JEAN-PIERRE CUIF

MICROSTRUCTURE *VERSUS* MORPHOLOGY IN THE SKELETON OF TRIASSIC SCLERACTINIAN CORALS

CUIF, J. F.: Microstructure *versus* morphology in the skeleton of Triassic scleractinian corals. Acta Palaeont. Polonica, 25, 3/4, 361—374, January 1981.

The systematics of Triassic corals based on morphological characters (Alloiteau 1952, Wells 1956) has been examined. It has been shown that microstructural characters are more valuable than morphological ones as systematic criteria for scleractinian corals. An outline of Triassic coral evolution has been presented and the premises, on which the classic concept of independent rugosan and scleractinian phylogenies is based, are refuted.

Key words: Corals, Triassic Scleractinia, systematics, phylogeny.

Jean-Pierre Cuif, Université de Paris-Sud, Centre d'Orsay, Laboratoire de Paléontologie, Bâtiment 504, 91405 Orsay-Cedex, France. Received: September 1979.

INTRODUCTION

According to the classic concept of Haeckel (1896), the post-Palaeozoic corals (Scleractinia) form a group completely independent of the Rugosa (Palaeozoic corals), which are considered to become extinct in the late Permian. In this diphyletic scheme, it is generally agreed that the Rugosa differ from the Scleractinia in three fundamental respects: (1) Ontogeny: bilateral development and serial septal insertion in the Rugosa; radial symmetry with cyclic and alternate septal insertion in the Scleractinia; (2) Mineralogy: it is generally agreed that Palaeozoic corals had a calcitic skeleton but from the Triassic onwards, the skeleton was composed of aragonite; (3) Histology of skeleton: the size and morphology of the skeletal elements are usually taken to support the diphyletic theory. The Scleractinia are considered to have fibres exclusively of small diameter (up to 1 micrometre) and to lack lamellar elements, whereas the Rugosa are supposed to have much thicker fibres and to have lamellar elements.

The diphyletic theory is also supported by the fact that at the end of the Palaeozoic the rugose corals display progressive extinction: at the end of the Upper Permian (Flügel 1970) the number of genera decreases from 23 in the *Yabeina* Zone to 15 in the *Codonofusiella* Zone and to 8 in the *Palaeofusulina* Zone, which marks the end of the Permian.

Thus, according to this theory the Scleractinia are a group of independent origin, comprising the families which have evolved during the Mesozoic and Tertiary and leading to the coral faunas of the Present Day. The definition of taxa of higher rank (family groups) is therefore particularly important. The most recent works on the general systematics of fossil Scleractinia (Alloiteau 1952 and Wells 1956) are clearly in agreement on this subject: a comparison of the classifications advocated by these two authors shows a significant similarity in the grouping of genera, although the family names may differ. The families, however, are very differently placed within the general classification, reflecting the divergence of opinion between these authors on the general evolution of the main coral groups during the Mesozoic. Thus it is the validity of the family groupings which must be resolved before the general phylogeny of the Triassic Scleractinia can be considered.

CONSEQUENCES OF THE INTRODUCTION OF MICROSTRUCTURAL CRITERIA FOR THE CLASSIFICATION OF TRIASSIC SCLERACTINIANS

The influence of microstructural criteria on the present classification of Triassic scleractinians is illustrated by three families which are considered among the best defined: Stylophyllidae Volz, 1896, Montlivaltiidae Dietrich, 1926 and Procyclolitidae Wells, 1943.

1. Studies on the family Stylophyllidae Volz, 1896

The type genus of the family, *Stylophyllum* Volz, includes corals united by well defined morphological characteristics: superposed concave tabulae pierced by vertical septal spines. Microstructurally, these corals are formed of undifferentiated fibrous tissue in continuous concave laminae. Vertical digitate invaginations of successive fibrous laminae are in contact to form the characteristic septal spines (fig. 1).

Features of the same general pattern are found in another genus of the family, *Stylophyllopsis* Frech, 1890, the only difference being a regular arrangement of the septal spines in the latter.

The third genus assigned by Alloiteau (1952) and Wells (1956) to the Styllophyllidae is *Protoheterastraea* Wells, 1937, the taxon separated out of *Hexastraea* Volz, 1896 but limited by Montanaro-Gallitelli to specimens comparable to *Hexastraea leonhardi* Volz, 1896 (Volz 1896: pl. 11: 21—25, except 24).

The microstructure is very variable in *Protoheterastraea* in comparison with that in the two previous genera: three distinctly differentiated microstructural regions may be distinguished. The major septa are formed by divergently arranged more or less elongated axes of convergence. The septa are inserted on the internal face of the wall through an intermediate zone in which the divergence between the fibre fascicles is always very distinct. This is also true of the septa of the second and third cycles. The wall structure is entirely different from that of the septa: it is formed by radially oriented fibres growing centripetally. This type of microstructure,

which is known in specimens from the Dolomites and from Turkey, is thus very different from that in *Stylophyllum,* close to which *Protoheterastraea* has been recently classified (fig. 2).

