Chapter 9
Cameral Membranes in Carboniferous and Permian Goniatites: Description and Relationship to Pseudosutures

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1 Introduction

During the last century, cameral membranes have been reported in many different ammonoids (Grandjean, 1910; Schoulga-Nesterenko, 1926; Hölder, 1952, 1954; Schindewolf, 1968; Erben and Reid, 1971; Westermann, 1971; Bayer, 1977;

Kulicki, 1979; Weitschat and Bandel, 1991; Tanabe and Landman, 1996). Cameral membranes include two main varieties: chamber linings coating the inside surfaces of each chamber, and three-dimensional structures suspended within the chambers (Landman et al., 2006). In the Mesozoic, cameral membranes have been observed in phylloceratids, lytoceratids, and ammonitids. More recently, similar membranes have been observed in Paleozoic prolecanitids (Mapes et al., 2002; Tanabe et al., 2005). Until recently, however, it was unclear whether such membranes occur in goniatites (Landman et al., 2006). Schoulga-Nesterenko (1926) reported membranes associated with the siphuncle in the Artinskian goniatite *Agathiceras uralicum* (Karpinsky, 1889); however, the illustration of the specimen, which shows a central siphuncle, puts its identification as a goniatite in doubt.

We describe suspended cameral membranes in the phragmocones of two species of goniatites: (1) *Crimites elkoensis* Miller et al., 1957, from the Permian Arcturus Formation near Buck Mountain, Nevada, and (2) *Cravenoceras fayettevillae* Gordon, 1965, from the Carboniferous (Mississippian) Fayetteville Shale in northwestern Arkansas. The membranes are similar in some ways to those observed in other ammonoids, but are much less complex and are present only in the immediate vicinity of the siphuncle. We refer to them as siphuncular membranes, which are defined as cameral membranes attached to and surrounding the siphuncle (Landman et al., 2006).

The presence of pseudosutures in several specimens of *Cravenoceras fayettevillae* further allowed us to investigate the relationship between siphuncular membranes and pseudosutures. Pseudosutures are markings between septal sutures that form incomplete replications of the suture. Some workers have hypothesized that pseudosutures are the preserved vestiges of pseudosepta, that is, thin, organic structures, which in most cases decomposed early in diagenesis (Hewitt et al., 1991; Westermann, 1992). Pseudosepta have been interpreted as membranes that resulted from the desiccation of a cameral gel and replicated the shape of the septum (Hewitt and Westermann, 1987; Hewitt et al., 1991), while pseudosutures are the preserved margins of the pseudosepta where they contacted the interior of the shell wall (Hewitt et al., 1991). Some authors have suggested that siphuncular membranes such as the ones described herein are in fact the remains of pseudosepta (Hewitt and Westermann, 1987; Hewitt et al., 1991; Landman et al., 1993). Although siphuncular membranes have been observed in a wide variety of ammonoids, the identification of these membranes as pseudosepta is unclear. Because both siphuncular membranes and pseudosutures are present in some of the goniatites we examined, we investigated the relationship between them.

1.1   Background

Three main types of suspended cameral membranes have been described: transverse, horizontal, and siphuncular (Weischat and Bandel, 1991). Of these, siphuncular membranes are the most common, and they are the only type documented in the goniatites described in this study. Weitschat and Bandel

(1991) described siphuncular membranes as sheets extending from the outermost layer of the siphuncle to the inside surface of the ventral wall, and commonly attached to the septal surface as well. They further noted that the edges of the sheets are projected adorally. This description is similar to what Landman et al. (2006) noted in prolecanitids from Nevada. Although the siphuncular membranes in goniatites are much less complex than those in other ammonoids, these membranes also extend between the siphuncle and ventral floor of the chamber, and are commonly projected adorally.

Pseudosutures were first described by John (1909) as markings ("*Pseudolobenlinie*") between sutures on the steinkerns of Triassic ceratites. Pseudosutures have since been described in a variety of Paleozoic and Mesozoic ammonoids, and they most often occur on the venter or flanks (Hölder, 1954; Vogel, 1959; Schindewolf, 1968; Bayer, 1977; Zaborski, 1986; Hewitt et al., 1991; Landman et al., 1993; Lominadze et al., 1993).

The significance of pseudosutures for understanding the mode of chamber formation also has been examined (Zaborski, 1986; Seilacher, 1988; Hewitt et al., 1991; Landman et al., 1993; Lominadze et al., 1993). The most detailed model proposed that the animal secreted a cameral gel, which supported the back of the body during translocation and formed cameral membranes (=pseudosepta) due to differences in the viscosity of the gel, and subsequent desiccation (Hewitt et al., 1991). The pseudosutures are interpreted as the margins of these membranes on the inner surface of the shell wall. Of the two goniatite species we examined, pseudosutures are present only in *Cravenoceras fayettevillae*.

2   Material

2.1   *Crimites elkoensis* Miller et al., 1957

Crimites elkoensis Miller et al., 1957, is an adrianitid goniatite from the Lower Permian (Wolfcampian = Sakmarian) of eastern Nevada. The genus *Crimites* has a cosmopolitan distribution in the Permian (Sakmarian to Kazanian). Several species of this genus occur in Lower Permian deposits in Nevada (Miller et al., 1957). Although other ammonoids are more common at this site, *Crimites elkoensis* is the most abundant goniatite.

The shell of *Crimites elkoensis* is relatively small, globular, and involute, with reticulate ornament and four or five constrictions per whorl (Fig. 9.1A). The whorl width is commonly greater than the whorl height. The suture is relatively simple, with about 14 lobes (Fig. 9.1B).

Specimens were collected near Buck Mountain in east-central Nevada (Figs. 9.2, 9.3). The strata containing ammonoids are part of the Lower Permian Arcturus Formation and are located on the south side of the mountain in three
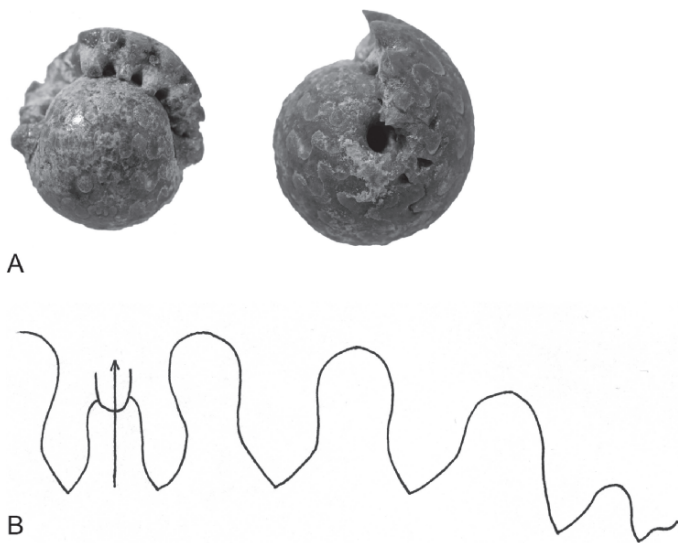
Fig. 9.1 Crimites elkoensis *Miller et al., 1957, SUI 39000, Rib Hill-Arcturus Formation, Lower Permian, Buck Mountain, Nevada.* **A**. *Apertural view and right side. Maximum diameter = 8.8 mm.* **B**. *Partial suture of the same specimen at shell diameter = 8.8 mm. From Lee (1975: 105).*

Fig. 9.2 *Localities of* Crimites elkoensis *Miller et al., 1957, and* Cravenoceras fayettevillae *Gordon, 1965. Map of the USA with asterisks indicating the sites at Buck Mountain, Nevada, and Fayetteville, Arkansas.*

