

7 | Ammonoid Shell Structure

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Abstract: Early ontogenetic stages of ammonoids vary in morphology but show a remarkably uniform shell structure. The protoconch, the proseptum and the first whorl are built up of two successive stages of irregular or prismatic structures. Nacreous structures appear at the nepionic constriction, which is thought to indicate the beginning of post-embryonic life.

The post-embryonic shell consists typically of an outer prismatic layer, a nacreous layer and an inner prismatic layer. This pattern may be modified in coiled forms by dorsal wedging-out of the two outer layers. In some strongly ornamented ammonoids the inner prismatic layer forms hollow floored spines and keels. Constrictions are formed by thickening of the nacreous layer. Septa are mainly nacreous, but may possess an adoral prismatic layer.

Shell structures of Palaeozoic and Triassic ammonoids are rather poorly known. Among Jurassic and Cretaceous ammonoids Phylloceratidae differ significantly from others by having extremely thin ribbed outer prismatic and nacreous layers and a much thicker, smooth inner prismatic layer. The marked difference between the sculpture of outer and inner surfaces together with the presence of "false septal necks" are features shared by many Palaeozoic and Triassic ammonoids and support the idea of an early origin of the phylloceratid stock, independently of other Mesozoic ammonoids.

Dactyloceratidae are so far unique among Jurassic and Cretaceous ammonoids in possessing an inner shell, and Triassic Trachyceratidae may show a similar construction. The presence of outer encrusting layers, mainly umbilical and dorsal, has been recognized in many Palaeozoic and Triassic ammonoids and also in some Mesozoic forms.

The highly variable morphology of the ammonoid siphuncle is described and evidence for different types of calcification discussed.

INTRODUCTION

Knowledge of shell structures of ammonoids was sparse before the age of electron microscopy. Nevertheless, the main characteristics of the ammonoid shell were recognized in a number of early papers. Thus, Hyatt (1872, p. 107, pl. 4, figs 2-3) recognized three different layers in the ammonoid shell, later confirmed by Böhmers (1936) and Hölder (1952a), and Cornish and Kendall (1888) stated that the ammonoid shell was composed of aragonite. Cayeux (1916, p. 492, pl. 54, figs 4-5) and Bøggild (1930, p. 323, pl. 14, figs 2-4) were among the first to describe the prismatic and nacreous structures of the layers.

Studies with the aid of electron microscopy started in the late sixties. However, work is often hampered by diagenetic alteration of the metastable aragonite, resulting in dissolution of the aragonite altogether or its replacement by calcite. Although many ammonoid shells may look promising, with shiny mother-of-pearl preserved, closer investigation and analysis of the aragonite/calcite content often reveal diagenetic alteration. For this reason the shell structures of Palaeozoic and Triassic ammonoids are very poorly known and virtually all detailed knowledge is based on Jurassic and Cretaceous ammonoids.

According to Kennedy and Hall (1967) the most important factor in the preservation of aragonite is the shielding effect of the organic membranes surrounding the individual crystallites in the shell wall. These conchiolin membranes are most likely to be preserved in a slightly acid, reducing environment with low permeability such as that of pyritic clays and black shales (Bucharadt, 1977); but at the same time this is why many otherwise well preserved ammonoid shells are partly spoiled through impregnation by pyrite.

Early investigations by electron microscope were mainly concerned with the initial part of the ammonoid shell (e.g. Birkelund, 1967; Erben *et al.*, 1969; Drushchits and Khiami, 1970), and this is still the subject of close study and discussion (e.g. in Kulicki, 1979). Details of the finer structures of the crystallites of the nacre and of the organic matrix of ammonoids have been described first and foremost by Gregoire and co-workers (e.g. Gregoire, 1958, 1966; Grandjean *et al.*, 1964; Gregoire and Voss-Foucart, 1970), but many papers on the structure of nacre in other molluscs have

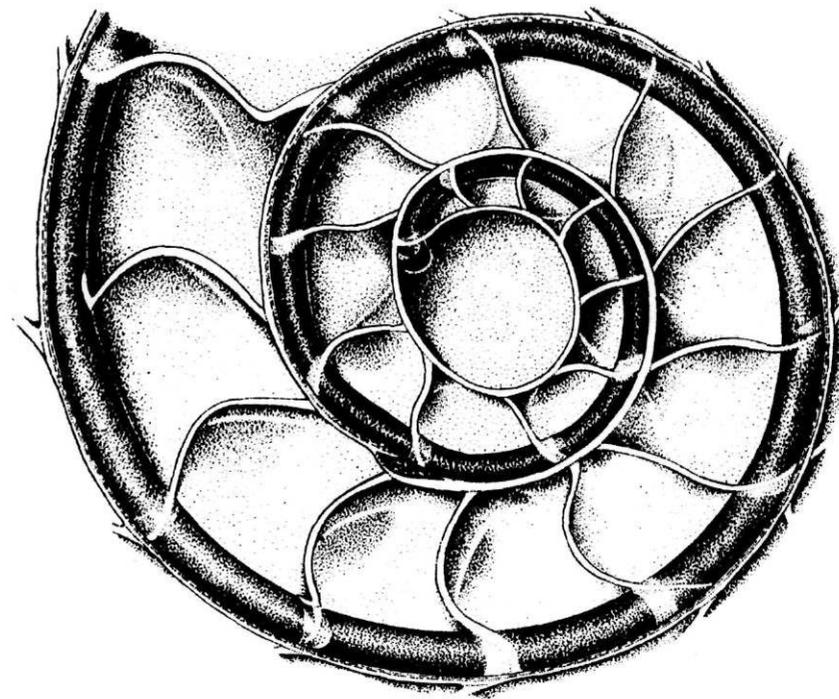


Fig. 1. Early growth stages of *Discoscaphites*. Polished section. The caecum and the siphuncle are visible through the transparent calcite filling. $\times 57$.

also a strong bearing on the nacre of ammonoids (Wise, 1970; Erben, 1972a; Erben and Watabe, 1974).

The post-embryonic shell tends to be constructed in a way which is very uniform in many Jurassic and Cretaceous ammonoids. Some groups, however, show significant differences in shell and siphonal structure, e.g. Phylloceratidae, Dactylioceratidae and *Gaudryceras*. Some of these structures may have a bearing on hypothesis of phylogeny and ecology of the ammonoids.

AMMONITELLA

1. Protoconch and First Whorl

The protoconch and first whorl are separated from later parts of the shell by the nepionic constriction (Figs 1,2) and was called

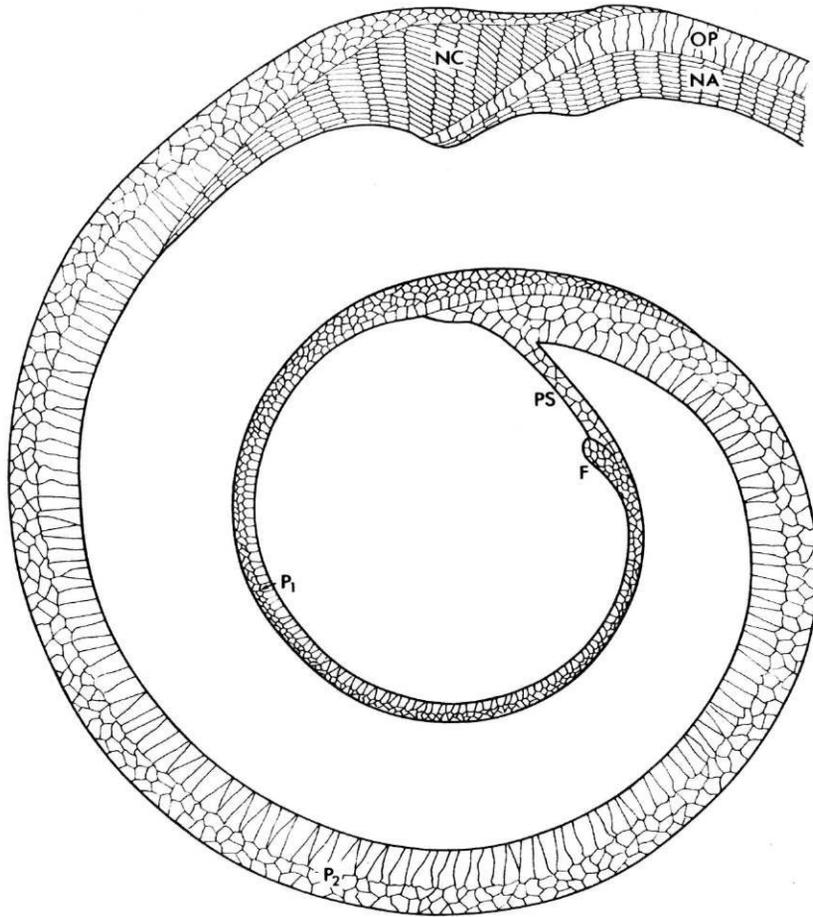


Fig. 2. Shell structures of early growth stages of *Saghalinites*. The section is slightly asymmetrical and not to scale. Dorsal wall, siphuncle and septa (except proseptum) are not shown.

Abbreviations to all figures: C, connecting ring; CA, cavity; F, flange; FN, false septal neck; IN, inner nacreous layer of inner shell; IP, inner prismatic layer of main shell; IPD, inner prismatic layer of dorsal wall; J, junction between two connecting rings; KP, outer prismatic layer of inner shell; N, septal neck; NA, nacreous layer of main shell; NC, nepionic constriction; OP, outer prismatic layer of main shell; P1, prismatic layer of protoconch; P2, prismatic layer of first whorl; PS, proseptum; SE, septum; SP, septal prismatic layer; W, wrinkle layer.

ammonitella by Drushchits and Khiami (1970). The nepionic constriction is present in all Ammonoidea and is thought to have played an important role in their ontogenetic development. The shell structures of the pre- and post-nepionic shell are fundamentally different.