Cyathocoenia, the fourth genus assigned to the *Stylophyllidae,* shows microstructural characteristics confirming the heterogeneity of this family group. In fact, this genus includes two species which differ very strongly from each other and have nothing in common with *Stylophyllum:*

— *C. andraeai*: this is a cerioid form, in which the septa are formed by perfectly centered vertical trabeculae of small diameter which are slightly disjointed distally; (see Cuif 1972, 1977*b*);

— *C. milchi*: very small corals in which the theca is formed of two distinct layers: the external one is thin, fibrous, invaginating radially to form septa of typical
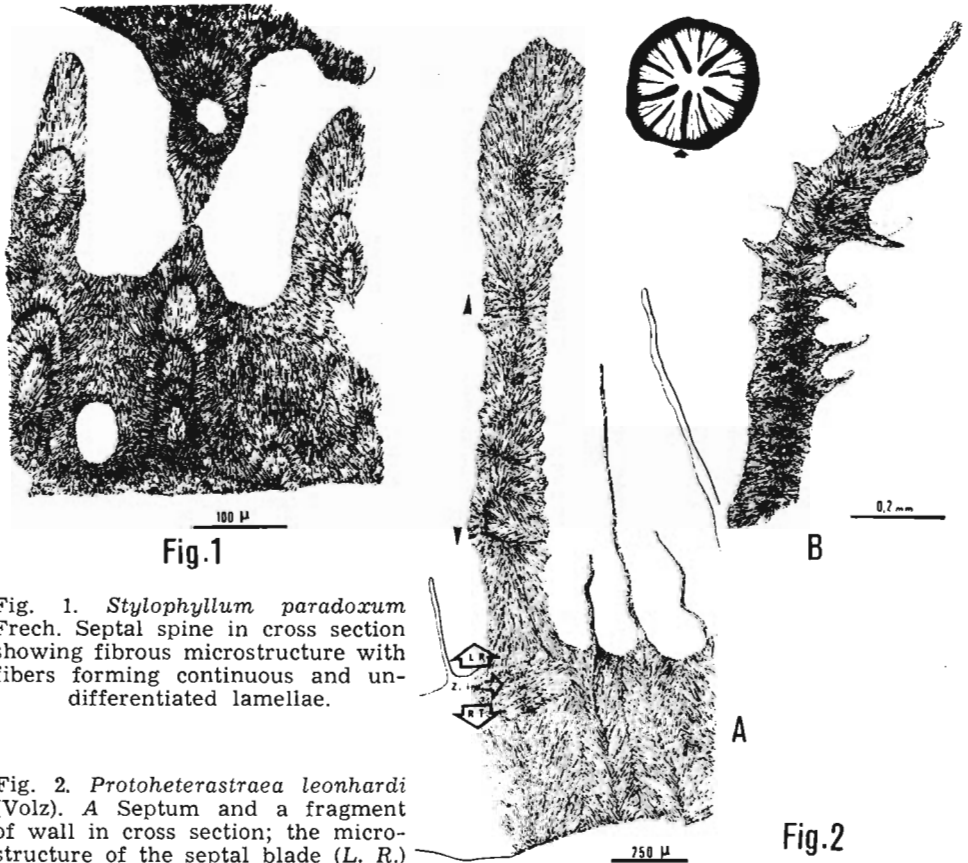

Fig.1

Fig. 1. *Stylophyllum paradoxum* Frech. Septal spine in cross section showing fibrous microstructure with fibers forming continuous and undifferentiated lamellae.

Fig. 2. *Protoheterastraea leonhardi* (Volz). A Septum and a fragment of wall in cross section; the microstructure of the septal blade (*L. R.*) is differentiated, an intermediate zone (*Z. int.*) composed of fine centres of convergence is developed between the septal blade and wall (*R. T.*); the wall is formed of radial fiber fascicles which continue centripetally as septa of the second cycle. B Cross section of the septum of the second cycle in the zone of gemmation: axes of convergence well defined, diverging; lateral spines develop.

archaeothecal development; the inner layer is lamellar and abuts against the septa (see Cuif 1972, 1977b).

Coccophyllum comprises phaceloid or cerioid colonial corals in which the septal apparatus is weakly developed in contrast to the very strong endotheca. Within the very thick wall of these corals vertically centred systems are differentiated forming nontrabecular septa, whilst slightly concave downwards tabulae continue into the fibrous layers of the wall (see Cuif 1972, 1977b).

Value of the family Stylophyllidae. — An analysis of the main characters of the genera constituting the family Stylophyllidae shows that this taxon as currently understood, is highly heterogeneous even if the analysis is limited to the Triassic members of the family.