PERIOD	N. AMERICAN SERIES	EURO-PEAN SERIES	EASTERN NEVADA		NORTHWEST ARKANSAS	
Permian	Leonardian	Artinskian	Arcturus Group	Riepetown-Rib Hill-Arcturus-Pequop-Formation	Unconformity	
	Wolfcampian	Sakmarian		Unconformity		
Carboniferous / Pennsylvanian	Desmoinesian	Westphalian	Ely Group	Tomera Formation		
	Atokan			Moleen Formation	Atoka Formation	
	Morrowan				Bloyd Formation	
					Hale Formation	
Carboniferous / Mississippian	Chesterian	Namurian		Diamond Peak Formation	Imo Fm/Unconformity	
					Pitkin Fm	
					Fayetteville Shale	Upper Fayetteville
						Weddington Sandstone
						Lower Fayetteville
					Mayes Group	Batesville Sandstone
						Unconformity
						Moorefield Formation
	Meramecian	Visean		Chainman Formation	Unconformity	
	Osagean			Not exposed	Boone Formation	

Fig. 9.3 *Stratigraphic column for Buck Mountain, Nevada, and Fayettevillae, Arkansas. The specimens of* Crimites elkoensis *Miller et al., 1957, are from the Arcturus Group (Permian). The Arcturus Group has been referred to by various names, as shown. The specimens of* Cravenoceras fayettevillae *Gordon, 1965, are from the lower Fayetteville Shale (Mississippian). Modified From Tomastik (1981: 18) and Manger (2004: 5, 14).*

ridges just east of Beck Springs. The fossils, which include marine invertebrates and vertebrates, occur in carbonate and phosphate concretions. Prolecanitid ammonoids are the most abundant fossils, followed by goniatites and nautiloids. During deposition of these strata, the lower part of the water column may have been anoxic and slightly acidic (Landman et al., 2006). These conditions would have allowed for rapid phosphatization of cameral membranes in ammonoids very early in diagenesis (Briggs, 2003; Landman et al., 2006). The originally aragonitic shell material of the goniatites was transformed into calcite, while the originally organic membranes were replaced by phosphate.

2.2 *Cravenoceras fayettevillae* Gordon, 1965

Cravenoceras fayettevillae Gordon, 1965, is a goniatite from the Upper Mississippian (Chesterian = early Namurian) of northwest Arkansas. The shell is relatively small, evolute, and globular, with a small umbilicus, thin, closely spaced ribs, and three or four constrictions per whorl (Fig. 9.4A). The body chamber is approximately 1.5 whorls long, and the suture is simple and very similar to that of *Cravenoceras articum* (Fig. 9.4B). Growth occurs in three stages (Fig. 9.5). This species is present only in the Fayetteville Shale (Fig. 9.3), although the genus has a cosmopolitan distribution (Eurasia, North Africa, and North America) during the Late Mississippian and Early Pennsylvanian.

   The specimens we studied came from the lower part of the Fayetteville Shale along the White River near Durham, Arkansas (Fig. 9.2). Many of the specimens were obtained from carbonate concretion "halos" that occasionally surround the body chambers of large (up to 3 m in length) actinoceratids. The concretions were slabbed with a diamond saw to expose the goniatites (Mapes and Dalton, 2002). Most of the ammonoids appear to be *Cravenoceras fayettevillae*, although specimens of other taxa, such as *Tumulites* and *Paracravenoceras*, have been observed.
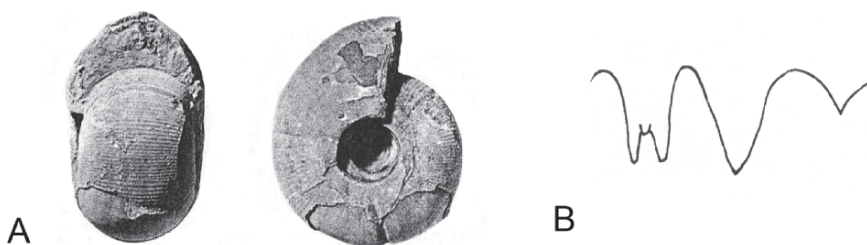

Fig. 9.4 A. Cravenoceras fayettevillae *Gordon, 1965, UA 77–205–1, lower Fayetteville Formation, Upper Mississippian (Chesterian), Fayetteville, Arkansas. Apertural view and left side, maximum diameter = 24 mm. From Saunders et al. (1977: 129).* **B**. *Partial suture of a closely related species,* Cravenoceras articum *Librovich, 1938, Middle Carboniferous (Namurian), Novaya Zemlya, Russia. From Ruzhentsev (1962: 589).*
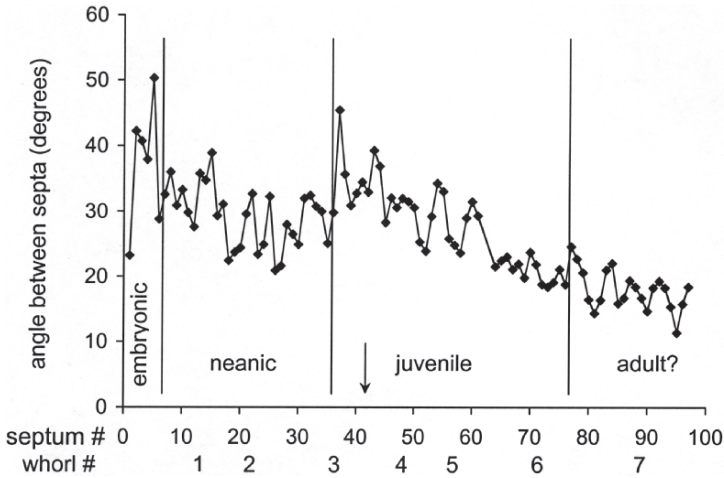
Fig. 9.5 *Plot of septum number versus septal angle (angle between septa) in* Cravenoceras fayet-tevillae *Gordon, 1965, AMNH 51239, lower Fayetteville Formation, Durham, Arkansas. Vertical lines demarcate three growth stages as described by Bucher et al. (1996). The arrow indicates the point at which siphuncular membranes appear at about 3.5 whorls. Siphuncular membranes may have appeared even earlier, but this is impossible to determine as the siphuncle is missing between septa 30 and 40.*

The Fayetteville Shale is a black, concretionary marine shale with a primarily molluscan fauna dominated by cephalopods (Gordon, 1965; Saunders et al., 1977). Nautiloids and ammonoids occur as pyritized casts, or alternatively, in carbonate concretions. The environment most likely was a deep, muddy shelf with anoxic bottom conditions. As with the specimens of *Crimites* from Nevada, such conditions were conducive to the preservation of soft tissue. The shells of *Cravenoceras fayettevillae* are calcitic. Rapid burial and an abundance of phosphorus resulted in the preservation of the originally organic membranes, through replacement by phosphate or through the development of phosphatic coatings on the surfaces.

