Chapter 8
Ammonoid Shell Microstructure

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8.1 Introduction

This chapter is not devoted to shell microstructure alone. In addition to presenting a description of the structure of the individual layers that compose the ammonoid shell, we also discuss the distribution and relationships of these layers to one another as well as their ultrastructure whenever possible. Because aragonite, the chief mineral that makes up the ammonoid shell, is metastable and transforms into calcite as a function of time, pressure, and temperature (Dullo and Bandel 1988), it is difficult to obtain specimens for study, which are preserved well enough to observe fine details of their microstructure. The oldest known occurrence of shells with pristine aragonite preserved derives from the Pennsylvanian Buckhorn Asphalt, USA. This explains why nearly all micro- and ultrastructural studies of ammonoids have been conducted on materials collected from Mesozoic platform deposits.

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8.2 Embryonic Stage

8.2.1 Existing Structural Models

The term "*ammonitella*" was proposed by Drushchits and Khiami (1969) to denote the initial chamber plus the first shell whorl up to the primary constriction. Additional internal structure elements of ammonitella are proseptum, prosiphon, and cecum. Therefore, the term ammonitella is generally understood as an ammonite embryonic shell (compare De Baets et al. 2015). Prior to Drushchits and Khiami (1969), the same structure was known as "*protoconch*" (Ruzhentsev and Shimanskij 1954; Makowski 1962, 1971) though the later term should rather be refereed to initial chamber than to entire ammonitella. Because of controversies on the structure and relationships of the layers in the wall of the ammonitella, and because of diverse opinions on the embryogenesis of ammonoids, the problem of the microstructure of the ammonitella is of special interest.

The distinct morphological and microstructural features of the ammonitella had already been observed in the nineteenth century (Hyatt 1872; Branco 1880), but knowledge on the subject rapidly improved with the use of electron microscopy. Birkelund (1967) and Birkelund and Hansen (1968) were the first to apply transmission electron microscopy (TEM) in studies of the microstructure of ammonitellae of Late Cretaceous *Saghalinites* and *Scaphites*. The preparation method was described by Hansen (1967) and depended generally on slight EDTA etching of the surfaces of polished cross-sections and then removing the colloidal replicas and sputtering them with carbon. By means of this method, the following was determined: (1) The wall of the initial chamber is built of two layers without a distinct boundary in-between; (2) The inner layer consists of crystals perpendicular to the inner shell surface, whereas crystals in the external layer are distributed without a distinct orientation; (3) Both layers of the initial chamber wedge out in the vicinity of the proseptum base.

The wall of the first whorl appears as a prismatic layer on the inner surface of the initial chamber. After the wall of the initial chamber wedges out, the wall of the first whorl continues without much change to the primary constriction. It is similar in construction to the wall of the initial chamber; i.e., it consists of two sublayers, an inner sublayer having more regular crystals perpendicular to the inner shell surface and an external, thinner sublayer with less regularly oriented crystals. The terminal part of the ammonitella aperture is delimited by a structure known as a primary constriction. The prismatic and subprismatic sublayers of the first whorl become much thinner, and the nacreous primary varix develops beneath them. The proseptum is constructed of the same crystalline matter as that of the internal prismatic layer of the initial chamber and the wall of the first whorl.

Erben et al. (1968, 1969) first introduced scanning electron microscopy (SEM) to study the shell microstructure of ammonoids. This technique is much easier in specimen preparation and generally more appropriate than TEM. Based on SEM observations, Erben et al. (1968, 1969) proposed a model for the structure and

development of the ammonitella. According to this model, the wall of the initial chamber initially consists of two subprismatic layers. These wedge out, and only somewhat later the fully prismatic sublayers appear on the inner surface of the initial chamber. Two of these sublayers also wedge out, and only the sublayer beyond the base of the proseptum continues until the end of the primary constriction. The dorsal part of the proseptum consists of an additional layer on the inner surface of the initial chamber, whereas the ventral part of the proseptum is a continuation of the innermost layer of the initial chamber and the first whorl. The flange is composed of a prismatic layer and is separated from the proseptum and the wall of the initial chamber by a discontinuity surface, and according to this model it is suggested that the flange was formed later in ontogeny.

Another model of ammonitella formation has been presented by Kulicki (1979) based on excellently preserved material of *Quenstedtoceras* and *Kosmoceras* from Łuków (Callovian, Poland). In this model, the wall of the initial chamber has two layers, best seen in its dorsal and apical parts. The inner layer has a regular prismatic structure and represents the wall proper of the initial chamber, continuing into the outer prismatic layer of the first whorl up to the ammonitella edge. The outer layer of the wall of the initial chamber is a continuation of the mural part of the proseptum and represents the dorsal wall of the first whorl of the ammonitella. This layer is thickest opposite the primary varix and is subprismatic. Crystallites in this layer are oriented in parallel, diagonally, or perpendicularly to the shell surface. The boundary between this layer and the wall proper of the initial chamber is not distinct. A distinct boundary between the dorsal wall and the outer prismatic layer of the first whorl develops at the appearance of the tuberculate sculpture characteristic of the ammonitella in Mesozoic ammonoids.

In medial and paramedial cross sections through the outer saddle of the proseptum on the inner surface of the venter of the initial chamber, there is an inner prismatic layer of regular structure linked to the base of the proseptum. This layer is separated from the wall proper of the initial chamber by a thin layer of microcrystalline structure. This thin layer is thickest in the middle part of the base of the proseptum. The prismatic layer of the proseptum commonly continues as one of the main components of the wall of the first whorl ("medial prismatic layer" of Kulicki 1979).

All of the above models assume simultaneous secretion of the organic phase of the shell together with mineralization. This is what occurs in the formation of the postembryonic shell in Recent mollusks. In contrast, Bandel (1982, 1986) presented a model based on shell development in some Archaeogastropoda in which the larval shell is formed in two phases. In the first phase, the shell consists only of elastic, organic matter, and in the second phase, the organic primary shell is calcified. The direction of calcification may not have been consistent with the direction of secretion of the organic shell. In the case of the ammonitella, the wall of the first whorl and umbilical walls of the initial chamber would have been calcified first. Only later would the remaining wall of the initial chamber and proseptum have been mineralized.

Bandel's (1982, 1986) interpretation has been confirmed by well-preserved ammonitellae of *Aconeceras* (Albian) representing different calcification stages (Kulicki 1989; Kulicki and Doguzhaeva 1994). Four stages of calcification of the ammonitella have been recognized.

Stage 1 is represented by specimens in which the wall of the first whorl, including the primary constriction and the lateral walls of the initial chamber are calcified.

Stage 2 is represented by specimens in which, in addition, the part of the wall of the initial chamber that separates the interior of the initial chamber from the lumen of the first whorl is calcified.

Stage 3 is represented by specimens that have a calcified first whorl, initial chamber, proseptum, and nacreous primary varix. In *Quenstedtoceras* ammonitellae from Łuków, there is another septum adapertural of the proseptum (the first nacroseptum).

Stage 4 is represented by ammonitellae of larger, postembryonic specimens. This stage is characterized by a distinct thickening from the inside of the inner prismatic layer and commonly by the addition of extra prismatic layers from the inside.

Another model has been proposed by Tanabe (1989), which assumed that the embryo of Mesozoic ammonoids might have temporarily had an endocochliate body plan late in embryonic development during which the outer prismatic layer with tubercles was secreted from the outer reflected mantle. Finally, Tanabe et al. (2008), after investigation of exceptionally well preserved embryonic shells of *Aconoceras*, returned to the model of Bandel (1982) and Kulicki and Doguzhaeva (1994) but refined the timing of formation of the outer prismatic layer and tubercles. Tanabe et al. (2008) demonstrated for the first time the presence of amorphous calcium carbonate (ACC) in the wall of the embryonic shell.

8.2.2 Structure of the Ammonitella Walls

A cross section through the wall of the first whorl in Paleozoic and Mesozoic ammonoids is shown in Fig. 8.1–8.3. The outer layer has a regular prismatic structure and a thickness of about 1–3 μm in Mesozoic ammonoids while in the Pennsylvanian Buckhorn Asphalt goniatite it is indistinct. Prisms consist of aragonitic needles 0.1–0.2 μm in diameter oriented perpendicular to the outer surface. The diameter of the crystallites is 0.2 μm .

