

Morphogenetic origin of radial lirae and mode of shell growth in *Calliphyloceras* (Jurassic Ammonoidea)

HUGO BUCHER¹, RÉGIS CHIRAT² & JEAN GUEX³

Key words: radial lirae, growth, *Calliphyloceras*, Ammonoidea

ABSTRACT

The microstructure of the shell wall of *Calliphyloceras* reveals the morphogenetic origin of radial lirae, a character commonly encountered in both Paleozoic and Mesozoic ammonoids. The outer prismatic layer consists of projected and overlapping tile-shaped, radial slats. The free, arched and projected adoral end of each slat implies that secretion must have been interrupted and followed by a withdrawal of the periostracal groove of the mantle back to the junction line with the preceding slat. Secretion resumed with a new increment of thin outer prismatic layer and periostracum, and the adoral secretion of the underlying, continuous nacreous layer proceeded only after this new cycle initiated. The junction lines between consecutive and overlapping slats were subsequently moulded by the nacreous layer, thus forming the radial lirae. These must be seen as fabrication noise originating from the discontinuous secretion of the outer prismatic layer and periostracum. The hitherto unclear morphogenesis of these radial lirae is now unambiguously distinguished from that of ordinary –and smaller– growth lines, which do not involve such discontinuities accompanied by partially overlapping increments of the outer prismatic layer. It also differs structurally from megastriae, which cut across the periostracum, outer prismatic and nacreous layers. Small and acicular fibro-radiated deposits in the cylindrical cavities of the outer prismatic layer of *Calliphyloceras* also suggest that ‘remote biomineralization’ (i.e. without direct control of mantle) occurred inside the shell wall.

RESUME

La microstructure de la paroi coquillière de *Calliphyloceras* révèle l’origine morphogénétique des lirae radiales, caractère fréquemment observé chez diverses ammonites jurassiques et crétacées. Chez *Calliphyloceras*, la couche prismatique externe est disposée en lattes radiales imbriquées et projetées. L’extrémité adorale de chaque latte arquée et projetée est libre, impliquant une interruption de la sécrétion suivie d’un retrait du sillon périostacal jusqu’à la ligne de jonction avec la latte précédente. La reprise de la sécrétion se fait avec un nouvel incrément composé de périostacum et de couche prismatique externe, la sécrétion adorale de la couche nacréée sous-jacente et continue ne se pouvant se produire qu’après le démarrage de ce nouveau cycle. Les lignes de contact entre les lattes successives sont moulées par la couche nacréée sous-jacente nouvellement sécrétée, formant ainsi les lirae radiales. Ces dernières sont donc assimilables à du bruit fabricationnel résultant simplement de la sécrétion discontinue du périostacum et de la couche prismatique externe. La morphogenèse jusqu’ici mal comprise des lirae radiales est clairement différenciable de celle des lignes de croissance ordinaires, bien plus petites, et n’impliquant pas de telles discontinuités et imbrications de la couche prismatique externe. Les lirae radiales se différencient également des mégastries, discontinuités plus importantes impliquant conjointement la couche prismatique externe et la couche nacréée. Des dépôts de structure aciculaire et fibro-radiée dans les cavités résultant de l’imbrication des lattes de la couche prismatique externe suggère la présence d’un mécanisme de biominéralisation à distance, indépendant d’un contrôle direct par le manteau.

1. Introduction

Among the usual ornamental characters of the ammonoid shells, Arkell (1957, L91) gave a first, rather loose definition of the lirae: ‘In many shells the growth lines are accentuated or raised as lamellae, which may be crinkled, or they appear as fine radial lines (lirae) or they are accompanied by them’. Following this first definition, Arkell (1957) also used the same term but in reference to the longitudinal or spiral lines that occur in some genera (e.g. *Amaltheus*). Any possible confusion between these two distinct features will be here avoided by systematically specifying the radial orientation of the lirae that

are the focus of this work. Arkell’s definition of radial lirae appears somewhat equivocal because it refers indifferently to marked growth lines as well as to independent structures intercalated between them. This ambiguous definition has led to some confusion resulting in the interchangeable use of the terms growth lines or lamellae, with lirae (e.g. Doguzhaeva 1982; Korn & Price 1987; Bond & Saunders 1989; Bucher & Guex 1990; Bucher et al. 1996). However, the distinction between growth lines and radial lirae was later illustrated by Bucher et al. (1996), who emphasized the different scales of these structures, but without any further distinction pertaining

¹ Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, CH–8006 Zürich. E-mail: Hugo.Bucher@pim.unizh.ch

² U.F.R. Sciences de la Terre, Université Claude Bernard Lyon 1, 27-43 Bd. du 11 novembre 1918, F–69622 Villeurbanne Cedex. E-mail: Chirat@univ-lyon1.fr

³ Institut de Géologie et Paléontologie, BFSH2, Université de Lausanne, CH–1015 Lausanne. E-mail: Jean.Guex@igp.unil.ch

to the mode of growth. Spacing of growth lines varies around $1\ \mu\text{m}$, while spacing of radial lirae may range from 0.1 to 1.5 mm, depending on the size of the specimen and on the whorl height at which measurements are taken. If growth lines actually reflect intermittent growth at the cellular level, a similar underlying morphogenetic process for the more widely spaced radial lirae is unlikely. Another difference between these two structures can be seen in their respective lateral continuity or extension: both are parallel to the growing edge but single growth lines may not systematically extend all around the apertural edge, being generally more numerous on the venter than on flanks and with variable strength, as opposed to radial lirae, which are continuous all around the aperture (except in repaired shell breakages), of relatively uniform strength, and with a sharp outline in cross section. Although the shells of the Early and Middle Jurassic *Calliphyloceras* described here are calcified, layer boundaries can be readily recognized and the unusual preservation of an undescribed outer layer covering the lirata surface lead us to infer a very distinctive morphogenetic process for these radial lirae.

