Dorsal shell wall in ammonoids

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In ammonoids, a soft body organ (possibly a supracephalic mantle fold), extending from the conch aperture secreted aragonitic wrinkles, forming a layer on the surface of the preceding whorl. The dorsal shell wall consists of the outer and inner components which were deposited sequentially, beginning at the aperture of the living chamber inwards. The dorsal wall attains its full thickness near the last septum. The outer component is visible in the apertural region and is smooth or wrinkled; it is called the wrinkled layer in the latter case. The wrinkles may be continuous, interrupted, or form isolated patches arranged in rows. The wrinkles are usually triangular in cross section. A further stage of dorsal wall development involves filling in the space between the apices of triangles, and then adding one or more inner prismatic layers from the inside of the living chamber. This pattern occurs at least in the postembryonic stage of all genera studied, belonging to five suborders of Ammonoidea ranging from Late Carboniferous to Late Cretaceous. In many genera, the outer component of the dorsal shell wall exhibits remarkable ontogenetic change in its ultrastructure and micro-ornament. It may be compared with the black film of Recent *Nautilus* shells with respect to place of formation. The outer component of the ammonoid dorsal shell wall is regarded as a product of organic secretion and carbonate precipitation in the area of the supracephalic mantle fold.

Key words: Ammonoidea, dorsal shell wall, ultrastructure, wrinkle layer, biomineralization.

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Introduction

In openly coiled ammonoids, where the shell walls of adjacent 'whorls' do not overlap, the dorsal wall of the 'free whorls' usually has the same structure as do other parts of the shell. In normally coiled ammonoids, on the other hand, the structure of the dorsal wall changes, and the dorsal wall is a layer covering the previous whorl from the outside.

Kulicki (1979) distinguished two components in the structure of the dorsal wall of a Callovian ammonoid *Quenstedtoceras* with respect to the position of formation: an outer one, and an inner one, representing usually the inner prismatic layers. The first one may have a complex microstructure, and micro-ornamentation, as shown by Walliser (1970).

The term 'Runzelschicht' (wrinkle-layer) was introduced by Sandberger & 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 & Sandberger (1850–1856) also used another expression 'Ritzstreifen' to denote the markings preserved on internal moulds 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 should be referred to as the dorsal or ventral wrinkle-layer, respectively. According to Tozer (1972), the wrinkle-layer (Runzelschicht) and Ritzstreifen do not represent the same features. The former is formed on the dorsal side of normally coiled ammonoids and, in some instances, it has been observed beyond the aperture (Senior 1971; Tozer 1972). The latter, as also defined by Sandberger & Sandberger (1850–1856), is situated at the back of the body chamber and, therefore, the zone of its formation lies behind the secretory zone of the nacreous layer. 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.

The development of the dorsal wall, including the wrinkle-layer, was first described in the body chamber of *Quenstedtoceras* (Kulicki 1979: figs. 7D, 9). A similar wrinkle-layer – dorsal wall developmental sequence has been traced in the Triassic *Proarcestes* by Doguzhaeva & Mutvei (1986). In the present paper ultrastructure of the dorsal shell wall of 13 Late Paleozoic and Mesozoic ammonoid genera was examined, providing, for the first time, an overview of dorsal shell wall development and ultrastructures in the Ammonoidea.

Materials and methods

The study is based on specimens of Late Paleozoic goniatitids from the United States, Triassic ceratitids from Arctic Siberia and Spitsbergen, and Cretaceous lytoceratids, phylloceratids and ammonitids from Hokkaido (Japan) and Russia, all showing aragonitic preservation, except for the Spitsbergen material. They represent 13 Late Paleozoic and Messozoic genera.

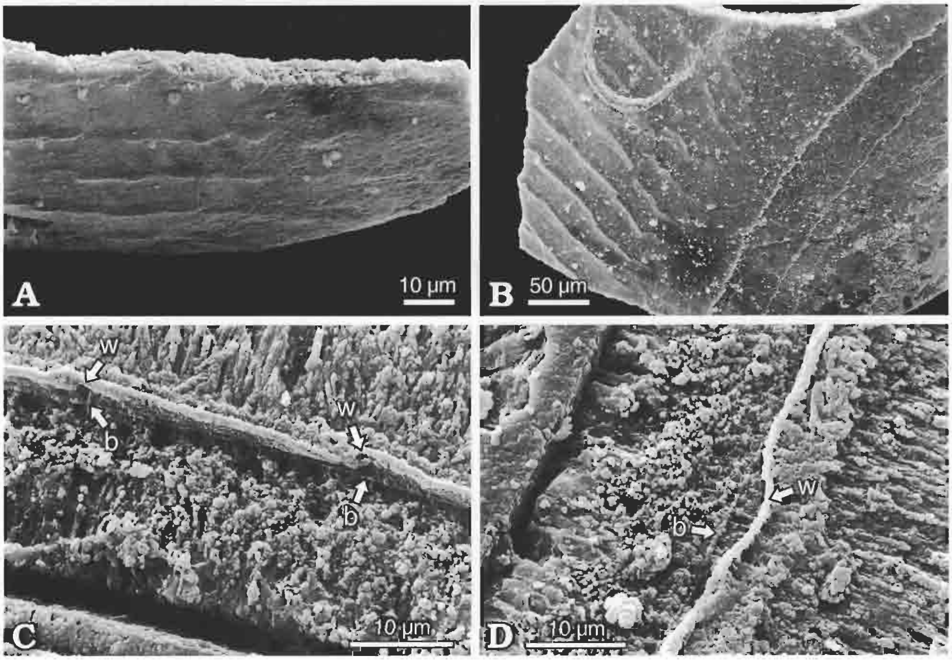

Fig. 1. Goniatite ammonitellae. **A**. Ventral wall of the initial chamber showing the wrinkle layer, its earliest occurrence in ontogeny. The layer is deposited in the apertural zone of the ammonitella, below the primary varix, AMNH 46552. **B**. Left lateral view of the ammonitella whorl just adapical of the primary varix. The wrinkle layer does not reach the umbilical seam. It indicates that the zone of deposition was narrower than the aperture width, AMNH 46609. **C**. Longitudinal section through the ammonitella whorl. The dorsal wall is separated by a distinct boundary from the smooth ventral wall. Two wrinkles are visible. The inner prismatic layer is relatively thin, AMNH 46550. **D**. As in C but earlier in ontogeny, AMNH 46550. Abbreviations: **b**, boundary between dorsal and ventral wall; **w**, wrinkle.

Most specimens excluding one goniatite embryonic shell were cut and polished along the median dorsoventral plane with a graded series of carborundum and diamond paste. The sectioned surface was etched with 1% hydrochloric acid solution for about 20 seconds, washed with distilled water, coated with platinum after drying, and then observed by scanning electron microscopy (Hitachi model S-2300 and Philips model XL-20). The goniatite embryonic shell shows a hollow preservation, so that pieces of the shell wall were carefully removed with a needle and were observed for the dorsal wall microstructure with SEM without etching.

The specimens utilized are housed in the University Museum of the University of Tokyo (UMUT), American Museum of Natural History (AMNH), and Institute of Paleobiology, Polish Academy of Science (ZPAL).

Goniatitine dorsal wall

Nassichuk (1967) assumed that the wrinkle-layer of *Clistoceras* may have been organic. This is not confirmed by our study on other Carboniferous material. Three em-

