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**Geometrical constraints in foraminiferal architecture:**
consequences of change from planispiral to annular growth

(Figs 1–8)

**Abstract.** Large-sized, porcelaneous, planispiral-involute foraminifera react to the loss of alar chamber extensions in the transition from reniform to cyclical growth stages by compensating the abrupt loss of alar apertures with the production of meandrine lateral chambers fed from apertures in the ultimate alar prolongation. This is an analogy common to Late Cretaceous meandropsinids and Late Tertiary archaiasines. In genera with an early annular growth due to oblique-overcrossed stolon systems, the chamberlets of the main layer have oblique-retrovert stolons feeding lateral chamberlets disposed according to a chessboard pattern over the whole lateral surface of the discoidal shell, as in so many orbitoïdiform genera. In lamellar foraminifera developing a median supplemental skeleton with radial canal systems, spiral marginal crests are laterally covered by a single, retrovert-spiral string of supplemental chamberlets per growth step, forming step by step a complete lateral cover as in *Biplanispira*. Early annular-concentric median supplemental skeletons are laterally covered by successive expanse chambers as in *Vaughanina*. The function of some, not all, lateral shell compartments as greenhouse for vegetal symbionts is briefly discussed.

**Key words:** foraminifera, architecture, chamber arrangement, planispiral-involute, annular, lateral chamberlets, cubicula.

**INTRODUCTION**

Foraminifera are unicellular, eucaryotic organisms living an individually autonomous life in the sea. They have a mechanically resistant cell envelope with a single or multiple apertures (foramina) in the envelope through which rhizopods extrude. On one hand, the envelope is a protective device complemented by an organic inner lining. On the other hand, the mechanical stability of the shell provides the cell body a permanent shape at low costs of energy. This is in contrast to hydro-
static constructions like the amoeboid cell body, where actine fibers below the cell wall produce a flexible envelope permitting motility and phagocytosis by the change of cell shape (Gutmann 1986). Where the foraminiferal shell is biomineralized, the quantity of nutrients permanently fixed in shell proteins and unavailable for recycling is also very low.

Permanent cell shape has autecological functions (Hottinger, 2000). This is suggested by the numerous repetitions of basic shapes (such as discs or cones) in the evolutionary process during earth history in so many parallel, more or less unrelated lineages. These repetitions are interpreted as analogies and represent therefore adaptations to autecological requirements (adaptive convergence).

Mechanically stable, permanent cell envelopes call for particular procedures when the cell body is growing: either, the old shell is abandoned and a new, larger one is constructed (as in the process of molting in arthropods), or new parts of envelope are added to the previous one (as in many mollusc shells). Keeping the advantages of low energy and nutrient consumption as well as avoiding repeated interruption of protection during ontogeny, most foraminifera growing for more than 100% of their initial volume keep to adding new envelope parts to the existing one. Wherever foraminiferal reproduction was observed in vivo, the proloculus represents the initial volume of the individual. Wherever there is further growth, the volume is approximately doubled in the following instar as documented by the volume of the deutoconch. In unilocular lagenids, there are no calcified proloculi, just single-chambered shells exhibiting often complex ornaments (Lagnea) demonstrating their adultness. These shells remain always very small. Wherever there is an ontogeny resulting in gaining sizable amounts of volume, we observe discontinuous, chamberwise growth. Each “chamber” is defined as all envelope parts added to the previous shell by the same growthstep (instar).

Chamberwise growth of the envelope provides the cell body with a permanent compartmentation at lowest possible costs of energy and nutrients. The shell compartments permit to keep units of protoplasm within the range of ordinary cell size when the adult organism reaches sizes corresponding to multicellular organisms (up to 15 cm discoidal diameter). Thus, compartmentation of the foraminiferal shell is a prerequisite for the long, true ontogeny so uncommon in the world of unicellular organisms.

Shell shape has autecological functions. If these functions are to remain constant during ontogeny, shell shape has to remain constant during additive growth. This involves heavy geometric constraints. In contrast to gastropod or cephalopod shells with similar, additive growth, but with a single, widely open aperture, foraminifera have a comparatively narrow aperture on an apertural face, or multiple apertures. This modifies the geometric constraints in a fundamental way: the angle of the apertural face in respect to the rest of the shell and the position of the aperture or multiple apertures on the apertural face are an important additional functional element modifying the constraints.