2. Analysis of the Triassic representatives of the family Montlivaltiidae Dietrich, 1926

The second important family represented in the Triassic coral fauna is the Montlivaltiidae, in which recent authors (Alloiteau 1952 and Wells, 1956) have placed many solitary and phaceloid to dendroid forms. A great diversity of structural types is found in the Triassic representatives.

a. Triassic Montlivaltia:

Example: Montlivaltia norica Frech, 1890. — The detailed analysis of examples of this species is particularly important because the structural development of the septa during ontogeny follows a pattern common to many Triassic forms, which is therefore of great significance in establishing phylogenetic relationships (fig. 3*ABC*).

In early ontogenetic stages, septa in *M. norica* are formed of undifferentiated fibrous tissue, the fascicles of which are inserted on an irregularly undulating continuous medioseptal plane. Very short axes of convergence deviate highly obliquely from this plane. They are few, irregularly disposed and always well separated from each other.

At the end of their ontogenetic development, septa in *M. norica* have a quite different structure that is nevertheless directly based on the structure of the juvenile stage. During development the medioseptal zone takes on a very regularly zigzag form. Furthermore the lateral axes deviate consistently from the longitudinal crests formed by the zigzags. These lateral axes are always parallel, regularly developed and in contact, thus producing on both sides of the medioseptal plane a double layer that results in the considerable thickness of the major septa.

Thus true trabeculae are lacking in this species: during septal ontogeny the medioseptal plane never separates into the distinct and centered axes of convergence characteristic of the type species of *Montlivaltia* — *M. caryophyllata* from the Bathonian of Ranville (Alloiteau 1957; Gill and Lafuste 1971).

In true *Montlivaltia* the lateral axes deviate symmetrically from the trabecular axis, whereas in *Montlivaltia norica,* in the absence of true trabecular axes, the lateral axes alternate because of their location along the crests of the undulating
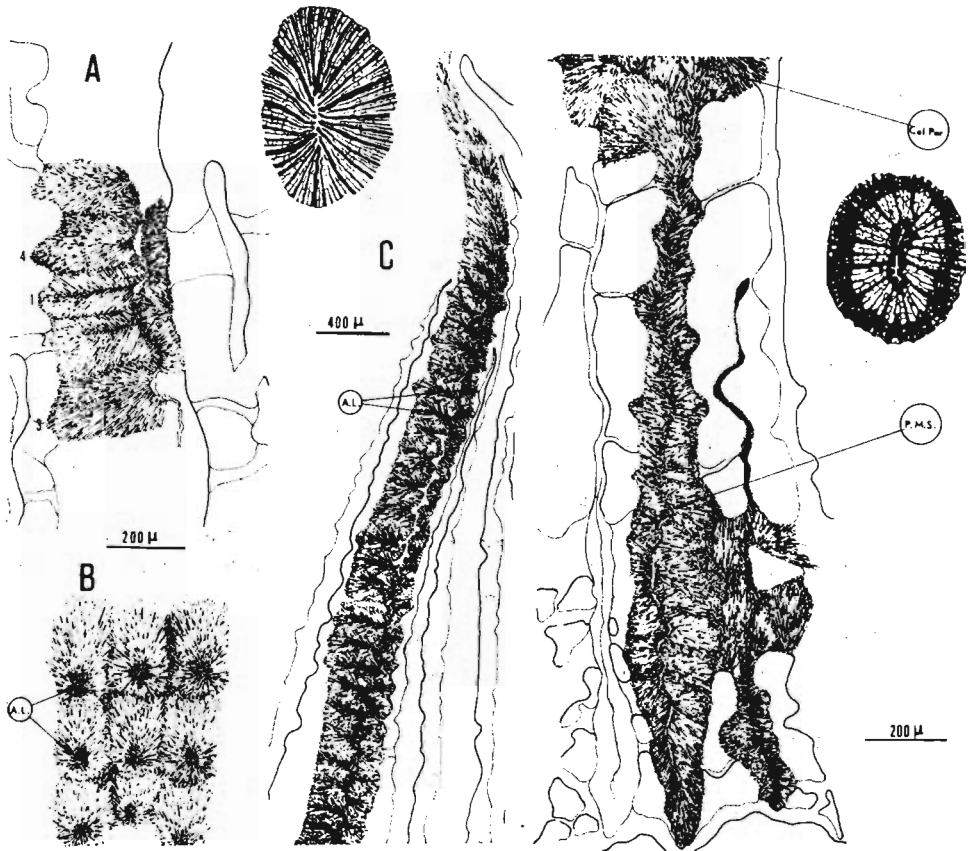
Fig. 3

Fig. 4

Fig. 3. Microstructure of *Distichophyllia norica* (Frech). *A* Lateral septal axes cut transversally on different levels: *1* sagittally and *2, 3, 4* parasagittally. *B* Major septum in longitudinal radial section showing lateral axes (*A. L.*) in subperpendicular section. *C* Major septum in cross section; a continuous medioseptal plane undulates forming vertical alternating crests from which lateral axes subperpendicular to the medioseptal plane diverge.