The medial layer, sandwiched between the outer and inner prismatic layers, has an irregular, grainy structure. The irregular, grainy structure of the medial layer results most likely from the limiting effect of organic matter on the growth of aragonitic crystals. In transverse cross sections through the initial chamber and first whorl, the outer prismatic layer and the medial layer wedge out on the umbilical seam, and only the inner prismatic layer continues across the dorsum forming the lateral walls of the initial chamber, which are two or three times thicker than the walls covered by the following whorl. This confirms earlier assumptions of Bandel (1982, 1986) and Kulicki (1979). In Mesozoic ammonoids, the crystallites of the outer layer in the outer wall of the first whorl of the ammonitella and lateral parts of the initial
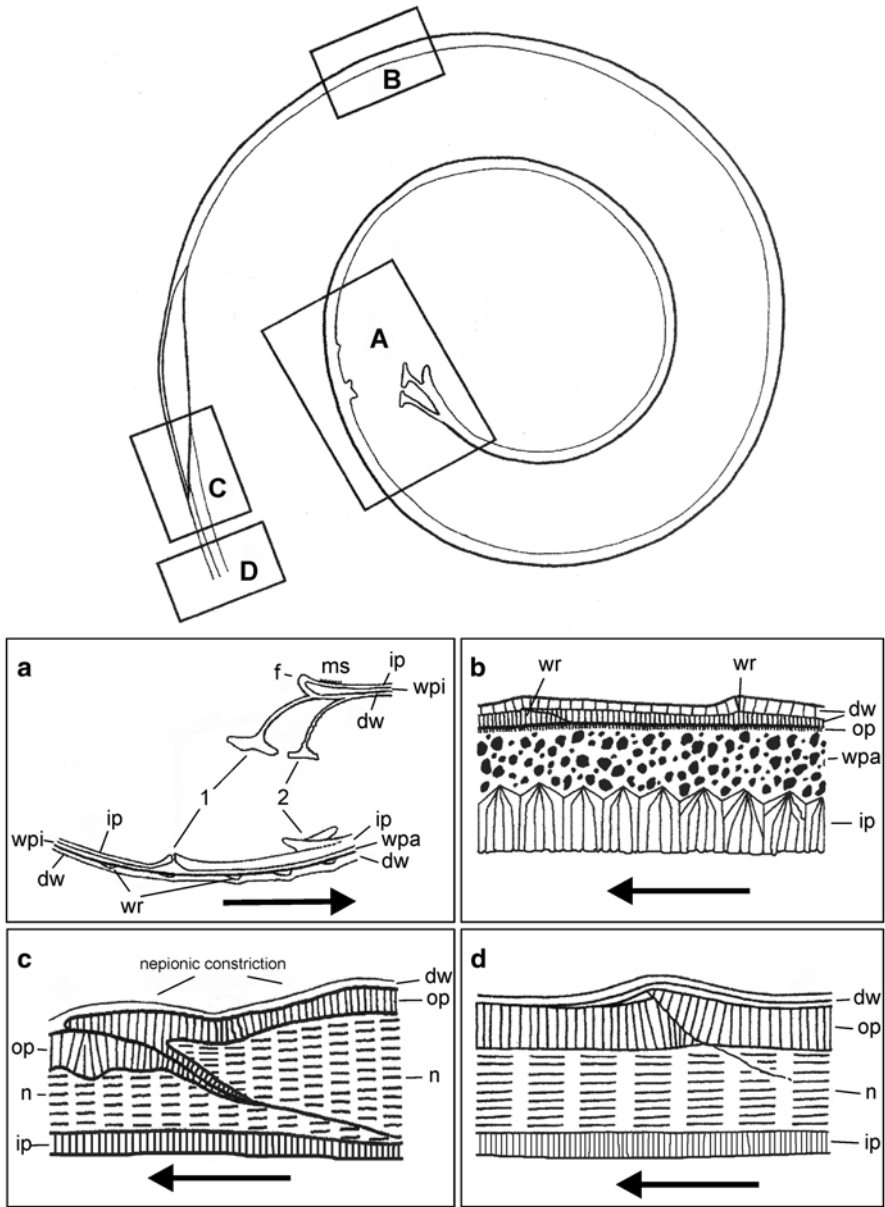
Fig. 8.1 Schematic drawing of median cross-section through ammonoid ammonitella and early postembryonic shell (modified after Kulicki et al. 2002). The arrows indicate adoral direction. **a** Overview figure with the places of close-ups indicated. **b** Close-up of the initial chamber in the vicinity of the first two septa. **c** Close-up of the wall of the first whorl. **d** Close-up of the ammonitella edge. **e** Close-up of the wall of the post-embryonic shell showing a lira in the outer prismatic layer (open arrowhead). Abbreviations: *dw*, dorsal wall; *f*, flange; *ip*, inner prismatic layer; *ms*, muscle scar; *n*, nacreous layer; *op*, outer prismatic layer; *wpa*, wall proper of the ammonitella; *wpi*, wall proper of the initial chamber; *wr*, wrinkle layer; *1*, first septum (proseptum); *2*, second septum
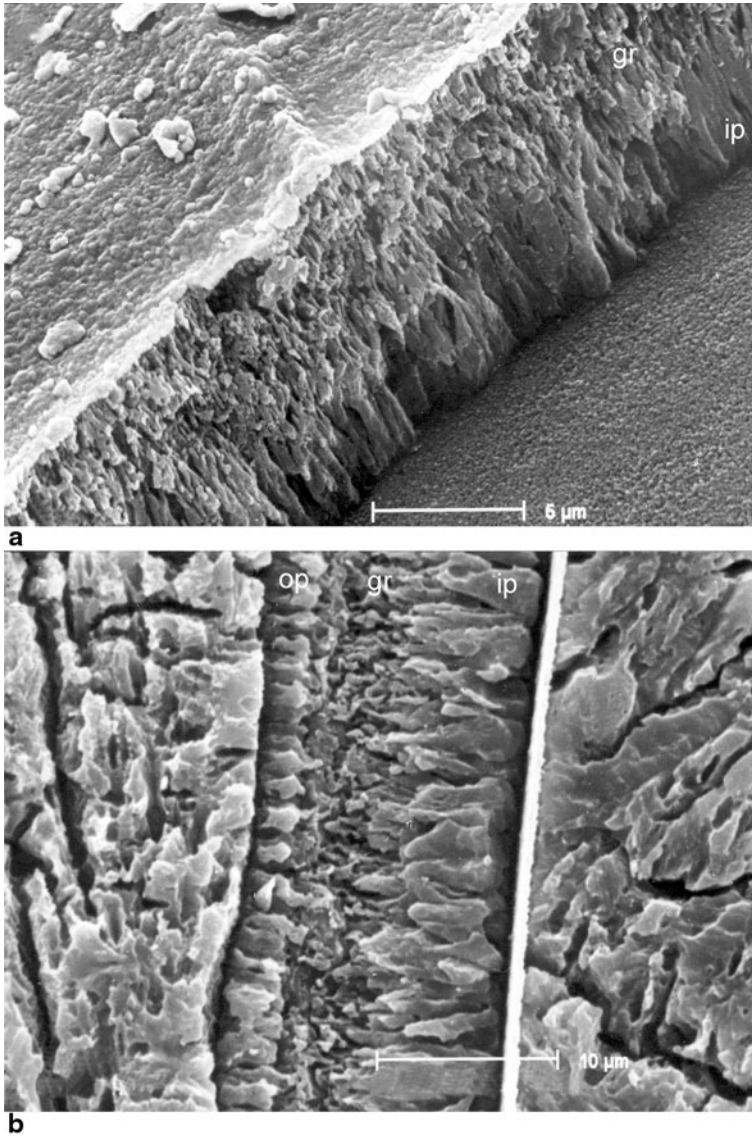
Fig. 8.2 a View of the broken wall of the first whorl of a goniatite ammonitella, Pennsylvanian, Buckhorn Asphalt quarry, Oklahoma. **b** Longitudinal section through the first whorl of the ammonitella of *Damesites sugata* Forbes, 1846, Coniacian, Cretaceous, Nakafutamata Rivulet, Haboro area northwestern Hokkaido. In case of Mesozoic ammonitellae the outer prismatic layer is more distinct and better developed. Abbreviations: *gr*, granular layer; *ip*, inner prismatic layer; *op*, outer prismatic layer
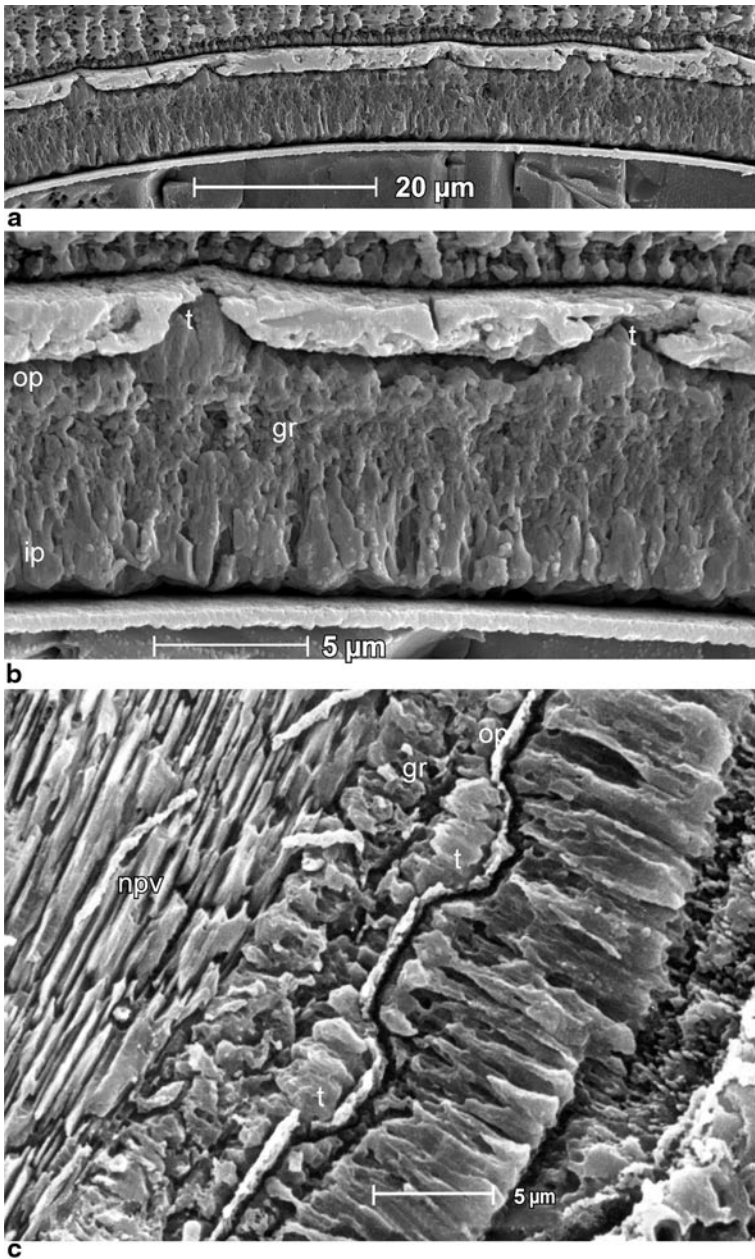
Fig. 8.3 a, **b** *Ptychoceras* sp. Aptian, Cretaceous, Khocods Rivier, NW Caucasus. Longitudinal section through tuberculate ventral wall of ammonitella whorl. **c** *Damesites sugata* Forbes, 1846, Coniacian, Cretaceous, Nakafutamata Rivulet, Haboro area northwestern Hokkaido. Longitudinal section through tuberculate ventral wall of ammonitella whorl above primary varix. Abbreviations: *gr*, granular layer; *ip*, inner prismatic layer; *npv*, nacreous layer of the primary varix; *op*, outer prismatic layer; *t*, tubercule

chamber become aggregated into structural elements of a higher order, the so-called pseudohexagonal trillings (Kulicki and Doguzhaeva 1994; Tanabe et al. 2008, 2010).

8.2.3   Apertural Zone of the Ammonitella

The terminology used here to describe different structural and morphological elements of ammonoid embryonic shells is derived from Drushchits et al. (1977) and Landman and Waage (1982). The morphological-structural distinctness of the apertural zone of ammonitellae was first recorded by Hyatt (1872). Please note, however, that the significance of this zone in terms of the ontogeny of ammonoids is beyond the scope of this chapter (see De Baets et al. 2015 for a review).

   Fully developed ammonitellae terminate in a structure called the nepionic constriction, where they form, for the first time in ontogeny, the nacreous layer comprising the so-called nepionic swelling (primary varix; Fig. 8.4a). The outermost thin prismatic layer continues until the ammonitella edge, where it forms a short return section directed toward the shell interior underlying internally the nacreous layer of the nepionic swelling or primary varix (Fig. 8.4a). The middle, granular, or subprismatic layer decreases in thickness towards the aperture and wedges out in
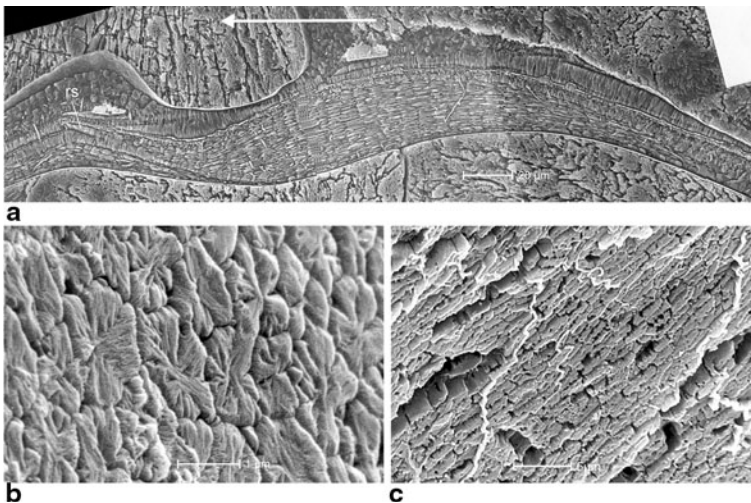

Fig. 8.4   a *Damesites sugata* Forbes 1846, Coniacian, Cretaceous, Nakafutamata Rivulet, Haboro area northwestern Hokkaido, primary varix (nepionic constriction), **b** *Gaudryceras tenuiliratum* Yabe, 1903, Campanian, Abeshinai River, Nakagawa Town, north Hokkaido, view of outer prismatic layer from the outside. Aggregation in form of pseugohexagonal trillings is clearly visible. **c** *Phyllopachyceras ezoense* (Yokoyama 1890), Middle Campanian, Cretaceous, Osoushunai Rivulet, Nakagawa Town, Hokkaido, view of outer prismatic layer from the outside. Fuselar aggregation is visible

the middle of the primary varix zone. The inner prismatic layer of the ammonitella terminates at the appearance of the nacreous layer. The border between the granular layer and the inner prismatic layer is indistinct and the structure of the prismatic layer itself is characterized in this zone by a slightly spherulitic distribution of the crystals with the center located at the interface with the granular layer. The lamellae of the nacreous layer form a characteristic arrangement, described for the first time by Kulicki (1974). The most external lamellae of the nacreous layer are relatively short and end on the inner surface beneath the outer prismatic layer on the posterior side of the shell while on the anterior side they reach the return section of the outer prismatic layer. The inner lamellae reach further backward and are generally longer. The plates of the nacreous layer of the primary varix are arranged in vertical stacks, similar in structure to those of the nacreous layer of the postembryonic shell. The vertical stacks in the nacreous layer of the primary varix have been illustrated by Birkelund and Hansen (1974); Drushchits et al. (1977); Drushchits and Doguzhaeva (1981), and Ohtsuka (1986).