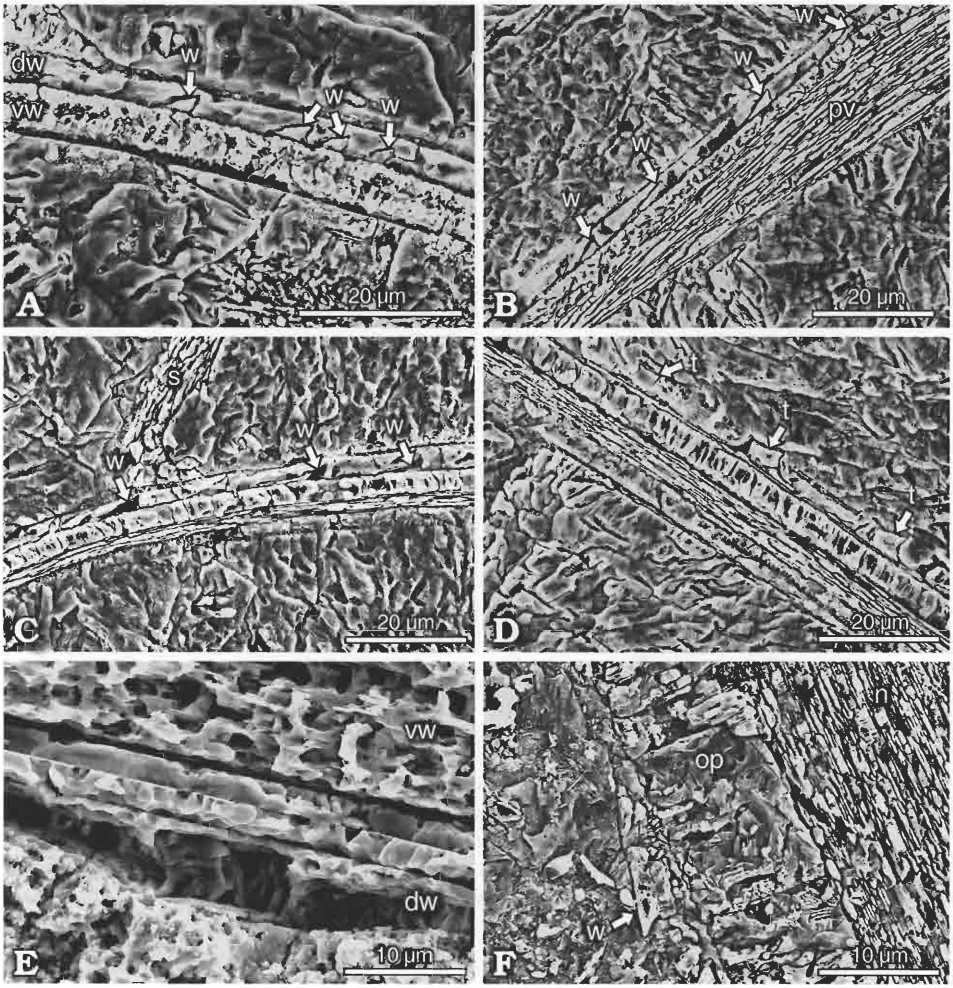

Fig. 2. **A–E**. *Subolenekites altus* (Mojsisovics, 1886). UMUT MM72836 (longitudinal section). **A**. Dorsal wall with distinct wrinkles, ammonitella whorl 100° adoral of the caecum. **B**. As A but above the primary varix. **C**. Dorsal wall on postembryonic shell just adoral of the primary varix. **D**. Dorsal wall 480° adoral of the primary varix. Triangular wrinkles are transformed into two-horned elements. **E**. Close-up of two-horned element. The crystal arrangement is clearly seen. In the left half of the section, crystal axes are perpendicular to the ventral wall surface, whereas in right half of the section the axes are arranged parallel to the wall surface. **F**. *Stolleyites tenuis* (Stolley, 1911). Triangular wrinkle element inside the body chamber, UMUT PM 72837. Abbreviations: **dw**, dorsal wall; **n**, nacreous layer; **op**, outer prismatic layer; **pv**, primary varix; **s**, septum; **t**, two-horned element; **vw**, ventral wall; **w**, wrinkle.

bryonic specimens (AMNH 46550, 46552, 46609) too small for generic and specific identification, from Buckhorn Asphalt, Arbuckle Mountains, Oklahoma; Middle Pennsylvanian (Desmoinesian) provide insight into the non-altered microstructure of Paleozoic ammonoid conchs.

Gen. et sp. indet. (ammonitella), AMNH 46550, 46552, 46609. — The wrinkle layer covers the embryonic whorl starting from the ventral part of the initial chamber

(Fig. 1A) until the end of the primary varix. The wrinkle layer (= outer component of the dorsal wall) does not reach the umbilical seams and two narrow bands are visible along the umbilical seams on both sides of the shell (Fig. 1B). In longitudinal cross section wrinkles have a typical triangular outline (Figs. 1C, D, 13). A thin prismatic layer fills the space between triangles. Near the ammonitella edge the outer layer of the dorsal shell wall loses its wrinkled appearance.

Ceratitine dorsal wall

***Subolenekites altus* (Mojsisovics, 1886)**. — One specimen (UMUT MM 72836) from the Olenekian at Mengilyakh near the mouth of the Olenek River, Arctic Siberia was studied. The ventral wall of the ammonitella is covered by the typical wrinkle layer with triangular elements, embedded in the inner prismatic layer (Fig. 2A, B). Identical triangular elements are visible on the postembryonic dorsal wall until the end of the first whorl (Fig. 2C). Further in ontogeny, already 120 degrees after the primary varix, the triangular elements are replaced by two-horned elements (Figs. 2D, E, 13).

***Stolleyites tenuis* (Stolley, 1911)**. — One specimen (UMUT MM 72837) from the Early Carnian at Kongressfiellet, Spitsbergen was studied. Only the typical wrinkle layer characterized by triangular elements occurs in this genus (Fig. 2F).

***Sibrites eichwaldi* (Keyserling, 1845)**. — One specimen (UMUT MM 72838) from the Late Spathian at Mengilyakh near the mouth of the Olenek River, Arctic Siberia was studied. The typical triangular elements of the wrinkle layer were observed on the primary varix (Fig. 3A). They are covered by one or two thin layers of the inner prismatic layer (Fig. 3B, C).

***Pseudosageceras* sp.** — One specimen (UMUT MM 72839) from the Olenekian at Mengilyakh, near the mouth of the Olenek River, Arctic Siberia was studied. The specimen examined retains dorsal wall structures similar to those described in more detail in *Aconeceras* (Fig. 3D).

Lytoceratine dorsal wall

Zakharov & Grabovskaya (1984) assigned the wrinkle-layer in *Zelandites japonicus* to the nacreous layer, a fact which is not clearly shown in their figure (Zakharov & Grabovskaya 1984: fig. 3).

***Gaudryceras tenuiliratum* Yabe, 1903**. — One specimen (UMUT MM 72840) from the Early Campanian, Abeshinai River, Nakagawa Town, north Hokkaido. A typical wrinkle layer consisting of triangular elements begins to appear at 120 degrees adoral of the primary varix (Figs. 4A, B, 5A). The ventral wall at that stage of development is devoid of the inner prismatic layer. The outer prismatic layer is twice as thick as the nacreous layer and is equal in thickness to the dorsal shell wall. The wrinkles are covered by the inner prismatic layer. Along with development of a dense micro-ornamentation, one and half whorls adoral of the primary varix, the wrinkles disappear and the dorsal wall smoothes the ornamentation. (Figs. 4C, 5C).

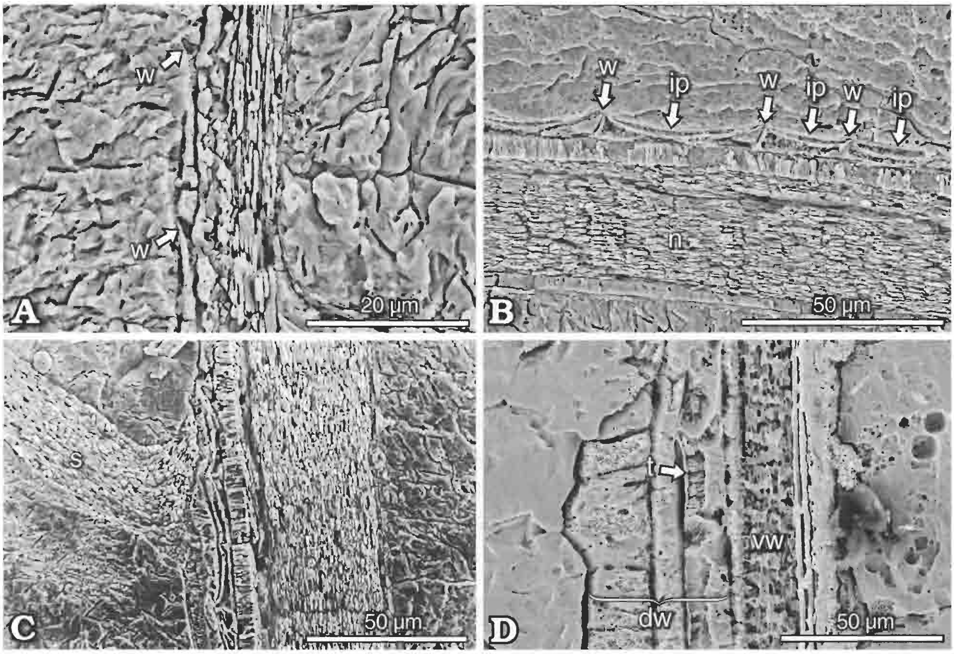

Fig. 3. **A–C**. *Sibirites eichwaldi* (Keyserling, 1845). UMUT MM 72838 (longitudinal section). **A**. Dorsal wall with distinct triangular wrinkles above the primary varix. **B**. Dorsal wall with well preserved wrinkle and inner prismatic layers, 630° adoral of the primary varix. **C**. As B, but 720° adoral of the primary varix, below septum attachment. **D**. *Pseudosageceras* sp. UMUT MM 72839. Dorsal wall, 720° adoral of the caecum. The dorsal wall is as thick as the ventral one and shows a poorly preserved two-horned element. Abbreviations: **dw**, dorsal wall; **ip**, inner prismatic layer; **n**, nacreous layer; **s**, septum; **t**, two-horned element; **vw**, ventral wall; **w**, wrinkle.

The outer shell surface is covered by dark dyed coating layers. They rest on the whole surface of the umbilicus and smooth the umbilical seams (Fig. 5D). Viewed from the outside, these layers exhibit a multilayered structure (Fig. 5F). Densely cracked coating layers shown in Fig. 5E presumably appeared in vacuum, during sputtering or microscoping. The dark color and tendency to crack during dehydration indicates that the layer is rich in a hydrophilic organic substance.