2. Material

Observations presented here are derived from three phragmocones of immature specimens of *Calliphyloceras* cf. *C. nilssoni* from the paleontological collections of the Université Claude Bernard Lyon 1 (France). The morphology of the outer shell is well preserved but pervasive re-crystallization has partially obscured the details of the shell microstructure. These specimens were collected by De Riaz and Rebours in the late nineteenth century from pink micritic limestone of late Toarcian age at Saint-Romain-au-Mont-d'Or, 15 kilometres northwest of Lyon (France). Additional Callovian representatives of *Calliphyloceras disputabile* from Madagascar are also used in this study. A large calcitized specimen, first described for taxonomic purposes by Joly (1976, pl. 13, fig.1), comes from locality 51 of the Collignon collection housed at the Université de Bourgogne, Dijon (France). An additional fragmentary specimen of *Calliphyloceras* sp. indet. of Upper Oxfordian-Lower Kimmeridgian age from the Morondava Basin (Madagascar) with a preserved aragonitic lirata shell allowed further investigation of the microstructure. All specimens were examined with light microscopy; only the aragonitic specimen was studied with SEM.

3. Shell structure and mode of growth

As in some other phylloceratids, the shell of *Calliphyloceras* bears the sharp, continuous and sinuous raised lines designated as radial lirae. The distance between two consecutive lirae increases progressively from the umbilical shoulder to the venter. The spacing of radial lirae generally increases with shell size, but may display some superimposed, short term fluctuations affecting up to ten consecutive lirae. Among ammonoid workers, there is an implicit assumption fuelled by the confu-

sion with growth lines, that the lirata surface of the shell corresponds to the outermost calcareous layer, namely the outer prismatic layer. In fact, close examination of many specimens of *Calliphyloceras* reveals that a few of them have a lirata-bearing layer still partly covered with a thin, brittle and wavy layer (Fig. 1A and 1B). Further preparation of shell sectors still embedded in limestone consistently indicates that this additional layer rests directly on the lirata surface of the shell all around the whorl. Median sections also reveal that this layer is preserved on the earlier whorls, where protected by whorl overlap (Fig. 1C and 1D). As illustrated in Figure 1B, the unusual morphology of this layer results from the juxtaposition of parallel tubular units whose trajectories are strictly parallel to those of the radial lirae, with an invariable one-to-one correspondence. Following the spacing of lirae, the spiral length of the tubular units increases from the umbilical margin to the venter.

Closer examination of this outermost layer, where superficially cracked away (see Fig. 1B) reveals that each unit is a hollow structure filled with sparry calcite. This justifies the term 'tubular' as a first approximation for its general outline. For each unit, the enfolding layer is very thin (from 10 to $50\ \mu\text{m}$). This layer rises up from the crest of the preceding lirata and then gently arches towards the aperture. The adapical side of each folded layer is generally steeper and shorter than its adoral side. It also appears that the adoral limit of the folded layer is free, i.e. not in contact with the next adoral unit, nor with the lirata layer. Hence, the morphology of this discontinuous layer is better described as consisting of imbricated, tile-shaped slats.

The single aragonitic, fragmentary specimen of *Calliphyloceras* has a well-preserved lirata shell with angular periodic thickenings, but the outermost layer has been dissolved. The periodic varices of the shell displayed by some of the phylloceratids are known to develop only in the nacreous layer (Birkelund 1981). SEM examination of a thin section confirms that the lirata layer is in fact the nacreous layer, with typical columnar stacks of aragonitic crystals. It also shows the absence of any internal discontinuities linked with the superficial radial lirae. These observations strongly support the recognition of the next overlying, tile-shaped layer of other calcified specimens as being the outer prismatic layer.

As seen on calcified specimens, thin sections perpendicular to this outer, presumably prismatic layer, do not disclose other preserved microstructure (Fig. 1C and 1D). Nevertheless, these sections highlight the structurally discontinuous secretion of the outermost layer of *Calliphyloceras*, thus implying a similarly discontinuous secretion of the periostracum. A complete outer prismatic layer unit starts at the sharp bending point of the preceding unit marked by an angle of about 90° , extending forward with a shallow curvature until it rises up abruptly with a sharp angle and projects forward into a low, arched shape. No shelly material is deposited beyond the projected end of the segment.