8.2.4 Structure of the Initial Chamber Wall and Proseptum

The umbilical walls of the initial chamber in ammonitellae of Mesozoic and Paleozoic ammonoids are relatively thick, being comparable in thickness to that of the first whorl wall. With respect to their structure, they are also alike; i.e. they are composed of the same three layers. Transverse cross sections through the first whorl of ammonitellae of *Aconeceras* (see Kulicki and Doguzhaeva 1994) and *Quenstedtoceras* (see Kulicki 1979; Bandel 1982, 1986) show that the most external components of the umbilical wall of the initial chamber and of the lateral wall of the first whorl wedge out at the umbilical seam. Only the internal regular prismatic layer of the umbilical wall goes under the umbilical seam as the primary wall of the initial chamber (Fig. 8.4). In the apical part of the initial chamber of the ammonitella of *Quenstedtoceras*, the 3.0–3.5-μm-thick wall made of organic matter is penetrated through its entire thickness by needle-like aragonitic crystallites. In longitudinal cross section, this layer appears to reach the end of the flange.

In medial and paramedial cross sections through the ventral wall of the initial chamber, one or two prismatic layers are visible under the wall proper of the initial chamber (Fig. 8.5b; Kulicki 1979). Kulicki (1979) and Kulicki and Doguzhaeva (1994) claimed that the wall proper of the initial chamber continues as the middle granular or subprismatic layer of the first whorl. Birkelund (1967, 1981); Birkelund and Hansen (1968); Erben et al. (1969); Tanabe et al. (1980, 1993b), and Tanabe and Ohtsuka (1985) concluded that the wall of the initial chamber wedges out in the vicinity of the base of the proseptum. According to Bandel (1982, 1990), in median section, the inner prismatic layer of the initial chamber extends from the base of the proseptum and continues as the primary wall of the initial chamber, ending in the flange. These observations of Bandel are contradictory to those of Kulicki (1979) conducted on the same material, namely, *Quenstedtoceras* from Łuków.
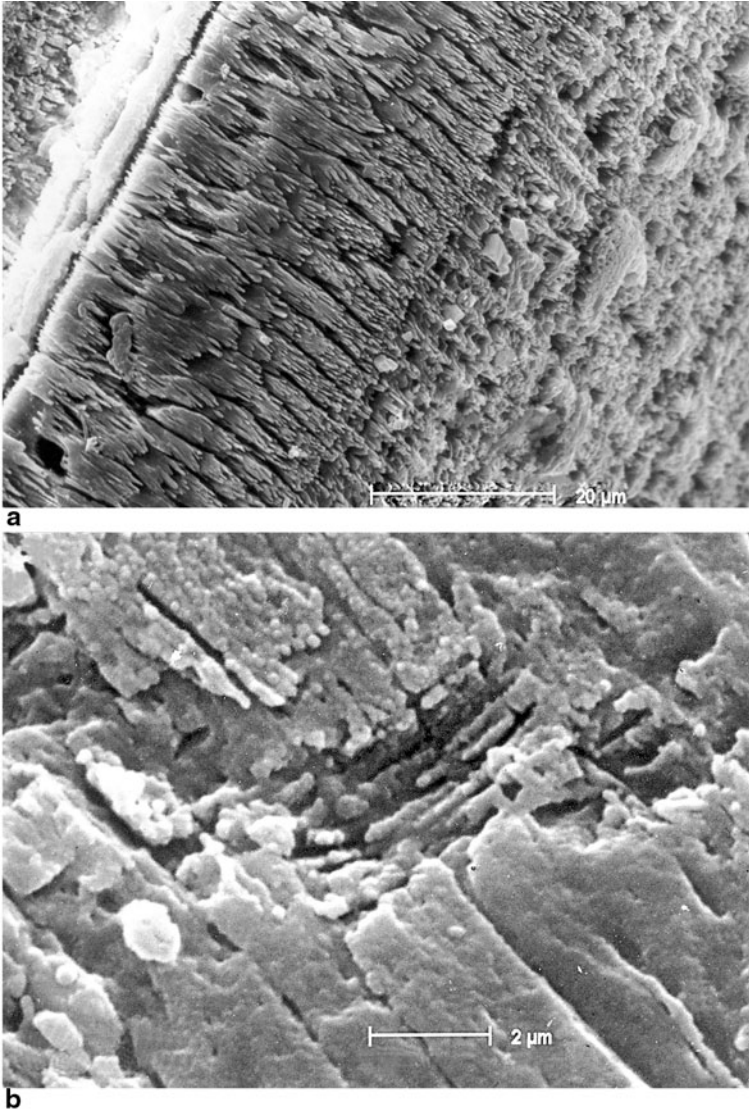
Fig. 8.5 *Tetragonites* sp. Campanian, Cretaceous, Abeshinai River, Nakagawa Town, Hokkaido. **a** Outer prismatic layer showing acicular primary structure. **b** Outer prismatic layer with nacre like intercalation

Opinions concerning the relationship between the proseptum and the shell wall are not consistent either. Some authors, such as Grandjean (1910); Miller and Unklesbay (1943); Arkell (1957); Birkelund and Hansen (1968); Erben et al. (1969); Kulicki (1975, 1979), Drushchits and Doguzhaeva (1981); Bandel (1982), and Landman and Bandel (1985) have considered the prismatic proseptum to be continuous with the internal layers of the whorl and initial chamber of ammonitella while Hyatt (1872); House (1965); Erben (1962, 1966), Drushchits and Khiami (1970),

and Drushchits and Doguzhaeva (1981) have suggested that the relationship of the proseptum to the shell wall is the same as that of all other septa.

In the dorsal region, the proseptum has a very long prismatic mural part that covers a large area of the wall proper of the initial chamber. Bandel (1982, 1990) interpreted the mural part of the proseptum as continuing to the ammonitella aperture; this is consistent with the occurrence of a dorsal wall in the ammonitella whorl. As shown in paramedial cross sections distant from the plane of bilateral symmetry, the ventral part of the proseptum continues as the inner prismatic layer of the first whorl (Birkelund and Hansen 1974, Fig. 2; Kulicki 1979, Fig. 10C). Most authors consider the proseptum to be a one-or two-layered structure made of aragonitic prisms oriented perpendicular to the outer surface. Only Landman and Bandel (1985, Fig. 33) illustrated the three-layered structure of the proseptum in *Euhoplites* sp., in which the irregularly prismatic proseptal layer is sandwiched between two layers of a more homogeneous prismatic material that originally may have been organic. These authors (1985, Fig. 21) also noted distinct wrinkles on the surface of the proseptum in *Baculites* sp.

8.2.5 Dorsal Wall of the Ammonitella

Birkelund (1967, 1981), Birkelund and Hansen (1968, 1974), and Erben et al. (1969) have denied the existence of a dorsal wall in the ammonitella. However, Kulicki (1979) has shown that the outermost layer overlying the wall proper of the initial chamber as seen in medial and paramedial cross sections is the dorsal wall of the first whorl. Its structure is subprismatic, and it is not separated from the wall proper of the initial chamber by a sharp boundary (Fig. 8.1a, 8.1b, 8.3a, 8.3b, 8.3c). The dorsal wall is reduced in thickness in the apertural region of the ammonitella and the distinct boundary between the dorsal wall and the ventral wall of the previous whorl appears with the advent of tuberculate sculpture.

In the terminal stage of the ammonitella in *Quenstedtoceras* there are two septa and a nacreous primary varix. Kulicki and Doguzhaeva (1994) have shown that in this developmental stage the outer surface of the initial chamber in the apertural region is covered by distinct structures resembling those of the wrinkle layer. Inside the living chamber these structures reach about 90° from the aperture. In longitudinal cross section, these structures are triangular, with the gentle slope pointing adapically and the much steeper slope facing adaperturally. These triangular elements have a prismatic structure with the long axes of the prisms perpendicular to the overall surface of the wall of the ammonitella rather than to the surfaces of the gentle adapical slopes of the triangles.

Kulicki (1979) and Doguzhaeva and Mutvei (1986b) investigated the complex structure of the dorsal wall. Kulicki (1979) distinguished two components, outer and inner ones in the dorsal wall. The wrinkle-like layer of the ammonitella is the outer component. It was produced by the anterior part of the mantle and, later in ontogeny, was covered by more internal components that were produced by the posterior part of the body. Generally, the ammonitellae available for studies are in

the final calcification stage; i.e., they are the apical parts of large specimens. Thus, the dorsal wall at what had been the edge of the ammonitella has the thickness and structure characteristic of the posterior part of the living chamber. On the basis of such specimens, Kulicki (1979) stated that the dorsal wall of the ammonitella covers the outer surface of the wall proper of the initial chamber, that the dorsal wall has a subprismatic structure, and that the boundary between these two layers is not too distinct. The outermost component of the dorsal wall, i.e., a wrinkle-like layer of Paleozoic ammonitellae is present in the apertural region and it is characterized by a specific ornamentation described by Tanabe et al. (2010).

8.2.6   Ornamentation of the Ammonitella

The presence of a tuberculate micro-ornamentation in Mesozoic ammonitellae has been already documented in the early works of Brown (1892); Smith (1901), and Smith (1905) . More detailed investigations were possible due to use of SEM techniques (Kulicki 1974, 1979; Bandel 1982; Bandel et al. 1982; Landman 1985, 1987, 1988; Tanabe 1989; Tanabe et al. 2001; Tanabe et al. 2008, 2010). All investigated Mesozoic ammonitellae possess this characteristic tuberculate micro-ornamentation (De Baets et al. 2015), which is limited to the outer surface and is not observed on the initial chamber covered by the whorl of the ammonitella. However, there is wide variation in the density of tubercles, their size, and their distribution on the shell surface (Tanabe et al. 2010).

Bandel et al. (1982, p. 387) found that "*some smaller tubercles appear to be emergent ends of single large prisms, but the larger ones show the complex spherulitic structure.*" On the basis of cross sections through the walls of ammonitellae of *Quenstedtoceras*, Kulicki (1979) determined that tubercles are a continuation of the prisms of the outer prismatic layer and that they are not separated from the outer shell surface by any discontinuity (Fig. 8.2b, 8.3a, b, c).

Tanabe (1989, Fig. 5) presented the tubercles as separate elements on the surface of the outer prismatic layer or, as in the umbilical wall of *Anapachydiscus,* sometimes fused into a continuous layer, forming a smooth outer surface. On this basis, Tanabe (1989) formulated an endocochliate embryo model in which the tuberculate micro-ornamentation, or the layer corresponding to it, was formed by a fold of the mantle covering the outside of the ammonitella.

