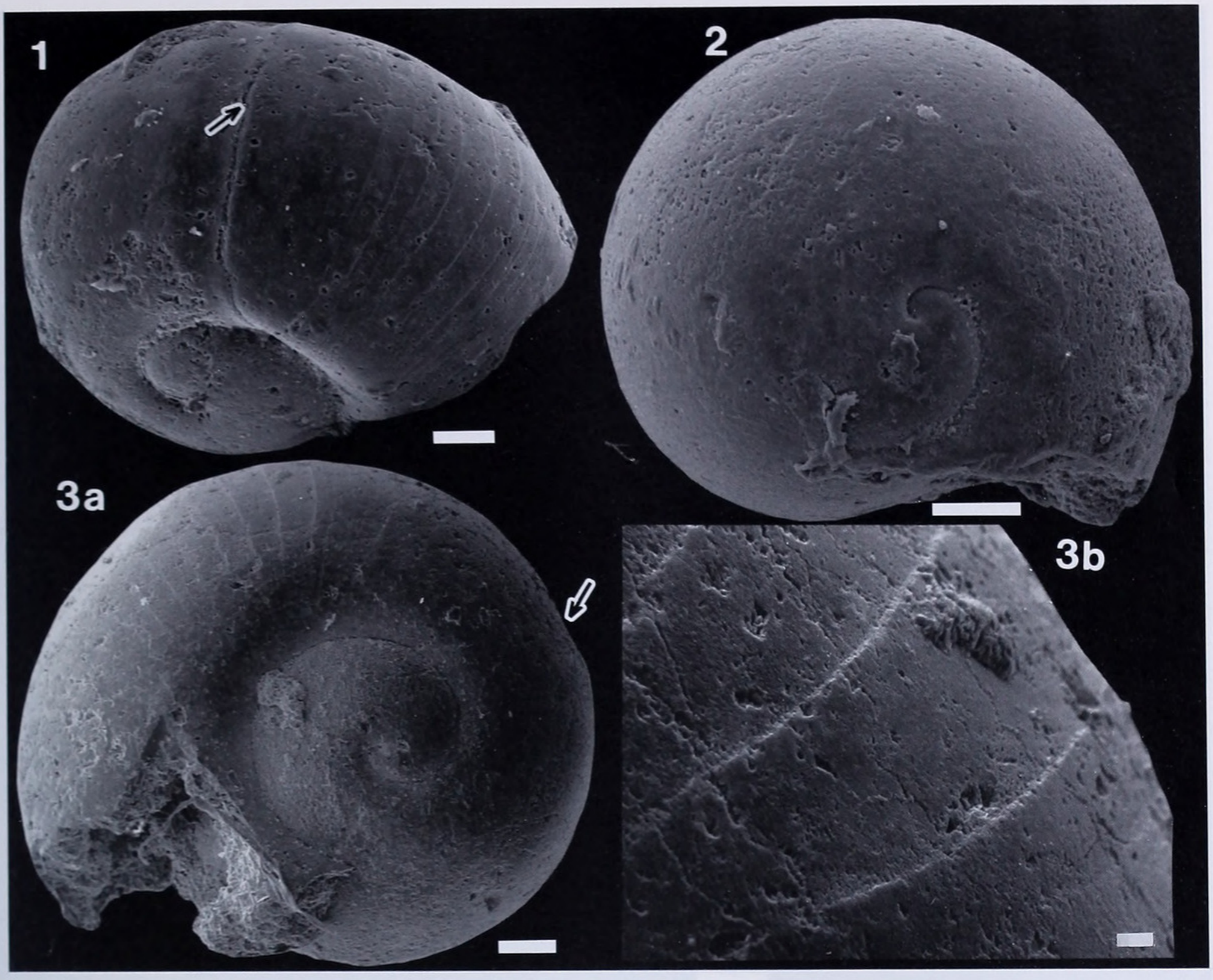