Fig. 4. *Retiophyllia fenestrata.* (Reuss). Cross section showing costo-septum formed of convergent fiber fascicles determined by vertical undulations of perfectly continuous medioseptal plane (*P. M. S.*).

medioseptal plane. Thus, the septal structure in the Triassic *"Montlivaltia"* differs fundamentally from that in the type species. Furthermore, the structural development of the septa during ontogeny provides good evidence of affinity with forms in which the medioseptal plane is undifferentiated.

A similar situation may be observed in the majority of the Triassic species assigned to *Montlivaltia* which indicates that during the Triassic this type of septal structure is representative of an important part of the fauna and must be reflected in the systematics.

b. Triassic Thecosmilia:

Investigation of Triassic species assigned to *Thecosmilia* confirms the results found in Triassic *Montlivaltia* but with a greater degree of variation.

Example: Variation of septal microstructure within the species group T. subdichotoma — T. sublaevis — T. badiotica. — In this group of phacelo-dendroid forms, microstructural analysis of serial sections shows the following general characteristics:

— septa: on both sides of the continuous medioseptal plane, fibre fascicles are inserted perpendicularly to form septa showing very little variation. In places, short lateral axes result in an irregular ornamentation (fig. 8).

— wall: thick, formed of fibre fascicles with centripetal growth, orientated radially and obliquely upwards.

This type of microstructure is very variable, even within the same corallite (development of ornamentation, relationship of the septum to the wall). It is evident that these forms cannot be assigned to *Thecosmilia,* the microstructure of which is identical to that of true *Montlivaltia.*

Example: Thecosmilia fenestrata. — This form, known from the Zlambach marls, has a microstructure similar to that of the previous group but differing in the following points (fig. 4):

— the medioseptal plane is continuous but irregularly undulating, corresponding to the flexures of the distal edge in the vertical plane;

— correspondingly fibres are grouped into fascicles centered along the edge of the resultant crests;

— lastly, the wall is reduced to a thin epithecal layer resting on the external wedge-shaped edges of the septa.

This type of microstructure cannot be maintained within the family Montlivaltiidae as defined on the microstructure of the type species.

These observations are valid for the majority of the forms presently assigned to the Montlivaltiidae, which no more than the previous family (Stylophyllidae), can be considered as representative of Triassic coral evolution.

3. Investigation of the family Procyclolitidae Vaughan et Wells, 1943 (= Conophyllidae Alloiteau, 1952+Procyclolitidae Vaughan et Wells, 1943 emend. Alloiteau, 1952)

This complex family comprises seven Triassic genera and constitutes according to Wells (1956) a major group in the fauna of this period. He regards the family Procyclolitidae as having given rise to the most important branches evolving during the Mesozoic. Two of these genera (*Margarophyllia* and *Margarosmilia,* see Cuif 1974b) have a microstructure similar to that in the Triassic "*Montlivaltia*" discussed above. A third (*Triadophyllum*), with a very brief diagnosis, has not been found in the beds I have examined. The remaining four genera, as in previous cases, have very different septal microstructures.

— *Procyclolites*: septal structure continuous, with very large fibre fascicles inserted in a medioseptal zone which is organized into regularly alternating sectors to form typical lateral carinae (fig. 5).
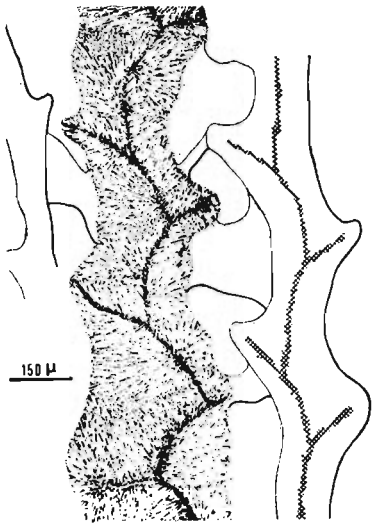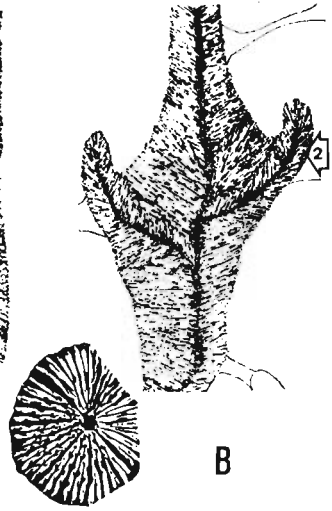
Fig.5

Fig.6

Fig. 5. *Procyclolites triadicus* Frech. Longitudinal section perpendicular to the septal plane showing fiber fascicles perfectly convergent which diverge from the medio-septal plane; microstructure resembling that of *Craspedophyllia*.