In foraminifera, the cell envelope may be single-layered or exhibit a bilamellar wall, where the two layers may be partially independant, producing primary cham-
ber cavities delimited by a primary, double-layered wall, and additional cavities delimited in part at least by the outer lamella only, by the so-called supplemental skeleton. The independance of shell layers provides a much larger morphological potential to foraminiferal architecture.

Main chamber cavities are connected by single or multiple intercameral foraminina in order to provide connection within the cell’s protoplast housed in the the shell compartments. Transport between chamber cavities is carried out by protoplasmic streaming supported by microtubuli, which have a linear extension. Thus, the connections in the shell’s septa have to be aligned. The axes of the intercameral foraminina in successive chambers form basic patterns which are genetically fixed as deduced from their taxonomic importance on generic and higher levels (Hottinger, 2001).

Reduction of transport distances are an important additional functional requirement for the shell’s architecture (Brasier, 1982). On the other hand, the position of the apertures on the apertural face has autecological functions related to the cell’s life in its ambient environment (food gathering, particle collection, motility, protection of offspring etc). These “extern” requirements have to be balanced with the “intern” ones related rather to the cell’s metabolism and growth.

Lamellar foraminifera may produce – by complex folds of the independant inner and outer lamellae (Hottinger & Leutenegger, 1980) – interlocular spaces transformed by local resorption of the shell into extensive canal systems. These house pseudopodial protoplasm extruding to the ambient environment through orifices on the shell surface. Often, we observe a division of functions: the apertures, open only during the growth process, determine the growth of the subsequent chamber, while the canal orifices, tending to be distributed over the whole shell surface and remaining permanently open, are reflecting autecological functions, in particular motility (Hottinger, 2000).

Along the lines of the above considerations we will focus our attention in the following pages on selected examples of foraminiferal architecture, where so-called lateral chamberlets cover a discoïdal main chamber layer on both sides. Of particular interest are the consequences of change from planispiral main chamber arrangement to annular arrangement during ontogeny. What happens in involute shells to their alar prolongations with their apertural face? What is the difference in the constraints in single- and double-layered walls? The comparison of the reactions to a change of spiral to concentric growth in the construction of three-layered shells exhibiting an equatorial layer covered by two lateral layers will point out the role of geometry determining the architectural patterns of their shell.

LATERAL SHELL CAVITIES IN PORCELANEOUS, PLANISPIRAL-INVOLUTE FORAMINIFERA CALL FOR A MEANDRINE ARCHITECTURE

Late Cretaceous Meandropsinidae (Ciry, 1964) and Eocene to recent Archaiasiinae (Hottinger, 2001) are two unrelated groups exhibiting planispiral-involute
shells with radial foraminal axes determining their radial endoskeleton. They have in common the tendency to extend their apertural face by the peripheral extension of their spiral chambers during ontogeny: a first, spiral, peneropline growth stage ends with the first chamber overgrowing the spiral periphery of the previous chamber (1 in Fig. 1B, D). The second, reniform growth stage ends where a chamber produces the first time a complete annulus (2 in Fig. 1B, D).

In the equatorial plane of the shell (Fig. 1B), the peripheral extension of the apertural face grows successively in cadence with the overall size of the shell. In involute shells however, the alar prolongations produce on both sides of the shell additional apertural faces (Fig. 1C) with additional apertures. The alar chamber extensions have a similar tendency to extend, forming a spiral vortex on both sides around the spiral axis of the shell (Fig. 1E). Where vortices are produced, the total number of apertures exceeds by far the number of apertures available on the peripheral apertural face in the equatorial plane. This is in accordance with the general tendency of all discoidal foraminifera subject to nepionic acceleration (radial foraminifera sensu Drooger, 1993).