8.3   Postembryonic Stage

8.3.1   Products of the Anterior Mantle Edge

Ammonoids resemble Recent *Nautilus* and other Recent mollusks (e.g., bivalves, gastropods, and monoplacophorans), both in the products of secretion and in the morphology of the apertural edge of the shell. This similarity makes it possible to

argue that these groups are almost identical with respect to the processes of biocalcification taking place at the mantle edge. Biocalcification in *Nautilus* has been described by Crick and Mann (1987) and Gregoire (1987) and is briefly summarized below. In *Nautilus* the epithelium of the mantle edge is typically folded. The outer fold is separated from the rest of the mantle by a periostracal groove, where the outermost layer of the mollusk shell, the periostracum, is secreted. The inner wall of the periostracal groove adheres strongly to the outer surface of the periostracum, thus protecting the space filled with extrapallial fluid from the external environment. In this way, all the products of secretion participating in the construction of the outer shell pass through the underlying epithelium before being exuded into the extrapallial fluid. The periostracum insures the isolation of the secretory environment and is, at the same time, a substrate for the nucleation of mineral components. The first zone lying immediately behind the periostracal groove is where the outer prismatic layer is produced, and the deposition of the nacreous layer is associated with another zone, located farther away. Production of $CaCO_3$ is controlled by the disequilibrium of the extrapallial fluid as the CO_2 content varies. The organic matrix accounts for the crystal orientation. The deposition of the inner prismatic layer is confined to the zone of the myoadhesive epithelium (Mutvei 1964).

The anterior mantle edge is responsible for the production of sculpture in ammonoids. Some sculptural elements, e.g., ribs and nodes, are formed from both the outer prismatic and middle nacreous layers, so that convex shapes on the outer surface correspond to concave ones on the inner surface. Both layers generally retain the same thickness throughout the extent of the rib or node. In the posterior part of the body chamber and in the phragmocone, where the inner prismatic layer is present, a certain smoothening out of the interior surface of the sculpture may occur. Occasionally, as in *Hypophylloceras,* sculptural elements are composed mostly of the outer prismatic layer so that the inner surface of the shell wall remains flat (Birkelund and Hansen 1974, 1975; Birkelund 1981). Protruding sculptural elements-spines or a sharp keel-may be totally cut off from the cavity of the body chamber by the inner prismatic layer; as a result, the space within such elements remains free (Hölder 1952a, 1952b; Erben 1972b). Numerous Paleozoic and Mesozoic ammonoids produce regularly spaced varices, which are thickenings of the nacreous layer. Such varices appear as constrictions on inner molds. Constrictions as outer sculptural elements may occur alone or can be accompanied by varices. Mature growth stages of micro- and macroconchs may show modifications related to the thickenings of the apertural edge; these thickenings are composed chiefly of the nacreous layer.

Periostracum This is the most external layer of the shell wall, which is made of an organic substance in the majority of mollusks. In the case of *Yokoyamaoceras* from Hokkaido, the periostracum is thick (5 μm), multilayered and made of stabilized ACC matrix (Fig. 8.6b) similar to the black film of Recent *Nautilus* (CK unpublished data). Periostracum is produced in the periostracal groove of the mantle. In the ontogeny of ammonoids, the periostracal groove would have already been formed in the final stage of embryonic development. The periostracum in extant
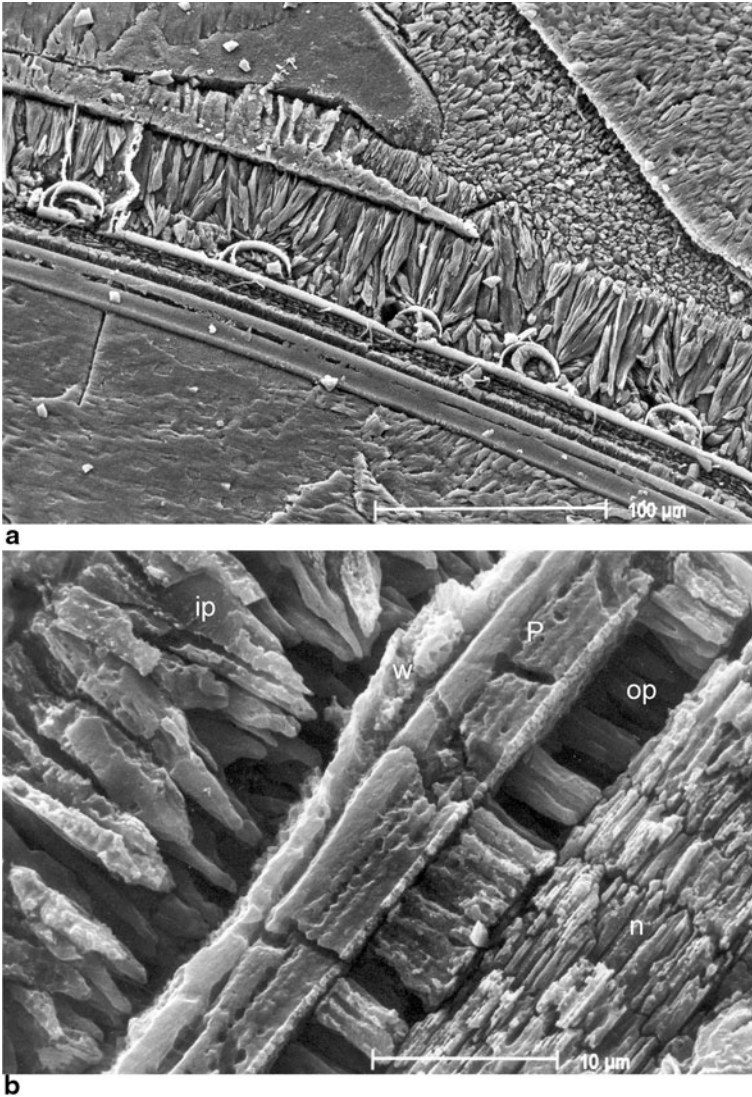
Fig. 8.6 a *Phyllopachyceras ezoense* (Yokoyama 1890), Middle Campanian, Cretaceous, Osoushunai Rivulet, Nakagawa Town, Hokkaido. Longitudinal section through the ventral wall covered by distinct periostracum showing periodically free periostracal edges directed adapically. **b** *Yokoyamaoceras jimboi* Matsumoto 1955, Middle Campanian, Cretaceous, Abeshinai River, Nakagawa Town, Hokkaido. Thick multilayered periostracum composed with stabilized amorphous calcium carbonate. Abbreviations: *ip*, inner prismatic layer of the next whorl; *n*, nacreous layer; *op*, outer prismatic layer; *p*, periostracum; *w*, wrinkle layer

mollusks may have a complex, multilayered structure as in, e.g., *Mytilus edulis* (see Dunachie 1963), be double-layered as in *Nautilus macromphalus* or very thick as on the lower half of the shell in *N. scrobiculatus* (see Ward 1987). In phylloceratids *Phyllopachyceras* and *Hypophylloceras* the periostracum does not form a continuous layer (as in many other ammonoids) but displays periodic bending outwards of the outer layers with small collars inclined posteriorly (*Phyllopachyceras*) or anteriorly (*Hypophylloceras*) (Kulicki et al. 2001).

Outer Prismatic Layer The mantle zone directly behind the periostracal groove is responsible for formation of the outer prismatic layer. It is deposited directly on the inner surface of the periostracum. In all normally coiled ammonoids (Erben et al. 1969; Kulicki 1979), this layer occurs in the ventral, lateral, and umbilical portions of the wall but wedges out at the umbilical seam. Earlier reports of the total lack of an outer prismatic layer in some normally coiled ammonoids (e.g., Bøggild 1930; Mutvei 1967; Birkelund and Hansen 1974) are based on incompletely preserved material (Erben et al. 1969; Birkelund and Hansen 1975). In heteromorphs in which a portion of the shell has no contact with the shell of earlier developmental stages, the outer prismatic layer occurs not only ventrally and laterally but also in the dorsal part (Doguzhaeva and Mikhailova 1982; Doguzhaeva and Mutvei 1989). In early postembryonic stages, the outer prismatic layer comprises a considerable percentage of the total thickness of the shell wall: over 75 % in *Aconeceras,* and about 50 % in *Quenstedtoceras.* During later development, the thickness of the outer prismatic layer decreases considerably to only a small fraction of the total shell wall thickness. In the Cretaceous heteromorph *Ptychoceras,* the thickness of the outer prismatic layer is about 1 μm. From the microstructural point of view, the outer prismatic layer consists of regular prisms, each with needle-like crystallites 0.2–0.5 μm in diameter; these are perpendicular to the outer shell surface (Fig. 8.5a). The relatively thick outer prismatic layer like the one in *Tetragonites*, indicates some irregularities in development of prisms, i.e. empty crystals or inclusions of nacre-like inserts (Fig. 8.5b).

The monolayered structure of the outer prismatic layer of ammonoids distinguishes this layer from the outer prismatic layer of the present-day *Nautilus,* which consists of two sublayers with different ultrastructure (Mutvei 1964). Namely, the outer sublayer has a grainy structure; each grain is made of crystallites that are mutually parallel in arrangement or slightly spherulitic.

Nacreous Layer As in *Nautilus,* the nacreous layer of ammonoids was·produced in two secretory zones located in the shell wall and in the septa respectively. The first of these has a belt-like shape, encircling the inside of the aperture except for its dorsal part in the normally coiled ammonoids. The second zone of nacreous secretion is a large area at the posterior part of the body. Although the secretory product is the same in both zones, the relationship of the surface of secretion to the elements of the nacreous layer (lamellae) varies. Generally, the growth direction in the zone of septal secretion is perpendicular to the surface of the septum and to the interlamel-

lar membranes. On the other hand, in the shell wall, the interlamellar membranes occur in very long sections parallel to the inner surface of the outer prismatic layer, and the growth zone cuts them diagonally (see Erben 1972a, Fig. 1). In fossil and modern gastropods and nautilids, as well as in Paleozoic ammonoids, the mineral component of the nacreous layer is characterized by a uniform orientation of the crystallographic axes (crystallographic texture) while in Mesozoic ammonoids the aragonite crystals display variable orientations of the crystallographic axes (Frýda et al. 2007, 2009).

According to these authors the molecular mechanism driving the origin and the development of gastropod and nautilus nacre are thus extremely old and remained unchanged for at least 220 million years. A quite different crystallographic texture of the nacre is known from each of the Mesozoic ammonoid suborders Ammonitina, Phylloceratina, and Lytoceratina. The presence of different nacre textural patterns in nautiloid and ammonoid lineages as well as the extreme stability of those patterns supports the conclusion that this patterns can be used as a tool to resolve cephalopod phylogenetic relationships (Frýda et al. 2007).

The basic structural elements of the nacreous layer are aragonitic hexagonal plates, which are arranged in sheets separated by interlamellar membranes (Fig. 8.7a). These plates are placed one on top of another, forming vertical stacks (Fig. 8.7c). Such a columnar arrangement of nacre is characteristic of ectocochliate cephalopods and of gastropods. The growth surfaces of columnar nacre described by Wise (1970) and Erben (1972a) show that the nuclei of newly formed plates are always deposited in the central part of subordinate plates and afterwards accreted. The lateral walls of neighboring hexagonal plates are separated from each other by intercrystalline membranes of conchiolin. According to Mutvei (1980), the hexagonal tablets of stack nacre are composed of a variable number of crystalline sectors, which are separated from one another by vertical radial organic membranes. These sectors represent contact and interpenetrant twins. The central portion of each tablet in the stack is occupied and connected vertically by a central organic accumulation (Mutvei 1980, 1983); these accumulations commonly occur in ammonoid nacre (Fig. 8.7b).