The shell wall of the protoconch and the first whorl is thin – the thinnest part of the protoconch being only about $4\ \mu\text{m}$ thick – and often badly recrystallized. This may be the main reason why the structure of this part of the shell has been variously interpreted.

Figure 2 shows the interpretation given by Birkelund (1967) and Birkelund and Hansen (1974), mainly based on well-preserved material of *Saghalinites* from the Maastrichtian of West Greenland. The protoconch consists of two sublayers; the inner always built up of coarser crystallites than those of the outer sublayer. In the proximal part of the protoconch the crystallites are rather irregular, but they become gradually more regularly prismatic towards the adoral part of the protoconch. The crystallites of the outer sublayer are morphologically completely disorganized and retain the same appearance throughout the protoconch. The boundary between the two sublayers becomes gradually more distinct towards the distal end but is never sharp. Where the boundary can be studied in detail, intermingling crystallites can always be seen.

In the distal part of the protoconch a new layer appears abruptly on the inside. This stage can be correlated with the first change in growth (“1. Wachstumsänderung”) as described by Erben (1964) in early ammonoids. The new layer gradually grows thicker at the expense of the protoconch layer which slowly wedges out on the adoral side of the proseptum. This new layer is also differentiated into two sublayers. The inner sublayer is always built of coarser crystallites than is the outer sublayer. The crystallites of the inner sublayer tend to form somewhat regular prisms while the outer sublayer retains a completely irregular structure. Thus, in the adoral part of the protoconch and the apical part of the first whorl four units can be distinguished in the shell wall (Figs 2, 10A).

The proseptum belongs genetically to the prismatic layer of the first whorl, the transition between the shell wall and the septum being gradational (Fig. 10A). Thus, it was formed very early in ontogeny and differs fundamentally from later septa. It is attached to the so-called flange of the proximal part of the protoconch.

Erben *et al.* (1968, 1969) interpreted the shell of the protoconch

and the first whorl in a different way. They suggested the formation of the sublayers of the protoconch successively and stated also that the flange is formed late – together with the proseptum shortly before the second stage in growth – and thus that it belongs to an inner, secondary wall of the protoconch which also formed the early part of the whorl following the protoconch (Erben *et al.*, 1969, fig. 5).

Kulicki (1979) interpreted the shell layers of the protoconch and first whorl differently again. He confirmed the bipartite nature of the wall of the protoconch described above but interpreted the internal prismatic sublayer as the wall proper of the protoconch and the external sublayer with less regularly distributed crystallites as the dorsal wall of the next (first) whorl. Kulicki's studies do not confirm the wedging out of the protoconch wall in the beginning of the first whorl, but he claims that the external prismatic layer of the first whorl represents a continuous extension of the external wall proper of the protoconch. The boundary between the two sublayers of the protoconch is, however, never sharp (see Birkelund and Hansen, 1974, pl. 1, figs 1–2; pl. 16) and cannot therefore be the boundary between the protoconch proper and the dorsal wall as suggested by Kulicki. Moreover, the mural parts of the septa may cover the sublayers and this cover is not shown in the schematical drawings (Fig. 2), which may be the cause of the misinterpretation. The wedging-out of the protoconch layer is shown in Figs 10A–C. It is very slow and the protoconch layer continuous over a considerable distance as a very thin prismatic cover, which finally breaks up and disappears.

Kulicki found also a discontinuity separating the flange from the proximal part of the protoconch, and claimed that the flange was laid down at the same time as the “mid-layer” formed ontogenetically later than the prismatic wall of the protoconch, in the vicinity of the proseptum (Kulicki, 1979, fig. 7b).

Different preservations and methods of preparation (especially by etching) may very well be the reason why the structures are interpreted differently. Thus, the irregularities in the shape of crystallites connected with the formation of the proseptum could give rise to a slightly different appearance of the shell in that region, which might then be separated as a special unit. Also, the mode of formation of the flange has been uncertain up to now. Birkelund and

Hansen (1974, p. 9) stressed that it is not quite clear from their material whether the proseptum wedges out on the outer side of the protoconch (as claimed, for example, by Drushchits and Khiami, 1970; Howarth, 1975; and now also by Blind, 1978, 1979), or whether the flange is separated from the protoconch proper, as first suggested by Erben *et al.* (1969). As support for the last-mentioned point of view, Kulicki's figures are not very convincing.

In the first whorl Kulicki separates the following units:

- (1) An external prismatic layer, representing a direct extension of the wall proper of the protoconch (discussed above).
- (2) A middle prismatic layer differentiated into an external part (with more regular crystallites) and an internal part with less regular crystallites.
- (3) An internal prismatic layer.

These layers, together with the mid-layer of the protoconch, correspond to P2 (prismatic layer of second ontogenetic stage) described by Birkelund and Hansen (1974) and in that paper separated into only two sublayers, as described above and shown in Figs 2, 10B–C. The layers differentiated by Kulicki have such diffuse boundaries and are so indistinct that a complicated terminology is best avoided.

2. The Nepionic Constriction

The characteristic constriction in the adoral part of the first whorl was already recognized and illustrated by Hyatt (1872, pl. 4, fig. 11). Terms like “primary constriction” and “primary varix” have also been used for this structure. A change in the spiral growth at this stage has been described, e.g. by Currie (1942) and Erben (1964), and is clearly seen in Fig. 1. The nepionic constriction has the form of a swelling of the shell wall and appears as a marked constriction on the internal cast (Figs 2, 3). The most characteristic change in shell structure at this point is the appearance of a nacreous layer on the inner side of the shell. This layer thickens gradually, while the thickness of the irregular prismatic layer of the first whorl (P2) decreases proportionally. The nacre reaches its greatest thickness in the adoral part of the constriction, corresponding to the deepest part of the constriction on the internal cast. Here a thin prismatic layer appears on the inner side and crosses obliquely to the outer side where it continues as the outer prismatic layer of the later whorls.

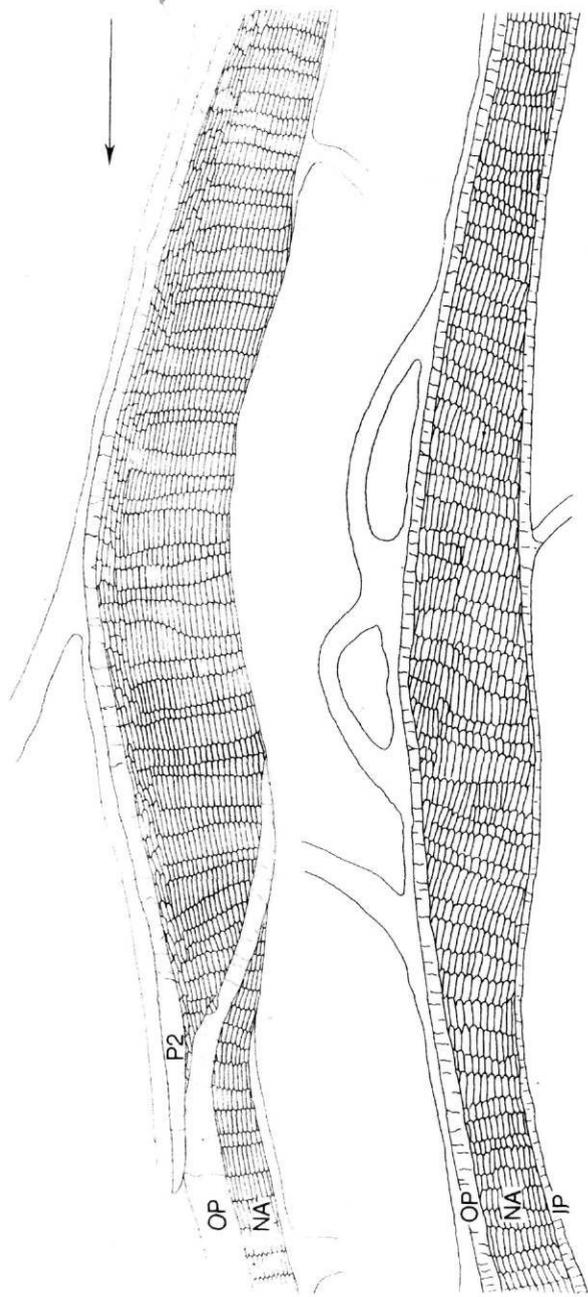


Fig. 3. Schematic drawings of the nepionic constriction (A) and a post-embryonic constriction (B) in *Saghalinites*. Not to scale.

Following the description by Birkelund (1967) of the shell structure of the nepionic constriction of *Saghalinites* and *Scaphites*, similar shell structures have been described and illustrated in many other genera. The main structure of the nepionic constriction is the same in all the ammonoids investigated up to now, but the structure differs in details, especially in the adoral region, where the sub-prismatic layer of the first whorl (P2) is replaced by the outer prismatic layer of the succeeding whorls. Although discontinuities between the two layers are always seen somewhere, they may in some parts be more or less continuous.