When the involute chambers reach an annular growth stage, no alar extension can be produced as long as the apertures remain confined in the peripheral apertural face. Thus, the progress of apertural numbers during ontogeny is drastically re-

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Fig. 1. Planispiral-involute chamber arrangement in Meandropsinidae and Archaiasinae reaching annular growth during ontogeny. A – lateral view of chamber sutures. Shaded: Ultimate spiral chamber with alar prolongation forming vortex. B – equatorial section, outline of septa only. Shaded: ultimate spiral chamber in equatorial plane. C – oblique view of late planispiral-involute stage showing spiral shell periphery, peripheral part of free frontal chamber wall bearing extended apertural face and alar prolongation with its apertural face, forming vortex. D – schematic view of shell in transparency showing growth stages ending at arrow points 1 and 2, the last spiral chamber (stippled) with its ultimate alar prolongation, giving rise to earliest meandrine chambers 1–5 (in darkening shades) on the lateral shell surface. Note the tendency of meandrine chambers to overgrow the vortex. E – schematic, three-dimensional view of ultimate spiral chamber with last alar prolongation. Note extension and position of apertural faces. The respective position of detailed structural models is indicated with F and G. F – structural model of a sector of an alar prolongation. Note the similarity with the structure of a chamber of Pracalveolina (Reichel, 1936). This is due to the positioning of the chamber on a free outer surface of the imperforate shell. The chamber wall deposited on this surface is “basal”, corresponding to the basal layer in Alveolinidae. G – structural model of sector of late spiral chamber. Note in both models the large annular passage in lateral-preseptal position, double in the chamber, single in its alar prolongation. The large annular passages distinguish the involute Meandropsinidae from the Archaiasinae (Hottinger, 2001). Abbreviations: Ax – shell axis; a – aperture; af (alp) – apertural face of alar prolongation; af (ch) – apertural face of chamber; alp – alar prolongation (of chamber); ap – (double) lateral annular passage in preseptal position; as – annular septum; bw – basal wall; ch – chamber; lw – lateral wall; per – (spiral) periphery; pi – pillar; pr – proloculus; prp (single) preseptal passage in alar prolongation; raf – (functionally) restricted sectors of apertural face (in ultimate alar prolongation); s – septum; sl – septulum; soc – socculus; ss – septal suture; ult – ultimate; v – vortex. Arrow 1 – End of peneropline growth stage by overgrowing the spiral periphery of the previous chamber; arrow 2 – end of reniform growth stage with appearance of first annular chamber, loss of alar prolongation. All figures schematic, not to scale.
duced by the suppression of additional alar prolongations. In order to avoid a regression of the numbers of apertures during ontogeny, additional apertural faces are produced by additional lateral shell compartments fed from apertures of the last alar prolongation (Fig. 1D). There may be one or several restricted domains within these alar apertural faces nucleating the procession of at first semilunar and later meandering chambers on the lateral shell surface. The morphology of the non-lamellar, imperforate shell provides unfortunately no indication whether the annular chambers in equatorial position and the additional meandrine chambers in lateral posi-

[Images of diagrams A to G]
tion may be correlated (Fig. 1D) by their successive number within the annular growth stage and may thus belong to the same instar.

Large-sized Meandropsinidae (*Larrazetia, Meandropsina*, Fig. 2A–C) from the Late Cretaceous and large Archaiasines (*Pseudotaberina, Miarchaias*, Fig. 2D–F) from the Late Tertiary thus respond to cyclical adult growth not only by meandrine lateral chambers but have in common also structural patterns, subdividing the elongated chambers by septula (see Fig. 1F, G; Fig. 2), a structure similar to the fusiform
alveolinids. The connection between the chamber compartments is ensured by pre-
septal passages also as in alveolinids. Therefore, the extremely elongate chamber
shape and the chamber’s position on a former external wall produces also similar
structural patterns independent of shell shape, discoïdal or fusiform. The similari-
ties between Meandropsinidae and Archaiasinae are so striking, that Henson (1950)
united both groups in the same family. They are distinguished however by the na-
ture of their microspheric embryos and by some details in their architecture.