2.3 Phosphatization of Organic Material

Preservation of soft tissues and delicate organic structures, such as cameral membranes, is relatively rare in the fossil record. Briggs (2003) discussed the circumstances under which such preservation is likely to occur: warm, shallow, marine environments with high organic productivity, episodic sedimentation, fluctuating salinity, and low oxygen. The presence of active bacterial decomposers or microbial mats appears to be a key factor in mediating the rapid mineralization of soft tissues (Briggs and Kear, 1993; Briggs, 2003; Martin et al., 2004). Phosphatization of organic material such as siphuncular membranes most likely occurs where bottom

conditions are poor (probably anoxic and slightly acidic). This would allow postmortem precipitation of phosphate in the ammonoids as well as precipitation of phosphate concretions around suitable nuclei. The following scenario represents one possible pathway for the fossilization of the organic membranes in the goniatites we studied. After death, some of the ammonoids sank to the bottom and were rapidly buried. This rapid burial prevented destruction of soft tissue by scavengers. Dissolved phosphate in the sediment diffused into the phragmocone via the siphuncle (Weitschat and Bandel, 1991), and additional phosphate was liberated by bacteria from the soft tissues of the ammonoids. Decay resulted in the production of bicarbonate, which combined with phosphate to form apatite. Briggs (2003) has shown that when the concentration of phosphate is high, calcite or aragonite precipitation is inhibited, and apatite replaces soft tissue. Briggs (2003) further has shown that bacterial mediation and a significant external source of phosphate (e.g., from decomposing phytoplankton) are probably necessary for soft-tissue fossilization.

3   Methods

To study siphuncular membranes, we prepared 26 specimens in three different orientations. Sixteen specimens (10 *Crimites elkoensis* and 6 *Cravenoceras fayettevillae*) were ground in a median section coincident with the plane of the siphuncle; this provided a lateral cross section of the membranes. One specimen of *C. elkoensis* and one of *C. fayettevillae* were ground in a dorsoventral cross section perpendicular to the plane of symmetry to reveal the siphuncular membranes in transverse cross section. The eight remaining specimens (all *C. fayettevillae*) were left intact. We etched the specimens with dilute acetic acid (5%) to expose the membranes. Because the membranes are phosphatic, etching revealed the preserved membranes in three dimensions. The etching process was monitored and stopped as soon as the membranes were adequately exposed. Etching time varied from 2 min up to 3 h. Further etching resulted in the destruction of the membranes.

The exposed membranes included the organic lining of the chamber, the wall of the siphuncle, and the siphuncular membranes. In whole (unground) specimens, the only structure visible after dissolution is commonly the smooth outer surface of the chamber lining. This lining must be partly removed to observe the siphuncle and its associated membranes. Removal of the delicate lining usually resulted in destruction of the underlying siphuncle and associated membranes, but sometimes the lining was serendipitously removed, exposing the siphuncular membranes. The specimens with siphuncular membranes were examined by scanning electron microscopy (SEM).

To examine pseudosutures, four specimens of *Cravenoceras fayettevillae*, in which only the phragmocones had been preserved, were prepared by carefully separating the phragmocone from the surrounding matrix. In general, the shell wall adhered to the matrix, resulting in an external and internal mold (steinkern). Both

the external and internal molds of two specimens were etched, while the molds of the two other specimens were not etched. By etching, we hoped to determine the original nature of the pseudosutures (mineralized or organic). The molds were examined by SEM. All illustrated specimens are reposited in the American Museum of Natural History (AMNH), the Department of Geology of the University of Arkansas (UA), and the Department of Geoscience of the University of Iowa (SUI).

4 Observations

4.1 *Crimites elkoensis* Miller et al., 1957

The membranes in this species consist of a series of small, adorally concave sheets that extend from the outer layer of the siphuncle to the inner surface of the ventral part of the chamber (Figs. 9.6, 9.7).

They are usually evenly spaced along the siphuncle in each chamber, although in some specimens they are more common in the adapical part of the chamber. The
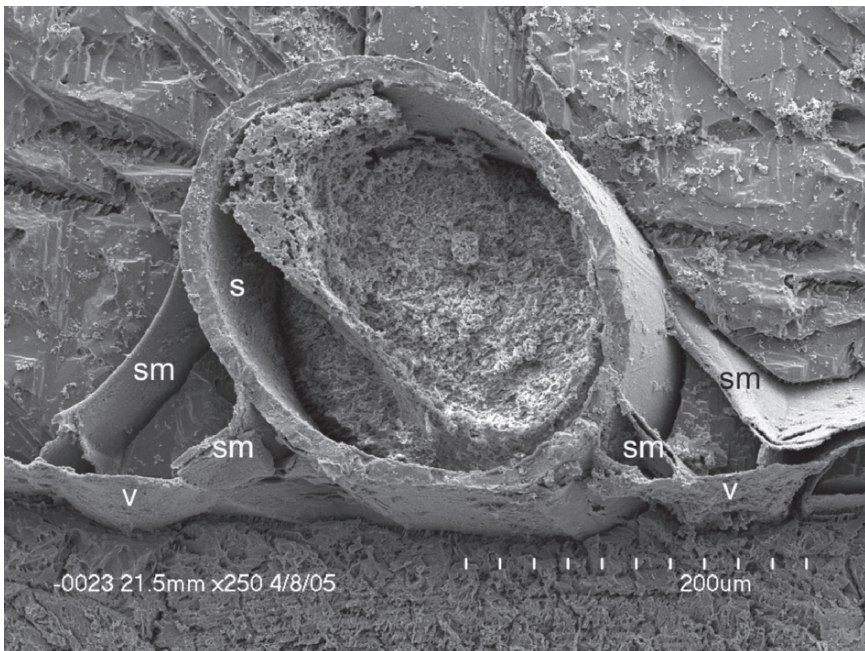

Fig. 9.6 Crimites elkoensis *Miller et al., 1957, AMNH 51223, Arcturus Formation, Buck Mountain, Nevada. Dorsoventral section showing the siphuncle (s) and siphuncular membranes (sm). The membranes form sheets between the siphuncle and the ventral floor of the chamber (v).*
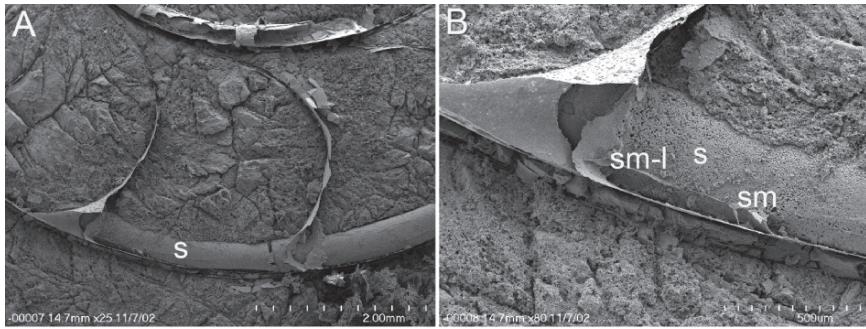
Fig. 9.7 Crimites elkoensis *Miller et al., 1957, AMNH 51240, Arcturus Formation, Buck Mountain, Nevada. Median views of the siphuncle and siphuncular membranes. A. The siphuncle (s) is visible in two chambers. Adoral direction is to the right. B. Close-up of the siphuncular membranes (sm) in A. A fragment of a siphuncular membrane (sm-l) that connects multiple siphuncular membranes is visible.*

membranes sometimes appear to have two layers (Fig. 9.6), although in most instances, they appear as one solid sheet. The bilayered structure may indicate that the original membrane was coated with phosphate on both sides during early diagenesis. When the original membrane decomposed, the two phosphatic layers remained with a small space between them.

Figure 9.7 indicates that the membranes may merge dorsally into a thin sheet parallel to the floor of the chamber. However, the fragmentation of the specimen makes it difficult to determine this for certain. Such sheets, formed by the merging of several elements, are common in ceratites and prolecanitids (Weitschat and Bandel, 1991; Landman et al., 2006).