3. The Nepionic Constriction in Ammonoid Ontogeny

The nepionic constriction has been extensively discussed in connection with ammonoid ontogeny. Earlier views were reviewed by Erben (1964) and Birkelund and Hansen (1974). Two main points of view are still under debate:

(i) Erben (1964, 1966) suggested that the protoconch was embryonic and that the first whorl (up to the nepionic constriction) belonged to a larval stage, as of a trochophore or veliger. A metamorphosis from the larval to the post-larval stage then took place when the nepionic constriction was formed. This distinction of three ontogenetic stages was supported, for example, by Makowski (1971), Lehmann (1976) and Kennedy and Cobban (1977).

(ii) Drushchits and Khiami (1970) distinguished only two principal ontogenetic stages in ammonoids: an embryonic and a post-embryonic. The embryonic shell consists of the protoconch and the first whorl to the nepionic constriction – the ammonitella. This view was supported, for example, by Bogoslovskiy (1969), Birkelund and Hansen (1974), Blind (1978, 1979) and Kulicki (1974, 1979).

Erben (1964, 1966) based his interpretation of the early ontogeny on detailed studies of bactritid and early goniatitid cephalopods. His distinction of an embryonic stage, for the protoconch, followed by a larval stage, for the first whorl to the nepionic constriction, was partly based on the two characteristic changes in growth observed, and partly on the absence of a ventral modification of the aperture in the first growth stage while in the second growth stage a wide ventral sinuous bend is developed. According to Erben *et al.* (1969) the presence of both an embryonic stage and a larval stage is supported

by the remarkable changes in shell structures found between the stages. Further support for their point of view was seen in the early appearance of the nacreous layer in nautiloids, together with the lack of any metamorphosis in shell morphology – in agreement with the lack of free-living larval stages in nautiloids.

Kulicki (1974) has now shown however that there is no change in micro-ornamentation and no discontinuity of any sort on the shell surface between Erben's "embryonic" and "larval" stage in Mesozoic ammonoids. This is in contrast with recent mesogastropods, in which larvae with a protoconch hatch from the egg. Here the hatching-point is marked by a change in surface ornament or the onset of growth lines (Robertson, 1971). The wide ventral sinus in the growth – lines of Erben's larval stage could equally well be interpreted as related to the development of a funnel in the embryonic stage as with a velum (Bogoslavskiy, 1969, p. 66).

Drushchits and Khiami (1970) supported their view that the embryonic stage – the ammonitella – continued to the nepionic constriction mainly by citing (i) its small size (0.6–1.1 mm in Cretaceous ammonoids, up to 2.0 mm in Devonian ammonoids); (ii) the completely smooth protoconch and first whorl of the forms investigated by them; (iii) the discovery of large numbers of embryos in the Lower Aptian of Ulyanovsk, consisting of protoconch, first whorl, prosepium, prosiphon and caecum. The growth lines observed by Erben on the first whorl could then equally well have developed during embryonic growth, as there is evidence for this in the juvenile sculpture observed on the first whorl of the shell in coiled nautiloids; and it was considered more likely that ammonoids developed directly without a larval stage, as do all living cephalopods, than that they passed through trochophore or veliger stages.

Kulicki (1974, 1979) further mentions the possibly adaptive significance of the nepionic constriction, serving to and acting as ballast to the apertural margin during the first phase of development after hatching: i.e. the ammonitella has a nearly spherical shape with centre of gravity and centre of buoyancy close together, and the nepionic swelling shifts the centre of gravity towards the aperture (Kulicki, 1979).

Further finds of profuse ammonitellas with nepionic constrictions fully developed accompanied by no shells at earlier stages and but few at later stages of development, in Oxfordian limestones of the Jagua Formation in Cuba (Kulicki, 1979) and Maastrichtian chalk

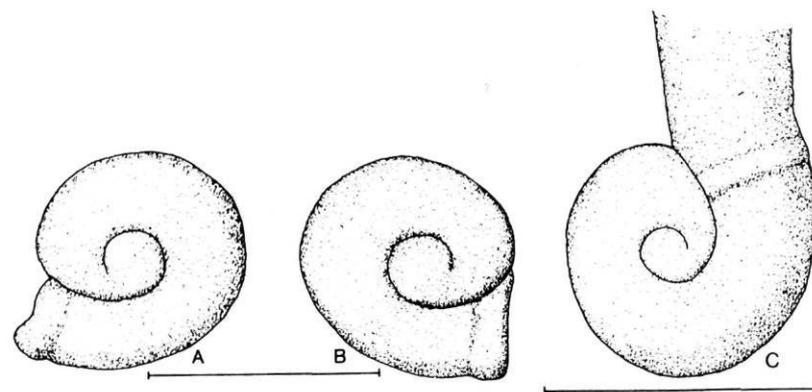


Fig. 4. Ammonitellas of *Hoploscaphites* or *Baculites* (A–B) and juvenile stage of *Baculites* (C). Bars 1 mm.

in Stevns Klint, Denmark (Birkehund, 1979) suggests widespread mortality at time of hatching. It is also interesting to note that uncoiling in heteromorphs often begins just after the formation of the nepionic constriction, but never before (see Fig. 4; and *Leptoceras studeri* in Wiedmann, 1969).

Finally, Lehmann (1966, 1976), Müller (1969) and Zacharov (1974) have described the supposed eggs of ammonoids, and these turn out to be very similar in size to ammonitellas. In recent coleoids the size of the eggs varies a great deal from species to species. Forms with small eggs, after hatching, pass through an inactive planktic stage in which the animal is often slightly modified compared with later stages. The ammonitella corresponds very well in size with such small eggs and it may well have been that the ammonoids passed through a similar inactive planktic "larval" stage (called pseudolarval by Kulicki, 1974) bounded by the nepionic constriction. The duration of this pseudolarval stage may have been crucial for the geographical distribution of ammonoids, just as it is in many other marine invertebrates with planktic stages, including recent coleoids (Mangold-Wirz, 1963; see also Thorson, 1946).

4. Morphological Variation in Early Shell Growth

While shell structures seem to be remarkably uniform in early ontogenetic stages, there is a certain variation in size and morphology of

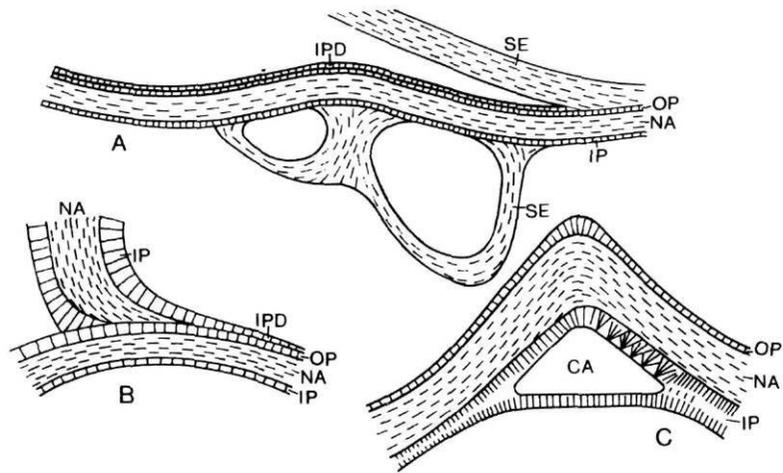


Fig. 5. A, ribbed wall of *Discoscaphites*; longitudinal dorso-ventral section; B, umbilical edge of *Saghalinites*, the outer prismatic layer and the nacreous layer wedge out dorsally; transversal dorso-ventral section; C, floored hollow spine of *Kosmoceras*. Schematic drawings, not to scale. C, after Erben (1972b).

the shells as a whole. Thus Bogoslovskiy (1969) mentions a general reduction in size of the protoconch upwards in the geological column, although the absolute size of the ammonitella may oscillate. Drushchits and Khiami (1970) mention ammonitellas of 0.6–1.1 mm in the Cretaceous and up to 2.0 mm in the Devonian. However, ammonitellas equal in size or even smaller than those in the Cretaceous appear already in the Late Devonian (Kulicki, 1979).

Tanabe *et al.* (1979) describe significant differences in early shell growth in different taxa at or above superfamily level in Cretaceous phylloceratids, lytoceratids and ammonitids, including shape of prosiphon, morphology of septal neck and ontogenetic change of siphuncular position. Such differences are also clearly seen in the representatives of Lytoceratidae and Phylloceratidae described by Birkelund and Hansen (1974); differences between these two groups are treated in further detail by Drushchits and Doguzhayeva (1974). Various complicated structures of caecum and prosiphon have also been described by Zacharov (1972). The most complex were found

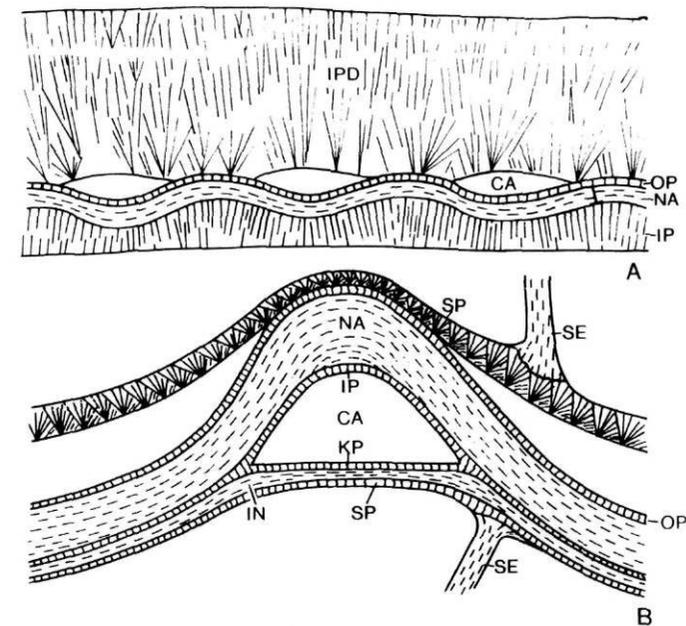


Fig. 6. Schematic drawings of the shell of *Hypophylloceras* (A) and the main shell and inner shell in Dactylioceratidae (B). B, after Howarth (1975, fig. 2D). Not to scale.

in *Desmophyllites*, which shows a cone embracing the caecum, a ligament connecting the cone to the inner wall of the protoconch and a housing surrounding the cone.