**DISCOÏDAL SHELLS WITH EARLY CYCLICAL GROWTH CALL FOR EXPANSE CHAMBERS**

Discoïdal foraminifera with crosswise-oblique stolon axes usually produce
early annular growth or start annular from the first growth stages following an em-
byronic apparatus with multiple apertures. The annular chamberlet cycles exhibit
retrovert stolons piercing in oblique direction the lateral wall of the chamberlet in
the equatorial main chamberlet layer. The retrovert stolons are positioned at the
most proximal corner of the main chamberlet (Fig. 3). This can be observed in por-
celaneous *Orbitolites transitorius* - *Somalina* (Hottinger & Krusat, 1972) as well as
in lamellar-perforate *Orbitoides* (Caus et al., 1996). The direct connection between
main and lateral chamberlet lumina by intercameral foramina indicates a close cor-
respondence between a particular annular cycle in the main layer with its lateral
chamberlet layer. They are formed during the same growth step. Therefore, we call
the elements of a cycle in the equatorial main layer “chamberlets” and not (as Droo-
ger, 1993) “chambers” in spite of the lack of annular communication in the median
layer of the shell. By way of the lateral chamberlet layers, they are however comm-
unicating within their cycle by intercameral foramina.

The lateral chamberlets of one generation form a network extending over the en-
tire lateral shell surface. They are comparable to expanse chambers of permanently

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**Fig. 2.** Analogous, meandrine lateral shell compartments in large, microspheric, porcelaneous
shells: *Larrazetia* from the Upper Cretaceous, *Miarchaias* and *Pseudotaberina* from the Middle-
Upper Miocene. A–C – *Larrazetia larrazeti* (Munier-Chalmas), Meandropsinidae. Upper Creta-
ceous, Catalonia, Spain. A – tangential section perpendicular to shell axis showing meandrine
disposition of supplementary lateral chambers. B – transverse section perpendicular to shell equator,
at low angle to shell radius, showing septa of annular chambers in oblique section. C – detail of A
showing annular and meandrine chambers in oblique section. D, E – *Miarchaias meander* Hottinger.
Uppermost Miocene, Dominican Republic, Caribbean. D – lateral view of eroded shell showing
meandrine disposition of supplementary lateral chambers. E – tangential section perpendicular to
Oblique section. Middle-Upper Miocene. Iran, Neotethys. **Abbreviations:** alp – alar prolongation (of
chamber), b – beam (of exoskeleton); f – intercameral foramen; lw – lateral wall (of inner whorl); lw1
– lateral wall of annular chambers; lw2 – lateral wall of supplementary meandrine chambers; pi –
pillar; psp – preseptal space; s – septum; sch – supplementary, meandrine chamber and chamberlet;
soe – socculus; v – vortex
sessile, incrusting foraminifera (Fig. 4A; Fig. 5), using the free periphery of the median layer and the previous expanse chambers on both sides of the shell as a kind of substrate. In subsequent layers, they occupy alternating positions as in the main layer, not in a linear circle but on a two-dimensional, discoïdal surface. This produces roughly a chessboard pattern where the white fields correspond to one, the black fields to the following generation of lateral chamberlets. Within an expanse chamber, tubular restrictions may form passages connecting the different branches while subsequent expanse chambers are connected by true foramina, oblique stolons resulting from the overgrowth of regular, basal apertures. The so-called stacks of lateral chamberlets seen in so many axial sections of three-layered orbitoidal genera represent every second growth step. In Sphaerogypsina globulus (Fig. 4C) this pattern is quite regular, but when in the same time piles (of lamellae = “pillars”) are formed, it may be much more irregular, closer to polygonal fields. It is not clear, whether the retrovert, oblique stolons are always primary apertures covered by the lateral chamberlet or products of resorption prior to each growth step (as for example the masked equatorial main aperture in nummulites or fusulinids), transformed after the formation of the next chamber into a tiny tunnel.

In larger-sized forms expanse chambers appear, where volume accretion rates (per growth step) permit considerable acceleration during ontogeny. Expanse chambers may cover the total surface of a discoïdal shell in one step (Fig. 4A). In particular, they appear in encrusting lamellar foraminifera such as Planogypsina squamiformis (Fig. 5A, B). In very large shells they may become broadly annular where there is a need for rapid radial growth in competition for space with other encrusting organisms (Gypsina plana, Fig. 5C, D). In the porcelaneous kera-mosphaerids, expanse chambers of particularly irregular-vermicular outline may cover part or all of the spherical surface of the shell. They need additional studies.
Fig. 4. Response to concentric-annular or concentric-spherical growth in lamellar foraminifera. 

A – expanse chamber covering by a single growth step a complete lateral surface of a discoidal shell. Schema, not to scale, inspired by *Planogypsina squamiformis* (Chapman), recent. 