Perhaps because goniatites are relatively rare in the Buck Mountain concretions, we were unable to find a specimen with preservation adequate to determine the morphology of the siphuncular membranes throughout ontogeny. The goniatite *Crimites elkoensis* is present in the same deposits as the prolecanitid *Akmilleria electraensis* Plummer and Scott, 1937, whose membranes do not appear until the end of the neanic stage (at or near the beginning of the third whorl, corresponding to a shell diameter of approximately 3 mm). The membranes in *A. electraensis* first appear as simple sheets, similar to those of the goniatites, and then become more complex during ontogeny (Landman et al., 2006). Until better-preserved specimens are examined, it is impossible to state whether there is any consistent ontogenetic pattern in *C. elkoensis*.

4.2   *Cravenoceras fayettevillae* Gordon, 1965

The siphuncular membranes in *Cravenoceras fayettevillae* also appear as a series of simple, evenly spaced, adorally concave sheets between the siphuncle and ventral
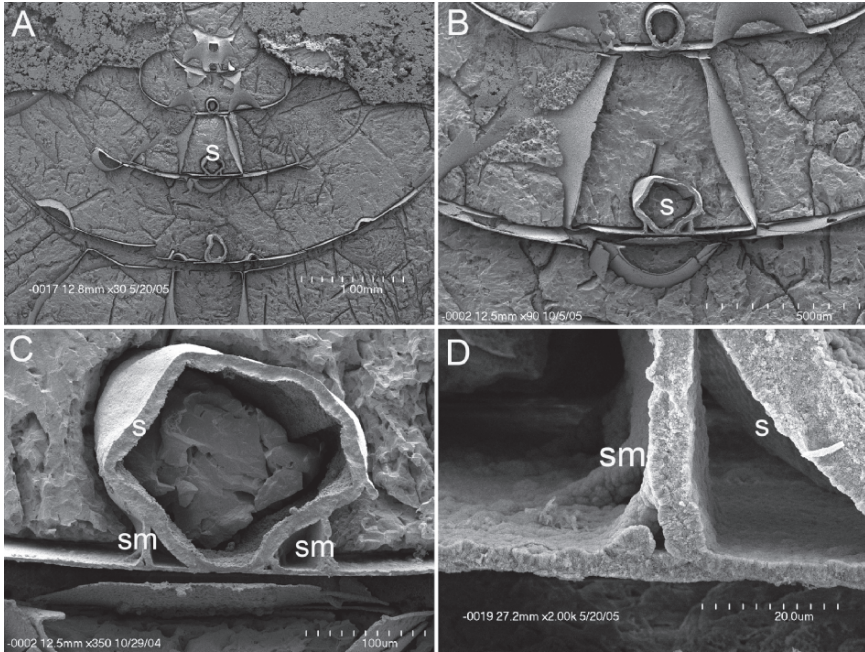
Fig. 9.8 Cravenoceras fayettevillae *Gordon, 1965, AMNH 51233, lower Fayetteville Shale, Fayetteville, Arkansas. Dorsoventral views of the siphuncle and siphuncular membranes. A. Overview of several whorls. B. Close-up view of a portion of the siphuncle (s), showing siphuncular membranes. C. Close-up view of the central portion of B, showing the siphuncular membranes (sm) on either side of the siphuncle (s). D. Close-up view of the siphuncular membranes in C, showing tiny podial attachments along the length of the siphuncular sheet.*

floor of the chamber (Figs. 9.8–9.10). In the dorsoventral view in Fig. 9.8, tiny "podia" are visible attaching the membrane to the inner lining of the shell. Such podia are very common on the siphuncular membranes in prolecanitids (Landman et al., 2006). In the specimen of *C. fayettevillae* in Fig. 9.8, the membranes are oriented perpendicular to the chamber floor, with no adoral projection. The median sections of *C. fayettevillae* confirm, however, that the siphuncular membranes are adorally concave and projected forward, as in specimens of *Crimites elkoensis* (Fig. 9.9).

In Fig. 9.9C, D, a thin, fragmented sheet is visible along the ventrolateral portion of the siphuncle. This is probably similar to the sheet described in *Crimites elkoensis*, in which the smaller, ventral membranes merge dorsally into a single sheet. Part of the siphuncle has been ground away, so the connection between the smaller sheets and the larger sheet is no longer visible. Figure 9F, H additionally shows that the larger sheet is not continuous, but shows numerous gaps (at least five in Fig. 9.9H).

Fig. 9.10 illustrates several examples of specimens in which the venter of the phragmocone was etched whole without first being ground, revealing the cameral membranes. In these specimens, the orientation of the siphuncular membranes in
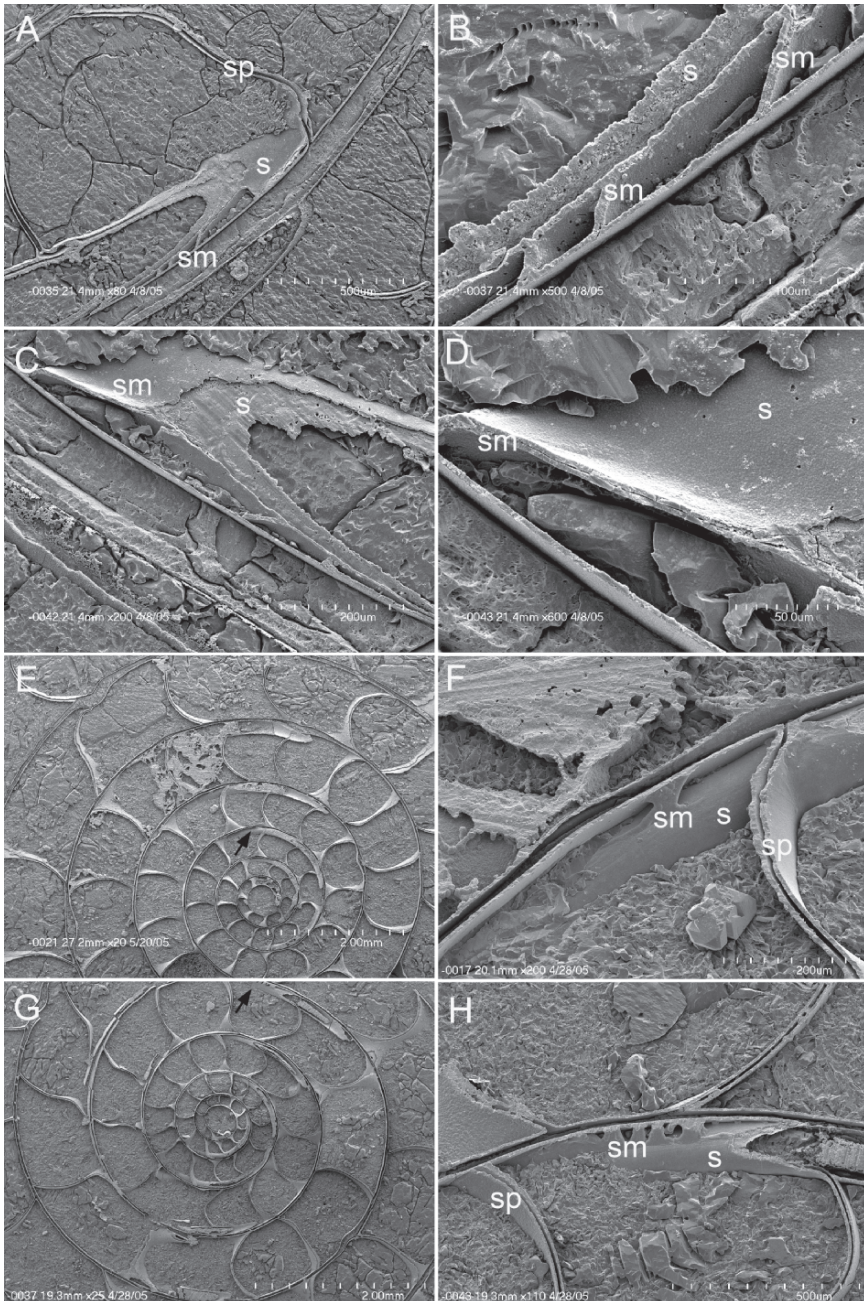
Fig. 9.9 *Median views of siphuncular membranes in* Cravenoceras fayettevillae *Gordon, 1965, lower Fayetteville Formation, Durham, Arkansas. A–D. AMNH 51229; E–F. AMNH 51237; G–H. AMNH 51239. A. Siphuncle (s) and associated siphuncular membranes (sm). The adoral direction is to the left. sp = septum. B. Close-up view of A, showing the adoral projection of the membranes (sm),*

relation to the siphuncle and chamber floor is visible. The siphuncular membranes appear as a series of adorally concave sheets between the siphuncle and the ventral lining of the chamber. The sheets are projected forward and commonly merge ventrolaterally.