Early stages of sexually dimorphic pairs of Jurassic ammonoids described by Palframan (1966, 1967) show no differences.

THE POST-EMBRYONIC SHELL

1. The Three Main Layers

In all ammonoids so far investigated the post-embryonic shell consists of three principal layers: the outer prismatic layer, the nacreous layer and the inner prismatic layer. This is the nomenclature of most authors, and other terms have been avoided as they have been used in conflicting senses, as for example “ostracum” and “hypostracum” (see Howarth, 1975, p. 63).

The outer prismatic and nacreous layers are secreted at the aperture by the front edge of the mantle. The inner prismatic layer is formed behind the aperture. In juvenile specimens it is formed in the apical part of the body chamber but sufficiently forward of the last septum to be fully developed before the next septum is formed. A continuous adoral transition may be seen from the mainly nacreous septa, secreted by the apical part of the mantle, to the inner prismatic layer. In adult shells the inner prismatic layer is secreted closer to the aperture (see e.g. Blind, 1975; Howarth, 1975; Birkelund and Hansen, 1975; Kulicki, 1979 and Fig. 7 herein). Kulicki (1979) has described discontinuities in the outer prismatic layer and sometimes in the nacreous layer of *Quenstedtoceras* indicating breaks in secretion of the shell. Similar discontinuities were never found in the inner prismatic layer, reflecting its subsequent formation.

2. The Nacre

The tabular crystallites of the nacre of ammonoids and of *Nautilus* are deposited in vertical stacks as in gastropods (Fig. 10F), but the structure differs from that in the last in the orientation of the crystallites. Thus, the alignment of *a*- and *b*-axes of the tabular crystallites is parallel in cephalopods, but random in gastropods (Wise, 1970). The micro-architecture of the nacre of both gastropods and cephalopods differs markedly from the imbricate and row-stack pattern found in pelecypods (Wise, 1970; Erben, 1972a). Stacking may represent a relatively primitive character as crystal stacks are already present in monoplacophorids, the most primitive class of molluscs (Erben *et al.*, 1968), and also in primitive pelecypods such as *Nucula*. The micro-architecture of nacre has also a bearing on growth, as a thick layer can be formed within a narrow area of growth by stacking. However, neither in ammonoids nor in *Nautilus* have the growth surfaces been identified.

Conchiolin membranes between crystallites have been described especially by Gregoire in a number of papers (see above). The fabric of nacreous conchiolin of ammonoids can in some cases be shown to differ from that of nautiloids, e.g. in material from the Pennsylvanian Buckhorn asphalt (Gregoire, 1966). The fabric of the ammonoid conchiolin differs mainly in having broader and shorter trabeculae. Chemical investigations show that the amino acid patterns in the

polypeptide remains of nacreous conchiolin in all fossil cephalopods – from the Tertiary to the Devonian – differ from that in *Nautilus* because of early diagenetic alterations (Voss-Foucart and Gregoire, 1971; Weiner *et al.*, 1979).

3. The Outer and Inner Prismatic Layers

In well-preserved specimens it can be seen that the prisms are formed as continuations of the stacks of tabular crystallites of the nacre. They seem also to have a similarly polygonal cross-section (Fig. 10E). The prisms are orientated conformably with the crystallites of the nacre, the *c*-axis being perpendicular to the shell surface, or nearly so. This is in contrast with orthoceratid cephalopods, in which, according to Ristedt (1971), the *c*-axis of the prisms is oriented parallel to the surface in the inner prismatic layer.

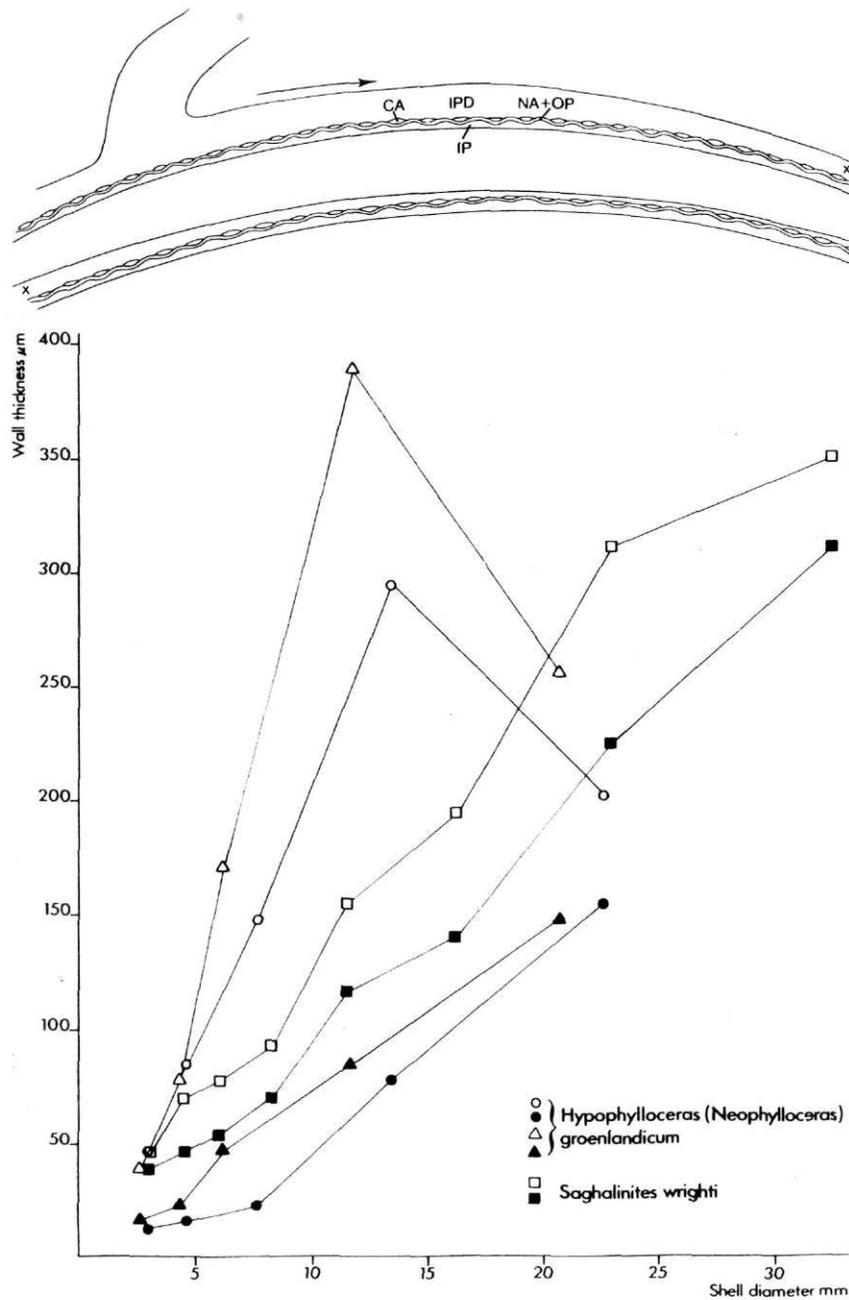
In the early part of the post-embryonic shell the prisms of the prismatic layers extend from the nacreous layer to the inner and outer surfaces of the shell (Fig. 10D), but in later whorls several levels of prisms may be found. In some forms the orientation of the prisms may be quasi-spherulitic.

4. The Extent of the Three Main Layers

The nacreous layer and the outer prismatic layer commence at the nepionic constriction. The inner prismatic layer may in some cases be already present at the nepionic constriction (e.g. *Eleganticeras elegantulum*, see Erben *et al.*, 1969, p. 27), but usually appears rather later – in the second or third whorls (Erben *et al.*, 1969, Table 2). This means that the myo-adhesive epithelium was not formed until the early post-embryonic stage (Blind, 1978).

Dorsally, in coiled forms, the outer prismatic and nacreous layers always seem to wedge out towards the spiral plane while the inner prismatic layer usually continues across it although with some thinning (Fig. 5B). In Dactylioceratidae the dorsal shell may be reduced to nothing on the brow of the previous whorl (Howarth, 1975, p. 53).

The septa are mainly nacreous. With the exception of the primary septum, which according to Erben *et al.* (1969) is prismatic, as is the prosepium, only nacreous structure has been found in most



of the ammonoids investigated so far. In a few groups, however, a prismatic layer has also been found on the adoral side of the nacreous septa: in a member of the Phyllocerata (*Hypophylloceras*) a very well developed prismatic layer can be seen from $2\frac{1}{2}$ whorls onwards adoral of the nepionic constriction (Birkelund and Hansen, 1974, pl. 10; Fig. 11D herein); and late septa of the lytoceratid ammonoid *Saghalinites* may show an incipient prismatic layer (Birkelund and Hansen, pl. 3, fig. 6). A prismatic layer may also be developed in Dactylioceratidae (Howarth, 1975, fig. 1; pl. 5, fig. 3), and prismatic or prismatic-spherulitic structures have been seen in *Kosmoceras* and *Quenstedtoceras* (Kulicki, 1979, p. 123).