***Tetragonites glabrus* (Jimbo, 1894)**. — One specimen (UMUT MM 72841) from the Early Campanian, Abeshinai River, Nakagawa Town, north Hokkaido.

A wrinkle layer was observed in the area 90 degrees adoral of the adapical termination of the primary varix (Fig. 6A). The wrinkles presumably consist of an organic fabric. In outline they are triangular, with the acute angle oriented adapically, and the steep side of the triangle forming its adoral side. The triangles at this ontogenetic stage are 2–3 µm high and 7–9 µm long. The wrinkle layer is covered by a thin layer of the inner prismatic layer, and its prisms show a slightly spherulitic arrangement. The thickness of the whole dorsal wall is 8–10 times smaller than the ventral wall it covers. In ontogeny, the wrinkles increase in size and their inner spaces become filled with calcium carbonate, presumably aragonite, the same material as the rest of the shell. The orienta-

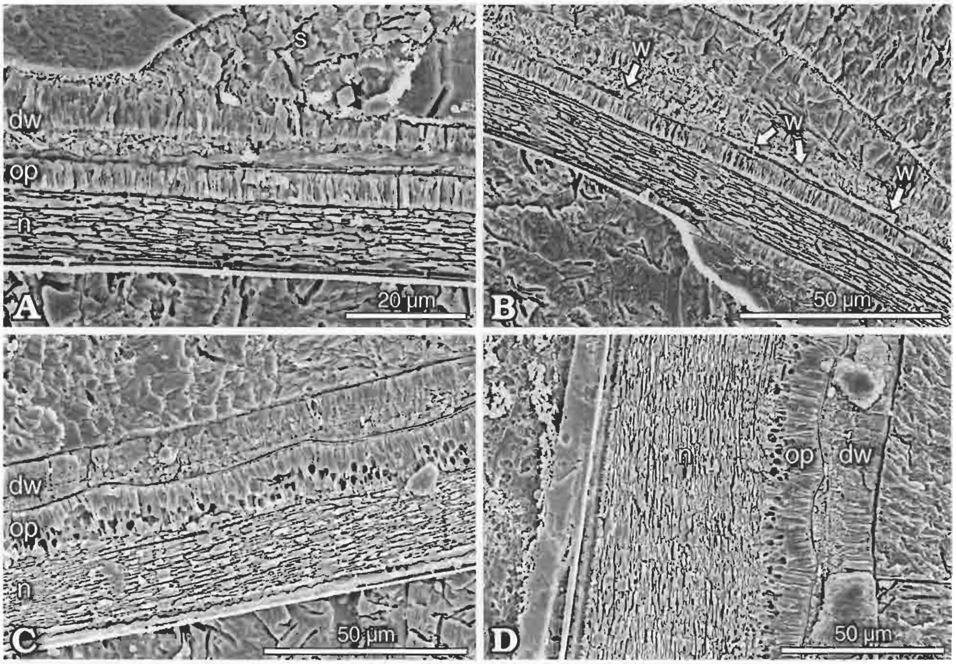

Fig. 4. *Gaudryceras tenuiliratum* Yabe, 1903. UMUT MM 72840 (longitudinal section). **A**. Ventral wall covered by dorsal one 90° adoral of the primary varix. Dorsal wall consists of two layers. No wrinkles are observed in this stage of development. **B**. 120° adoral of the primary varix. Small indistinct wrinkles are observed directly adhering to the ventral wall of the previous whorl. **C**. Ventral wall covered by dorsal one, 595° adoral of the primary varix. No wrinkles are observed in the outer component of the dorsal wall. **D**. 720° adoral of the primary varix. Abbreviations: **dw**, dorsal wall; **n**, nacreous layer; **op**, outer prismatic layer; **s**, septum; **w**, wrinkle.

tion of the long axes of the crystals is more or less perpendicular to the adoral steep slope as well as to the adapical, longer and gentle slope of the triangle (Fig. 6B–D). The relative thickness of the dorsal wall in relation to the ventral one increases toward the adoral direction, and at the end of the third postembryonic whorl, it is only 2.5 times thinner than the ventral wall (Fig. 6C).

Phylloceratine dorsal wall

***Phyllopachyceras ezoense* (Yokoyama, 1890)**. — One specimen (UMUT MM 72842) from the Middle Campanian, Osoushunai Rivulet, a tributary of Abeshinai River, Nakagawa Town, north Hokkaido.

In early ontogeny (1.75 postembryonic whorls), the thickness ratio of the dorsal shell wall versus the ventral wall exceeds 1.3. During growth this ratio increases considerably up to 2.3 at 2.2/3 p.wh. (p.wh. = ammonitella plus postembryonic whorl). The first wrinkle-like elements have been observed at stage 1.75 p.wh. (Fig. 7A). They consist of a short outermost periostracal layer, elevated above the surface of the

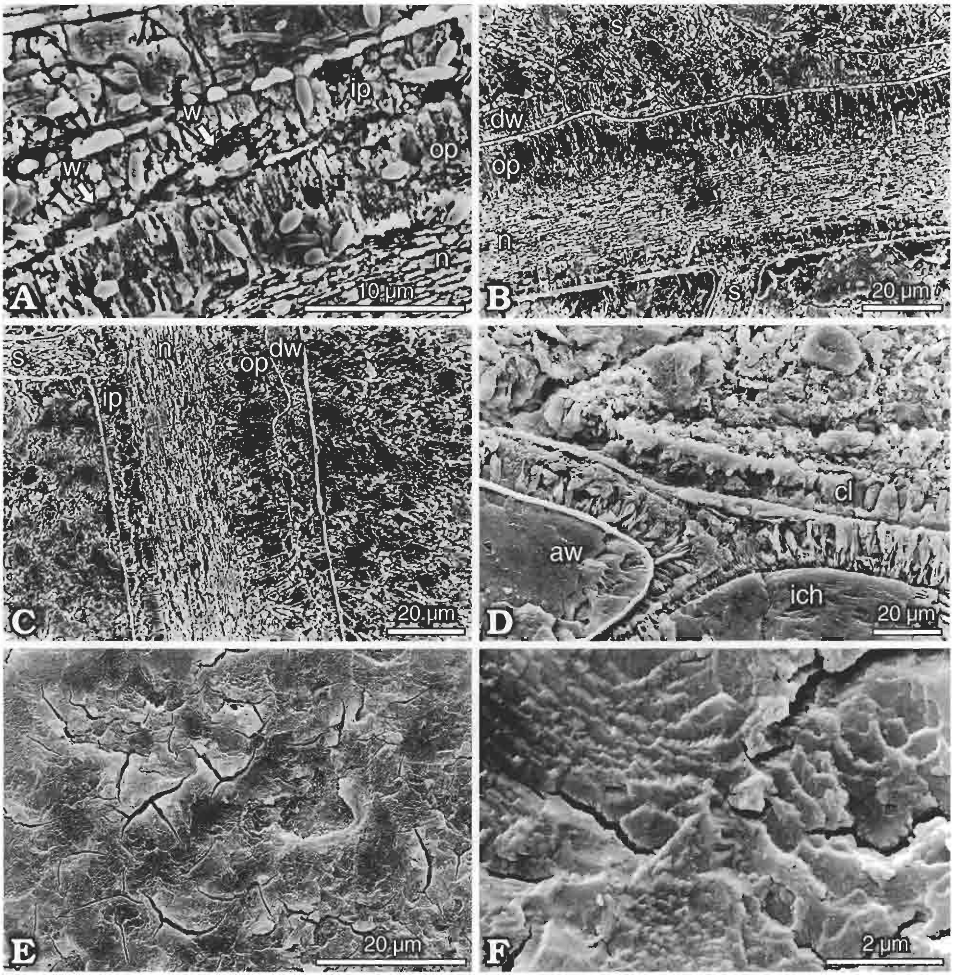

Fig. 5. *Gaudryceras tenuiliratum* Yabe, 1903. UMUT MM 72840 (longitudinal section). **A**. Dorsal wall, 440° adoral of the primary varix. Close up of wrinkle layer. **B**. Dorsal wall 800° adoral of the primary varix. No wrinkle layer is observed. **C**. Dorsal wall 890° adoral of the primary varix. **D**. Cross section through the initial chamber and ammonitella whorl. The coating layer covers the shell from the outside. It contains calcium carbonate crystals oriented perpendicular to its outer and inner surfaces. **E**. Coating layers viewed from the outside. Visible cracks arise as a result of dehydration processes. It indicates that the coating layer is presumably enriched in organic substances. **F**. Close-up of the coating layers. Multi-layered structure is visible. Abbreviations: **aw**, ammonitella whorl; **cl**, coating layer; **dw**, dorsal wall; **ip**, inner prismatic layer; **n**, nacreous layer; **op**, outer prismatic layer; **s**, septum; **w**, wrinkle.

shell, forming an acute angle with the shell surface. The inner component of the dorsal wall at this stage represents a thick spherulitic prismatic layer consisting of relatively coarse crystals. At the end of the second postembryonic whorl, the triangles formed by the free periostracal margins projecting from the shell surface are filled with aragonitic crystals, which are smaller than those in the rest of the dorsal wall (Fig. 7B, C). At stage 2.1–2.2 p.wh., the projecting periostracal elements start to be