Hence, the open space between the oral termination of a

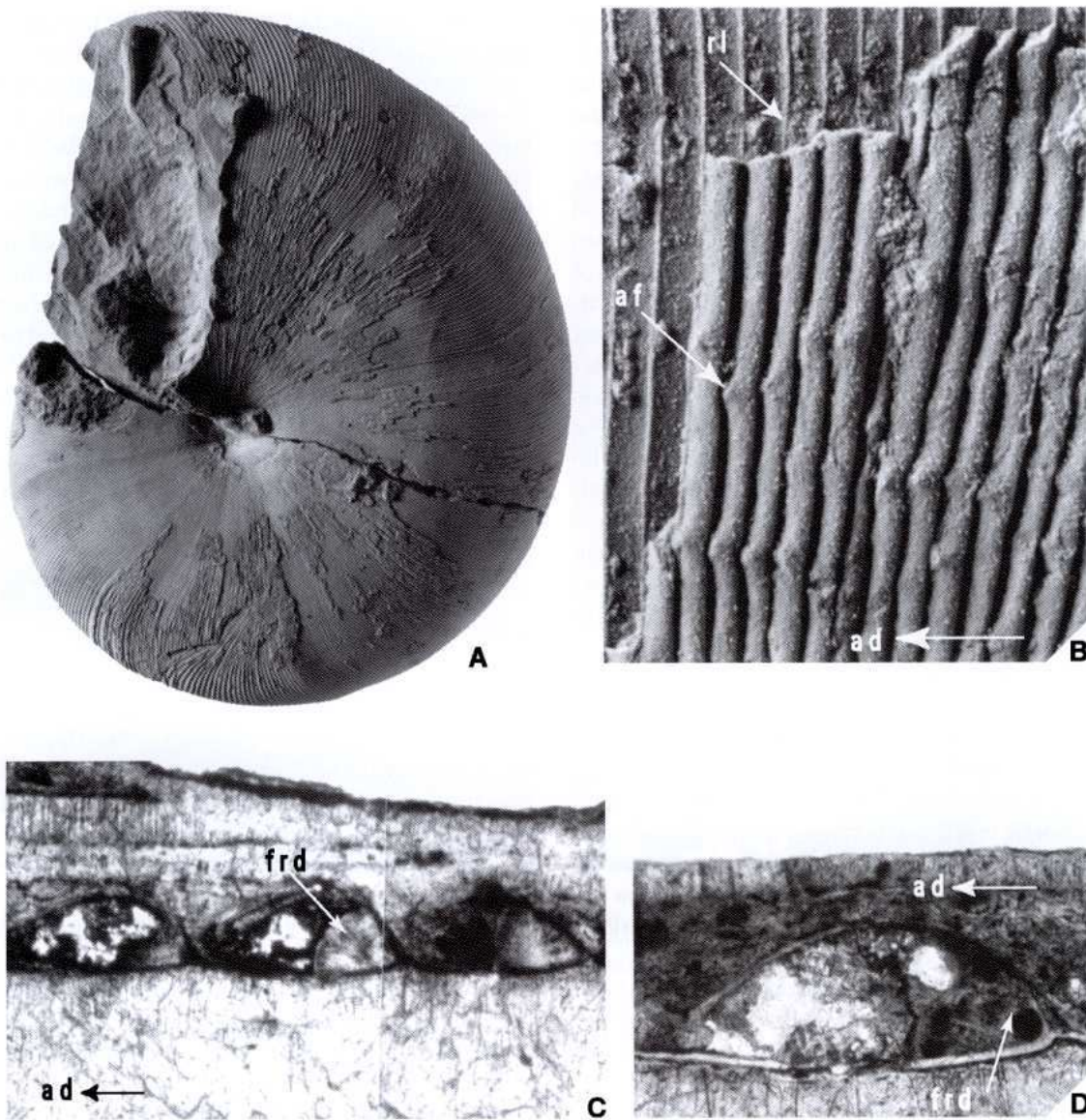


Fig. 1. A, *Calliphylloceras disputabile* (ZITTEL) from the Callovian of Madagascar (GD 13067, Université de Bourgogne); lateral view ($\times 0.5$) showing partial preservation of the outer prismatic layer covering the lirate, calcified nacreous layer. B, *Calliphylloceras* cf. *C. nilssoni* (HÉBERT) from the Toarcian of Saint-Romain-au-Mont-d'Or (France) FSL 431113; close-up view ($\times 10$) of the right flank showing slats of preserved outer prismatic layer covering the lirate surface of the calcified nacreous layer (direction of growth to the left). C-D, *Calliphylloceras* cf. *C. nilssoni* (HÉBERT) from the Toarcian of Saint-Romain-au-Mont-d'Or (France) FSL 99932; thin sections ($\times 50$ and $\times 20$) perpendicular to the shell wall showing the imbrication of the outer prismatic layer. Abbreviations: ad: adoral direction; af: adoral fold; frd: fibro-radiate deposit; rl: radial lira.

unit and the rear of the arched part of the next unit (see Fig. 1C), as well as the space between the uppermost part of the projected outer layer and the dorsal layer of the next overlapping whorl (see Fig. 1D), set an uppermost limit for the thickness of a periostracal sheet. As displayed by the section illustrated in Figure 1D, the thickness of the empty space filled by opaque, organic matter below the dorsal layer of the next overlapping whorl amounts to *c.* 80 μm , which gives a maximum order of magnitude for the thickness of the periostracum. As pointed out by Kulicki (1996), no periostracal layer has ever been documented among ammonoids, which can be easily

explained because of the dominantly proteinaceous composition of molluscan periostracum. In *Calliphylloceras*, the adorally open, cylindrical cavities formed by the overlap of two consecutive units as well as the space between the projected outer layer and the dorsal layer of the next overlapping whorl often display concentrations of dark, opaque organic matter. Beside the microfolds visible on the outer prismatic layer of some exceptionally well-preserved ammonoids (Landman & Lane 1997), this particular concentration of organic matter provides further evidence for the presence of a periostracal layer in ammonoids.