B – detail of sector with 5 successive expanse chambers. Front of stereograph cut in oblique direction, inclined in respect to shell axis. Note the “opportunistic” use of previous empty spaces filled preferentially by the next chamber and producing an alternating pattern when sectioned. 

C – detail of alternating chamberlets covering by successive cycles a sphere. Stereograph inspired by *Sphaerogypsina globulus* (Reuss), recent. Note the chessboard pattern produced and the fact that in this case not only the ultimate but also the penultimate chamberlet cycle may have apertures into the ambient environment. 

**Abbreviations:** 

*a* – aperture; 

*f* – (intercameral) foramen; 

*puch* – penultimate chamber or chamberlet cycle; 

*sut* – chamber suture; 

*tpa* – tubular passage (within expanse chamber); 

*uch* – ultimate chamber. Lamellae and piles omitted.
Fig. 5. Expanse chambers in recent Acervulinidae from the Gulf of Aqaba, Red Sea. SEM graphs. 

**A, B** – *Planogypsina squamiformis* (Chapman). **A** – dorsal side of shell showing surface of attachment where the chamber arrangement is clearly visible: early spiral stage of 5 chambers, the apertures in the distal part of the dorsal spiral suture revealing the relationship with the Cibicididae. The postnepionic stage exhibits the successive expanse chambers producing on the surface of attachment the alternating pattern of orbitoidal chamberlet cycles. **B** – free ventral side of the test showing superposed expanse chambers of the ultimate and penultimate generation. **C, D** – *Gypsina plana* (Carter). Surface of large, encrusting specimen with broadly annular expanse chambers, the double arrows indicating their radial extension, and fragment showing the superposition of expanse chambers, their connections within the same chamber by tubular passages, the connections between subsequent chambers by oblique stolons. 

**Abbreviations:**
- **a** – aperture
- **k** – keel
- **orbch** – expanse chambers producing a pattern similar to orbitoidal chamberlets
- **p** – pore
- **puch** – penultimate expanse chamber
- **sa** – sutural aperture
- **spch** – (nepionic) spiral chamber
- **st** – stolon
- **tpa** – tubular passage (within expanse chamber)
Other open questions concern the detailed pattern of lateral chamberlet arrangement, their eventual taxonomic significance (Schweighauser, 1953) and the formation of broad equatorial collars at the periphery of the discoïdal shell lacking lateral chamberlets, as in the latest lepidocyclinids. There might be transitions between chessboard arrangement of lateral chamberlet layers and so-called expanse chambers (see below) difficult to distinguish where the shell cavities are filled with calcitic transparent cement.

Banner & Hodgkinson (1991) have introduced the term cubicula for “lateral chamberlets” traditionally used for orbitoidiform, “three-layered” foraminifera. They have restricted the term lateral chamberlets to spiral-involute foraminifera, where the alar prolongation of a spiral chamber would be subdivided into a string of secondary cavities, i.e. chamberlets. I do not follow these authors for the following reasons. In their restrictive redefinition of the “lateral chamberlets”, the example of Tansinhokella tatauensis is given in pl. 6. The “lateral chamberlets of subrectangular shape” (p. 256) visible in the oblique sections pl. 6, figs 1, 2 and 4, are in my view oblique sections of ordinary equatorial chamberlets as in all involute heterosteginids. The “subdivisions” of the alar cavities as seen in axial sections correspond in my view to non-radial, i.e. inclined or sigmoidal septa obliquely cut by the radially directed axial section. On the other hand, the lateral chamberlets of Spiroclypeus are indeed alar prolongations transformed into a string of very low cavities with a rounded basal outline alternating in radial position from one chamber to the next.

DISCOÏDAL SHELLS WITH A MARGINAL CREST

Marginal crests are produced by radial extension of an enveloping canal system (Hottinger, 2000). Restrictions in space of such radial extensions are common: the restriction to narrow sectors of the equatorial plane produces the canalicular spines (as in Siderolites calcitrapoides), the restriction to a small, equatorial disc is found in many spiral (Pellatispirines) and annular (Pseudorbitoidids) shells. Since they are the product of folding of outer lamellas, their basic geometric configuration is independant from the spiral or annular chamber arrangement of the shell.