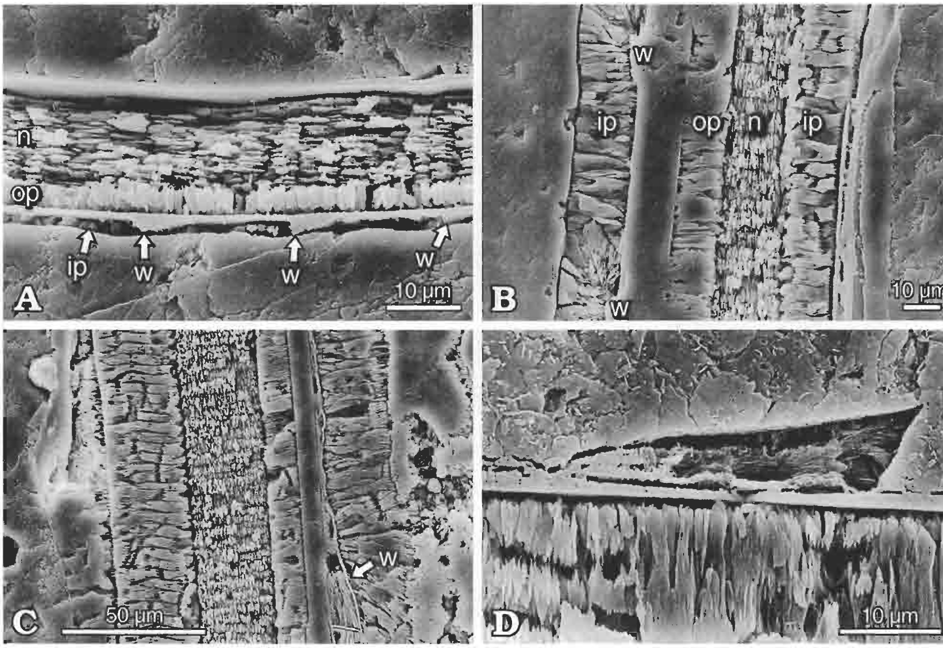

Fig. 6. *Tetragonites glabrus* (Jimbo, 1894). UMUT MM 72841 (longitudinal median section). **A**. Ventral wall covered by thin dorsal one, 90° adoral of the primary varix. Triangular small wrinkles, composed of organic matrix are visible. The inner prismatic layer is very thin. **B**. Dorsal wall 2.5 whorls adoral of the primary varix. The inner prismatic layer consists of crystals oriented perpendicular to the surface of the ventral wall. Prismatic crystals directly covering triangular organic wrinkles are oriented differently and their outline is triangular too. There is no distinct boundary separating these triangles from the outer prismatic layer at this stage. **C**. Dorsal wall 3 whorls adoral of the primary varix. The full outline of the triangular element is separated from the rest of the dorsal wall by a thin layer. **D**. Single triangular element of the dorsal wall, 3.5 whorls adoral of the primary varix. Clearly visible is its central organic triangular core and calcium carbonate crystals oriented perpendicular to its sides. Crystals based on steep short side are much longer than those covering the long slope of the triangle. Abbreviations: **ip**, inner prismatic layer; **n**, nacreous layer; **op**, outer prismatic layer; **w**, wrinkle.

directed backward (in an adapical direction) (Fig. 7D). In a still later ontogenetic stage (2.5–2.67 p.wh.), the dorsal wall (Fig. 7E) consists of two distinct prismatic layers, indicating a different spherulitic arrangement of crystals. These two layers were presumably precipitated in two different zones inside the living chamber. Our specimen of *P. ezoense* shows an even more complicated form of periostracal micro-ornamentation (Figs. 7F, 13).

***Hypophylloceras subramosum* (Shimizu, 1934)**. — One specimen (UMUT MM 72843) from the Middle Campanian, Osoushunai Rivulet, a tributary of Abeshinai River, Nakagawa Town, north Hokkaido.

The dorsal shell wall of *H. subramosum* is comparatively thick as in *Phyllopachyceras*. In the early postembryonic stage (end of the first whorl), the dorsal wall is as thick as the ventral one or is somewhat thinner (Fig. 8A). No triangular elements were observed. At the end of the second whorl the ventral wall shows wavy ornamen-

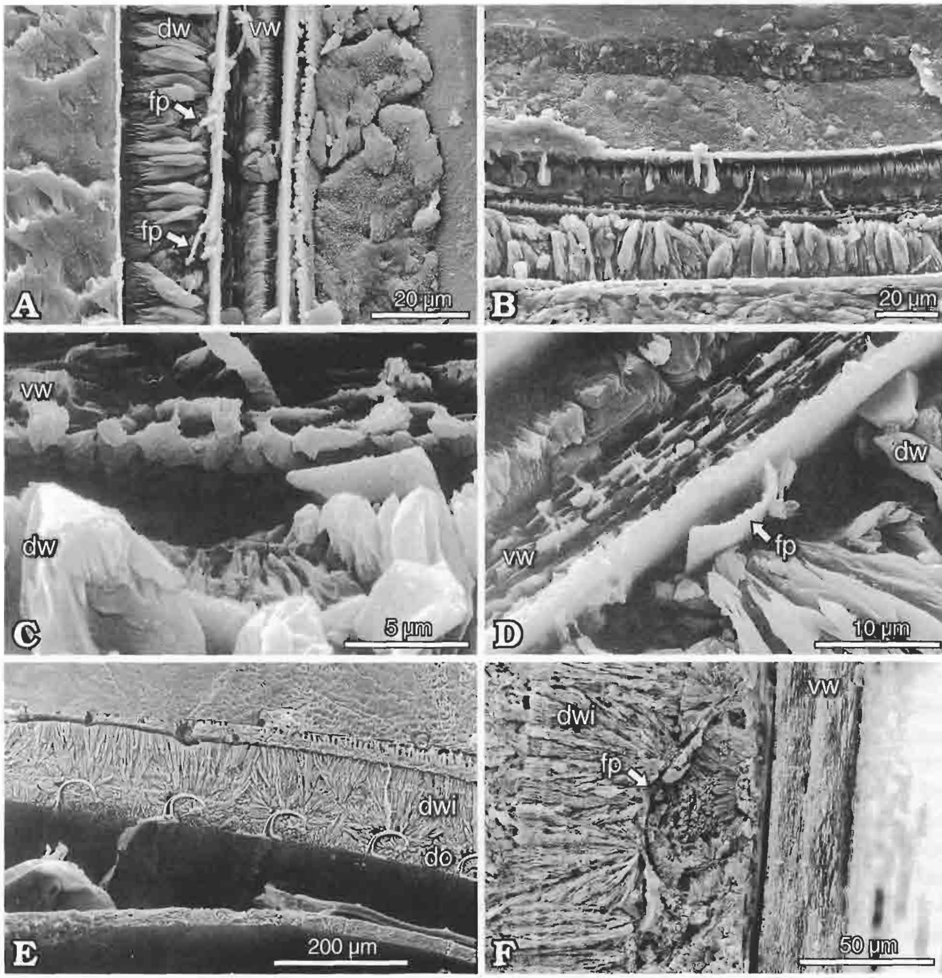

Fig. 7. *Phyllopachyceras ezoense* (Yokoyama, 1890). UMUT MM 72842 (longitudinal section). **A**. Ventral wall covered by dorsal one 1.75 whorls adoral of the primary varix. The periostracum covering the ventral wall shows more or less evenly spaced free periostracal edges elevated above its surface and forming triangles. The inner prismatic layer is as thick as the whole ventral wall and is built of relatively coarse spherulitic prismatic crystals. **B**. 2.1 whorls adoral of the primary varix. Periostracal edges form mild bows directed adorally and they are covered by fine prismatic crystals having a triangular outline. **C**. Close-up of triangular element. The fine prismatic crystals covering from the outside the periostracal edge are perpendicular to the free periostracal edge. **D**. The place 2.1 whorls adoral of the primary varix. The free periostracal edge is projected adapically, and does not show the triangular fine crystalline deposit. **E**. Dorsal wall of 3.67 whorls detached from ventral one of 2.67 whorls. The dorsal wall consists of two layers differing in size and crystal arrangement. Free periostracal edges are directed adapically and are limited only to the outer sublayer of the dorsal wall. Their basal portions are seen on outer, detached surface of the dorsal wall. **F**. Dorsal wall 3.5 whorls adoral of the primary varix. Two layered dorsal wall with more complicated periostracal edge. Direction of growth directed downwards. Abbreviations: **dw**, dorsal wall; **dwi**, inner sublayer of the dorsal wall; **do**, outer sublayer of the dorsal wall; **fp**, free periostracal edge; **vw**, ventral wall.

tation, and periostracal modifications are associated with the ornamentation. Free and elevated outermost periostracal margins are directed adorally (Fig. 8B–D).