The free adoral end of each unit of outer prismatic layer implies that its secretion must have been interrupted and followed by a withdrawal of the periostracal groove back to the junction line with the preceding slat. Then, secretion of the outer prismatic layer resumed with a new unit, and the nacreous layer was secreted only after this new cycle initiated. Only such a sequence of events explains why the lirata surface of the nacreous layer does not faithfully reflect the inner surface of the projected outer prismatic layer but only the image of the juxtaposed adapical parts of each slat of the outer prismatic layer. Apart from oblique growth lamellae, absence of any major coincident discontinuities in the lirata nacreous layer clearly supports that its deposition took place after completion of the last folded slat of the outer prismatic layer. Thus, radial lirae arise as a structural by-product of the secretion of elementary and overlapping tile-shaped slats of the outer prismatic layer.

Such a by-product is highly significant for the analysis of the morphogenetic processes underlying the growth of an organism and is an example of what Seilacher (1973) called "fabricational noise". The morphogenesis of lirae in *Calliphylloceras* is thus clearly distinct from that of ordinary growth lines, which first occur on the periostracum when expelled from the periostracal groove and prior to its mineralization, as well illustrated by Checa (2000) for freshwater unionid bivalves. Moreover, ordinary growth lines do not involve discontinuities in the outer prismatic layer. Interestingly, although cross sections of the lirata, nacreous layer of the aragonitic specimen do show growth lamellae, no growth lines are visible between the lirae on the surface of the nacreous layer of either aragonitic or calcified specimens.

Ward (1987, 1988) and Ward and Saunders (1997) documented the variation in the thickness and structure of the periostracum in *Nautilus* and *Allonautilus*. In *N. macromphalus* and *N. pompilius*, the periostracum is a very thin (1–5 μm thick), continuous sheet resting on the underlying prismatic shell layer. This topology is similar in *N. belauensis*, even though the periostracum is much thicker (c. 1 mm). In *Allonautilus scrobiculatus* the periostracum is strikingly different, being composed as a series of long (up to 10 mm in length) sheets extending outward from the shell wall and splitting into numerous thin layers from a thicker layer, which is itself sandwiched between increments of outer prismatic layer. Although the shape of the outer prismatic layer of *Calliphylloceras* is very different from that of *Allonautilus*, the topology of the discontinuities affecting the periostracum and the outer prismatic appears equivalent. However, the question of whether or not the periostracum of *Calliphylloceras* extended outward from the outer shell wall cannot be solved at present.

The common occurrence of small-sized open folds at the adoral end of each slat of outer prismatic layer is an additional feature of the outer prismatic layer in *Calliphylloceras* (Fig. 1B). The hinge and opening of the folds are oriented adorally. Large enough intact surfaces are not available for recognition of any pattern in the spatial distribution of the adoral

folds. Preserved surfaces only permit us to notice that they are apparently isolated or may be aligned, thus defining crude rows either parallel or oblique to the direction of growth. There are no imprints of these folds on the lirata nacreous layer. These features could theoretically be compatible with the accommodation of lateral compressive stress generated by the folding of the periostracum into an arched shape, combined with its anchoring all around the curved apertural margin. However, these adoral folds also occur on the flanks of the shell, where curvature is minimal and almost nil. Hence, the apparently ubiquitous occurrence of adoral folds along the apertural perimeter makes it difficult to consider compressional stress as a unique explanation. Strikingly similar adoral folds have been documented in the newly expelled outer periostracum of *Unio elongatus* (see Checa 2000, fig. 3), prior to any calcification. Such adoral folds may also conceivably accommodate a local excessive production of periostracum, an interpretation which is favored here.

4. Microsculptures

The surface of the nacreous layer of *Calliphylloceras* displays numerous and minute creases or wrinkles (Fig. 2A). In well-preserved ammonoids, Checa (1994) described and defined eight types of these fold-like irregularities called 'microsculptures'. In *Calliphylloceras*, these folds are generally perpendicular to the lirata, bounded by pairs of consecutive lirata and are somewhat off set from one lira to the next. Their length and strength are variable. They generally begin either on the adoral crest of a lira or within an inter-crest space, and disappear on the adapical slope of the next crest. Their adapical end is usually thin and extremely sharp, and they tend to broaden adorally. However, some of these microfolds may bridge two consecutive crests, without change either in shape or in strength. They may fall into the microsculpture category 1 of Checa (1994, p. 866), i.e., the 'longitudinal wrinkles' described as 'tiny, closely spaced, low-relief wrinkles which appear at the intercostal valleys when ribs are more or less straight, and which fade out towards both rib slopes. They are without exception longitudinal, i.e., perpendicular to ribs'.