VARIATION IN STRUCTURE OF THE POST-EMBRYONIC SHELL

In most ammonoids investigated up to now the nacreous layer builds up the main part of the shell, while the inner and outer prismatic layers only form rather thin covers (seen typically in Fig. 10D) of varying relative thicknesses (Erben *et al.*, 1969). In the early post-embryonic parts of the shell the prismatic layers are usually relatively thicker than in later parts.

1. Sculpture

It is a characteristic feature of most post-Triassic ammonoids that the sculpture of the outer surface is also that of the inner surface, although usually somewhat smoothed out. This is one of the reasons why internal casts of ammonoids are so much more informative and useful than internal casts of pelecypods and gastropods, which usually show very few characters. Such a construction of the ammonoid shell is very economic in mass and may reflect the nektonic mode of life. A parallel may be seen in swimming scallops with ribs on the inner side of the shells. Ribbing of a *Discoscaphites* is demonstrated in Fig. 5A.

Fig. 7. Above: dorsal apical part of body chamber of *Hypophylloceras* showing the adoral wedging-out of the inner prismatic layer of the dorsal wall. The diagram shows shell thickness in relation to shell diameter in *Hypophylloceras* and *Saghalinites*. The black dots indicate the thickness of the ventral wall and the white dots the thickness of the ventral wall plus the dorsal shell wall of the succeeding whorl. The last measurement of the dorsal shell wall in all three specimens is situated in the body chamber.

In very strongly sculptured forms, the sculpture may be almost wholly smoothed out internally by the formation of floored hollow keels and spines (e.g. described by Hölder, 1952a). The cavities are formed within the inner prismatic layer, which is divided into an outer part, in contact with the nacreous layer and an inner part, forming the floor (Erben, 1972b; Fig. 5C herein) (see also p. 197).

2. Constrictions and Flares

Shell structures of constrictions or varices are known in a number of ceratitids, phylloceratids, lycoceratids and desmoceratids. In all cases the constrictions are formed by thickening of the nacreous layer, much as in the nepionic constriction, and the inner prismatic layer may tend to become thinner (Figs 3, 11A). Unlike the nepionic constriction, however, there is never an interruption by a discordant prismatic layer.

In some forms with flares developed in connection with the constrictions, e.g. *Gaudryceras*, the ammonoid dissolved the part of the collar where the new whorl contacted the previous one (Drushchits *et al.*, 1978).

3. Conellae

Conical or pyramidal structures found in the ammonoid shell have been called conellae since they were first described by Quenstedt (1884) and later by Hölder (1952b). Erben and Reid (1971) have reviewed these and shown that all ammonoid conellae originate in the inner prismatic layer and are the result of prediagenetic dissolution and – in some cases – later recrystallization, and hence of little independent relevance to the subject of shell structures as a whole.

4. The Shell Wall of *Hypophylloceras*

The post-embryonic shell wall of *Hypophylloceras* differs fundamentally from the normal type described above in having (i) completely different relative thicknesses of the main shell layers; (ii) a smooth inner surface, leaving a smooth internal cast despite the fine ribbing on the outer surface; (iii) cavities between the inner

prismatic layer of the dorsal shell and the outer prismatic layer of the corrugated ventral wall of the preceding whorl, the dorsal wall thus bridging the ribbing interspaces (Fig. 6A).

At the adoral part of the nepionic constriction the shell consists of a relatively thick outer prismatic layer and a thin nacreous layer. Then, already in the first whorl after the nepionic constriction, the outer prismatic layer becomes very thin relative to the nacreous layer, and about two whorls from the nepionic constriction its thickness is about a third of that of the nacreous layer. In yet younger whorls it may be so thin as to be only occasionally distinguishable, and has been missed in the past (Birkelund and Hansen, 1974, 1975).

The inner prismatic layer, on the other hand, is already prominent in the first whorl after the nepionic constriction, and two whorls from the nepionic constriction it makes up about two-thirds of the total thickness of the shell; further adorally it makes up even more (Fig. 6A). From the very onset of ribbing which begins about $2\frac{1}{2}$ whorls after the nepionic constriction, it smooths the inner surface of the shell and hence varies considerably in thickness (Fig. 11D).

Dorsally the outer prismatic layer and the nacreous layer wedge out, but the inner prismatic layer (= “the quasi-spherulitic outer prismatic layer” of Birkelund and Hansen, 1974) is well developed. The structure of this layer is remarkable in being composed of several sublayers of intermingling quasi-spherulitically arranged prisms. The layer is only in contact with the ventral part of the preceding whorl on the crests of the ribs as described above. Cavities are also developed in the innermost whorls where the dorsal inner prismatic layer covers the venter of previous whorls that are still smooth. Perhaps these cavities represent a transverse projection into the dorsal region of the interspaces of the ribbing on the lateral and ventral faces of the shell.

On the adoral sides of the septa a gradual transition from the nacreous or prismatic/nacreous structure of the septum to the prismatic structure of the inner prismatic layer may be seen at the confluence of septum and wall (Birkelund and Hansen, 1975, pl. 1). Here the inner prismatic layer may be thickened by an amount equal to about a quarter of the thickness of the septum. In the dorsal walls of the body chambers of nearly adult specimens the thickness of the inner prismatic layer decreases adorally by $\frac{3}{4}$ in the first quarter of the whorl following the last septum (Fig. 7). It seems therefore that

the mantle renewed growth of the inner prismatic layer at the apical end of the body chamber.

The structure of the *Hypophylloceras* shell has a decisive influence on estimates of the thickness of the phylloceratid shell. Figure 7 shows measurements of thicknesses of phylloceratid and lytoceratid shells taken in the ventral region. It is clear that the phylloceratid shell is thinner than the lytoceratid shell if the dorsal shell wall is excluded, but considerably thicker when the dorsal shell wall is included. The thick phylloceratid shells described by Westermann (1971) may have included the dorsal parts of the inner prismatic layer, which is difficult to distinguish when a shell is recrystallized. Because of the involute coiling of the Phylloceratina most of the chambered part of the shell is in fact considerably strengthened by the subsequent superposition of thick dorsal shell wall. The wall of the body chamber and the youngest part of the phragmocone are, in contrast, extremely thin – accounting for the rarity of fossilized Phylloceratina with their body chambers preserved.

5. The Inner Shell of *Dactylioceratidae*

Howarth (1975) has described the unusual inner shell found in this group, unique so far among Jurassic and Cretaceous ammonoids (see Fig. 6B). It constitutes an additional lining within the main shell.

The main shell of *Dactylioceratidae* is of the usual type, dominated by a thick nacreous layer and with relatively thin outer and inner prismatic layers (see Fig. 6B). The inner prismatic layer is much thicker than the outer prismatic layer. Near the adult aperture the shell is thickened internally by an additionally strong growth of the nacreous layer which forms a constriction. The dorsal part of the main shell is thin. It is still well developed and fully in contact with the previous whorl at the umbilical seam, but further in towards the spiral plane it bridges the tops of the secondary ribs of the previous whorl as soon as these have attained any significant relief, and then quickly wedges out. Such wedging-out of the outer prismatic and nacreous layers is found also in other groups, but the wedging-out of the inner prismatic layer is exceptional and is related to formation of a “septal prismatic layer” described below.

The inner shell consists of two layers (Fig. 6B: KP and IN): a thin

outer prismatic layer and a thick nacreous layer. These two layers are very similar to the two outer layers of the main shell, except that the outer prismatic layer of the inner shell may have a more irregular structure and is not always continuous between the ribs. The inner shell forms the floor of the rib cavities (CA) and is thus homologous with the special modification of the main inner prismatic layer seen in many ammonoids as floors of hollow keels and spines (compare Figs 5 and 6). The ontogenetic development of the inner shell in *Dactylioceratidae* shows that it in fact evolved from that layer. It began to develop from the inner prismatic layer at the same time as the ventral ribs first appeared, after about $3\frac{1}{2}$ whorls. First, the inner prismatic layer thickened beneath the ribs. Shortly after, the inner prismatic layer divided in the middle under the ribs, leaving a cavity exactly as in floored hollow keels and spines. After a further period of growth (about $\frac{1}{4}$ whorl) a nacreous layer began to form in the middle of the inner prismatic layer of the floor, and this was the start of the inner nacreous layer (IN) of the inner shell. In this way floors of the rib cavities become made up of three parts: the prismatic layer (KP) that forms the floor itself and hence was called the “outer prismatic layer of the inner shell” by Howarth (1975); the middle “inner nacreous layer” (IN) which thickens during further ontogenetic development; the third, innermost prismatic layer (SP), which soon becomes closely connected with the attachment of the septa. This layer is called the “septal prismatic layer” by Howarth, who kept it as a separate component of the inner shell (see Howarth, 1975, fig. 2). It appears from Howarth’s description that the septal prismatic layer belongs ontogenetically to the inner prismatic layer as does the rest of the inner shell.