We were able to examine changes in the morphology of the membranes in the ontogeny of two specimens (Fig. 9.9E, G). Although the siphuncle was missing in places, it is clear that membranes are not present in the earliest chambers. The earliest appearance of membranes is at approximately 3.5–3.75 whorls. This corresponds to the end of the neanic stage (Fig. 9.5). In the prolecanitid *Akmilleria electraensis* from Buck Mountain, Nevada, membranes also appear at the beginning of the third whorl, which marks the end of the neanic stage, that is, the end of the first postembryonic stage (Bucher et al., 1996).

In one specimen, two phosphatized, presumably originally organic, layers are present in the body chamber (Fig. 9.11). Because the specimen is fragmented, it is impossible to determine in which part of the body chamber the layers occur. One layer, located on the outside of the shell wall, is presumed to be the periostracum (p), while the other, on the inside of the shell wall, is most likely the chamber lining (cl).

We observed pseudosutures in many specimens of *Cravenoceras fayettevillae* (Figs. 9.12–9.14), though none are visible in *Crimites elkoensis*. The pseudosutures occur on the ventral and/or ventrolateral parts of the specimen, adoral or adapical of the first saddle and the first and second lobes. They are generally quite close to the suture. Pseudosutures do not occur in every specimen or in every chamber, although, if present at all, they generally occur in more than one chamber. No pattern in the number or location of pseudosutures within or among specimens is apparent.

The pseudosutures in *Cravenoceras fayettevillae* appear as ridges on the inside surface of the shell on the external mold (Fig. 9.13A, B), and as grooves on the corresponding steinkern (Fig. 9.13C, D). They are sometimes very well defined (Fig. 9.13B), but more commonly they are indistinct (Fig. 9.14). The ridges, especially when well developed, are asymmetrical in lateral cross section, with an abrupt adapical slope and a longer, more gradual adoral slope (Fig. 9.12C, D).

In etched specimens, we noted that the pseudosutural ridges on the inside surface of the external mold are sometimes dissolved and sometimes intact. Similarly, the

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Fig. 9.9 (continued) *which is characteristic of ceratites, prolecanitids, and goniatites.* C. Siphuncular *membrane (sm) along the length of the siphuncle (s). The adoral direction is to the right. D. Close-up view of C, showing that the membranes sometimes consist of two layers and are continuous with the layer surrounding the siphuncle (s). E. Overview of a specimen with the initial chamber preserved. The arrow indicates the first appearance of siphuncular membranes. F. Close-up view of earliest siphuncular membranes (sm). The adoral direction is to the left and down. G. Overview of another specimen with the initial chamber preserved. The first appearance of siphuncular membranes is indicated by the arrow. H. Close-up view of the siphuncular membranes in G, showing how they appear when unbroken. Several siphuncular sheets may form parallel to the floor of the chamber, with the vertically directed sheets shown in A and B hidden underneath. The adoral direction is to the right.*
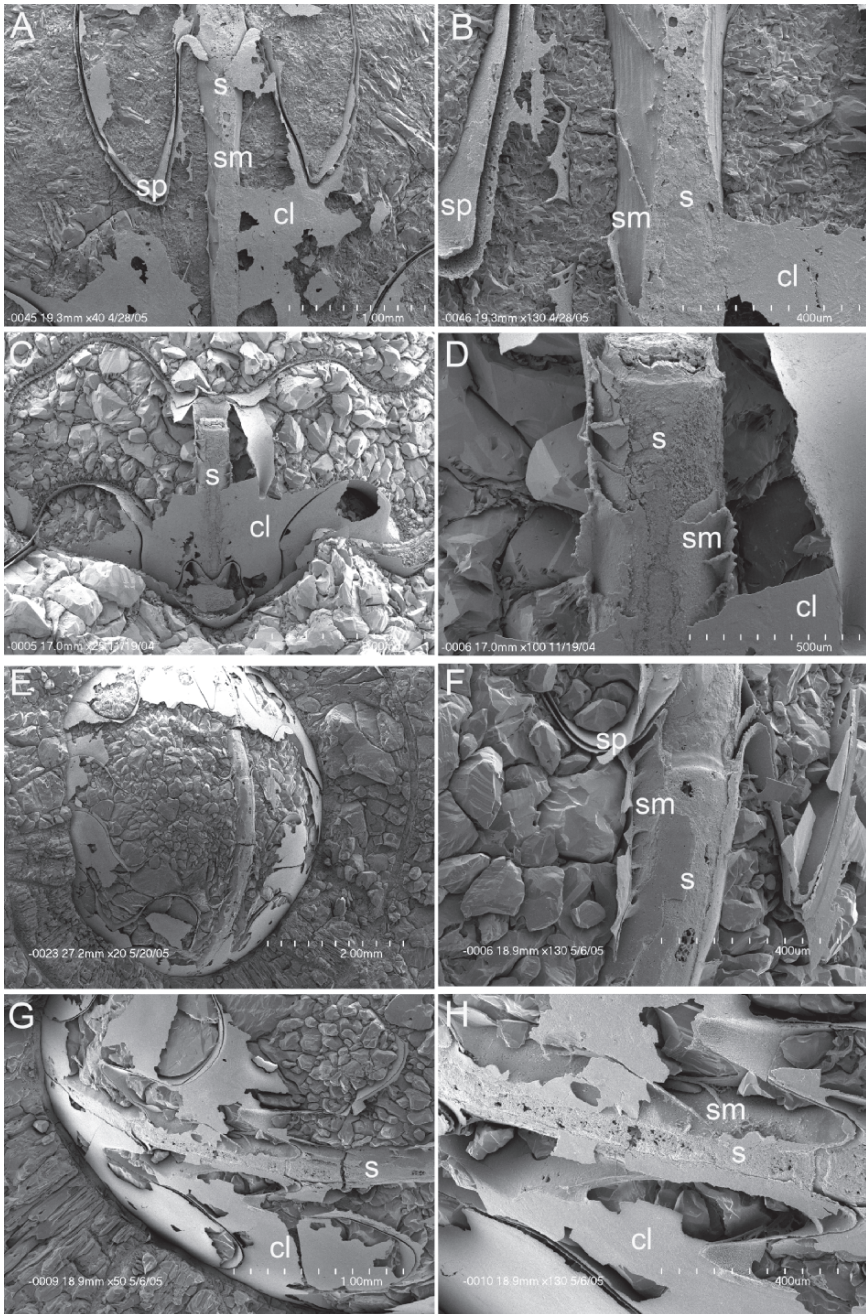
Fig. 9.10 Cravenoceras fayettevillae *Gordon, 1965, lower Fayetteville Formation, Durham, Arkansas. A–B. AMNH 51241; C–D. AMNH 51225; E–H. AMNH 51242. The venter has been etched to expose the siphuncle and siphuncular membranes. A. Siphuncle (s) with traces of siphuncular membranes (sm). Adoral direction is up. sp = septum, cl = chamber lining. B. Close-up*

pseudosutural grooves on the internal mold, which we expected to disappear as the calcite mold etched, are sometimes preserved. These observations suggest that either the mineral composition of the pseudosutures varies among specimens from the same location (and even from the same concretion), or, more likely, that a non-calcitic layer occurs between the shell wall on the inside surface of the external mold and the matrix of the internal mold (see section 5.2). The mineral composition of the pseudosutures is presumably calcitic, with regular crystals oriented perpendicular to the inner surface of the shell wall in well-developed pseudosutures (Fig. 9.12C), and with irregular crystals oriented at random in less well-developed pseudosutures (Fig. 9.12D). The pseudosutures may also be secondarily mineralized (see section 5.3).