In a repaired injury (Fig. 2B), this longitudinal pattern is somewhat modified. Some wrinkles radiate from a single point forming an adorally divergent bundle, thus resulting into a 'drapery-like' pattern. This pattern is reminiscent of microsculpture category 3 of Checa (1994, p. 866), described as 'wrinkles associated with concave primary ribs'. In *Calliphylloceras*, the adorally concave repaired injury is obviously the cause of this mimetic pattern. The nacreous layer is formed after the secretion of a tile-shaped slat of the outer prismatic layer, and conforms to its shape. Thus, the microsculpture on the nacreous layer probably corresponds to the imprint of similar structures in the adoral part of each unit of outer prismatic layer. However, no specimens were available to study such a relationship.

Checa (1994) convincingly argued that these microsculp-

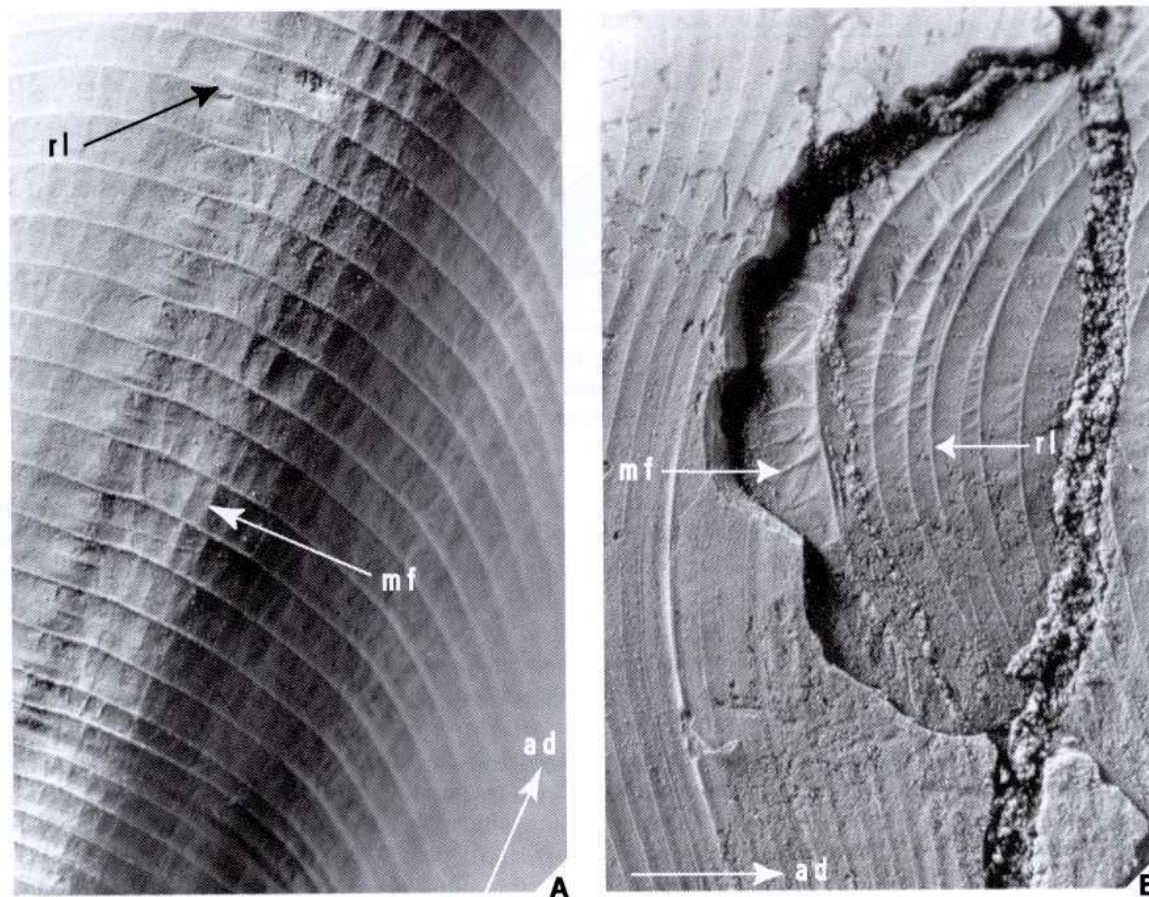


Fig. 2. *Calliphyloceras* cf. *C. nilssoni* (HÉBERT) from the Toarcian of Saint-Romain-au-Mont d'Or (France), FSL 99931. A, ventral view (*c.* $\times 12$) of the radial lirae between which longitudinal minutes creases intercalate; the raised rounded line follows the siphonal line (direction of growth up). B, repaired shell breakage on the lower left flank (*c.* $\times 12$); the newly secreted shell shows that the directions of microfolds converge towards the direction of maximal growth (direction of growth to the right). Abbreviations: ad: adoral direction; mf: microfolds; rl: radial lira.

tures initially formed in the periostracum prior to calcification of the shell as the result of stresses during growth. However, he hypothesized that the mantle initially extended beyond the last-formed apertural calcified margin and subsequently retracted, giving rise to a non-calcified rib in the periostracum. This rib was subsequently 'imprinted' on the outer prismatic layer. Checa interpreted the microsculptures as the result of compressive stresses that occurred on the uncalcified, passively-pulled-backward periostracum. This morphogenetic model for ammonite ribs generated by compressional folding was questioned by Bucher (1997) and Hammer & Bucher (1999) because it leaves many other ornamental characters unexplained. Furthermore, similar microsculptures documented on the smooth shell of *Baculites* by Henderson et al. (2002) also led these authors to discard the 'retraction' model for rib morphogenesis.