The septal prismatic layer is a layer of large prismatic crystals. On the lateral and ventral parts of the whorl it is attached directly to the inside of the inner nacreous layer of the inner shell and is fairly thin. On the dorsal side the layer is much thicker and only in contact with the crests of the ribs on the previous whorl, bridging the spaces between the ribs and leaving yet further crescent-shaped cavities. In this way the relief of the ribs on the venter of one whorl is reduced to approximately half in the floor of the next whorl. The structure of the dorsal part of the septal prismatic layer is quasi-spherulitic, consisting of radiating arrays of small prisms. The septa are formed by continuation of the growth of the septal prismatic layer. Thus,

the prismatic crystals in this layer change into the tabular crystallites of the nacre of the septa without a sharp boundary in the outer part of the layer. Adorally of the septa the septal prismatic layer is thickened by approximately the thickness of the septum.

The septal prismatic layer appears dorsally already in the first whorl and loses contact with the previous whorl between the ribs as soon as these are well developed. In small immature ribbed specimens the septal prismatic layer extends only the width of one or two ribs in front of the last septum while in larger specimens and in adult body chambers it extends 1/8 whorl in front of the last suture.

The septal prismatic layer of Dactylioceratidae resembles in many ways the inner prismatic layer of Phylloceratidae: (i) in its quasi-sperulitic structure; (ii) by being in contact with the ventral part of the preceding whorl only on the crests of the ribs, leaving cavities where it bridges the rib interspaces; (iii) in the gradual transition from the nacreous or prismatic/nacreous structure of the septa to the prismatic structure of the septal prismatic layer; (iv) in the thickening of the layer adorally of the septa; (v) in the rapidly decreasing thickness of the layer in the body chamber. Nomenclaturally it is however best to preserve the terms "septal prismatic layer" in Dactylioceratidae and "inner prismatic layer" in Phylloceratidae because of the highly differentiated construction of the inner prismatic layer *sensu lato* in the former, and the simple construction of the inner prismatic layer in the latter.

An inner shell seems also to be developed in Triassic Trachyceratidae (Tozer, 1972). The function of the inner shell was discussed by Tozer (1972) and Howarth (1975). Smoothing of the inside of the body chamber may have been its main function, but strength and distribution of weight of the shell may also have been important: it may have governed the attitude of the shell, as the inner shell is absent in the last 1/8–1/4 whorl before the aperture.

6. Encrusting Shell Layers

In a number of ammonoids, outer calcareous shell deposits may form an umbilical plug and in rare cases also encrust large parts of the outer surface of the shell. Other encrusting layers were formed at the border of the body chamber much like the black layer in *Nautilus*. These encrusting layers are secondary in the sense that

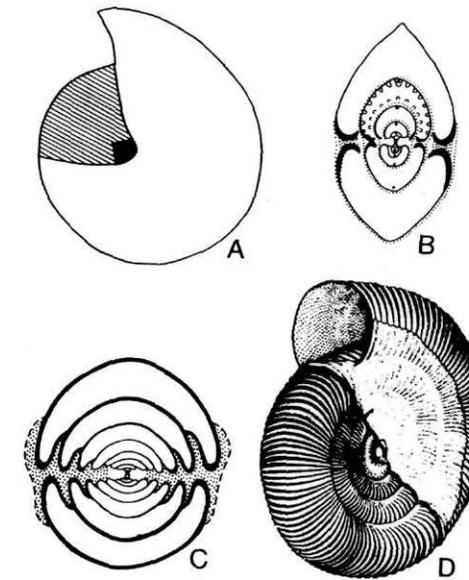


Fig. 8. Wrinkle layers and umbilical plugs. A–B, *Nathorstites*; lateral view and transverse section, the shaded part corresponds to the assumed distribution of the wrinkle layer, the black part to the preserved portion, after Tozer (1972); C, *Clistoceras*, transverse section showing the umbilical deposits, after Nassichuk (1967); D, *Gaudryceras*, distribution of encrusting layer, after Drushchits *et al.* (1978).

they were formed by the mantle after the main shell had been constructed.

Umbilical plugs are most common in involute forms with a deep narrow umbilicus and are comparable to the umbilical plug in *Nautilus pompilius*. Examples include *Nathorstites* and *Clistoceras* (Fig. 8A–C).

Some of the encrusting layers formed at the border of the body chamber show a structure resembling fingerprints which led Foord and Crick (1897) to introduce the term "wrinkle layer" for them. In the German literature these deposits have been called "Runzelschichten" from early times, but other names have also been used (see House, 1971; Walliser, 1970). The term "Ritzstreifen" was introduced by Sandberger and Sandberger (1850, p. 121) for markings preserved on the inner side of ventral and lateral parts of the shell,

but these structures may be kept separate from wrinkle layers for reasons discussed below.

House (1971) has reviewed the occurrence of wrinkle layers in Palaeozoic ammonoids and Tozer (1972) in Triassic ammonoids. Mesozoic examples were more or less neglected until a number of examples were described by Merkt (1966), Senior (1971) and Kulicki (1979).

House (1971) discussed the relations between "Runzelschicht" and "Ritzstreifen" and concluded that they are merely two expressions of the same structure. He found wrinkle layers *s.l.* present in all Palaeozoic suborders but only in smooth, unribbed forms. The course of the striae on a wrinkle layer is related neither to the growth lines nor to the form of the aperture. Only in two families, Anarcestaceae and Pharcicerataceae, did he note the presence of both dorsal and ventral wrinkle layers (? "Ritzstreifen"). The record of a ventral wrinkle layer is based mainly on specimens of *Manticoceras*, as originally described by Sandberger and Sandberger (1850) and Sandberger (1851). Thus, House figured a barytic shell replacement showing a wrinkled surface on the umbilical wall, the flanks and the dorsum (House, 1971, pl. 1, figs 1, 2).

Tozer (1972) kept "Ritzstreifen" separate from wrinkle layers and stressed that evidence from Triassic ammonoids suggests that wrinkle layers were deposited only on the dorsum and in the umbilical area. He found wrinkle layers in 19 families of Ceratitida, all smooth forms as in the Palaeozoic ammonoids. The relations between wrinkle layers and "Ritzstreifen" was studied by Tozer in very well-preserved examples of a *Nathorstites*. The "Ritzstreifen" on the flanks of this species show a pattern wholly unlike that of the wrinkle layer (seen also in *Maenioceras* and *Tornoceras*), while "Ritzstreifen" on the flanks of other forms (*Megaphyllites* and *Manticoceras*) do resemble the pattern of a wrinkle layer.

Wrinkle layers in Jurassic and Cretaceous ammonoids seem to be rarer than in Palaeozoic and Triassic ammonoids, although recognized in a number of groups.

A spiral pigmented ornament seen in *Amaltheus margaritatus* (de Montfort) has been compared with the black layer of *Nautilus* by Quenstedt (1849, p. 93, pl. 5, fig. 4a) and Walliser (1970, pl. 4, fig. 5), and a similar structure in *Caemisites turneri* (J. Sowerby) has been interpreted in the same way (Quenstedt, 1858, p. 96).

Unusually well-preserved material of another amaltheid, *Pleuroceras*, kindly put at my disposal by Dr R. Jordan, shows that the pigmented spiral ornament covers the body chamber down to the umbilical margin and it must therefore be interpreted as a pigment of the main shell (see also Birkelund and Hansen, 1974, p. 24). However, covering this pigmented layer at the aperture, in the same position as the black layer of *Nautilus*, a well-developed wrinkle layer can be seen (Fig. 11E-F). Unfortunately the shell structure of this layer is spoiled by recrystallization. The dark colour of the layer suggests a higher organic content than in the main shell.

The wrinkle layer of *Amaltheus* was described by Merkt (1966) as "Punktrasterung" together with similar occurrences in *Schlotheimia*, *Coroniceras*, *Euagassicerias*, *Promicroceras* and *Sonminia*, and Senior (1971) described it in Graphoceratidae. The surface ornament of all these forms tend to be finer and more discontinuous than the "wrinkles" in Palaeozoic and Triassic forms.

In *Quenstedtoceras* and *Kosmoceras* Kulicki (1979, pp. 121-122) has demonstrated the presence of a wrinkle layer in longitudinal dorso-ventral sections. Between the venter and the prismatic layer of the dorsal shell of the next whorl he found a layer consisting of triangular structures whose microstructure differs from that of prismatic and nacreous layers but is poorly understood.

The distribution of the wrinkle layer in all the Jurassic forms mentioned above is dorsal and seems to be very similar to the dorsal black layer of *Nautilus*. Only in Graphoceratidae has a ventral wrinkle layer been described (Senior, 1971), but this is very dubious.

7. Interpretation of Wrinkle Layers and "Ritzstreifen"

Earlier interpretations of the wrinkle layer were reviewed by House (1971), who himself regarded it as a dorsal nacreous layer of the shell. He supported this idea by analogy with the fact that dissolution of "ostracum" in *Nautilus* produces a wrinkled etched surface. It would also explain the presence of a "ventral wrinkle layer" as the apparent continuation of a dorsal nacreous layer. We know however from well-preserved Mesozoic ammonoids that the nacreous layer wedges out on the dorsal side of the whorl. There is further strong indication that the wrinkle layer does not belong to the main shell.

The origin of the dorsal wrinkle layer as in fact a deposit encrusting the main shell is evident from the occurrence of wrinkled ornamentation on the umbilical plug in *Nathorstites* (Tozer, 1972, pl. 125, fig. 2). Tozer (1972) found also that inside the body chamber and phragmocone of *Nathorstites* the wrinkle layer passes beneath the dorsal shell of the succeeding whorl. The same observation was made by Furnish and Glenister (1971) in *Mescalites*, and by Kulicki (1979) in *Quenstedtoceras* and *Kosmoceras*. The distribution of the dorsal wrinkle layer is very similar to that of the black layer in *Nautilus* and with which it has been compared from early times (see Tozer, 1972, p. 651). Nassichuk (1967) also claims that the wrinkle layer of a *Clistoceras* sp. may have been organic. House (1971) and Senior (1971) stressed that the wrinkle layer and the black layer cannot however be regarded as exactly the same because the wrinkle layer is calcareous and the black layer is composed of conchiolin. Tozer (1972) concluded that the dorsal wrinkle layer seems to be comparable with the black layer of *Nautilus* in position and was probably secreted by a comparable part of the mantle, but that the two are different in composition and texture.