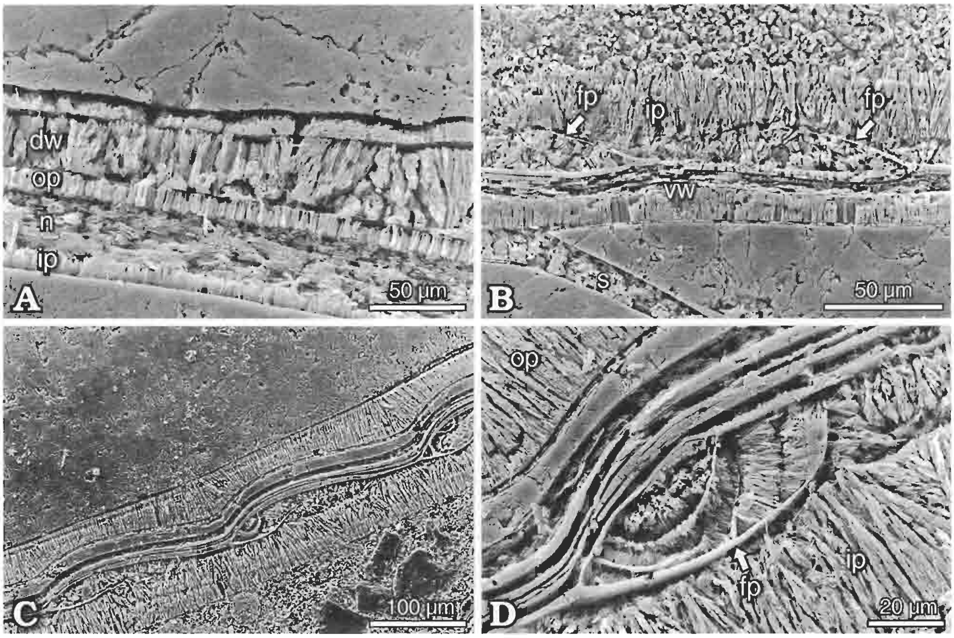

Fig. 8. *Hypophylloceras subramosum* (Shimizu, 1934). UMUT MM 72843 (longitudinal section). **A**. Dorsal wall as thick as ventral one 1 whorl adoral of the primary varix. Two layered inner prismatic layer. **B**. Dorsal wall of 2nd whorl adoral of the primary varix. Two layers distinctly seen and periostracal edges pointed adorally. **C**. Ventral wall covered by dorsal one 3.5 whorls adoral of the primary varix. Two layered structure of the dorsal wall is visible and the free periostracal edges are directed adorally. **D**. Close-up of periostracum modified edge. Spherulitic arrangement of calcium carbonate is seen inside the space between the free periostracum edge and ventral wall. Abbreviations: **dw**, dorsal wall; **fp**, free periostracum edge; **ip**, inner prismatic layer; **n**, nacreous layer; **vw**, ventral wall.

Ammonitine dorsal wall

***Quenstedtoceras* sp.** — Numerous specimens (ZPAL/Am. collection) from the Callovian, Łuków, Poland. The dorsal shell wall microstructure of *Quenstedtoceras* as well as its development was described by Kulicki (1979). It represents common features as observed in the majority of Mesozoic Ammonitina.

***Aconeceras trautscholdi* (Sinzow, 1870).** — One specimen (ZPAL Am. 17/1) from the Early Aptian, vicinity of Simbirsk, Russia. In early ontogeny, just adoral of the primary varix, the dorsal wall is rather thin and represents only 20% of the ventral wall thickness. The ventral wall is, at that stage, devoid of the inner prismatic layer and its nacreous layer is at least as thick as the outer prismatic layer (Fig. 9A). As far as 0.75 whorls adoral of the primary varix, the ventral wall already consists of three basic layers and is covered by a thin dorsal shell wall. The thickness of the dorsal wall is equal to about 15–18.5% of the ventral one (Fig. 9B). At this stage, in terms of the dorsal wall, small spots (patches, islands), about 5.5 µm in diameter, are firmly connected to the ventral wall. These spots consisting of calcium carbonate differ considerably from

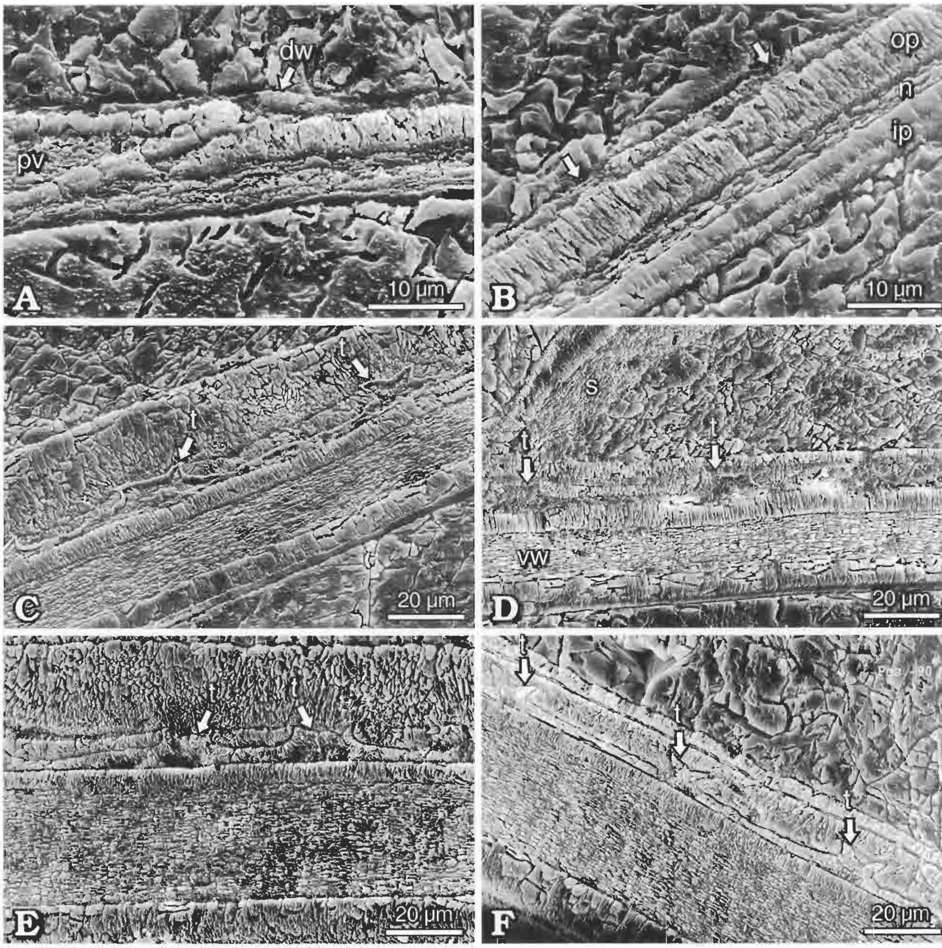

Fig. 9. *Aconeceras trautscholdi* (Sinzow, 1870). ZPAL Am. 17/1 (longitudinal section). **A**. Boundary between primary varix and postembryonic shell, covered by thin dorsal wall. **B**. Ventral wall at 0.75 whorls adoral of the primary varix covered by thin dorsal one. Two spots in dorsal wall are visible, differing in structure from the rest, marked by arrows. **C**. Ventral wall at 1.9 whorls adoral of the primary varix covered by dorsal one. The dorsal wall consists of two-horned elements whose basal parts are connected to each other. Each two-horned element contains a central core adjusted to the ventral wall of the previous whorl, and this is surrounded by prismatic crystals, perpendicular to the outer surface of the central core. The space between the two-horned elements is filled by inner prismatic layer and additional, thick inner prismatic layer covers the whole surface of the dorsal wall. **D**, **E**. The wall in different stages of ontogeny: respectively 1.75, 2.25 whorls adoral of the primary varix. **F**. At 3.60 whorls adoral of the primary varix inside the living chamber. Abbreviations: **dw**, dorsal wall; **ip**, inner prismatic layer; **n**, nacreous layer; **op**, outer prismatic layer; **s**, septum; **t**, two-horned element; **vw**, ventral wall; **pv**, primary varix.

the structure of the prismatic layer which fills the spaces between spots (Fig. 9B). At a stage 1.75 whorls adoral of the primary varix, the dorsal wall consists of two equally thick sublayers. The outer dorsal wall sublayer, adhering to the ventral wall of the underlying whorl, is less regularly built than the inner one.