Ultrastructural studies of the conchiolin of the mollusk nacreous layer have been conducted by many authors, but only Gregoire (1966, 1980) included ammonoids in his investigations. Experimental studies on the conchiolin of the mollusk nacreous layer show that it is thermoresistant. Even after having been heated to 900°C for 5 h, it is still biuret-positive (Gregoire 1966, 1968, 1972, 1980; Voss-Foucart and Gregoire 1971). During diagenesis, the chemical composition of mollusk conchiolin changes rapidly but afterwards can remain stable and unchanged over millions of years, even under metamorphic conditions (Voss-Foucart and Gregoire 1971; Weiner et al. 1979; Gregoire 1980). The mineral component of the hexagonal plates of nacre has been examined since the nineteenth century, but even present-day authors offer differing opinions on its structure.

In addition to its presence in ectocochliate cephalopods, stack nacre is characteristic of gastropods, monoplacophorans, and primitive bivalves such as *Nucula*
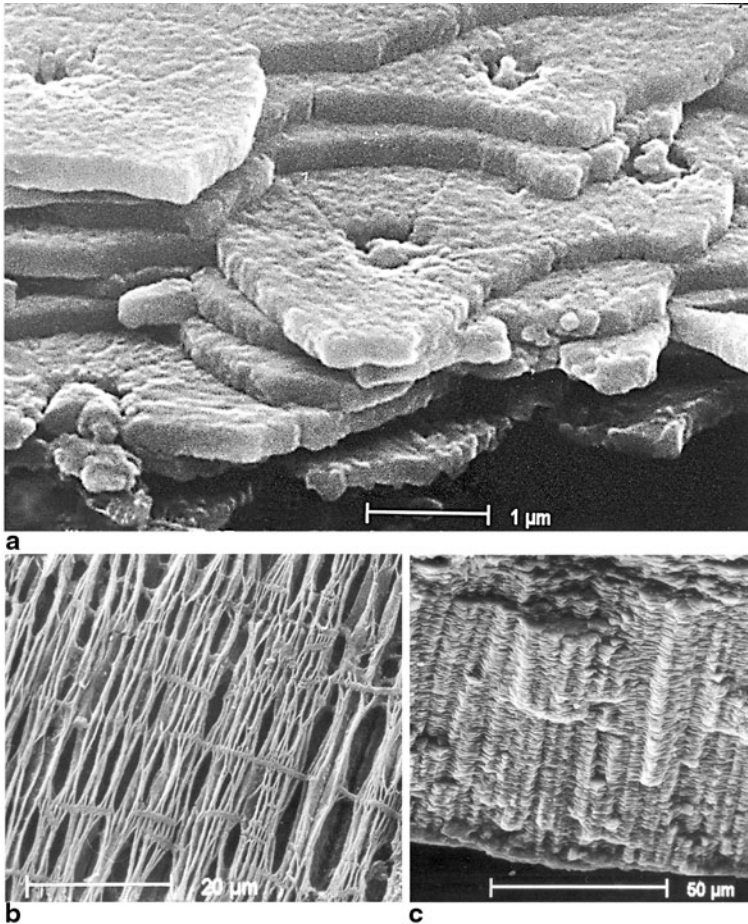
Fig. 8.7 a, **b** *Aconeceras trautscholdi* (Sinzov 1870), Aptian, Cretaceous, vicinity of Simbirsk, Russia. **c** *Bochianites neocomiensis* (d'Orbigny 1840), Valanginian, Cretaceous, Wąwał, Poland. **a**, Tablets of the nacre with central organic accumulations and sectors of tablets. **b**, Interlamellar organic membranes and central organic accumulations of stack nacre. **c**, Stacks of the nacre visible in broken specimen

and *Trigonacea* (see Erben et al. 1968). Orientation of axes *a* and *b,* respectively, in different plates is parallel in cephalopods (Gregoire 1962; Wise 1970) but random in gastropods (Wise 1970). Studies of the nacre in gastropods by Erben (1974) concluded that the hexagonal plates represent compact crystals rather than poly-crystalline aggregates, as suggested by Mutvei (1969, 1970, 1979). From a study of chromium-sulfate-treated shells, Erben (1974) also observed, apart from inter-lamellar and intercrystalline membranes, intracrystalline organic elements such as diagonal sheets or vertical pillars. Mutvei (1969, 1970, 1979), on the other hand,

interpreted these elements as acicular crystallites. Chromium sulfate preparation of the nacreous layer of *Quenstedtoceras* reveals detailed structural characters as seen in *Nautilus* (see Mutvei 1972a) and *Haliotis* (see Erben 1974, pl. 4, Fig. 1–5). The same *Quenstedtoceras* specimens prepared in H_2O_2 (the method used by Kulicki and Doguzhaeva 1994) display a great similarity in their nacre to that of modern *Mytilus edulis* treated with sodium hypochlorite solution and etched with 25 % glutaraldehyde solution for 2 days (Mutvei 1979). The lamellae of the nacreous layer of ammonoids are generally 0.25 μm thick in different parts of the shell, but are several times thicker in the transition zone to the outer prismatic layer. Doguzhaeva and Mutvei (1989) described pores in the nacreous layer of the heteromorph *Ptychoceras*. They considered them to be an inherent characteristic of these ammonoids. In the nacreous layer of the Early Cretaceous heteromorph *Bochianites,* similar pores are also observed, but it is difficult to dismiss the possibility that they were produced by boring organisms even though they display a "rowlike distribution" (Doguzhaeva and Mutvei 1989).

Inner Prismatic Layer This layer is situated on the inner surface of the nacreous layer at some distance from the apertural edge of the shell. In specimens in the final stages of ontogeny, the inner prismatic layer comes closer to the apertural zone (Doguzhaeva and Mutvei 1986b). This layer results from secretory activity of the myoadhesive epithelium (Mutvei 1964). Although the literature provides various data on the occurrence of the inner prismatic layer in the ontogeny of different ammonoids, in all ammonoids examined by us it starts to develop as far adapically as the second or third septum. In transverse cross sections of normally coiled ammonoids, the inner prismatic layer is the only shell layer that extends across the venter and dorsum; this is in contrast to the outer prismatic and nacreous layers, both of which wedge out at the umbilical seam and do not occur in some Phylloceratina; on the dorsum, this layer is more than twice as thick as the whole ventral wall of the previous whorl (Birkelund and Hansen 1974, 1975; Birkelund 1981).

There is not always a close contact between the inner prismatic layer and the overlying layer. The general tendency is to smooth out all unevenness or hollows, e.g., as in the floored hollow spines of *Kosmoceras* (see Erben 1972b), or to smooth out the fine ribbing on the exterior of the previous whorl (Birkelund and Hansen 1974, 1975: Howarth 1975). The inner prismatic layer generally consists of regular prisms with visible needle-like crystallites. In the heteromorph *Ptychoceras* it shows irregular nacre like inclusions (Fig. 8.8a, b). In the Triassic *Phyllocladiscites,* well-developed pores filled with crystalline matrix occur in the inner prismatic layer (Doguzhaeva and Mutvei 1986b). These pores are not visible in cross sections of the wall but can be seen only on the surface.
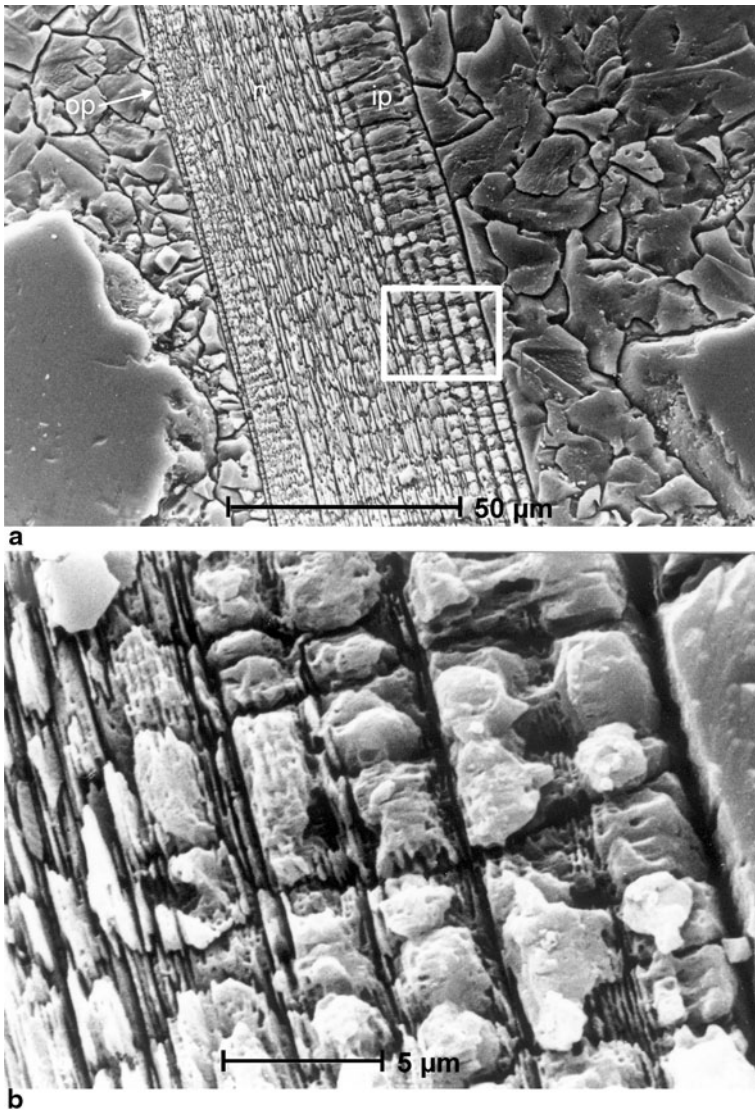
Fig. 8.8 *Ptychoceras* sp. Aptian, Cretaceous, Khocods Rivier, NW Caucasus. **a** Longitudinal section through ventral wall. Outer prismatic layer extremely thin and inner prismatic very thick. **b** Magnification of a indicating inclusions of nacre between prisms. Abbreviations: *ip*, inner prismatic layer; *n*, nacreous layer; *op*, outer prismatic layer

8.4   Modifications of the Shell Wall

8.4.1   Inner Shell Wall of the Dactylioceratidae

Howarth (1975) described the so-called inner shell wall in the Dactylioceratidae, a modification unknown in other groups of ammonoids. The main shell wall in representatives of the Dactylioceratidae consists of layers with a normal sequence: outer prismatic layer, nacreous layer, and inner prismatic layer. The inner shell wall consists of an outer prismatic layer and an inner nacreous layer. On the inside, the inner shell wall is covered by a septal prismatic layer.

The appearance of the inner shell wall coincides with the appearance of ornamentation. It is not closely attached to the inner surface of the main shell wall but smoothes out this wall from the inside, leaving empty spaces between it and the concave surfaces of ribs. The outer prismatic layer of the inner shell wall is not continuous—it is missing in some places. In ontogenetic development, the nacreous layer of the inner shell wall first appears as an insert in the inner prismatic layer of the main shell wall. The nacreous layer of the inner shell wall does not differ in its microstructure from the nacreous layer of the main shell wall (Howarth 1975). Although the inner prismatic layer is not split by a nacreous layer in other groups of ammonoids, there is an analogy to the splitting of the inner prismatic layer by the conspicuous organic membranes in *Nautilus* (see Doguzhaeva and Mutvei 1986b).

8.4.2   Dorsal Wall

In heteromorphs, where the shell walls of adjacent "whorls" do not join, the dorsal wall of the "free whorls" usually has the same structure as do other shell parts. In normally coiled ammonoids, on the other hand, the microstructure of the dorsal wall changes, and the dorsal wall is a wall covering the previous whorl and laterally limited by the umbilical seams. According to Kulicki (1979), the dorsal wall of ammonoids generally consists of two components: the outer wrinkle layer and the inner prismatic layer. The latter may have a complex microstructure, as discussed in the previous section.