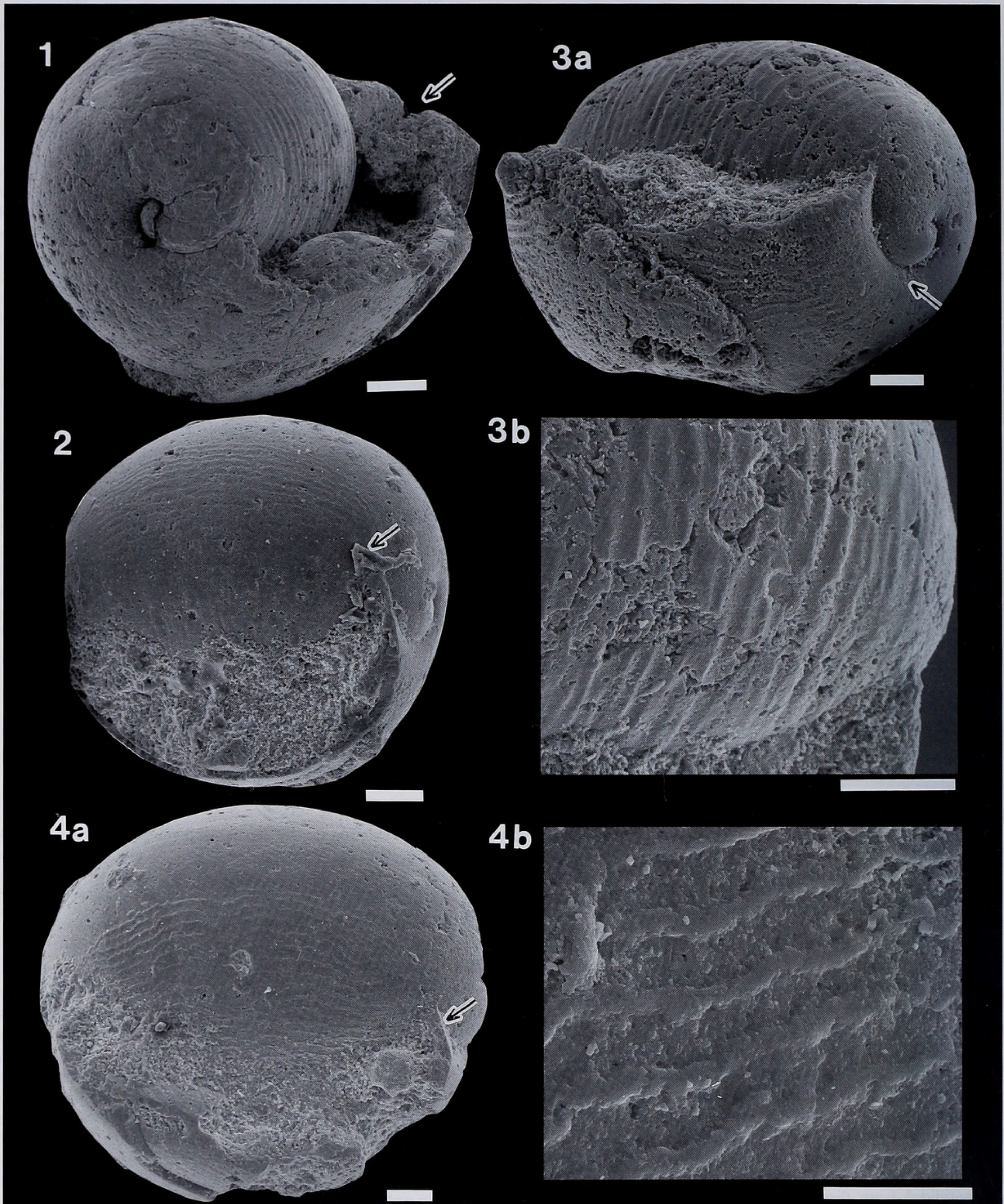