Fig. 6. *Craspedophyllia alpina* (Loretz). Longitudinal section (*B*) showing lateral axes forming lateral carinae (menianae) and (*A*) transversal section on the same level (*2*) showing the synchronously growing axes fused together laterally.

— *Craspedophyllia*: septa with lateral carinae, but formed here by the synchronous growth of lateral axes, a structure comparable with that in *Procyclolites* (fig. 6).

— *Conophyllia*: a complex genus comprising forms with true trabecular structure and well developed pennular ornamentation, e.g. *Rhopalophyllia* (see Cuif 1975*b*, 1977*b*).

— *Gigantostylis*: simple corals with a peculiar morphology and a microstructure differing from those of the preceding genera: centripetally orientated fibre fascicles are organised in concentric layers (see Cuif 1977*b*).

4. Conclusions

It follows that neither the classification of Alloiteau nor that of Wells reflects the real relationships of the principal groups during the initial phases of Scleractinian evolution. The introduction of microstructural data into the diagnoses shows that a fundamental conceptual modification of the major taxa of these authors is necessary.

This conclusion suggests a re-examination of the basis upon which the diphyletic scheme of Milne-Edwards and Haeckel is grounded. On the basis of many papers it has long been established that the three factors which support the fundamental subdivision of the major coral groups are much less decisive than suggested by the classic scheme.

The contrast in symmetry between the Rugosa and Scleractinia, respectively bilateral and radial, has been largely negated by embryological observations (Duerden for example) and by palaeontological work. Schindewolf's observations on the progressive change towards a cyclic arrangement of septa are well known, as are the investigations of Alloiteau's school which indicate that the septal apparatus develops bilaterally even in Recent corals. Thus, I was able to establish in *Caryophyllia cyathus*, the same species on which Milne-Edwards based his ontogenetic scheme, that septal insertion is related to a constant plane of symmetry during ontogeny. The cyclic aspect is the result of different rates of appearance of successive septal couples.

Secondly, the contrast in mineralogy between aragonite (Scleractinia) and calcite (Rugosa) cannot be used as a decisive discriminating factor for two reasons:

— arguments exist for a diagenetic origin of the mineralogical difference (Cuif 1974a). Briefly, the recrystallization of aragonitic fibrous tissue seen in several groups results in calcite crystallites (the "fibres à bosselures" of Lafuste) the dimensions and morphology of which are comparable to the structures observed in some rugosans.

— furthermore, even if this contrast in mineralogy existed and, as classically proposed, was connected to the advent of symbiosis with zooxanthellae, a biological novelty advantageous to those groups possessing it, it does not imply a break in phylogenetic continuity.

As the last point of difference between the two groups (the presence or absence of lamellae in Rugosa and Scleractinia respectively) is weakened by the study of the Triassic fauna (see below), it is clear that the fundamental criteria on which the subdivision currently accepted is based should be completely reconsidered and do not constitute an obstacle to a scheme of phylogenetic continuity as a better expression of the evolution of these corals.

EVOLUTIONARY SCHEME OF SCLERACTINIAN-RUGOSAN RELATIONSHIPS ESTABLISHED ON THE BASIS OF TRIASSIC CORAL MICROSTRUCTURE

In recent years the microstructural analysis of Triassic corals has revealed a number of forms with archaic characteristics, important in supporting the proposition that Palaeozoic types of microstructure survived the Permo-Triassic boundary, thus diminishing the importance of this classically accepted fundamental break.

The importance of this break had already been questioned during the Symposium in Novosibirsk (1971):

Montanaro-Gallitelli had drawn attention to the archaic features of a small solitary coral from the Upper Triassic of the Dolomites then assigned to *Protoheterastraea leonhardi* Volz. On the basis of morphology and microstructure (see also Montanaro-Gallitelli 1973), this coral (*Zardinophyllum* Montanaro-Gallitelli, 1975)

would have been classified "not among the Scleractinia but among the Tetracoralla" (Montanaro-Gallitelli 1974: 221). At about the same time I drew attention to the archaic morphology, ontogeny and microstructure of a coral fauna from the Lower Norian of Turkey which significanctly enlarges the group with primitive character- istics at the beginning of the Mesozoic.