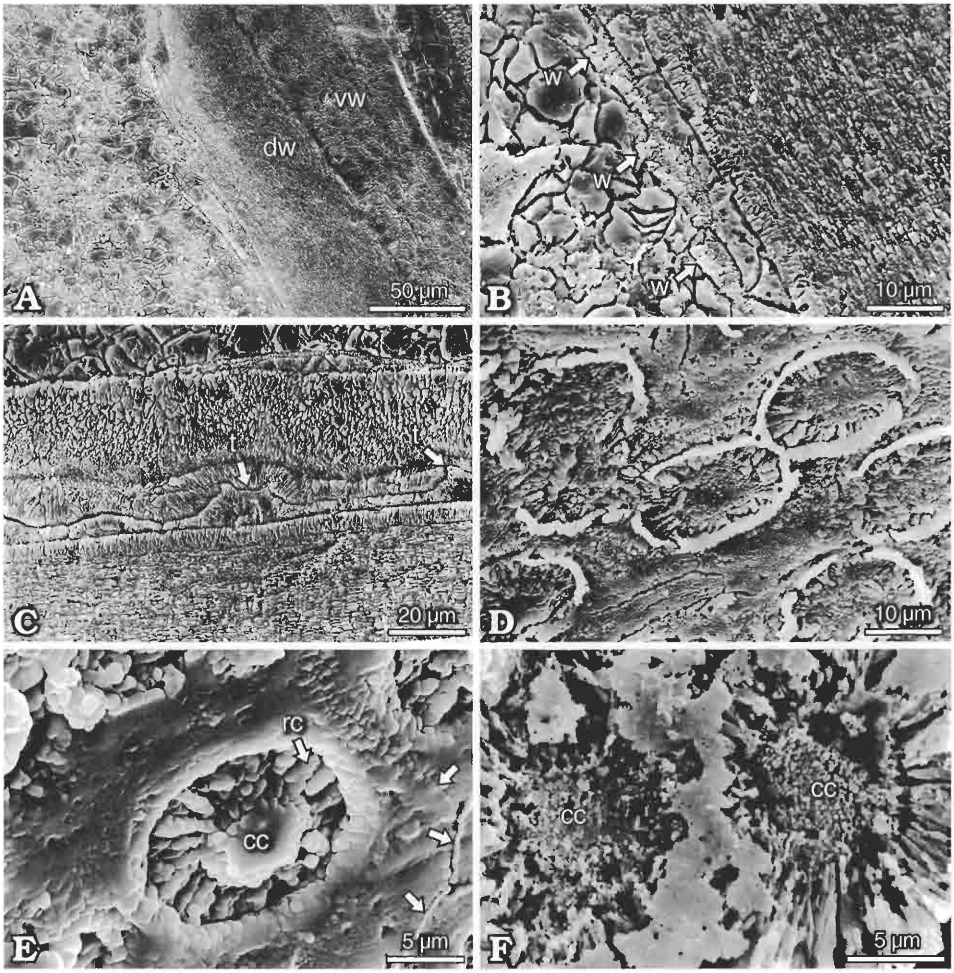

Fig. 10. *Aconeceras trautscholdi* (Sinzow, 1870). ZPAL Am. 17/1 (longitudinal section for **A**–**C** and dorsal views for **D**–**F**). **A**. Apertural part of adult specimen showing considerable thickening of dorsal wall deposit, marked by arrow. **B**. The place just before apertural thickening of the dorsal wall, showing regular, triangular wrinkles. **C**. The place at 3.15 whorls adoral of the primary varix. Dorsal wall with two-horned elements in posterior part of living chamber. **D**. View of the dorsal wall from the outside, after detaching from previous whorl. Rounded basal parts of two-horned elements are visible. **E**. Close-up of basal part of two-horned element. Radial arrangement of prismatic crystals around central core is visible, as well as lines demarcating individual units, marked by arrows. **F**. Close-up of two elements showing fine granular structure of central core. Abbreviations: **cc**, central core; **dw**, dorsal wall; **rc**, radial crystals; **t**, two-horned element; **vw**, ventral wall; **w**, wrinkle.

Later in ontogeny, the appearance of the outer layer of the dorsal shell wall in longitudinal section is illustrated in Fig. 9C–F. The characteristic two-horned elements are visible. The central part of each two-horned element is filled with calcium carbonate differing in structure from the rest of the layer (Fig. 9C–E). In cases where the dorsal wall is detached from the ventral one, we have a view of the surface of the dorsal wall from the out-

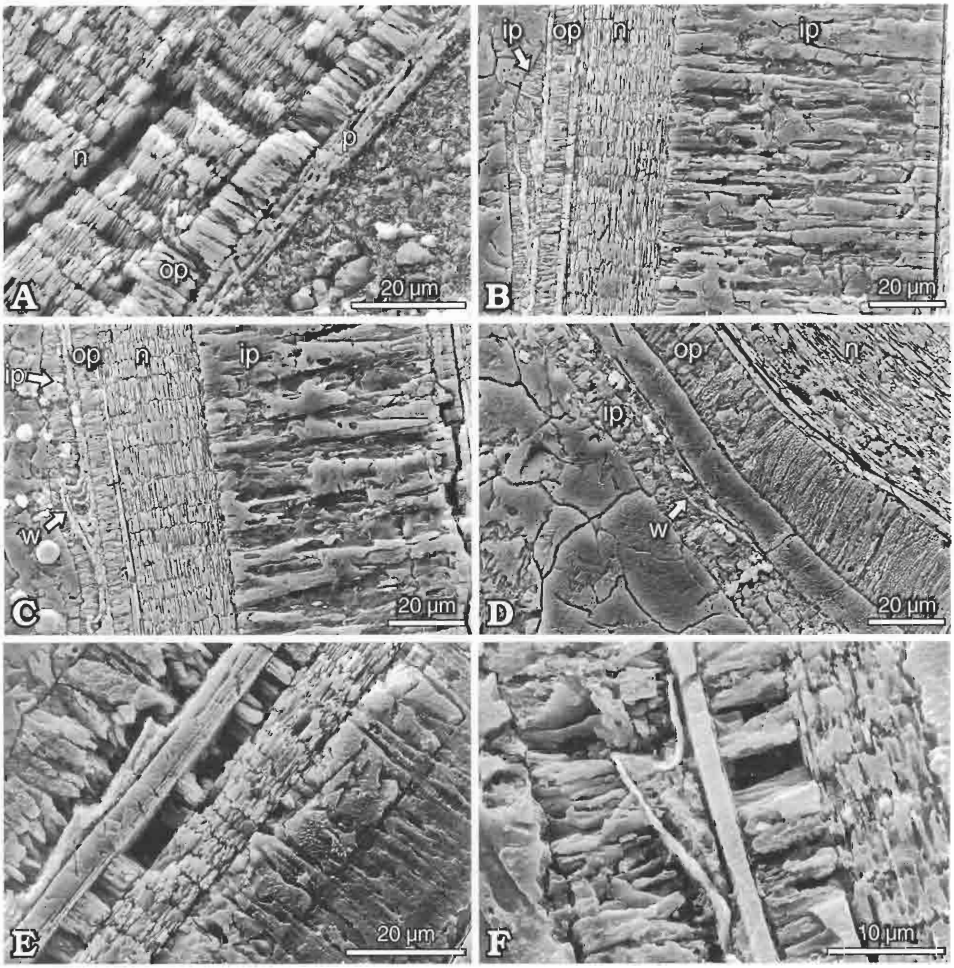

Fig. 11. *Yokoyamaoceras jimboi* Matsumoto, 1955. UMUT MM 72844 (longitudinal section). **A**. Apertural part of living chamber, at 5.2 whorls adoral of the primary varix, showing thick, multilayered periostracum. The wrinkle layer is not preserved in this part of the shell. **B**. Ventral wall of living chamber, at 4.58 whorls adoral of the primary varix, showing the abrupt appearance of the inner prismatic layer. **C**. Dorsal wall in living chamber at 4.57 whorls adoral of the primary varix with triangular elements covered by thin inner prismatic layer. **D**. Dorsal wall in living chamber in stage 4.51 whorls after primary varix. Wrinkle layer covered by thicker inner prismatic layer. **E**. Specimen at 2.6 whorls adoral of the primary varix. **F**. Specimen at 2.68 whorls adoral of the primary varix. Close-up of single wrinkle to show its structure, central triangular core and covering prismatic crystals. Abbreviations: **ip**, inner prismatic layer; **n**, nacreous layer; **op**, outer prismatic layer; **p**, periostracum; **w**, wrinkle.

side (Fig. 10D–F). In this view, it is clearly visible that the outer component of the dorsal shell wall in *Aconeceras* markedly differs from other ammonoids having a regular wrinkle layer. The equivalent of the wrinkle element in *Aconeceras* has a circular shape in plane view and a two-horned shape in cross section. In the central part of each circular spot, a hemispherical element consisting of fine granules, about 0.5 µm in diameter, occurs (Fig. 10F). The hemispherical elements are covered by the prismatic layer following