Figure 1. *Vidrioceras* sp. **1**. Oblique view of early postembryonic specimen showing slightly depressed primary constriction and adjacent embryonic shell edge (pointed by an arrow). The embryonic shell is smooth, while the postembryonic shell is sculptured by fine transverse lirae. UMUT PM19872-1. **2**. Lateral view of embryonic shell with smooth surface. UMUT PM19872-2. **3a, b.** UMUT PM19872-3. Lateral view of early postemebryonic shell showing abrupt appearance of fine transverse lirae after primary constriction (pointed out by an arrow) (**3a**) and close-up of lirae (**3b**). Scale bars: 100 μm (1, 2, 3a) and 10 μm (3b)

embryonic shells are characterized by fine transverse lirae parallel to the aperture (Beecher, 1890; Miller, 1938; House, 1965; Landman *et al.*, 1996; Klofak *et al.*, 1999). In the uncoiled Late Silurian and Devonian Bactritina and partly coiled Devonian ammonoids, the straight whorl after the initial chamber is also covered with transverse lirae (Erben, 1964). Mapes (1979) reported both smooth and longitudinal ornament on the initial subspherical chamber and early shaft of "bactritids" from the Carboniferous, and Mapes (1979) and Doguzhaeva (1996) reported a reticulate ornamentation on the earlier embryonic shaft portion of "bactritids" from the Carboniferous and Permian, respectively. However, Doguzhaeva *et al.* (1999) suggested that some of these specimens may eventually be reassigned to the Coleoidea. In the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, the embryonic shell lacks lirae and instead is covered with minute tubercles (Kulicki, 1974, 1979; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman and Waage, 1982; Landman, 1985, 1987; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press). To sum up these previous descriptions, at least three kinds of embryonic shell ornamentation have been recognized in the Ammonoidea excluding Upper Paleozoic "bactritids". Each ammonoid suborder, excluding the doubtful taxon Bactritina, appears to have its own characteristic pattern of ornamentation.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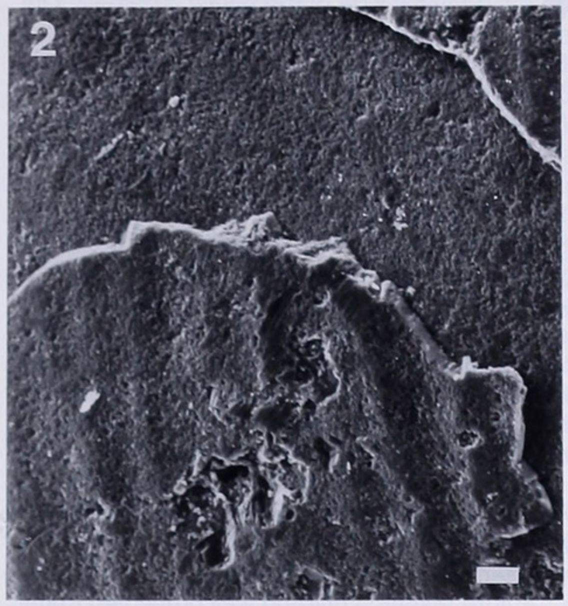

Figure 3. *Vidrioceras* sp. **3a.** Oblique view of embryonic shell with preserving interior dorsal wall sculpture of the first whorl with longitudinal ridges. **3b.** Close-up of longitudinal ridges on interior side of dorsal wall. Note that the boundary between ventral and dorsal shell walls is discernible in this specimen. UMUT MM19872-8.