The origin of the wrinkled surface of *Manticoceras* and other forms with wrinkles covering also the inner side of the venter is still puzzling and needs a different explanation, as was also stressed by Tozer. It may either be part of the main shell or be an encrusting layer formed in the close vicinity of the apertural border in continuation of the dorsal black layer, as in the narrow border of black layer at the apertural border of *Nautilus*. As the structure of the "ventral wrinkle layer" or "Ritzstreifen" in certain cases is similar to the dorsal wrinkle layer, I find this explanation the most likely.

8. Encrusting Layer of *Gaudryceras*

Drushchits *et al.* (1978) have described unusual encrusting layers in *Gaudryceras tenuiliratum* Yabe from Sakhalin. I have found similar encrustations in the same species from Sakhalin kindly put at my disposal by Professor H. Hirano. The encrusting layers are recrystallized but seem to show remnants of nacreous structure; they are 3–7 times thicker than the main shell. The surface of the third whorl (about 3 mm diameter) seems to be completely encrusted and the outer part of the encrustations continue along the

lateral parts of the fourth whorl (about 3.5 mm diameter). The encrusting layers do not completely follow the outline of the whorls and leave small cavities at the umbilical seam. The occurrence of these layers in *Gaudryceras* but not in other ammonoids from the same locality, the dark surface colour, and the structures of the encrustations have convinced Drushchits *et al.* that they are not of diagenetic origin. They must have been secreted by the mantle completely enveloping the shell during certain stages of growth. Their function may have been to strengthen the thinnest part of the test or to influence stream-lining. (Fig. 8D).

THE SIPHUNCLE

The construction of the ammonoid siphuncle shows much variation, and this seems greatest in the Palaeozoic. However, much of the work done so far does not include detailed studies on the structures. The discussion that follows, therefore, treats mainly forms which have been investigated in detail in recent years. A number of types are illustrated in Fig. 9.

Structural units of the siphuncle are septal necks, connecting rings and auxiliary deposits.

The septal necks are with few exceptions (see Fig. 11D) entirely nacreous like the septa. They are referred to as prochoanitic or retrochoanitic according to whether they are projected adorally or apically.

In some prochoanitic forms the septal necks are closely associated with calcified collars, forming apical prolongations. These collars have been termed "prolongements postérieurs" by Grandjean (1910), "connective" rings by Drushchits and Khiami (1970), and simply "auxiliary deposits" by Birkelund and Hansen (1968). In 1974 Birkelund and Hansen introduced the term "false septal necks" to avoid confusion with other auxiliary deposits. They have been found in many different Phylloceratidae and were already regarded as characteristic of that group by Grandjean (1910). They have been described in detail in *Partschiceras*, *Phyllopachyceras*, *Euphyllloceras* (= *Calliphylloceras*), *Salfeldiella* (? = *Holcophylloceras*) and *Ptychophylloceras* by Drushchits and Doguzhayeva (1974), and in *Hypophylloceras* by Birkelund and Hansen (1974). Similar prolongations seem also to occur in the Triassic Ussuritidae *Leiophyllites*

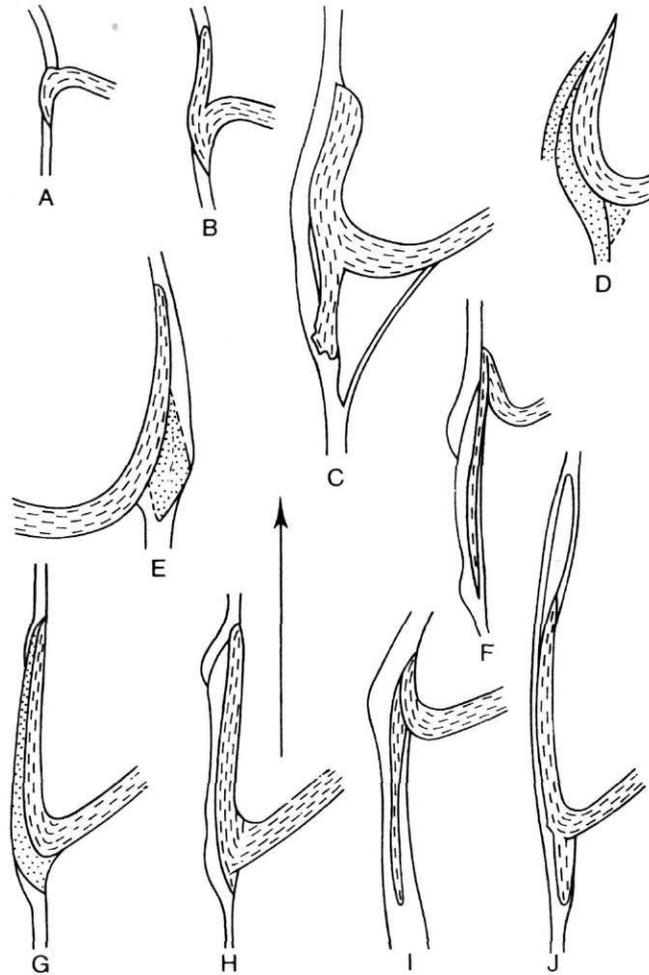


Fig. 9. Siphuncles of Mesozoic ammonoids. The schematic drawings show septal necks and false septal necks (dashed), connecting rings (blank) and auxiliary deposits (dotted). A–C, *Nathorstites*, after Kulicki (1979); D, *Quenstedtoceras*, after Kulicki (1979); E, *Promicroceras*, after Mutvei (1967); F, *Hypophylloceras*; G, *Tetragonites*, after Drushchits and Doguzhayeva (1974); H, *Saghalinites*; I, *Euphyllloceras*, after Drushchits and Doguzhayeva (1974); J, *Gaudryceras*.

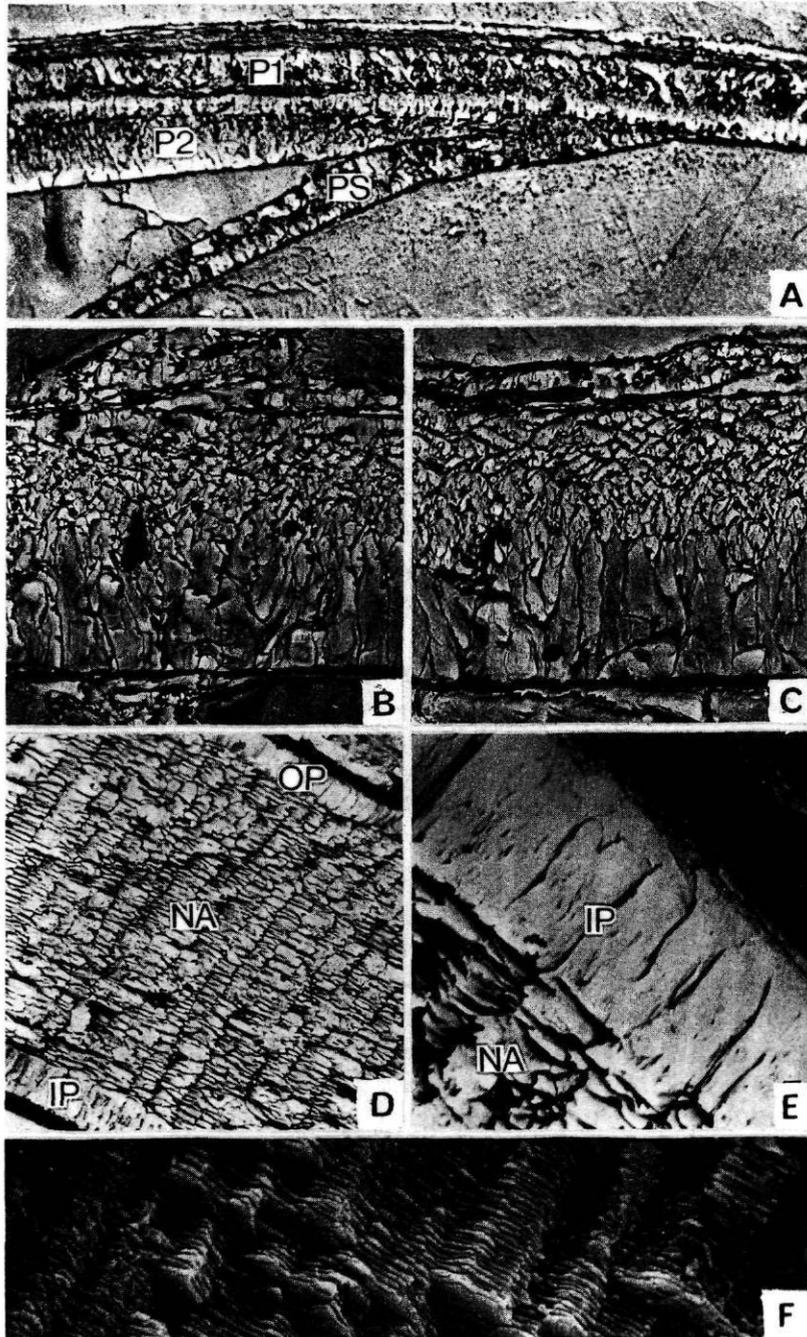
and *Discophyllites* (= *Rhacophyllites*) (Böhmers, 1936) and *Arcestaceae* (*Megaphyllites*) (Doguzhayeva, 1973). They have also been found in some Palaeozoic taxa according to figures in Miller and Unklesbay (1943, fig. 9A–F), e.g. in *Gonioloboceras* (*Goniatitidae*) and in *Neodimorphoceras* (*Dimorphocerataceae*).