Although the microsculptures visible on the nacreous layer of *Calliphyloceras* may well have initiated on the uncalcified periostracum, their morphology is more suggestive of tensional rather than compressional features. They may have developed

in the periostracum under tensile stresses as a result of differential traction generated by minor differential displacements between longitudinal lines of attachment of the mantle margin and the periostracum during forward movement of the periostracal groove. In *Calliphyloceras*, the tensional nature of the microsculptures is also supported by the 'drapery-like' pattern of wrinkles occurring in the repaired injury.

5. Fibro-radiate deposits

Small calcitic deposits typically occur in cylindrical cavities of the outer layer (Fig. 1C and 1D). Close examination with a polarizing microscope reveals relicts of an acicular fibro-radiate structure in these calcified deposits, therefore indicating that these were originally aragonitic (P. Bernier, comm. pers. 2001). They invariably radiate from the junction line between two consecutive slats toward the oral termination of the projected unit, and their outer, free boundary suggests a somewhat spherulitic outline. Similarities in size, position and structure of these fibro-radiate deposits support a primary rather than dia-

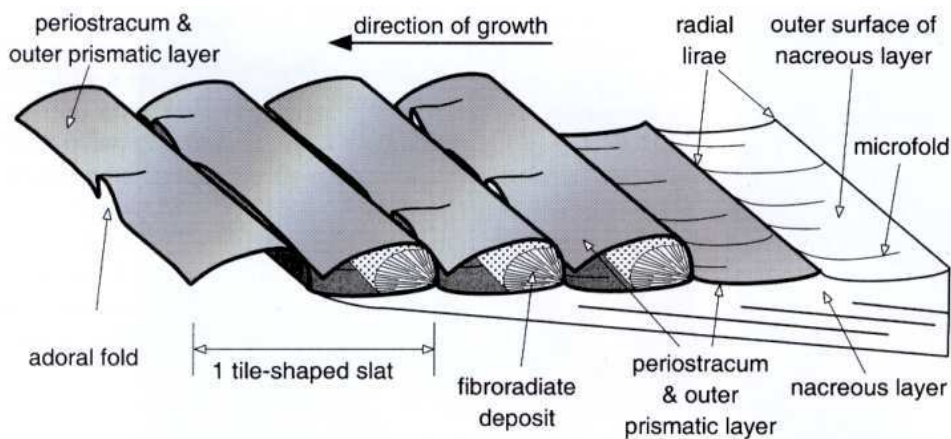


Fig. 3. Synthetic diagram of structures observed in the shell wall of *Calliphylloceras*. The shape of the periostracum is supposed to conform to that of the outer prismatic layer. The outer prismatic layer (grey) has been removed from the right part of the drawing in order to expose the radial lirae and microfolds visible on the nacreous layer.

genetic origin. Although organic sheets of periostracum acted as a matrix for the deposition of aragonitic crystals, the mineralization of these fibro-radiate deposits probably did not occur in the periostracal groove, nor in the extrapallial cavity. Their growth had to proceed without direct control of the mantle ('remote biomineralization') in the nearly closed cavities constructed by the overlapping slats of the outer prismatic layer. Remote biomineralized infillings separated from secreting tissues are thought to occur in other fossil and extant cephalopods, such as calcified pillars in the *Sepia* cuttlebone, a chalky layer connecting the septal necks of *Spirula*, the spicular layer of the connecting ring of *Nautilus* or the cameral deposits in some fossil nautiloids and belemnoids (Fischer & Teichert 1969; Bandel & Boletzky 1979; Crick 1982; Ward 1987; Bandel & Spaeth 1988; Seilacher & Chinzei 1993). However, this first evidence of remote precipitation of aragonite inside the shell wall of an ammonoid resembles the fill skeletons in cavernous oyster shells described by Chinzei & Seilacher (1993). The relative timing of precipitation of these deposits cannot be determined from the available material, although it can only have formed after completion of the next adoral unit composed of periostracal and outer prismatic layers.

4. Discussion

All our observations on the shell wall of *Calliphylloceras* are summarized in Figure 3. From a morphogenetic point of view, it appears that these overlapping, projected and relatively short growth increments are not easily compatible with elaborated ornamentation such as oblique ribs, tubercles, closed spines, or clavi. A likely explanation is that all such ornamental patterns require the secretion of long enough stretches of uninterrupted periostracum, because a minimal domain size is required for patterning under the control of activator-inhibitor processes (Hammer & Bucher 1999). Repeated and closely spaced retreats of the secreting edge of the mantle accompanied by cellular reorganization as imposed by the mode of growth of *Calliphylloceras* thus preclude the development of complex spatial patterning in which diffusion over minimal distances plays a critical role.