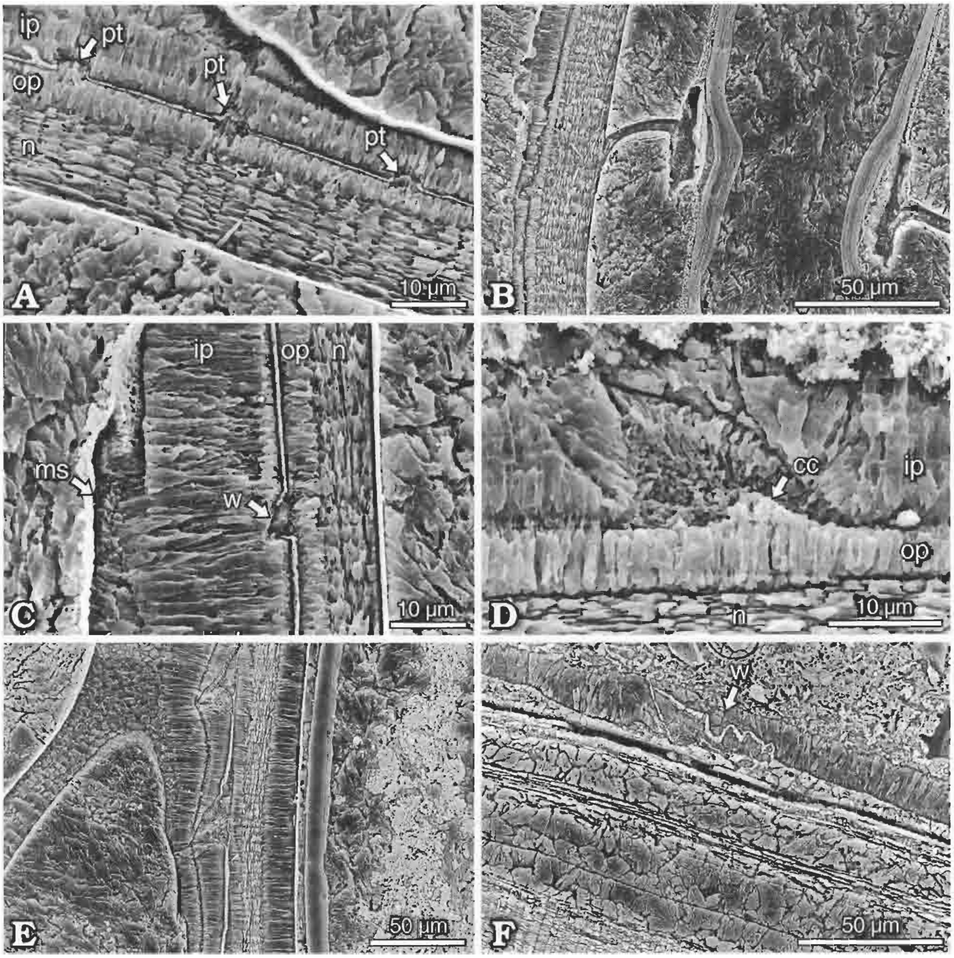

Fig. 12. *Damesites sugata* Forbes, 1846. UMUT MM 72845 (longitudinal section). **A**. Ventral wall covered by dorsal one at 0.25 whorls adoral of the primary varix. Prismatic tubercles belongs to outer component of the dorsal wall. **B**. Specimen at 0.33 whorls adoral of the primary varix. **C**. Specimen at 0.35 whorls adoral of the primary varix. **D**. Specimen at 1.30 whorls adoral of the primary varix. Close-up of a single wrinkle to show its structure. Central core in shape of tubercle, covered by prismatic crystals oriented perpendicular to its surface. General outline is triangular. **E**. Specimen at 1.5 whorls adoral of the primary varix. Note the adapical angles of wrinkles are relatively wide in comparison to other genera. **F**. Dorsal wall in living chamber. Triangular shape of the wrinkle in adapical portion shows irregularities. Abbreviations: **ip**, inner prismatic layer; **ms**, mural part of septum; **n**, nacreous layer; **op**, outer prismatic layer; **pt**, prismatic tubercle; **w**, wrinkle.

the shape of the central elements, forming an unusual two-horned outline in cross section. Prismatic crystals are arranged in radial rows (Fig. 10D, E). The basal parts of the round elements are broadly spread and connected to one another (Fig. 9C–E), though in outside view demarcating lines or ribbons are visible (Fig. 10E). The prismatic layer fills the space between the round elements. It smoothes the uneven tubercular surface. The top of the described structure is lined by the inner prismatic layer from the inside (Fig. 9F).

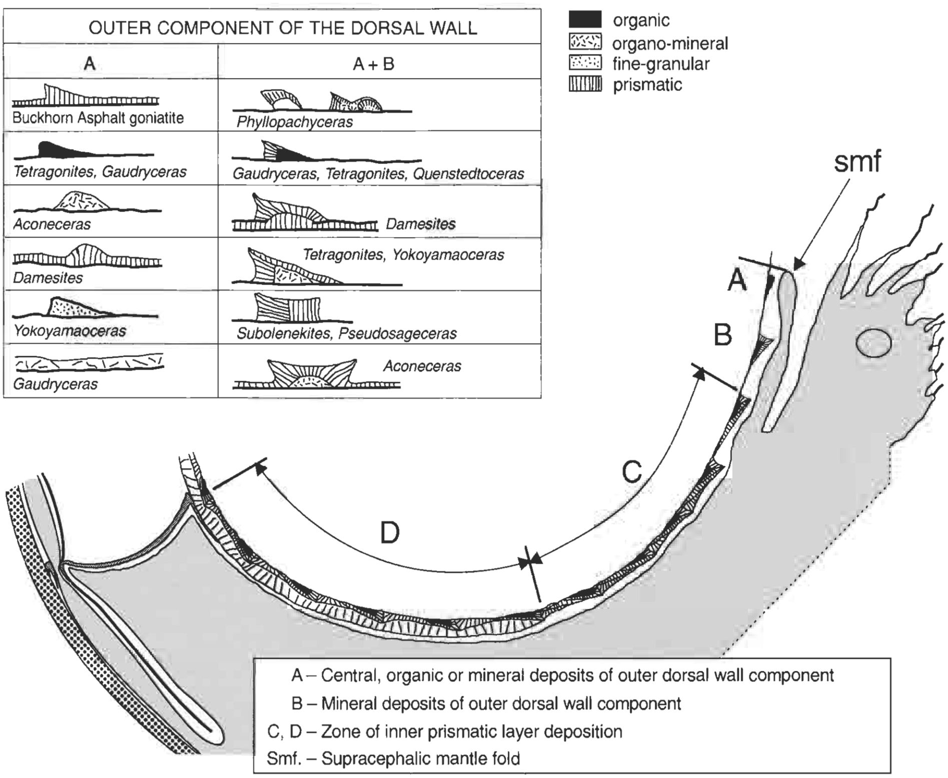

Fig. 13. Diagram showing the structural and morphological variation of the outer component of the dorsal shell wall and formation zones of the dorsal shell wall in ammonoids.

Formation of the dorsal wall was observed in the living chamber of adult microconchs. In the apertural region, a thickening of the dorsal shell wall occurs related presumably to arrested growth during this stage (Fig. 10A). Inside the living chamber, just adoral of the thickening, the normal triangles, typical of the 'triangular' wrinkle layer are visible (Fig. 10B). About 20 degrees farther in the living chamber, toward the last septum, a typical dorsal shell wall as in younger stages of *Aconeceras* occurs but is covered by only a thin inner prismatic layer (Fig. 9). Close to the last septum the inner prismatic layer increases considerably in thickness (Fig. 10C).

Yokoyamaoceras jimboi **Matsumoto, 1955**. — One specimen (UMUT MM 72844) from the Middle Campanian, Abeshinai River, Nakagawa Town, north Hokkaido. Shell structure is typical of Ammonitina except for a very thick, multilayered periostracum (Fig. 11A, E). In longitudinal sections through the periostracum a wedging out of individual lamellae is visible (Fig. 11A), consistent with the growth increments. The dorsal shell wall consists of two elements, the outer one, the wrinkle layer, which is typically developed (Fig. 11E, F) and the inner one, the prismatic layer. The prismatic layer inside the living chamber (Fig. 11B) gradually thickens toward the last septum (Fig. 11C, D). The wrinkle layer is entirely formed in the apertural region. Only the inner prismatic layer gradually increases in thickness toward the last septum.

***Damesites sugata* Forbes, 1846**. — One specimen (UMUT MM 72845) from the Coniacian, Nakafutamata Rivulet, Haboro area, northwestern Hokkaido. Small tubercles cover the outer surface of the ventral wall close to the 15th septum (A+0.25 p.wh.) (Fig. 12A). Tubercules were never observed as sculptural elements in this genus, hence they belong to the dorsal shell wall, rather than the ventral one. They represent an outermost element of the dorsal shell wall at the 1.25th whorl. In further development, tubercles become triangular in longitudinal section and resemble typical wrinkle elements (Fig. 12C). Later in ontogeny (3.5p. wh.), *Damesites* represents the typical ammonitic condition with respect to the sequence of layers, their thickness, and their development. The dorsal shell wall consists of the wrinkle layer and inner prismatic layer. The ventral wall of the previous whorl is devoid of the inner prismatic layer and is 4.3–6.5 times thicker than the dorsal wall covering (Fig. 12B). In a later ontogenetic stage (3.6 p.wh.), the dorsal wall is thicker, as thick as the ventral wall of the preceding whorl (Fig. 12E). The most striking difference with respect to the rest of the ammonoids investigated is the relatively wide apical angle of the wrinkle elements (Fig. 12D). In this genus, wrinkles were observed in the posterior part of the living chamber (first half of 6th whorl) (Fig. 12F), covered by the inner prismatic layer. Their shape is not so regular as in the previous stages. Irregularity appears in the adapical part of the triangles.