The term *"Runzelschicht"* (wrinkle layer) was introduced by Sandberger and Sandberger (1850) to denote a thin layer superimposed on the test of Devonian goniatites. This layer had been recognized earlier by Keyserling (1846). The descriptions of these authors leave no doubt that the layer described is connected with the dorsal wall. Sandberger and Sandberger (1850) also used another expression, *"Ritzstreifen,"* to denote the markings preserved on internal molds of the inside of the lateral and ventral parts of the ammonoid whorl. Subsequent authors have used the term *Runzelschicht* for both categories of elements. The problem of the wrinkle layer in Paleozoic goniatites was discussed by House (1971), who insisted that the terms *"Runzelschicht"* and *"Ritzstreifen"* denote the same structure and suggested

that this structure be referred to as the dorsal or ventral wrinkle layer, respectively. According to House (1971), all Paleozoic ammonoids possessing such structures are smooth and ribless: the Anarcestoidea and Pharciceratoidea display both kinds of wrinkle layers while the Cheiloceratoidea only the dorsal one, and the Clymeniina has just a narrow belt on the dorsal side. Tozer (1972) verified and precisely defined the meaning of these expressions.

The wrinkle layer occurs on the dorsal side of normally coiled ammonoids in the vicinity of the aperture; in some instances, it has been observed beyond the aperture (Senior 1971; Tozer 1972; Tanabe et al. 2001). The secretory zone of this layer is connected with the mantle edge, and, therefore, it is comparable to the black film of *Nautilus* with which it shares a similar microornamentation. *Ritzstreifen,* as defined by Sandberger and Sandberger (1850), are situated at the back of the body chamber, and, therefore, the zone of their formation lies behind the secretory zone of the nacreous layer.

Kulicki (1979) described the development of the wrinkle layer in the body chamber of *Quenstedtoceras*. A similar wrinkle layer and its developmental sequence have been presented in Triassic *Proarcestes* by Doguzhaeva and Mutvei (1986b). Walliser (1970) described the variability in ornamentation and occurrence of the *Runzelschicht* and *Ritzstreifen* without differentiating these two categories.

The main elements of the wrinkle layer of *Quenstedtoceras* are triangular in longitudinal cross section and are composed of prisms perpendicular to the surfaces of the steep adapertural sides of the triangles. Each triangle is filled with smaller prisms, arranged more chaotically as those known from perpendicular sections in *Damesites* and *Tetragonites* (Fig. 8.9). In addition to the prisms, the triangular elements contain abundant organic matter. Nassichuk (1967) assumed that the wrinkle layer of *Clistoceras* may have been organic. Zakharov and Grabovskaya (1984), however, assigned the wrinkle layer in *Zelandites japonicus* to the nacreous layer, but this feature is not clearly shown in their Figure (Zakharov and Grabovskaya 1984, Fig. 3). Bayer (1974) described the wrinkle layer of Mesozoic ammonoids as occurring only on the dorsal side. He argued that the wrinkle layer did not constitute a separate layer but was merely part of the inner prismatic layer. Kulicki et al. (2001) described the dorsal shell wall in many genera of Goniatitida, Ammonitida, Phylloceratida, and Lytoceratida. Apart from the external component of the dorsal wall expressed as wrinkle layer, there are also other forms of the external component as e.g., in *Aconeceras* illustrated herein (Fig. 8.10).

8.4.3 Umbilical Plugs and Encrusting Layers

Umbilical plugs comparable to those in *Nautilus pompilius* are observed in some Paleozoic and Triassic ammonoids, especially in strongly involute forms such as *Clistoceras* (see Nassichuk 1967), *Nathorstites* (see Tozer 1972), and a number of Triassic ammonoids and nautilids (Klug et al. 2004). In the present-day *Nautilus pompilius,* the surface of the umbilicus is partly covered by a black film on which
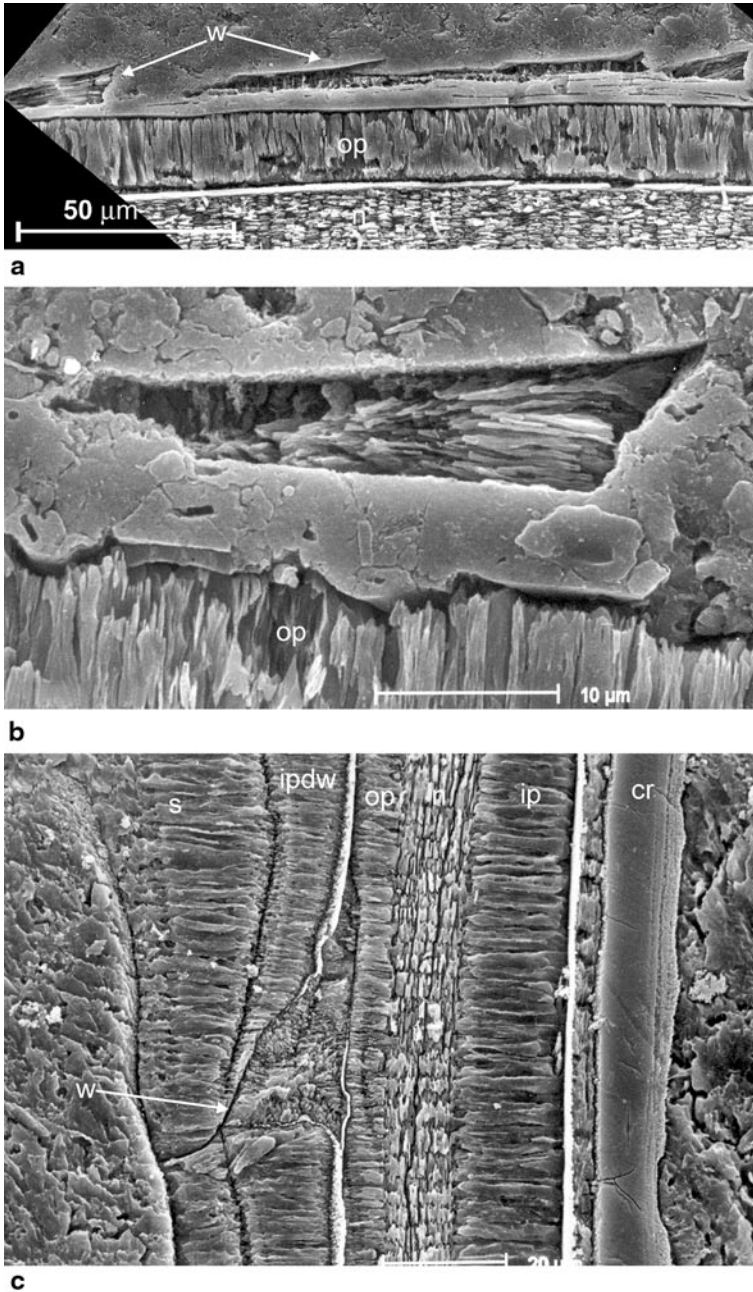
Fig. 8.9 a, **b**, *Tetragonites glabrus* (Jimbo 1894), Early Campanian, Cretaceous, Abeshinai River, Nakagawa Town, Hokkaido. **c**, *Damesites sugata* Forbes, 1846. Coniacian, Cretaceous Nakafutamata Rivulet, Haboro area northwestern Hokkaido. **a**, Longitudinal section through the ventral
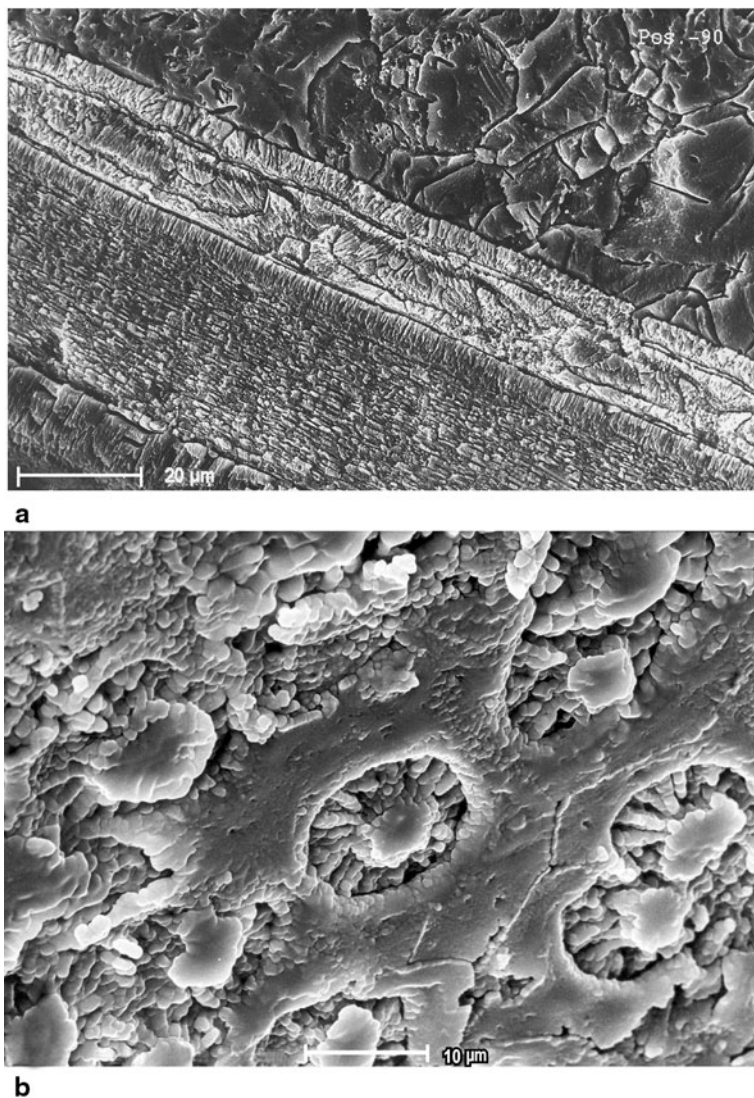
Fig. 8.10 *Aconeceras trautscholdi* (Sinzov 1870), Aptian, Cretaceous, vicinity of Simbirsk, Russia. **a**, Longitudinal section through ventral wall covered by dorsal one of the next whorl. **b**, View on exfoliated dorsal wall from the basal part

wall covered by triangular elements of the dorsal wall of the next whorl. **b**, Triangular element of the same specimen as **a**. **c**, Longitudinal section through the ventral wall covered by dorsal one, consisting of three constituents: triangular elements, middle prismatic layer and mural part of the septum. Abbreviations: *cr*, ventral wall of the connecting ring; *ip*, inner prismatic layer; *ipdw*, inner prismatic layer of the dorsal wall of the next whorl; *n*, nacreous layer; *op*, outer prismatic layer; *w*, wrinkle

the material of the umbilical plug lies. This umbilical callus consists of spherulitic prismatic deposits and elements of the nacreous layer (Gregoire 1966; CK, unpublished observations). In adult shells the umbilical plug does not fill the whole umbilical space but only the outer part. Nassichuk (1967) called the formations described in *Clistoceras* as "helicolateral deposits" but did not confirm their homology to the umbilical plugs in *Nathorstites* and *Nautilus pompilius*. Tozer (1972), in contrast, confirmed the close homology between the helicolateral deposits of *Clistoceras* and the umbilical plugs of *Nathorstites* and *N. pompilius*. There is no detailed description of the structure of the above mentioned deposits apart from the statement by Tozer (1972) that, in the formation of the umbilical callus in *Nathorstites,* a secondary nacreous material is included. Bogoslovsky (1969) illustrated specimens of *Prolobites* in which the umbilicus is covered by a calcium carbonate wall. Drushchits et al. (1978) described multilayered structures encrusting the umbilical surface in the Late Cretaceous lytoceratid *Gaudryceras*. These structures do not cover the entire shell surface in that some spaces are left out, especially at the umbilical seams. Starting from the third whorl, the encrusting layer separates the ventral wall of the third whorl from the inner prismatic layer of the fourth whorl. Birkelund (1981) confirmed the occurrence of such encrusting layers in specimens of *Gaudryceras* from Japan. The thickness of the encrusting layers may be several times thicker than that of the shell wall itself. Our reinvestigation of well-preserved material from Hokkaido suggests that the coating layers of *Gaudryceras* are homologous to the black film of *Nautilus*, being very similar both in color and the elemental composition (Fig. 8.11). There are significant amounts of Ca and variable amounts of C in these structural elements which may indicate that the primary material has been formed from more or less stabilized ACC (amorphous calcium carbonate). In case of *Gaudryceras* illustrated herein (Fig. 8.11b) some crystallization could occur as a result of diagenesis.