Among other phylloceratids, the structure of the shell wall of the Late Cretaceous *Hypophylloceras* (*Neophylloceras*) *groenlandicum* was first studied by Birkelund & Hansen (1974) and Birkelund (1981). Its shell wall also possesses cavities, but on the basis of these early studies, it is difficult to conclude if these are homologous or not with those resulting from the imbricated slats of outer prismatic layer in *Calliphylloceras*. However, recent investigations of the shell wall of *Phylloperoceras ezoense* and *Hypophylloceras subramosum* by Kulicki et al. (2001) unambiguously indicate that, in cross section, the so-called 'free periostracum' of these two genera agrees in plan with the outer prismatic layer (and periostracum) of *Calliphylloceras*. Kulicki et al. (2001) also note that the space engulfed by the partially overlapping slats of *Hypophylloceras subramosum* contains spherulitic calcium carbonate, which is an additional common trait shared with *Calliphylloceras*.

It is difficult to assert whether or not the structures so far described as radial lirae in other ammonoids are morphogenetically identical with those of *Calliphylloceras*. To our knowledge, a topology of the outer prismatic layer similar to that described in this genus has so far not been reported, which may simply reflect very rare preservation of this fragile layer. For instance, the lirae outer surface of the nacreous layer of other phylloceratids such as *Ussurites* and *Monophyllites*, both of Middle Triassic age and included into the Ussuritidae, compares well with that of *Calliphylloceras*, but no trace of any outer prismatic layer has been observed. If one makes the assumption that radial lirae are homologous within Triassic phylloceratids, then the smooth, lirae-free nacreous layer of Paleophyllitidae (*Paleophyllites*, *Leiophyllites*, *Stenophyllites*, etc.), which are the oldest known Phylloceratida of late Early Triassic age (Spathian), suggests that radial lirae represent a derived state of the mode of growth.

Some features labelled as radial lirae may possibly have formed under the control of a non-accretionary process, as proposed by Klofak et al. (1999) for the ammonitella of some Devonian ammonoids. These authors describe a Devonian *Archanarcestes obesus* in which the ammonitella and 0.75 whorls of the post embryonic portion are reported to preserve

the outermost shell layer, allowing a close examination of the external ornament of both the embryonic and post embryonic parts of the shell. The embryonic spaced lirae (average spacing of c. 50 µm) are described as symmetrical sharp ridges. Growth lines intercalated between lirae only occur on the post-embryonic shell of *Archanarcestes obesus*, whereas minute longitudinal creases or wrinkles resembling those observed on the post-embryonic nacreous layer of *Calliphylloceras* occur between the embryonic lirae. Absence of growth lines on the embryonic shell was used by Klofak et al. (1999) to support a non-accretionary mode of growth of the ammonitella, the consequence of which is that radial lirae and longitudinal microfolds may also form in a non-accretionary mode of growth. This illustrates the great difficulties in identifying homologous shell characters among ammonoids. Finally, the same topology of shell layers as that described here in *Calliphylloceras* is also found in some Cretaceous 'ribbed' nautilids (e.g. *Cymatoceras*, Chirat & Bucher, pers. observation), suggesting that this mode of growth occurred several times among coiled, externally shelled cephalopods.

Finally, the major discontinuities cutting across the shell of ammonoids can be grouped into three topologies, depending on what layers are affected. Absence of any major constructional discontinuities in all layers secreted at the aperture (periostracum, outer prismatic and nacreous layers) represents the simplest topology, thus implying a continuous secretion. Thin growth lines are then formed directly on the newly formed periostracum prior to calcification. Discontinuities involving simultaneously the periostracum and the outer prismatic layer represent a second topology, implying a moderate retreat of the mantle separating two consecutive growth increments. The imbricated slats made of outer prismatic layer in *Calliphylloceras* illustrate this category. Discontinuities cutting simultaneously across all three layers, termed megastriae by Bucher & Guex (1990), characterize a third topology, indicating a major withdrawal of the mantle between two consecutive growth increments. Such different topologies suggest that distinct morphogenetic mechanisms controlling the movements and secreting activity of the mantle edge were at play in the accretionary mode of growth of the ammonoid shell.

Acknowledgements

W. Weitschatt (Universität Hamburg) provided a specimen of *Calliphylloceras* preserved in aragonite. P. Bernier (Université Claude Bernard Lyon 1) gave us useful insights about remote biomineralization. N. Podelvigne (Université Claude Bernard Lyon 1) is thanked for photographic work. C. Klug and N. Landman improved a draft version of the manuscript. S. Lucas and F. Cecca are thanked for their constructive reviews, which improved the final version.