Marginal crests restricted to a narrow equatorial disc have the same basic geometrical configuration as a main chamberlet layer in orbitoidal foraminifera although they are of entirely different origin and constructed with different elements of the foraminiferal architecture: the marginal crests by complex folds of the outer lamella forming a supplemental skeleton, the main chamberlet layers by regular chamberlet cycles (Orbitoidiforms) or annular chambers (orthophragminiforms, Ferrandez Canadell & Serra-Kiel, 1995). Both produce so-called three-layered shells because the circular surface produced by the median layer has either retrovert canal orifices in the marginal crest or retrovert tubular foramina (oblique stolons) in the main chamberlet layer feeding the lateral shell compartments.

In particular, the lamellar-perforate pellatispirids from the Late Eocene produce planispiral shells with a dominant supplemental skeleton: the total volume of the
spiral chambers remains comparatively modest in respect to the volume of the canal system housed in an extremely broad marginal crest (Hottinger et al., 2001). Marginal crests ensure the positioning of numerous, radially directed orifices all around the shell’s periphery in spite of the spiral architecture of the shell. In *Biplanispira*, the marginal crest is overgrown by supplemental chamberlets added step by step in successive retrovert spirals (Figs 6, 7). The successive spirals of chamberlets produce a single lateral chamberlet layer covering the open space between successive whorls of the spiral main chambers on the marginal crest. Maybe, these lateral chamberlet layers compensate the modest main chamber volume. So far, no pellatispirid representative has been found where these lateral chamberlets produce regularly superposed layers on both sides of the discoidal shell.

In *Vaughanina* from the Caribbean Upper Cretaceous (Fig. 8), the spiral nepiont of sulcoperculinid nature is reduced to a few chambers followed by a supplemental

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**Fig. 6.** Supplemental chamberlets in lateral position produced by a planispiral lamellar shell (schl = “lateral chamberlets” in Hottinger et al., 2001) on a marginal crest (mcr) formed by an enveloping radial canal system, in transparent view. Growth stages roughly indicated for every five chambers. Corresponding chamberlets darkened. Chamberlets fed by retrovert orifices of the canal system. Note the retrovert spirals formed by the supplemental chamberlets of a single growth stage. Arrow — direction of growth. This corresponds to the retrovert spiral of alar prolongations forming a vortex in non-lamellar shells. Note also the alternating position of chamberlets corresponding to subsequent chambers. Schema, not to scale, inspired by Late Eocene *Biplanispira absurda* Umbgrove
skeleton substituting a main chamberlet layer, similar to *Biplanispira*. But with the loss of the spiral, the peripheral supplemental skeleton gets annular. Strong radial canals multiply in peripheral direction, forming a thickened periphery. On the lateral surface of this strictly annular and radial supplemental skeleton, piles of lateral chamber cavities appear which are fed probably by retrovert canal orifices, as observed in particularly well preserved pellatispirids (Hottinger *et al.*, 2001, pl. 4).
In contrast to the spiral pellatispirids, the concentric *Vaughanina* construct their lateral chamber system by superposed expanse chambers. Since the overall shell size in *Vaughanina* is comparably modest, the accretion rate per growth step remains within limits.

**THE FUNCTION OF LATERAL SHELL COMPARTMENTS**

In many if not most, non-lamellar, porcelaneous shells of larger foraminifera from shallow waters, symbionts are housed in lateral compartments of the chambers, avoiding places in the chamber where the protoplasm is circulating (endoskeletal realm). Protoplasmic streams may displace the symbionts from places where they can breathe (through thin and/or pitted lateral chamber walls) and where they are exposed to light. In Soritids, Leutenegger (1977) found a light regulation mechanism by active movement of the symbionts within the cell, changing place from one side of the disc to the other. This explains the epiphytic habit of the soritids: the dark surface of the vegetal substrate is a prerequisite to the light regulation mechanism in environments, where the carbonate sands at the bottom reflect a great amount of the light penetrating into the shallow waters.

Alveolinids living on the bottom of the sea house their symbionts in the last few whorls of their planispiral-fusiform shell. We do not know for sure, whether their
possibility to displace the symbionts into the inner whorls is used as light regulation device. The meandrine lateral chambers in porcelaneous larger foraminifera may be interpreted as symbiont greenhouse in analogy to outer whorls of the alveolinids. However, the discoïdal architecture of their shell prevents the displacement of the symbionts to the interior or to the opposite side of the shell. Consequently, the existence of a light regulation device in such shells is improbable and therefore also an epiphytic life habit. This is supported by the observation, that discoïdal porcelaneous forms with meandrine lateral structures are found in marls representing muddy substrates where a seagrass vegetation cover is usually absent.