The false septal necks resemble the true necks in being nacreous. They are in close connection with the true septal necks in the adoral part, although always separated from them by a boundary, while the apical part is free (Figs 9F, 11B). Drushchits and Doguzhayeva (1974) have described the ontogenetic evolution of the false necks in *Euphyllloceras*. They appear by partial displacement of retrochoanitic septal necks in the second whorl where the septa change from a retrochoanitic to a prochoanitic stage. They are short in the second whorl and longest in the third or fourth whorls, extending through a third to a half of the total length of the chambers. In the following whorls the length decreases again. In *Hypophylloceras* the necks measure about two-thirds the length of the chambers already in the second whorl. It is characteristic of the false septal necks that they are surrounded by the organic tissue of the connecting rings, and in this way they form a sort of calcification of the connecting rings.

Successive septal necks are joined by the connecting rings. These consist primarily of organic tissue and at the septal necks they may be joined together in annular ridges, as seen in *Saghalinites* and *Hypophylloceras* (Figs 9F, H, 11C).

In certain cases, and especially at early stages of growth, the connecting rings may be discontinuous at the septal necks (e.g. early stages of *Nathorstites*, shown in Figs 9A, B). In other cases the connecting rings are joined together by calcifications, some of which, at least, may be interpreted as calcifications of the connecting rings, for they may be shaped like these, with annular thickenings and jointings (see Fig. 9). In other cases, the calcifications seem to be more complicated in construction (see Miller and Unklesbay, 1943). All these calcifications are usually included in the term auxiliary deposits. The structures of these auxiliary deposits are uncertain.

Calcifications may also occur in other parts of the connecting rings, as discussed by Birkelund and Hansen (1974), who found prismatic calcifications in the connecting rings of *Saghalinites*. The calcitic or aragonitic composition of these calcifications has not



been proved, but the strontium content of the tube is distinctly higher than that of the calcitic matrix of the chambers and very similar to that of the prismatic layers of the shell wall, while the content in the nacreous layer is higher still. The prismatic calcification may be compared with the so-called spherulitic prismatic layer of the connecting rings of *Nautilus* (Mutvei, 1964, 1972).

Drushchits and Doguzhayeva (1974) and Kulicki (1979) describe phylloceratids (*Phyllopachyceras* and *Holcophylloceras*, respectively) showing the presence of a siphuncle projecting into the body chamber. The length of the siphuncle in the body chamber of *Phyllopachyceras* is remarkable, being equal to that of the two preceding chambers. These finds show that the construction of siphuncle apparently preceded the secretion of septal walls in the growing phragmocone by up to two chambers.

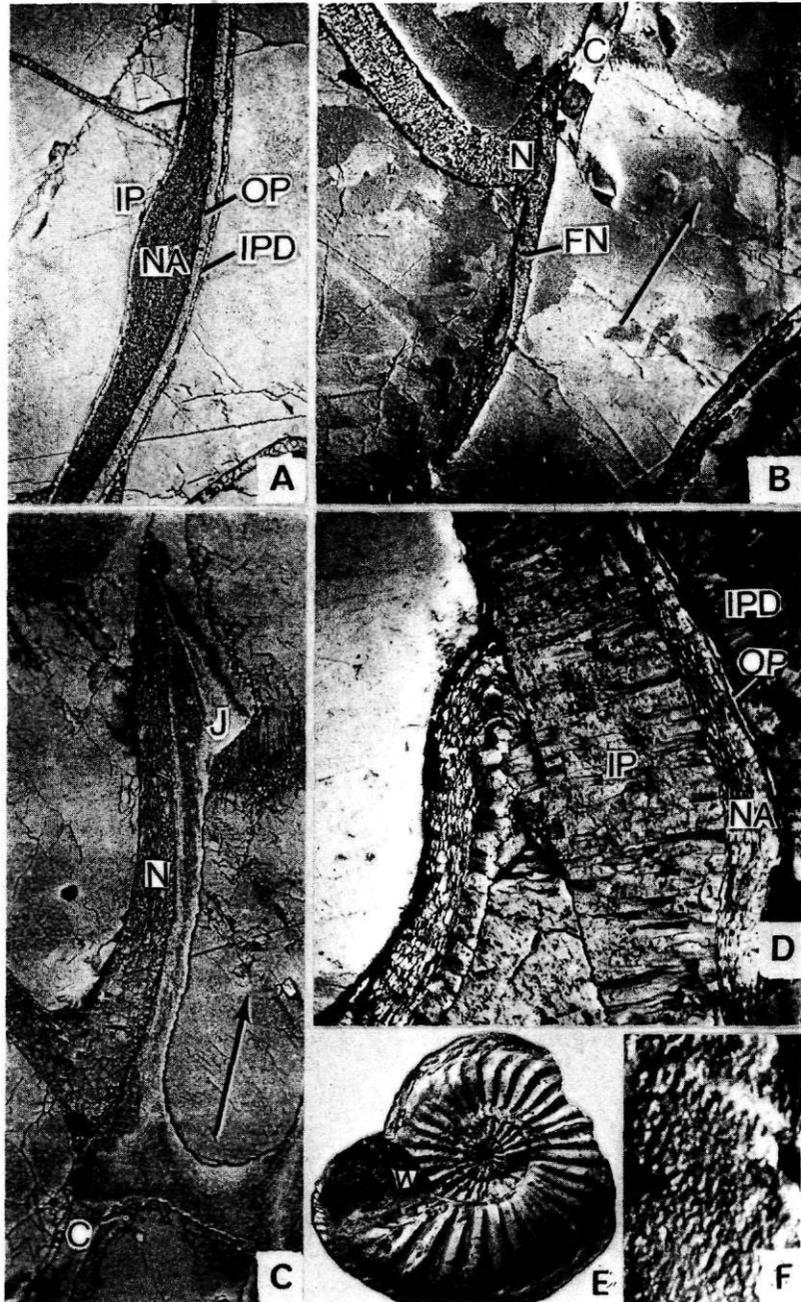
The siphuncle was connected to other elements of the shell by siphonal membranes. They have been well described by, for example, Grandjean (1910), Shulga-Nesterenko (1926), Miller and Unklesbay (1943), Hölder (1954), Schindewolf (1967), Westermann (1971), Erben and Reid (1971) and Kulicki (1979). They seem to have been uncalcified.

CONCLUSIONS

A fundamental feature of all ammonoids studied so far is economy of mass as a primary factor governing shell construction – the wedging-out dorsally of outer shell layers, the construction of hollow spines and keels and the development of cavities between different shell layers. All these reflect the nektonic way of life.

Other important functional characters are different methods of

Fig. 10. A, *Saghalinites*, the prismatic layer of the protoconch (P1), the beginning of the prismatic layer of the first whorl (P2) and its connection with proseptum (PS); $\times 650$. B, *Saghalinites*, early part of first whorl, showing P2 and a thin cover of crystallites belonging to P1; $\times 2100$. C, *Saghalinites*, slightly later part of first whorl only consisting of P2; $\times 2100$. D, *Discoscaphites*, the three main layers of the post-embryonic shell wall; $\times 900$. E, *Discoscaphites*, the nacreous layer and the inner prismatic layer of the post-embryonic shell wall, note the polygonal cross-section of the prisms; $\times 2500$. F, *Saghalinites*, fracture surface of stacked nacre; $\times 5000$.



strengthening some or all of the chambered part of the shell – the formation of umbilical plugs or other encrusting layers, or the development of a thick dorsal wall in involute shells, such as phylloceratids. The advantage of such constructions is that the weight of the latest part of the shell can be kept to a minimum during growth: a correspondingly heavier body chamber in mature specimens can then be compensated by loss of cameral liquid at maturity as described in recent nautiloids by Ward (1979).

To explain the function of the different types of ammonoid siphuncle known is hardly possible as long as many of the physiological aspects of the function of the siphuncle in recent *Nautilus* remain incompletely understood, but the different constructions reflect with little doubt differences in ecology.

Finally, the structures and evolution of shells and siphuncles are characters to be seriously considered in studies of the evolution of the ammonoids as a whole, something that has received little attention so far, no doubt because of the practical difficulties. First indications are that these characters may be of special value in establishing the phylogenetic relationships of the Phyllocerata and Lytocerata to the other ammonoids, which are still poorly understood (Tozer, 1971; Wiedmann, 1973).

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Fig. 11. A, *Saghalinites*, constriction in the early part of the post-embryonic shell; $\times 210$. B, *Hypophylloceras*, septal neck, false septal neck and part of the connecting ring; $\times 100$. C, *Saghalinites*, septal neck and junction between two connecting rings; $\times 450$. D, *Hypophylloceras*, inner part of the shell wall and adjacent septum, note the prismatic layer on the adoral side of the septum; $\times 420$. E, *Pleuroceras* with dark wrinkle layer; $\times 1$. F, *Pleuroceras*, surface of wrinkle layer; $\times c. 15$.

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