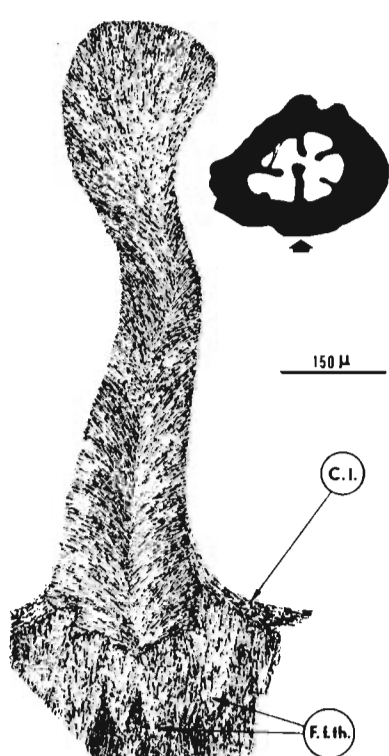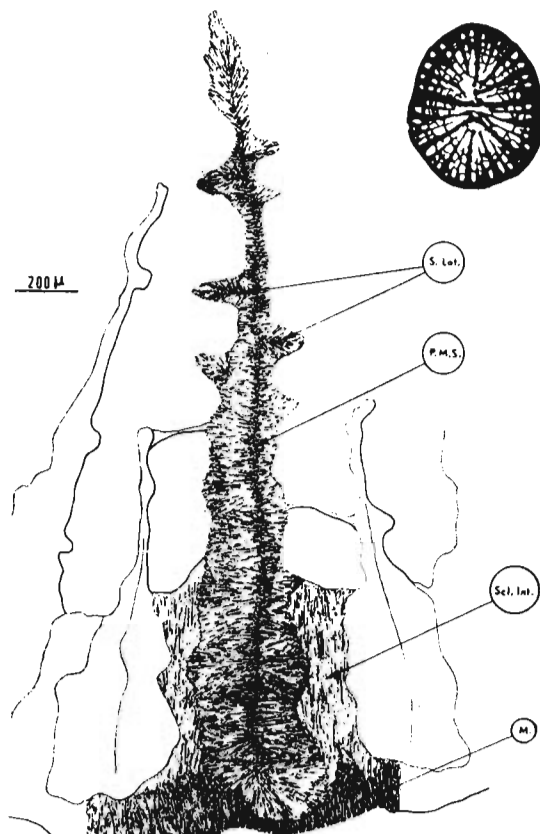These corals form the family Pachythecalidae Cuif, 1975 with the following characteristics (fig. 7):

Fig.7

Fig.8

Fig. 7. Pachythecalid type of structure in the septa-wall contact zone. Early deve- lopmental stage of the major septum of *Pachythecalis major* Cuif showing a direct type of contact of the medioseptal plane with the wall; septal fibers obliquely arranged due to their rapid growth (in adult septa fibers are subperpendicular to the medioseptal plane); wall fibers arranged in fascicles (*F. f. th.*.); lamellar tissue (*C. l.*) developed.

Fig. 8. Volzeid type of structure in the septa-wall contact zones. Fragment of *Volzeia badiotica* (Volz) corallite in cross section: medioseptal plane is isolated from the wall (opposite to the pachythecalid type); wall built of radial fibers (*M*), septum formed of fibers subperpendicular to the medioseptal plane (*PMS*); lateral axes of convergence sparse (*S. Lat.*); interseptal sclerenchyme (*Scl. Int.*) developed.

— simple and colonial forms, characterised by a very thick wall, formed by radially arranged, fibre fascicles of centripetal growth, directed obliquely upwards. Internal lamellar layer variably developed.

— throughout ontogeny, the wall is developed in advance of the septal apparatus; thus the septa abut against the already formed wall and the fibres of these two structures meet at a high angle, most often perpendicularly.

— the septal microstructure is of the continuous fibrous type; the medio-septal plane may appear discontinuous in adjacent growth zones in transverse section.

At the same time a fourth genus from the Dolomites, *Gallitellia* Cuif, 1975, was discovered and completes the family Pachythecalidae.

The morphological and particularly the microstructural characteristics of these corals are very close to those of genuine Permian corals, such as some Polycoeliinae:
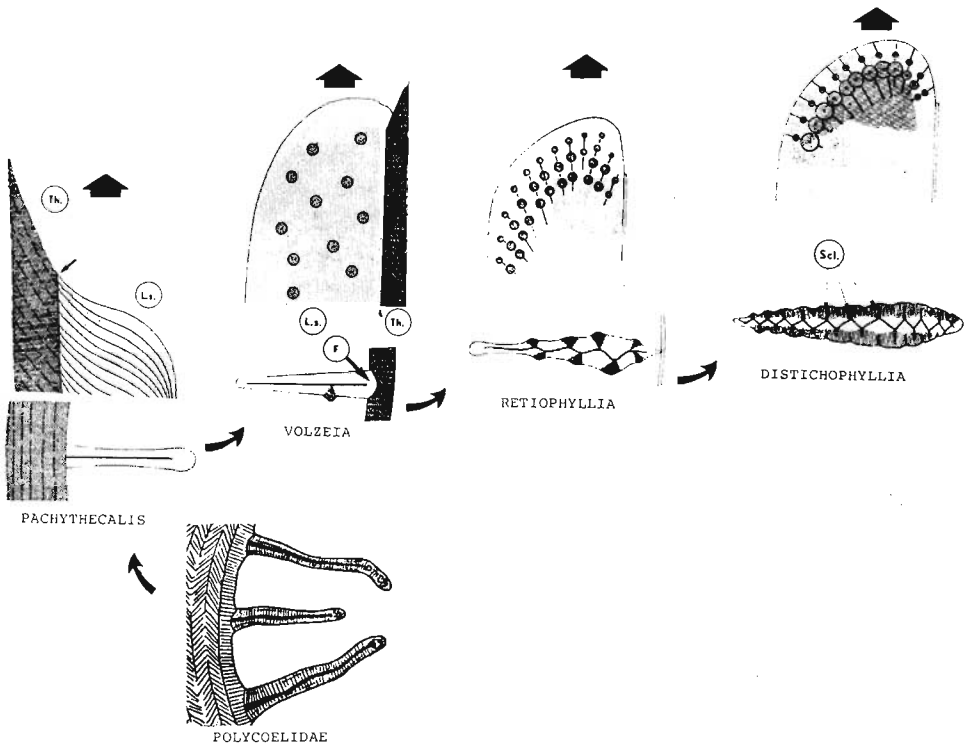