5   Discussion

5.1   Origin of Membranes

The origin of siphuncular membranes has been debated (Kulicki, 1979; Weitschat and Bandel, 1991; Westermann, 1992; Checa, 1996; Landman et al., 2006).
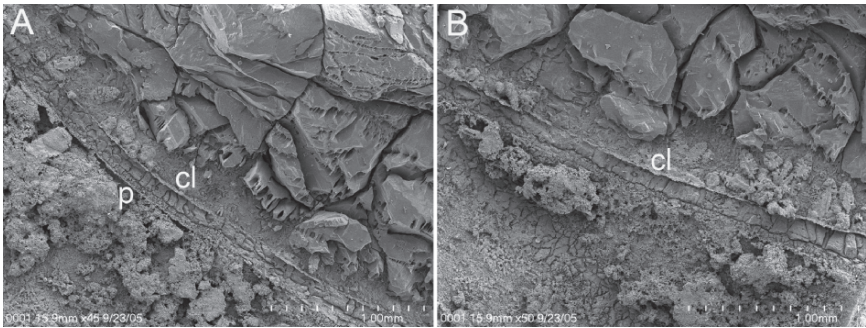

Fig. 9.11 Cravenoceras fayettevillae *Gordon, 1965, AMNH 51243, median cross section, lower Fayetteville Formation, Durham, Arkansas. Because the specimen is fragmented, it is unclear whether this is the adapical part of the body chamber or a more adoral portion. The shell wall exhibits two layers of phosphatized, presumably originally organic, layers. One of these layers (p) is assumed to be the periostracum, while the other (cl) is likely to be the chamber lining, similar to the chamber lining found in the phragmocone.*

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Fig. 9.10 (continued) *view of siphuncular membranes (sm) in A. C. Fragmented siphuncular membranes along the siphuncle (s). Adoral direction is up. D. Close-up view of siphuncular membranes in C (sm). E. Etched phragmocone with the siphuncle exposed. Adoral direction is up. F. Close-up view of siphuncular membranes in E (sm). G. Same specimen as in E, F, rotated 90° clockwise to show the siphuncular membranes in another chamber. Adoral direction is to the right. H. Close-up view of siphuncular membranes in G (sm).*
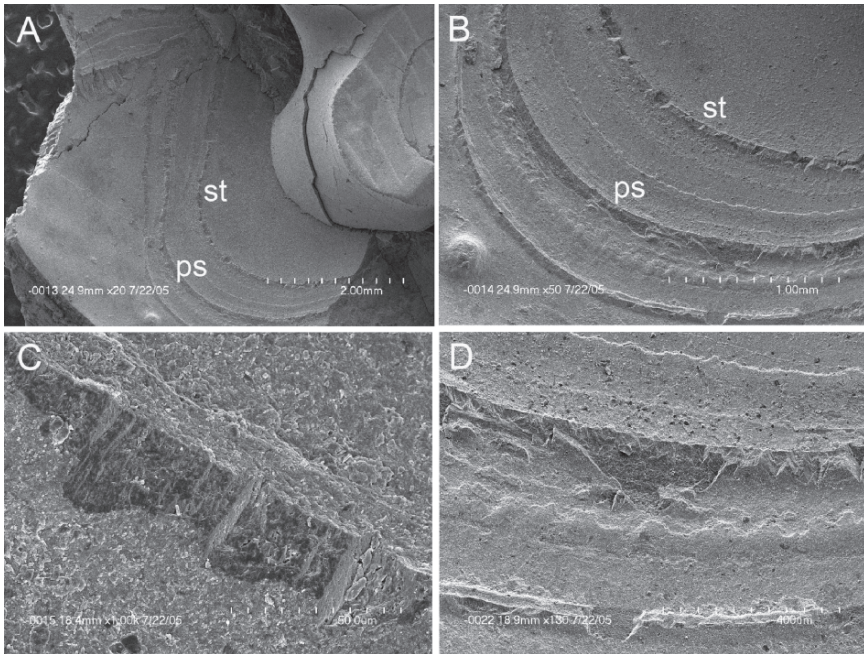
Fig. 9.12 *Pseudosutures in* Cravenoceras fayettevillae *Gordon, 1965, AMNH 51244, lower Fayetteville Formation, Durham, Arkansas. The adoral direction is down and to the left. A. The inner surface of the shell is exposed, showing the ridges or pseudosutures (ps). The specimen was not etched, st = suture. B. Close-up view of pseudosutures (ps), which appear on the adoral side of the suture (st). C. Close-up view of the most prominent pseudosuture, showing mineralization and an asymmetrical slope similar to the mural ridge in Nautilus. D. Close-up view of weaker pseudosutures, demonstrating the wide variability in the amount of material comprising each pseudosuture.*

Landman et al. (2006) argued that these membranes were secreted by the rear part of the mantle, and are not solely the result of desiccation of a cameral liquid or gel after formation of the septum. As evidence for this view, they noted: (1) the abrupt appearance of complex membranes at the end of the neanic stage; (2) the consistency of the ontogenetic pattern among individuals; (3) the surface morphology of the membranes, which lack features characteristic of desiccated gels; and (4) the presence of membranes of similar composition in the adapical portions of the body chambers of Cretaceous ammonoids (Tanabe et al. 2005: Fig. 9.1), which could not have formed by desiccation of cameral liquid after chamber formation.

The similarity in structure and composition of goniatite membranes to prolecanitid membranes strongly suggests that they were formed by similar processes. The four points of Landman et al. (2006) in support of the secretion hypothesis were also evaluated for the goniatites we studied.
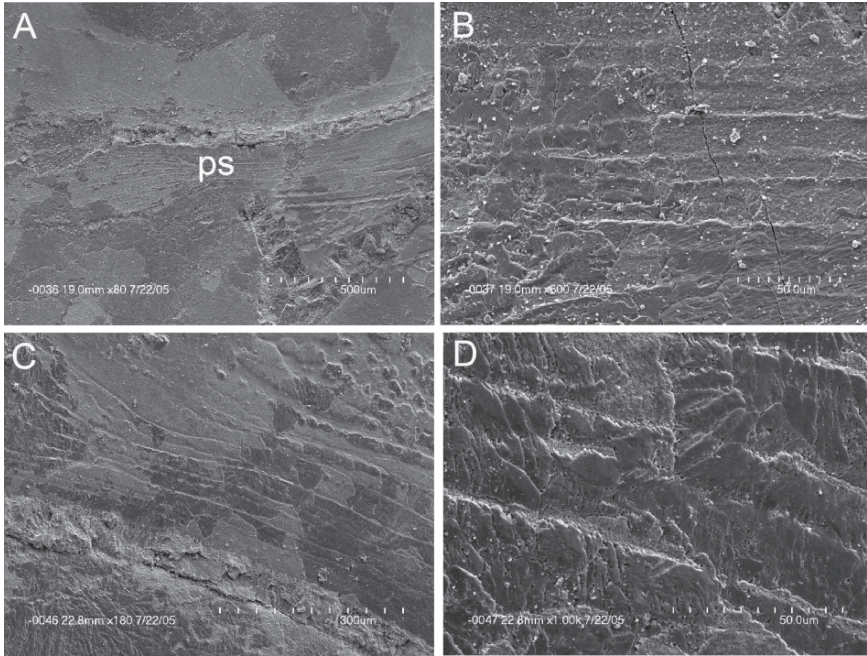
Fig. 9.13 *Pseudosutures on the external molds (A and B) and corresponding internal molds (C and D) of an unetched specimen of* Cravenoceras fayettevillae *Gordon, 1965, AMNH 51245, lower Fayetteville Formation, Durham, Arkansas. A, B. Overview and close-up of the pseudosutures (ps) on the inside surface of the shell (external mold). These pseudosutures are located on the adapical side of the saddle, and appear as ridges. The adoral direction is to the upper left. C, D. Pseudosutural grooves on the internal mold of the specimen. When specimens are broken, the pseudosutures appear as ridges on the external mold and as grooves on the internal mold.*