8.4.4 Septa

According to the commonly accepted view, the first two septa are called prosepta (Fig. 8.12). They were supposed to differ from all other septa in their relationship to the wall of the outer shell (Grandjean 1910; Böhmers 1936; Voorthuysen 1940; Miller and Unklesbay 1943; Miller et al. 1957; Arkell 1957; Drushchits and Doguzhaeva 1974; Tanabe et al. 1980). Miller and Unklesbay (1943) pointed out that prosepta are adaperturally concave in medial cross section, whereas all remaining septa are convex toward the aperture.

On the basis of SEM observations, Erben et al. (1969) confirmed the distinct microstructural character of prosepta in relation to all other septa. They also observed that the second septum (primary septum, "*Primarseptum*"*),* like all subsequent septa, is separated from the shell wall by a conchiolin layer.

A nacreous layer in the second septum has been identified by Birkelund and Hansen (1974); Kulicki (1979); Bandel (1982); Landman and Bandel (1985), and
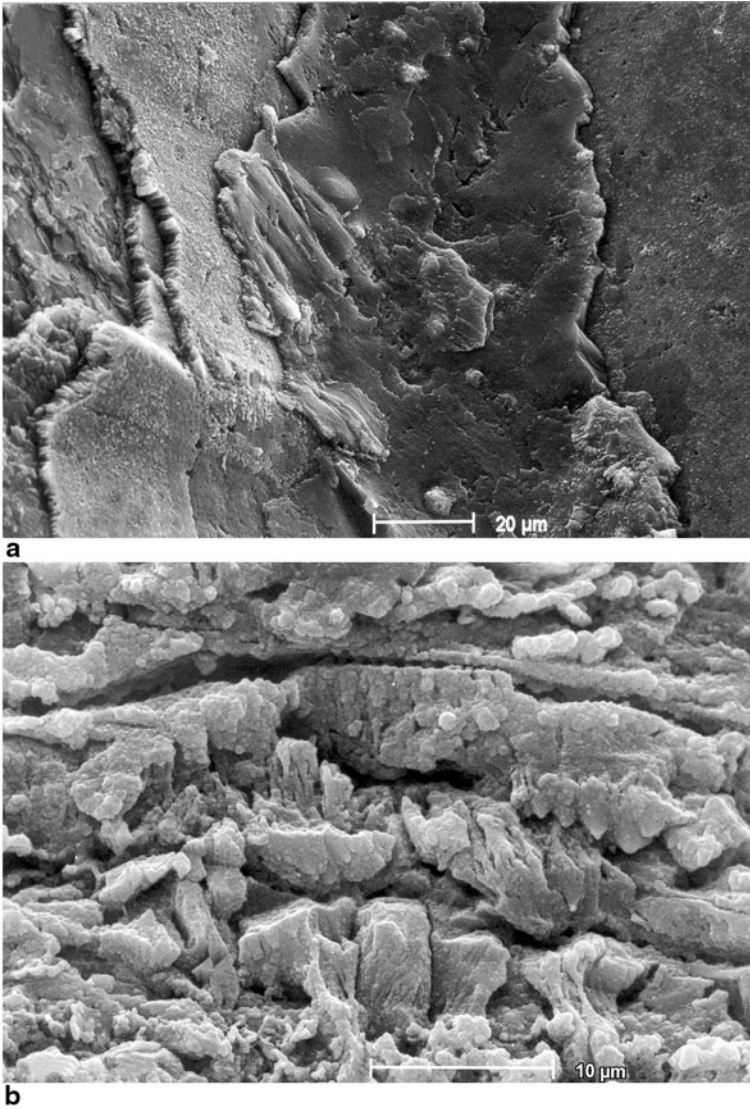
Fig. 8.11 *Gaudryceras tenuiliratum* Yabe, 1903, Campanian, Cretaceous, Abeshinai River, Nakagawa Town, north Hokkaido. **a**, Coating layers covering seam between two whorls. **b**, Broken view of several coating layers

Landman (1987). Erben et al. (1969), using strictly medial cross sections, may not have recorded the occurrence of a nacreous layer in the structure of the second septum. The main component in the construction of septa, with the exception of the proseptum, is the nacreous layer. Sporadically, the adapertural surface and, less commonly, the adapical one may be covered by a prismatic layer and, more rarely,

a spherulitic prismatic one (Birkelund and Hansen 1974; Howarth 1975; Kulicki 1979; Kulicki and Mutvei 1982). The connection between the septum and septal neck on the adapertural surface in *Quenstedtoceras* illustrates the prismatic layer passing collaterally and continuously into the lamellae of the nacreous layer (Kulicki and Mutvei 1982, text-Fig. 3, Pl. 5, Fig. 1). At the connection points of the septa and the shell wall a distinct boundary separating the two is visible. Lamellae of the nacreous layer bend strongly adaperturally and pass continuously into the prismatic layer, the so-called septal prismatic layer of Howarth (1975), which may be developed to different degrees.

8.4.5   Septal Neck-Siphuncular Complex

The expression "siphuncular complex," introduced by Tanabe et al. (1993a), includes the following elements: cecum and prosiphon, siphuncular tube (= connecting ring), siphuncular membranes, auxiliary deposit (= auxiliary anterior deposit), cuff (= auxiliary posterior deposit), and angular deposit.

Cecum and Siphuncular Tube The cecum (caecum) is the spherical ending of the siphuncular tube in the initial chamber. Originally composed of organic conchiolin, the cecum generally is phosphatized in the fossil state. The problem of preservation of the cecum applies equally well to the other organic elements of the siphuncular complex, i.e., the siphuncular tube and the siphuncular membranes. The main mineral in these elements is francolite (Andalib 1972; Hewitt and Westermann 1983). The siphuncular tube is very rarely calcified (Joly 1976; Kulicki et al. 2007; Tanabe et al. 2005). Nautiloids of the same age have non-phosphatized siphuncular tubes (Fukuda in Obata et al. 1980; CK, unpublished observations). Hewitt and Westermann (1983) presented a tentative interpretation of the ammonoid siphuncular tube as having been originally chitinous, but stiffened internally with phosphate crystals.

In its anterior part, the cecum in Mesozoic forms, e.g., *Kosmoceras* and *Quenstedtoceras,* is connected directly or by a calcareous deposit to the achoanitic proseptum (Kulicki 1979). In *Tornoceras* the relationship between the proseptum and the cecum was illustrated by House (1965, Fig. 2) and also by Bogoslovsky (1971, Fig. 6), and, although these two authors interpreted the described elements quite differently, they both indicated a retrochoanitic septal neck in the proseptum. Thus, it can be expected that the relationship between the conchiolin wall of the cecum and the proseptum is the same as that between the siphuncular tube and the retrochoanitic septal neck in *Nautilus*. The outer part of the cecum in many genera is covered by a calcareous deposit (Drushchits and Doguzhaeva 1974, 1981; Drushchits et al. 1983; Tanabe et al. 1979, 1980).

The cecum is connected to the inner surface of the initial chamber by means of the so-called prosiphon, which is an organic structure of complex construction. Prosiphons, even in the same species, may display considerable morphological variability. Apart from tube-like elements, which vary as to the degree of flatten-
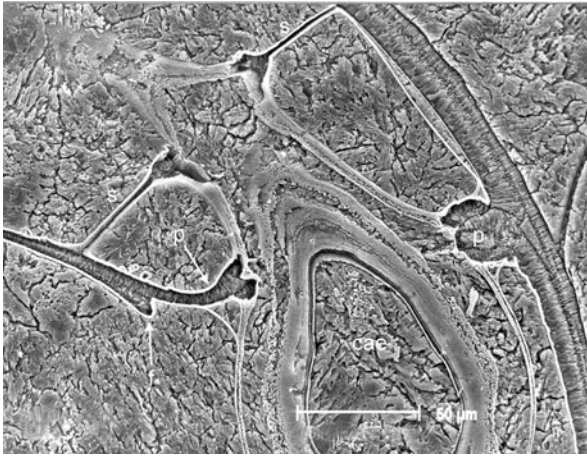
Fig. 8.12 *Damesites sugata* Forbes, 1846. Coniacian, Cretaceous, Nakafutamata Rivulet, Haboro area northwestern Hokkaido, Prosepta: prismatic proseptum and nacreous primary septum. Abbreviations: *cae*, caecum; *f*, flange; *p*, proseptum; *s*, first nacroseptun

ing and bending, there is another very variable element: membranes that join the tubular elements to the inner surface of the initial chamber (Kulicki 1979; Bandel 1982; Ohtsuka 1986; and citations above). The cecum in cross section may show a multilayered concentric structure (Ohtsuka 1986 and Fig. 8.12 herein). The cecum and prosiphon commonly exhibit wrinkles or tension lines, proving their former elasticity.

The siphuncular tube in ammonoids, as opposed to that in *Nautilus,* is constructed exclusively of organic matter, i.e., multilayered concentric membranes of conchiolin (Fig. 8.13a, c, d), each of which consists of lace-like, tuberculate microfibrils 1–2 μm in diameter with elongate pores (Obata et al. 1980; Gregoire 1984).

In the retrochoanitic condition, comparable to that in present-day *Nautilus,* the adapertural end of each segment of the siphuncular tube is a continuation of the organic membranes of the nacreous layer of the septal neck. The adapical end of each segment of the siphuncular tube terminates in an auxiliary deposit attached to the inner surface of the previous septal neck. In the prochoanitic condition, the only difference is the relationship between the siphuncular tube and the septal neck at the adapertural end of the tube segment. In this case, the organic segment of the siphuncular tube is connected with the cuff and not with the distal part of the septal neck.