Fig. 9. Possible relations between the types of Triassic coral microstructure. Beginning with the forms such as *Pachythecalis,* resembling in structure Polycoelidae, the evolution results in two phenomena: a) progressive reduction of the wall: in Polycoelidae and *Pachythecalis,* septa (*L. s.*) are inserted after the wall develops — the medioseptal plane contact directly with the wall (*Th.*). In *Volzeia* the wall is an important element but the precocious development of the septa results in closing (*F.*) of the medioseptal plane — the costo-septal type of structure is initiated. In the next stage the wall occurs only as an epitheca resting on the external edge of costo-septa; b) progressive development of the lateral axes: rare and disorderly arranged in *Volzeia,* the lateral axes (*Scl.*) diverge from the undulations of the medioseptal plane in *Retiophyllia* and become fused laterally in *Distichophyllia.* As a result two thick additional septal layers develop on both sides of the primary medioseptal plane.

for example according to Schindewolf (1942) *Polycoelia compressa* shows septal structure identical with that in the Pachythecalidae and a similar relationship between the wall and septa (fig. 9).

This similarity is the more interesting in that the Pachythecalidae have a development comparable to that of the Rugosa: for example the initial stages of *Pachythecalis* (type genus of the family), and equally *Pachydendron,* or again the layout of the septal groups in *Pachysolenia* and *Gallitellia,* display the bilateral insertion of successive pairs of septa, considered typical of Palaeozoic corals (Cuif 1975a: figs 2, 6, 7).

Under these circumstances, taking into account the morphological, mineralogical and microstructural resemblances, I have suggested that the Pachythecalidae as a group arose from Permian corals and developed in the Triassic across the Permo-Triassic boundary.

This idea is developed further by Melnikova and Roniewicz's (1976) work on four Jurassic coral families: the Carolastraeidae, Donacosmiliidae, Amphiastraeidae and Intersmiliidae. These authors recalled earlier ideas concerning the Amphiastraeidae and their archaic character, and considered that these four families could represent further differentiation of the Pachythecalidae and through this connection were thus related to Palaeozoic forms. According to these authors therefore corals survived across the Permo-Triassic boundary. Simultaneously, Montanaro-Gallitelli (1975) reached the same conclusion through an analysis of a single coral, *Zardinophyllum.* For this form she erected the family Zardinophyllidae and order Hexanthiniaria which she placed intermediate in position between the Rugosa and Scleractinia. More recently, Eliášová has suggested the inclusion of all the above forms and the Heterocoeniina of Beauvais, 1977 in the order Hexanthiniaria.

It is clear that several authors consider that there might exist a direct relationship between Rugosa and at least some Mesozoic corals.

However, the microstructural analysis of Triassic corals points to a relationship with the Rugosa not only for the forms displaying archaic characters (as in the Amphiastraeidae) but also for a number of forms whose structure does not suggest a link with the Rugosa.

THE STRUCTURAL EVOLUTION OF TRIASSIC CORALS OF PACHYTHECALID TYPE-DIFFERENTIATION OF TRABECULAR AXES

It is conceivable that a range of Triassic coral groups arose from the structural type characteristic of the Pachythecalidae as a result of two evolutionary phenomena: progressive reduction of the wall, and a process of differentiation of the trabecular axes in the septa (fig. 9).

As has been noted, the wall develops in advance of the septal apparatus in the Pachythecalidae. In the Upper Triassic are found forms (genus *Volzeia*) formerly assigned to the *Thecosmilia subdichotoma-T. badiotica* group, with a similar though

less accentuated development. The wall is fibro-radial, thick, deposited centripetally (as in the pachythecalids) but the septa are inserted before the wall develops completely (fig. 8). Moreover, the septa undergo a clearer development that in the Pachythecalidae: instead of being inserted into the wall with an open medioseptal plane, the external edge of the septa is reflexed. This means that the septa attach to the wall along a curve concave downwards whereas in the Pachythecalidae (as in the Permian Polycoeliidae) the septa are attached along a concave upwards curve. The septal apparatus here therefore shows accelerated development and this tendency is accentuated in later forms (Cuif 1977b: pl. 11). This is correlated with early differentiation of convergence of the fibre fascicles in the form of lateral granules on the septa, which are always lacking in the Pachythecalidae.