REFERENCES

- ARKELL, W. J. 1957: Introduction to Mesozoic Ammonoidea. In: Treatise on Invertebrate Paleontology. Part L (Mollusca 4), (Ed. by MOORE, R. C.). Geological Society of America and University of Kansas Press L81-L219.
- BANDEL, K. & BOLETZKY, S. VON 1979: A comparative study of the structure, development and morphological relationships of chambered Cephalopod shells. *The Veliger* 21, 313–354.
- BANDEL, K. & SPAETH, C. 1988: Structural differences in the ontogeny of some Belemnite rostra. In: *Cephalopods—Present and Past* (Ed. by WIEDMANN, J. & KULLMANN, J.). Schweizerbart'sche Verlagbuchhandlung, 247–271.
- BIRKELUND, T. 1981: The ammonoid shell structure. In: *The Ammonoidea* (Ed. by HOUSE, M. R. & SENIOR, J. R.). The Systematics Association Special Volume 18, Academic Press, 177–214.
- BIRKELUND, T. & HANSEN 1974: Shell ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their taxonomic implications. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* 20/6, 34pp.
- BOND, P. N., & SAUNDERS, W. B. 1989: Sublethal injury and shell repair in Upper Mississippian ammonoids. *Paleobiology* 15, 414–428.
- BUCHER H. 1997: Caractères périodiques et mode de croissance des ammonites: comparaison avec les gastéropodes. *Géobios, Mémoire Spécial* 20, 85–99.
- BUCHER H. & GUEX, J. 1990: Rythmes de croissance chez les ammonites triasiques. *Bulletin de la Société Vaudoise des Sciences Naturelles* 80, 191–209.
- BUCHER H., LANDMAN, N. H., KLOFAK, S. M. & GUEX, J. 1996: Mode and rate of Growth in Ammonoids. In: *Ammonoid paleobiology*. (Ed. By LANDMAN, N. H., TANABE, K. & DAVIS, R. A.). Plenum Publishing Corporation, 407–461.
- CHECA, A. 1994: A model for the morphogenesis of ribs in Ammonites inferred from associated microsculptures. *Palaeontology* 37, 863–888.
- 2000: A new model for periostracum and shell formation in Unionidae (Bivalvia, Mollusca). *Tissue and Cell* 32, 405–416.
- CHINZEI, K. & SEILACHER, A. 1993: Remote biomineralization I: fill skeletons in vesicular oyster shells. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 190, 349–361.
- CRICK, R. 1982: The mode and tempo of cameral deposit formation: evidence of orthoconic nautiloid physiology and ecology. *North American Paleontological Convention III*, 1, 113–118.
- DOGUZHAIEVA, L. 1982: Rhythms of Ammonoid shell secretion. *Lethaia* 15, 385–394.
- FISHER, A. G. & TEICHERT, C. 1969: Cameral deposits in cephalopod shells. *The University of Kansas Paleontological Contributions Paper* 37, 1–30.
- HAMMER, Ø. & BUCHER, H. 1999: Reaction-diffusion processes: Application to the morphogenesis of ammonoid ornamentation. *Géobios* 32, 841–852.
- HENDERSON, R.A., KENNEDY, W.J. & COBBAN, W.A. 2002: Perspectives of ammonites paleobiology from shell abnormalities in the genus *Baculites*. *Lethaia* 35, 215–230.
- JOLY, B. 1976: Les *Phylloceratidae* malgaches au Jurassique. Généralités sur les *Phylloceratidae* et quelques *Juraphyllitidae*. *Documents des Laboratoires de Géologie de Lyon* 67, 471 pp.
- KLOFAK, S. M., LANDMAN, N. H. & MAPES, R. H. 1999: Embryonic development of primitive ammonoids and the monophyly of the Ammonoidea. In: *Advancing research on living and fossil Cephalopods: Development and evolution: Form, construction and function: Taphonomy, paleoecology, paleobiogeography, biostratigraphy and basin analysis* (Ed. by OLÓRIZ, F. & RODRÍGUEZ-TOVAR, F. J.). Kluwer Academic/Plenum Publishers, New York, 23–45.
- KORN, D. & PRICE, J. 1987: Taxonomy and phylogeny of the *Kosmoclymeniinae* subfam. nov. (Cephalopoda, Ammonoidea, Clymeniida). *Courier Forschungsinstitut Senckenberg* 92, 5–75.
- KULICKI, C. 1996: Ammonoid shell microstructure. In: *Ammonoid paleobiology* (Ed. by LANDMAN, N.H., TANABE, K. & DAVIS, R.A.). Plenum Publishing Corporation, 65–101.
- KULICKI, C., TANABE, K., LANDMAN, N.H. & MAPES, R.H. 2001: Dorsal shell wall in ammonoids. *Acta Palaeontologica Polonica* 46, 23–42.
- LANDMAN, N. & LANE, J.A. M. 1997: Foldlike irregularities on the shell surface of Late Cretaceous ammonoids. *American Museum Novitates* 3197.

- SEILACHER, A. 1973: Fabricational noise in adaptative morphology. *Systematic Zoology* 22, 451–465.
- & CHINZEL, K. 1993: Remote biomineralization II: Fill skeletons controlling buoyancy in shelled cephalopods. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 190, 363–373.
- WARD, P. D. 1987: *The Natural History of Nautilus*. Allen and Unwin, Boston.
- 1988: Form and Function of the *Nautilus* shell: some new perspectives. In: *The Mollusca*, 11 (Ed. by BIGGELAR, P.), Academic Press, New York, 143–165.
- WARD, P. D. & SAUNDERS, W. B. 1997: *Allonautilus*: a new genus of living nautiloid cephalopod and its bearing on phylogeny of the Nautilida. *Journal of Paleontology* 71, 1054–1064.

Manuscript received June 25, 2003

Revision accepted September 28, 2003