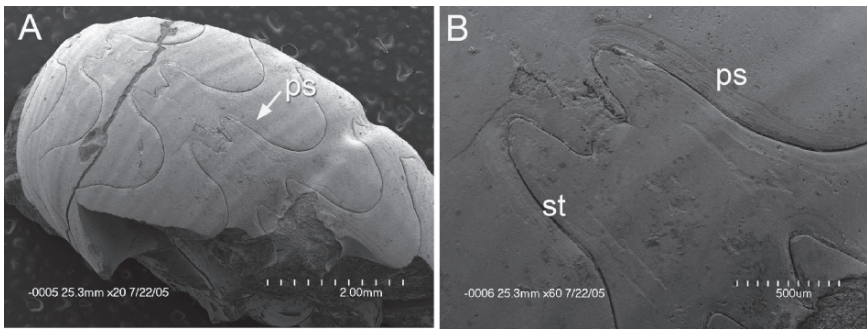**Fig. 9.14** Cravenoceras fayettevillae *Gordon, 1965, AMNH 51246, lower Fayetteville Formation, Durham, Arkansas. Internal mold with pseudosutures (ps) on the adapical side of the suture (st). The adoral direction is to the bottom right. A. Overview. B. Close-up of the pseudosutures (ps). The position and spacing of the pseudosutures do not correspond to the position and spacing of the siphuncular membranes.*

(1) If membranes were produced by desiccation after chamber formation, membranes would have formed in all chambers. However, the abrupt appearance of siphuncular membranes in *Cravenoceras fayettevillae* in the fourth whorl suggests that these features did not form by desiccation. Chamber linings are present starting from the initial chamber in both prolecanitids and in the goniatites we examined, which leaves open the question of whether the linings (as opposed to the siphuncular membranes) were formed by secretion or desiccation (but see point 4).

(2) In the goniatites we examined, the data are insufficient to determine whether a consistent ontogenetic pattern of membranes exists, although the uniform structure of the membranes in each chamber suggests secretion rather than the vagaries of desiccation.

(3) The surface of the membranes in goniatites is generally smooth, similar to that of membranes observed in other ammonoids. Features characteristic of a desiccated gel, such as wrinkles or tessellation, are absent.

(4) No body chambers were preserved in specimens of *Crimites elkoensis*, and so we cannot comment on the presence or absence of an organic lining in the body chambers of individuals of that species. Such linings, however, have been observed in body chambers of some individuals of *Cravenoceras fayettevillae* (Fig. 9.11). Thus, at least some chamber linings probably were secreted by the animal.

In summary, although additional data are needed, there is some evidence that the membranes formed by secretion rather than by desiccation.

5.2 Preservation of Pseudosutures

Whether or not pseudosutures are present in an etched specimen depends on the mineral composition of the pseudosutures and on how the fossil breaks. Pseudosutures that are preserved as calcite ought to dissolve, and in some cases this occurred. In a few instances, however, pseudosutures were not dissolved by acid etching. We attribute this to an overlying phosphatic coating sometimes left behind when the fossil broke out of the matrix (Fig. 9.15). When specimens are removed from the matrix, both the cameral lining and the shell wall may adhere to the external mold (a concave fragment; scenario 1, Fig. 9.15).

Alternatively, the cameral lining may adhere to the steinkern while the shell wall adheres to the surrounding matrix (scenario 2, Fig. 9.15). These different breakage patterns affect whether pseudosutures are visible after etching of the specimens. If the matrix breaks away from the internal mold with both the calcitic shell and the phosphatic chamber lining adhering to it (scenario 1), the pseudosutures will be visible as ridges on the inner surface of the external mold, and as grooves on the internal mold ("r" and "g," respectively, Fig. 9.15). If the pieces are then etched, the pseudosutures should still be visible on the external mold regardless of their
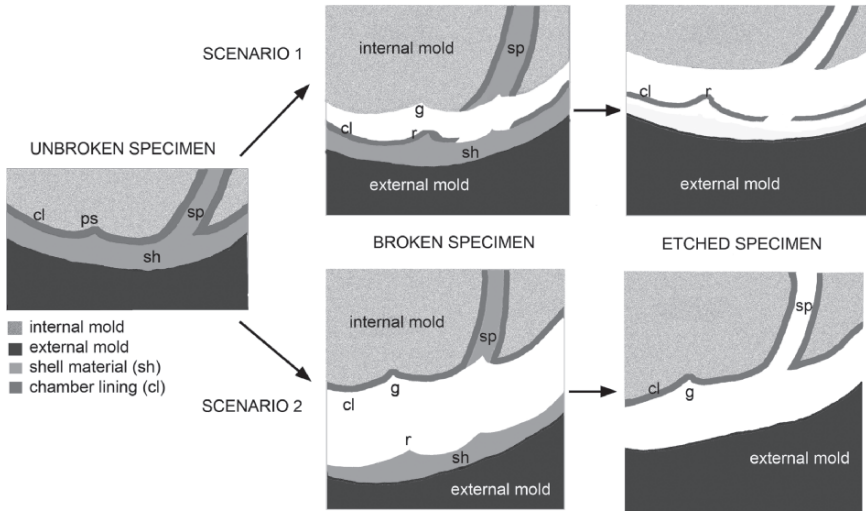
Fig. 9.15 *Illustration of two possibilities that may occur during preparation of a specimen, with the specimens shown in median cross section (parallel to the siphuncle). This diagram explains why pseudosutures sometimes remain visible after etching. In both scenarios 1 and 2, the unbroken specimen has a mineralized layer that includes the shell wall (sh) and the pseudosutures (ps) on the inside surface of the wall. There is a chamber lining (cl) overlying the mineralized layer. In scenario 1, both layers break away from the internal mold, and the pseudosutures are visible as grooves on the internal mold (g) and as ridges on the external mold (r). After etching, the grooves on the internal mold are no longer visible, but the impressions of the ridges on the external mold (r) are preserved by the overlying phosphatic layer. In scenario 2, the mineralized layer breaks away from the internal mold, but the phosphatic chamber lining (cl) adheres to the internal mold. As in scenario 1, the pseudosutural ridges (r) are visible on the external mold, and the impressions are visible on the internal mold as grooves (g). After etching, however, the mineralized ridges are dissolved away on the external mold, yet the impression of the ridges remains on the internal mold because the phosphatic lining (cl) resists etching.*

mineral composition, because the chamber lining protects and preserves the pseudosutures it overlies. On the internal mold, however, the grooves would disappear, as would all other calcitic material.