According to Mutvei (1972a), in present-day *Nautilus* there are no organic layers connecting the adjacent segments of the siphuncular tube. Therefore, Gregoire's (1987, Fig. 12) schematic drawing, in which the auxiliary ridge is connected to both the adapertural and adapical segments of the siphuncular tube is misleading. Ammonoids in the retrochoanitic condition do not exhibit such connections either while they were reported from the ammonoids with the prochoanitic condition (Kulicki and Mutvei 1982) as being present between adjacent segments of the siphuncular
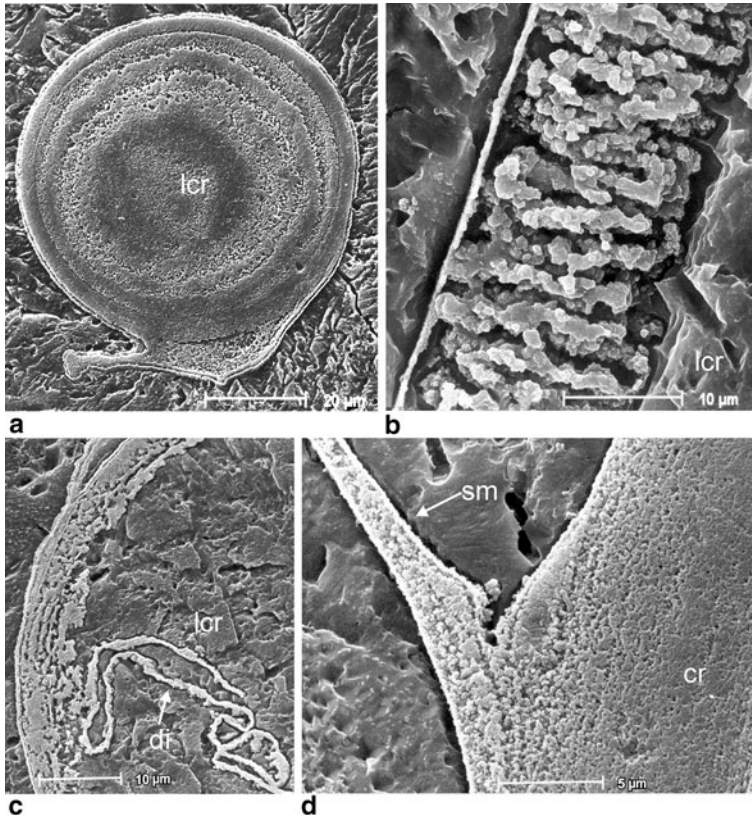
Fig. 8.13 **a**, **c**, **d**, *Damesites sugata* Forbes, 1846. Coniacian, Cretaceous, Nakafutamata Rivulet, Haboro area northwestern Hokkaido. **b**, *Aconeceras trautscholdi* (Sinzov 1870), Aptian, Cretaceous, vicinity of Simbirsk, Russia. **a**, **c**, Phosphatized siphuncular tube showing multilayered structure of the siphuncular wall. **b**, Cross section through partly phosphatized and partly calcified wall of the siphuncular tube. **d**, The outermost siphuncular layer passing in to siphuncular membrane. Abbreviations: *cr*, connecting ring; *di*, delaminated inner layer of the connecting ring; *lcr*, lumen of the connecting ring; *sm*, siphuncular membrane

tube via the basal lamella of the cuff. This phenomenon is easy to explain because the siphuncular tube protruding into the body chamber was longer than the distance between septa. In this case, after the soft body moved forward into a position appropriate to form a new septum, the basal lamella undergoing calcification became connected to both the adapical and adapertural segments of the siphuncular tube, which was already partially secreted. An additional connection of the outer layer of the siphuncular tube to the adapertural tip of the prochoanitic septal neck has also been reported by Kulicki and Mutvei (1982). According to Kulicki (1979), the siphuncular tube in the prochoanitic condition may have been secreted both from the inside, by the epithelium of the siphuncular cord, and from the outside, by the epithelium of the circumsiphonal invagination. The outermost layer of the

tube segment would have been secreted by the epithelium of the circumsiphonal invagination.

Birkelund and Hansen (1974) have described a double-layered siphuncular tube in a specimen of the Maastrichtian ammonoid *Saghalinites wrighti*. The inner, initially organic layer of this siphuncular tube displays a fibrous structure, whereas the outer layer is composed of calcium carbonate with a prismatic structure. The state of preservation of the specimen prevented these authors from determining whether the mineral of the outer layer was calcite or aragonite. But the fact that the strontium content of this layer differed from that in the surrounding rock was, in their opinion, a confirmation of the primary nature of this calcium carbonate layer and, hence, evidence of a similarity between the siphuncular structure in ammonoids and that in present-day *Nautilus*.

Septal Necks Siphuncular deposits in the Ammonitina are best known in *Quenstedtoceras* (see Kulicki 1979; Kulicki and Mutvei 1982) and *Gaudryceras* (Tanabe et al. 1993a; Tanabe and Landman 1996, 2010). Generally, the inner surface of the septal neck is covered by a cuff, which is the adapertural termination of the siphuncular tube segment. An auxiliary deposit, which is the adapical termination of the next segment of the siphuncular tube, frequently covers the cuff from the inside. In middle and late ontogenetic stages of *Quenstedtoceras* the outermost part of the cuff, called the basal lamella, is distinguished as a separate element. It remains in direct contact with the nacreous layer of the septal neck. Kulicki and Mutvei (1982) distinguished it because of the difference in its microstructure with respect to the rest of the septal neck and because it is connected to the wall of the siphuncular tube both adaperturally and adapically. They have also distinguished the basal lamella in the auxiliary deposit, which is connected at its distal end to the wall of the siphuncular tube.

The cuff and auxiliary deposit are identical in microstructure. They both show fine lamellae (about 1 μm thick) and a spherulitic-prismatic system of mineral components similar to the modified nacreous layer in the septal neck of *Nautilus* (see Kulicki and Mutvei 1982). The basal lamellae have a stronger spherulitic-prismatic calcification than the rest of the deposit, and, thus, the lamellar structure is less visible there (Kulicki and Mutvei 1982). These studies did not confirm the interpretation of Bandel and Boletzky (1979) and Bandel (1981, 1982) that the siphuncular deposits in the Ammonitina were originally porous.

In a newly formed septum, one commonly can observe that the basal lamella of the cuff is not in contact with the inner surface of the proximal part of the septal neck and that there is an empty space between these two elements (H. Mutvei and C. Kulicki, unpublished data). In more adapical septa, this space is filled by sparry calcareous material and forms so-called "angular deposit" (Kulicki 1979). Angular deposits are formed as a result of inorganic calcification; they are almost always present between the cuff and the adapical part of the prochoanitic septal neck, with the exception of the last septum. This suggests rapid formation of angular deposits during the lifetime of the animal (Kulicki 1979).

Intermediate Condition Septal necks characteristic of this condition represent an intermediate form between typical retro-and prochoanitic necks. Such necks have been described by Doguzhaeva (1973), Doguzhaeva and Mutvei (1986a), Drushchits and Doguzhaeva (1974), Kulicki (1979), Kulicki (1994), Tanabe et al. (1993a), and Tanabe and Landman (1996).

During the transition from retrochoanitic septal necks to fully prochoanitic necks, the secretion of the siphuncular tube became more independent of the secretion of the septum and septal neck than in the retrochoanitic condition. In the retrochoanitic condition, the siphuncular tube, septal neck, and septum must have been secreted simultaneously. In the prochoanitic condition, secretion of the siphuncular tube was independent of the formation of the septum. According to Kulicki and Mutvei (1982), the organic layers of siphuncular tube are formed prior to the appearance of the septum and siphuncular neck.

8.4.6   Intracameral Membranes

The inner surface of chamber walls and the adapical and adoral surfaces of septa are covered with phosphatized membranes that were originally organic. These are called, in general, intracameral, conchiolin, or cameral membranes. Those that remain in contact with the siphuncular tube are specifically known as siphuncular membranes. Siphuncular membranes have been described by Grandjean (1910); Schulga-Nesterenko (1926); Erben and Reid (1971); Westermann (1971); Bayer (1975); Kulicki (1979); Bandel and Boletzky (1979); Bandel (1981, 1982); Tanabe et al. (1982); Weitschat (1986); Weitschat and Bandel (1991), and Landman et al. (2006).

The ultrastructure of intracameral membranes was described by Tanabe et al. (1982) and Gregoire (1984). According to these authors, these membranes are composed of thin (0.015–0.15 μm) fibers that lack a distinct orientation. These membranes are comparable to the pellicle ("*brown membrane*") in *Nautilus* and *Spirula*. However, they differ considerably in having finer fibers that have no preferred orientation.

Siphuncular membranes display great variability among different ammonoid groups. Although Permian and Triassic genera seem to have especially well-developed and numerous siphuncular membranes (Schulga-Nesterenko 1926; Weitschat and Bandel 1991), they are less numerous and not-so-well-developed in Jurassic and Cretaceous forms. These membranes connect the siphuncular tube to both the adapical and adapertural surfaces of the septa. They may also form connections to the ventral or ventrolateral shell wall. Especially complex systems of siphuncular membranes have been described by Weitschat and Bandel (1991) in the Triassic genera *Anagymnotoceras* and *Czekanowskites*.

Horizontal membranes, as noted by Weitschat and Bandel (1991), represent a case of extremely well-developed siphuncular membranes. These horizontal membranes divide the phragmocone chamber into two main compartments of nearly

equal size, a ventral and a dorsal compartment. These membranes are connected to the siphuncular tube, to the septa at their mid-height, and to the inner surface of the outer shell wall flanks. These membranes are commonly perforated. There is another kind of intracameral membrane known as a transverse membrane (Weitschat and Bandel 1991). These membranes are not always connected to the siphuncle but generally separate the chamber into compartments. Transverse membranes also display perforations.

Zaborski (1986) and Hewitt et al. (1991) have described membranous structures, so-called "pseudosepta", in vascoceratids from Nigeria. Pseudosutures, i.e., the lines of attachment of pseudosepta to the shell walls, have been reported from Mesozoic ammonoids (John 1909; Hölder 1954; Vogel 1959; Schindewolf 1968; Bayer 1977) as well as from Paleozoic goniatites (Landman et al. 1993; Tanabe et al. 1998) and prolecanitids (Landman et al. 2006).

There are two interpretations for the formation of intracameral membranes. The first, accepted by the majority of researchers, posits that organic membranes are secreted in close contact with the mantle surface, like the periostracum or other mineral-organic layers of the shell, e.g., the nacreous layer. Weitschat and Bandel (1991) have critically assessed this point of view and they proposed an alternative interpretation which agrees with the former one that the organic matter of the intracameral membranes is secreted by the mantle surface but the membranes themselves are produced by dehydration of a jelly-like cameral fluid (Bandel and Boletzky 1979; Hewitt et al. 1991; Westermann 1992).

Functionally, hydrophilic intracameral membranes could have served either as pathways for transport of cameral fluid or as structures helping to maintain the fluid within certain reservoirs and preventing any overflow. This may have made it possible to keep cameral and circumsiphonal fluids in a state of decoupling, which may have been beneficial from the physiological point of view (Mutvei 1967; Kulicki 1979; Kulicki and Mutvei 1988; Ward 1987; Weitschat and Bandel 1991). For further discussion of intracameral membranes, see Polizzotto et al. (2015).

8.5   Conclusions

The major limitation to micro-and ultrastructural studies of ammonoids is diagenesis, i.e., the state of preservation of the specimens used. This explains why Jurassic and Cretaceous ammonoids are among the best studied, while the data on Paleozoic and Triassic forms are generally rare. It is only under exceptionally favorable conditions of preservation, such as those in the Buckhorn asphalts of Pennsylvanian age, that the study of the ultrastructure of orthoconic cephalopods was possible, revealing a great similarity between these forms and present-day *Nautilus* (see Mutvei 1972b). At the ultrastructural level, the three main layers of the postembryonic shell of ammonoids do not differ significantly from those known from the shell of present-day *Nautilus*. The same is also true for the septa. However, a clearly distinctive element is the ammonitella, which is now the focus of attention of many am-

monitologists. The new model of calcification of the ammonitellae, based on well-preserved specimens of *Aconeceras* (see Kulicki and Doguzhaeva 1994, Tanabe et al. 2008, 2010) and the importance of more or less stabilized ACC (amorphous calcium carbonate) as well as the remotely controlled development of the tubercles, requires further investigations. Knowledge of the ultrastructure of both the mineral and organic components in ammonoids is meager compared with what is known about Recent mollusks. Some results obtained in the course of ultrastructural studies by Gregoire (1984) and Obata et al. (1980) seem to show that such research is feasible.

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