In lamellar-perforate Baculogypsina, Hottinger & Leutenegger (1980) observed an accumulation of symbionts in shell compartments similar to lateral chamberlets. They are the only living representatives with a structure comparable to orbitoidiform foraminifera in spite of their lack of a main chamberlet layer. On the other hand, Planorbulinella larvata has no symbionts. This is a lamellar-perforate organism with an orbitoidiform chamber arrangement but lacking lateral shell compartments in spite of the presence of retrovert apertures (Hottinger et al. 1993, pl. 118). From this, one deduces the greenhouse function of the lateral chamberlets in all kinds of orbitoidal larger foraminifera with lateral shell compartments.

In foraminifera permanently fixed to a solid substrate and producing expanse chambers, no symbionts were observed (Leutenegger, personal comm.). This is also the case in Sphaerogypsina which must live without any differentiation of its spherical surface in an isotropic environment (Hottinger, 2000). In the benthic realm, isotropic environments exist only in the bottom sediment where light and oxygen gradients are too low to matter. It remains an open question, if the lateral shell compartments in foraminifera with a large marginal crest are greenhouses or recipients of chamber plasm substituting ordinary spiral chambers or main chamberlet cycles.

CONCLUSION

1. Planispiral involute porcelaneous shells loose their long, vortex-forming alar chamber extensions in the moment of transition from the reniform to the annular stage of growth. The loss of the alar apertural face produces an abrupt reduction of the number of apertures. This is compensated by the growth of additional lateral chambers fed from one or several restricted areas on the apertural face of the last alar prolongation. The sequence of lateral chambers starts with semilunar ones overgrowing each other by getting meandrine in later stages (Fig. 1D).

2. The particular chamber shape with its extremely elongate apertural face of the meandrine lateral shell compartments and the position of the chamber on previous lateral chamber walls lacking apertures is similar to the situation in Alveolinids with their (in the direction of growth) short chambers extending their long way from pole to pole and bearing a long apertural face with numerous apertures. Their position over a previous lateral chamber wall without apertures (of the previous whorl) is also very similar. The extreme geometry of such chambers obviously calls for
similar structural patterns: parallel septula arising from a basal layer and a preseptal passage for connecting the chamber compartments (Fig. 1F).

3. Early annular forms generated by oblique-overcrossing foraminal systems produce retrovert, oblique foramina at the proximal angle of the main chamberlets alternating their radial position in subsequent cycles (Fig. 3). These retroverse foramina feed cycles of lateral chamberlets covering the lateral surface of the shell in a chessboard pattern. Therefore, two lateral chamberlets superposed in a stack between piles so often observed in orbitoidiform shells correspond not to subsequent but to every second growth stage (Fig. 4C).

4. Lamellar-perforate, planispiral foraminifera may produce discoidal surfaces by extending a supplemental skeleton into much broadened marginal crests. These may be covered by a chain of supplemental chamberlets extending in retrovert spirals over the previously formed lateral surface of the crest. Subsequent spirals corresponding each to one spiral main chamber and indicating thus subsequent growth stages may form a complete cover of the lateral surface as in *Biplanispira* (Fig. 6). In forms with an early annular concentric supplemental skeleton, series of expanse chambers cover the lateral surface of the disc, as in *Vaughania* (Fig. 8).

5. Expanse chambers occur frequently in incrusting lamellar foraminifera fixed permanently on a solid foreign substrate. In free, three-layered, orbitoidiform genera, we may consider the surface of their own free shell margin and their own lateral chamberlet walls in earlier parts of the previous shell as a kind of substrate for chambers of successive growth stages (Fig. 5).

6. Lateral shell compartments may be interpreted by analogy to a few recent forms as greenhouse for the vegetal symbionts. Some of these structures however, in analogy to recent, lamellar, encrusting species, may represent a substitute for a much reduced number or for altogether absent ordinary, spiral or annular main chamberlets.

REFERENCES