The nature of the dorsal wall in normally coiled ammonoids

According to the position of formation, we distinguish outer and inner components in the dorsal shell wall of ammonoids: the outer component is formed in the apertural, dorsal region of the shell, whereas the inner one develops inside the living chamber (Kulicki 1979; Doguzhaeva & Mutvei 1986). The outer component may be developed in different ways according to the systematic position of the ammonoid or its ontogenetic stage. The most common occurrence is the wrinkle layer. The inherent character of the wrinkle layer is its wrinkled surface. In cross section each wrinkle has a triangular outline and is deposited on the periostracum of the preceding whorl. Some authors e.g., Walliser (1970), House (1971), Senior (1971), and Doguzhaeva (1981) reported the occurrence of the wrinkle layer in other places than the dorsal. In our material, we do not find this layer outside the dorsal side.

The inner structure of the basic wrinkle layer triangle is shown schematically in Fig. 13. Each triangular element consists of a central deposit, organic or mineralized, with a hemispherical or triangular shape. It is additionally coated by calcium carbonate crystals with a characteristic arrangement of crystal axes. The crystal axes are perpendicular to the triangle sides, and the general outline of these formations is triangular too. In most cases, a thin layer surrounds the triangles and separates them from the rest of the dorsal shell wall. In *Tetragonites* (Fig. 6B), the triangles are not separated from the rest of the dorsal shell wall by any layer, which makes them very indistinct. Such a wrinkle layer was observed in the preapertural regions of the ammonite dorsum (Senior 1971; Tozer 1972). Based on the shape and arrangement of wrinkle elements, Walliser (1970) elaborated a system, which is not in common use, but which gives an idea about the diversity in this respect, among Paleozoic ammonoids. Wrinkles may be more or less continuous, discontinuous, or may represent round patches (islands) arranged in rows, or irregularly scattered (compare Walliser 1970: fig. 3; II, 5).

The wrinkle layer with finger-print pattern and triangular outline of wrinkles in cross-section, represents the most common type of outer component of the dorsal wall in ammonoids. In middle and late ontogenetic stages of *Gaudryceras* the outer component of the dorsal wall forms so called coating layers of Druschits, Doguzhaeva & Mikhailova (1978) (Fig. 4A). In *Aconeceras* the patches of the outer component are circular or subcircular in plan (Fig. 13), and they have a peculiar two-horned shape in cross-section, with a central filling situated exactly in the middle. Similar two-horned elements of the outer component of the dorsal wall occur in *Subolenekites*. They differ from the *Aconeceras* elements in having an asymmetrical, eccentric arrangement of calcium-carbonate crystals. These features are very similar to those described by Doguzhaeva & Mutvei (1985: fig. 4A, B) as pores in the inner prismatic layer of Triassic *Phyllocladiscites ascheshbokensis* which actually represent wrinkle layer structures. The crystal arrangement, in *Phyllocladiscites* is also asymmetrical as in *Subolenekites*.

The earliest ontogenetic occurrence of the outer component of the dorsal shell wall, developed as the wrinkle layer, was reported in the apertural region of *Quenstedtoceras* ammonitellae (Kulicki 1979: pl. 44: 3; Kulicki & Doguzhaeva 1994: fig. 9C, D, F) and Late Carboniferous Goniatitines (Kulicki *et al.* in press), reproduced here (Fig. 1A, B). The dorsal wall adapical of this initial wrinkle layer only represents the inner prismatic layer in continuation with the mural part of the proseptum. The boundary between the initial wrinkle layer and the wall proper of the initial chamber is not sharp and is rather indistinct. Adoral of the initial wrinkle layer this boundary becomes distinct and well defined. This early wrinkle layer is most probably synchronously formed with the nacreous layer of the primary varix, and by analogy was formed in the late embryonic stage.

In the Cretaceous phylloceratids, *Hypophylloceras* and *Phyllopachyceras* small modifications of the periostracum were formed along the ventral and lateral apertural margins and produce micro-ornamentation on the outer shell surface. This micro-ornamentation was calcified from the outside presumably above the head by a supracephalic fold of mantle. The wrinkle like layer also occurs in the phylloceratines. Its triangular elements coexist with the calcified periostracum micro-ornamentation. The modified margins of the periostracum directed toward the posterior in *Phyllopachyceras* were interpreted by Druschits & Doguzhaeva (1981) as cilia, which is highly unlikely. In Recent *Nautilus*, the dorsal wall is built of three main components: the black periostracal film, the nacreous layer, and the inner prismatic layer (compare Mutvei *et al.* 1997). In ammonoids the nacreous layer was never observed as a component of the dorsal wall. A cross section through the ammonite shell reveals that it wedges out in the vicinity of the umbilical seam, so comparing the elements of the dorsal wall of *Nautilus* and the elements of the lateral wall of ammonite shells raises no objections. The zones of formation of both the inner prismatic and nacreous layers surround the whole mantle of *Nautilus*. In ammonites, this is true only with regard to the inner prismatic layer. The black film of *Nautilus*, secreted by the supracephalic mantle fold is homologous to the periostracum of ventral and lateral walls. The major difference in relative position of the mantle to the periostracum and black film is that the secretion environment for the organic fraction of periostracum is strictly isolated from the surrounding environment by tight contact between cells of the inner part of the periostracal rim. In the supracephalic region, however, the supracephalic mantle fold does not adhere tightly to the shell margin, and so the secretion environment is not fully isolated from the outer environment. Most ammonoids secreted as the first element of their dorsal wall the organic or organomineral central deposit of the wrinkles. It can be homologous to the black film of *Nautilus*. The mineral components of the wrinkles might be equivalents of the nacreous layer. The fingerprint pattern of the wrinkle layer probably reflects the subsequent extent of the margin of the supracephalic mantle fold. The triangular shape of the wrinkles in cross section would result from the shape of the space where aragonite has been precipitated.

Conclusions

1. The dorsal shell wall of ammonoids consists of outer and inner components. The outer formed in the apertural region and the inner represents the prismatic layer and covers the outer.

2. In the ammonitella shell, the interior of the living chamber is lined by the inner prismatic layers and the wrinkle layer occurs only below the primary varix. It is the first deposited outer component of the dorsal shell wall.

3. The ammonoid wrinkle layer is most commonly composed of wrinkles triangular in cross section but in some Ceratitina (*Pseudosageceras* and *Subolenekites*) as well as Ammonitina (*Aconeceras*) the outer component of the dorsal wall consists of circular and subcircular elements, which are two horned in cross section.

4. The area covered by the outer component of the dorsal wall may exceed the aperture width or be narrower.

5. The outermost coating of the *Gaudryceras* shell represents a well developed outer component of the dorsal wall, exceeding considerably the width of the aperture, and reaching the umbilical opening.

6. In ontogeny the outer layer of the dorsal shell wall may change its structure and micro-ornamentation. It may be compared with the black film of a Recent *Nautilus* shell with respect to place of formation.

7. The micro-ornamentation of the shell surface may serve as a calcification site for the mineral phase of the outer layer of the dorsal shell wall.

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Ścianka grzbietowa muszli amonoidów

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Streszczenie

U planispiralnie skręconych amonoidów, u których ścianka grzbietowa styka się bezpośrednio ze ścianką poprzedniego skrętu, mamy do czynienia z modyfikacją strukturalną ścianki grzbietowej w obszarze styku obu ścianek. Wymienione modyfikacje dotyczą w głównej mierze zewnętrznego składnika ścianki grzbietowej tzw. wrinkle-layer, położonego bezpośrednio na peryostrakum poprzedniego skrętu. Strefa zmarszczek (wrinkle-layer) znana była początkowo jedynie u amonoidów paleozoicznych, dopiero Senior (1971) i Kulicki (1979) odnotowali jej występowanie u amonoidów mezozoicznych. Na podstawie przebadanego materiału obejmującego 12 rodzajów należących do pięciu podrzędów Ammonoidea i występujących od późnego paleozoiku do późnej kredy nie stwierdzono występowania strefy zmarszczek poza ścianką grzbietową. Podobne struktury, obserwowane u paleozoicznych amonoidów w ściankach bocznej i brzusznej nosza nazwę „Ritzstreifen" i nie są homologiczne do zmarszczek „wrinkle-layer". Typowa zmarszczka „wrinkle-layer" w przekroju podłuznym zbudowana jest z elementu centralnego, organicznego lub organo-mineralnego, oraz pryzmatycznych warstewek, w których długie osie pryzm są prostopadłe do boków trójkąta skierowanych do wnętrza komory mieszkalnej. Obok typowych elementów strefy zmarszczek, opisano tzw. elementy dwurożne o zarysie okrągłym, lub owalnym u triasowych rodzajów *Subolenekites* i *Sibirites,* a także u wczesnokredowego *Aconeceras.* Te elementy były błędnie interpretowane (Doguzhaeva & Mutvei 1986) jako pory związane z przyczepami miękkich tkanek płaszcza do muszli. Typowa strefa zmarszczek wytwarzana przez fałd nadgłowowy płaszcza, została stwierdzona we wszystkich badanych podrzędach za wyjątkiem Phylloceratina. W wymienionym rzędzie opisano powszechnie występujące rytmiczne modyfikacje peryostrakum wbudowywane do ścianki grzbietowej. We wczesnych stadiach rozwojowych modyfikacje te mogą przypominać elementy strefy zmarszczek, lecz ich pochodzenie i budowa są różne.