Discussion

Observations of the early embryonic shells of extant *Nautilus* provide a reference point for discussions about the embryonic development of ammonoids. According to Arnold and Landman (1993) and Tanabe and Uchiyama (1997), the early embryonic shell development of *Nautilus* can be divided into two stages with different shell microstructure and ornamentation. In the first stage (=early organogenetic stage), a low cap-shaped shell with a distinct median depression (called cicatrix) is secreted in the sequence of outer conchiolin and inner prismatic layers. The cicatrix lacks growth lines, indicating uniform shell secretion by the mantle primordium (shell gland) on the posterior side of the embryonic body (see Tanabe and Uchiyama, 1997, fig. 1A). In the second stage (=middle organogenetic stage), a new shell consisting of outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers appears at the outer margin of the cicatrix, leaving a discontinuity in the shell structure at the boundary. It is sculptured by transverse growth lines and radial undulations. At this stage of development, the anterior mantle margin is well differentiated and possesses three folds, where shell secretion occurs (Tanabe *et al.*, 1991).

The absence of transverse lirae on the embryonic shells of the Goniatitina strongly suggests that the walls of the initial chamber and the first whorl were secreted synchronously by the undifferentiated shell gland. Bandel (1982) and Kulicki and Doguzhaeva (1994) hypothesized this kind of embryonic shell development in Mesozoic ammonoids, relying upon observations about the biomineralization of embryonic shells of modern "archaeogastropods". The longitudinal dorsal layer was probably secreted at a late stage of embryogenesis and occasionally at an early postembryonic stage. The appearance of transverse lirae on the postembryonic shell indicates an accretionary mode of growth. This event does not occur synchronously with the development of the dorsal wall with wrinkled ornamentation (Figure 2.1–2.4; Kulicki *et al.*, in press, pl. 2, fig. 3). Such a wrinkled dorsal wall has been extensively recognized in Paleozoic ammonoids in the postembryonic stage (House, 1971; Walliser, 1970). Kulicki (1979, 1996) and Kulicki *et al.* (2001) have pointed out that the dorsal wall of ammonoids consists of two components, namely, the outer component consisting of organo-prismatic material, sometimes with a wrinkled texture on the outside, and the inner prismatic component that covers the outer

← **Figure 2.** *Vidrioceras* sp. **1.** Lateral view of incomplete postembryonic shell, part of whose body whorl is lost. Dorsal wall of the first-second whorls exhibits longitudinally ridged ornament on the inner side. UMUT MM19872-4. **2.** Ventral view of early postembryonic shell showing change of interior dorsal wall sculpture from longitudinally ridged pattern to wrinkled pattern at embryonic shell/postembryonic shell boundary. UMUT MM19872-5. **3a, b.** UMUT MM19872-6. **3a.** Oblique view of incomplete postemebryonic shell, showing change of interior dorsal wall sculpture from longitudinally ridged pattern in embryonic stage to wrinkled pattern in postembryonic stage. **3b.** Close-up of longitudinally ridged dorsal wall structure in early postembryonic stage of same specimen. **4a, b.** UMUT MM19872-7. **4a.** Ventral view of embryonic (or early postembryonic) shell showing interior feature of dorsal wall with wrinkled ornamentation. **4b.** Close-up of wrinkled ornamentation in same specimen. Scale bars: 100 μm (1-4a) and 40 μm (4b). Arrows in 1, 2, 3a, and 4a point to the approximate position of primary constriction.

component on the adapical side of the body chamber. Our observations indicate that the inner dorsal wall component is absent in the embryonic shells of *Vidrioceras*. It presumably begins to appear in the postembryonic stage.

In view of the absence of transverse lirae, the mode of embryonic shell formation in the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina may also be explained by the "archaeogastropod model" of Bandel (1982) and Kulicki and Doguzhaeva (1994). The presence of fine transverse lirae on the relatively large embryonic shells of the Devonian suborders Agoniatitina, Anarcestina and Tornoceratina and on their postembryonic shells (see Landman *et al.*, 1996, appendix I) is, however, problematic. One possibility is that in the embryonic stage the mantle already was differentiated in the embryonic stage to secrete a shell with growth lines at its anterior margin. This type of embryonic shell development would be described as accretionary growth. A second possibility is that the embryonic shell was rapidly mineralised and an accretionary mode of growth characterized only the postembryonic shell (Klofak *et al.*, 1999). Future research utilizing well preserved material will resolve this problem.

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