Alternatively (scenario 2, Fig. 9.15), if the specimen breaks between the calcitic layer and the phosphatic cameral lining, the calcitic layer and pseudosutural ridges (r) would adhere to the external mold, and the cameral lining would adhere to the internal mold. Before etching, the pseudosutures would be visible as ridges on the external mold and as grooves on the internal mold, as before. After etching, however, the pseudosutural ridges on the external mold, if they are calcitic, would disappear, leaving nothing on the internal surface of the shell wall fragment, while the pseudosutural grooves would still be preserved on the internal mold as impressions in the cameral lining (scenario 2, Fig. 9.15). This model thus explains our observations of the variation in position and presence of pseudosutures before and after etching.

5.3   Origin of Pseudosutures

Differences in position, extent, and mineral composition suggest that pseudosutures and siphuncular membranes may have had different origins. In goniatites, siphuncular membranes are present only in the immediate vicinity of the siphuncle, whereas pseudosutures commonly extend across the entire venter and onto lateral portions of the shell (Fig. 9.14). The spacing and extent of pseudosutures differ from that of the membranes in *Cravenoceras fayettevillae*. Pseudosutures are located near the suture itself, in closely spaced series, and extend around the margin from the venter to the flanks. Siphuncular membranes, in contrast, are spaced evenly throughout the chamber and are confined to the area immediately surrounding the siphuncle (compare the position of the membranes in Figs. 9.9, 9.10 and the position of the pseudosutures in Figs. 9.12–9.14).

This lack of correspondence suggests that siphuncular membranes and pseudosutures were secreted either at different times, or by two different portions of the rear mantle. Because pseudosutures retain the general shape of the suture, it can be supposed that they were secreted by the margin of the rear mantle, at its peripheral contact with the interior of the shell wall. Siphuncular membranes would have been secreted by the rear area of the body immediately surrounding the siphuncle, not necessarily around the entire margin of the mantle. If the siphuncular membranes were secreted separately from the pseudosutures, then the siphuncular membranes would not necessarily have had contact with the pseudosutures. However, none of the specimens we examined contains siphuncular membranes and pseudosutures in the same chamber. Therefore, it is impossible to determine their relationship in the present material. That determination must await the examination of median or paramedian sections of specimens in which both structures occur in the same chamber. If additional data confirm that pseudosutures and siphuncular membranes contact each other and correspond in position and spacing, then the siphuncular membranes would be equivalent to pseudosepta.

If the siphuncular membranes in *Crimites elkoensis* and *Cravenoceras fayettevillae* are equivalent to pseudosepta, then it is reasonable to assume that they were deposited by a single process and may therefore have an equal chance of preservation. However, although the preservation of siphuncular membranes and pseudosutures is relatively common, the preservation of pseudosepta is extremely rare (for the sole published observation of pseudosepta, see Checa, 1996). Some workers have proposed explanations for these apparent contradictions. Even if these structures were parts of the same original structure, pseudosepta may have been quite thin and fragile, with thicker concentrations of proteinaceous or chitinous material near the margins of the chambers and immediately surrounding the siphuncle (Hewitt and Westermann, 1987). Greater accumulations in the areas close to the shell wall, as opposed to lesser accumulations within the open space of the chambers, would explain why only marginal traces, such as siphuncular membranes or pseudosutures, are preserved. In addition, increased bacterial activity near the siphuncle would explain why organic deposits in this region would have a much

greater probability of phosphatization in early diagenesis (Hewitt, 2005, personal communication). If siphuncular membranes and pseudosepta were parts of the same original structure, this would account for the preservation of siphuncular membranes even when pseudosepta are not preserved.

Nevertheless, the apparent differences in mineral composition of pseudosutures and siphuncular membranes are at odds with the hypothesis that these structures were formed by a single process and were originally continuous. It is, at first glance, unclear why the membranes are phosphatic whereas the pseudosutures are calcitic. It may be that the pseudosutures were originally secreted as a soft, organic substance that was secondarily mineralized (C. Kulicki, 2005, personal communication). Again, the proximity of the siphuncular membranes to bacteria that promoted phosphatization could explain why the membranes were phosphatized while the pseudosutures were not. Study of siphuncular membranes in specimens of the prolecanitid *Akmilleria electraensis* has confirmed that these membranes are phosphatic (Tanabe et al., 2000). An energy dispersive X-ray (EDX) analysis of the mineral composition of pseudosutures would shed light on their original composition. Analysis of pseudosutures in specimens with aragonitic preservation would show whether pseudosutures were originally mineralized (and therefore still aragonitic) or secondarily mineralized (and therefore calcitic). If pseudosutures were secondarily mineralized, a well-preserved aragonitic specimen ought to have pseudosutures composed solely of calcite. Future research should certainly include such specimens so that the question of mineralization of pseudosutures may be settled.

5.4   Implications for Chamber Formation

Some authors have suggested that, during the cycle of chamber formation, the soft body of the ammonoid crept forward incrementally (Seilacher, 1988). This creeping movement insured that the body was never entirely detached from the inner surface of the shell. Between movements, the animal would have paused within the chamber, which may have resulted in the accumulation of organic or mineral secretions from the mantle epithelium. It has been proposed that the siphuncular membranes formed as an accretion of organic material during such pauses (Landman et al., 2006). It is reasonable to assume that originally mineralized deposits or organic deposits that were later mineralized, could have accumulated at the peripheral contact of the rear body with the shell wall during such pauses as well. These ridges would be the pseudosutures, and could have served as sites for ephemeral attachment of the soft body.

Ward (1987: 85) proposed that the mural ridge in modern *Nautilus* serves as a site for temporary attachment of the periphery of the rear body during septal formation. The mural ridge is an aragonitic deposit formed as the first stage in septal morphogenesis (Blind, 1976, 1988; Ward, 1987: 85; Grégoire, 1987), and it is secreted by the mantle epithelium prior to the translocation of the body within

the chamber. The mural ridge becomes the margin of the new septum. The cross section of the mural ridge mimics the shape of the back of the body, which moves forward and away from the mineralized deposit. The asymmetric shape of the pseudosutures in cross section in *Cravenoceras fayettevillae* (Fig. 9.12) recalls the morphology of the mural ridge in *Nautilus*, and the pseudosutures in goniatites may have served as sites of temporary attachment of the soft body during translocation.

Siphuncular membranes and pseudosutures both appear to have formed as accretions during the incremental forward motion of the animal in the course of translocation. If they were secreted by different parts of the rear mantle, the membranes would not necessarily be continuous with the pseudosutures, although they may merge along the venter. It is impossible to verify this, however, given the fact that pseudosutures have not yet been observed on the mid-venter in *Cravenoceras fayettevillae*.

Although reasonable explanations can account for the differences in the extent and mineral composition of siphuncular membranes and pseudosutures, it is difficult to explain why the spacing of structures with presumably the same origin is so different. Examination of specimens in which both structures are visible in the same chamber is the only way to solve this apparent contradiction.

We propose that, as the animal moved forward in the chamber, the rear mantle secreted both siphuncular membranes and pseudosutures. Both structures replicated the shape of the rear mantle at the time of deposition, and at least some pseudosutures and siphuncular membranes may have been continuous. Pseudosutures may have been originally mineralized or may have been secondarily mineralized, but siphuncular membranes were probably originally organic. Future studies of the mineral composition of pseudosutures, and of specimens in which both pseudosutures and siphuncular membranes occur in the same chamber, will clarify the relationship between these structures.

Acknowledgments

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