This accelerated septal development shows in such forms as *Retiophyllia* in which the medioseptal plane remains continuous but is irregularly flexed in the vertical plane, producing dispersed lateral axes which form septal granulations. In these forms the septa have become perfect costosepta and the wall occurs only as an epitheca resting on the wedge-shaped external edges.

In the succeeding form (Distichophylliidae) the medioseptal plane is very regularly undulating and the lateral axes are inserted on the resulting vertical crests. This results in tripartite septal structure:

— in the centre the median lamina represents the initial stage of the distal edge,

— laterally, two layers (rarely symmetrical) develop as a result of the coalescence of the lateral axes.

The distal extremities of the axes result in ornamentation of the septal faces in the form of rows of granules. This ornamentation has been considered as identical to that in true *Montlivaltia*, but, as has been demonstrated, they do not have comparable microstructures.

It is significant that the succession Pachythecalidae-Volzeiidae-Distichophylliidae allows one to interpret the majority of the Triassic scleractinian fauna; these septal structures are found in many simple and colonial corals with diversified lateral ornamentation, and in particular a great variety of carinae. This assemblage, within which mutual relationships are well established on the basis of ontogenetic work and the progressive evolution of septal structure during development (Cuif 1974b: 306), constitutes a second group in addition to the Hexanthiniaria, the relationships of which with the Jurassic fauna must now be analysed in order to establish its significance in coral evolution.

However, it is clear that this group, with lateral axes diverging from a fundamentally continuous medio-septal plane (sometimes very reduced but always present), can hardly be ancestral to forms with true trabeculae which are already present in the Triassic. They show a perfect development of continuous vertical axes, which characterise trabecular structure, by the Upper Triassic. Well developed perforate structure is also found then (*Araiophyllum* Cuif, 1975). In our present state of knowledge it is not possible to reconstruct the progressive evolution of trabecular structure as can be done for distichophyllid structure. Only a detailed analysis of

structural characteristics in the youngest ontogenetic stages of known forms, or the discovery of older faunas, will reduce the present gap in our knowledge and complete the evolutionary scheme of the early Mesozoic corals.

GENERAL CONCLUSIONS

Recent researches by several authors in regions relatively distant from the Tethyan basin demonstrate that the classic systematic division of corals at the Permo-Triassic boundary, as well as the systematics of Triassic corals, cannot be maintained. The results of microstructural analysis show that the actual classification does not represent current evolutionary concepts of corals of this period. On the contrary, the microstructural data now available seems sufficiently in accord to suggest the existance of a phase of evolution initiated in the Palaeozoic and which probably developed during the Early and Middle Triassic.

It seems possible to distinguish the initial differentiation of a group with particularly archaic characters, the Hexanthiniaria, which comprises forms closely resembling Rugosa, in morphology, microstructure and ontogeny.

A second assemblage, the Distichophylliidae, appears later in which a gradually intensifying process of trabeculization begins, in the form of lateral axes inserted on a continuous medioseptal plane inherited from the Palaeozoic forms.

The trabeculization process may be observed in its typical form (with continuous vertical axes) in a third assemblage, established by the Upper Triassic but of obscure origin on the basis of present information.

Instead of the concept of a complete break between two successive entirely distinct assemblages, present research points to a process of rapid but continuous differentiation.

It is worth mentioning that this important evolutionary process might have been connected with a major palaeogeographical event of fundamental importance for the geological history of this period: the westward opening of Tethys which, through a fracture affecting the Afro-Eurasian block, was enlarged by a new marine environment. The correlation between the evolutionary phenomena mentioned above and the palaeogeographical data suggests the hypothesis that the differentiation of Upper Permian and Lower Triassic corals was a result of the colonization of western Tethys. In any case, it will be through research of this type that our knowledge of coral evolution, at this critical phase of its history, will progress.

REFERENCES

ALLOITEAU, J. 1952. Madréporaires post-paléozoïques. *In:* J. Piveteau (ed.), Traité de Paléontologie, 1, 539—684. Masson et Cie, Paris.
— 1957. Contribution à la systématique des Madréporaires fossiles. 1—462. Centre National de la Recherche Scientifique, Paris.

CUIF, J. 1972. Recherches sur les Madréporaires du Trias: I — Famille des Stylo-
　　phyllidae. — *Bull. Mus. Nation. Hist. Nat., sér. 3, Sci. Terre*, **17**, 211—291.

— 1974a. Indices de la nature aragonitique des fibres chez les Madréporaires
　　paléozoïques. — *C. R. Som. Soc. Géol. France*, **6**, 162—164.

— 1974b. Recherches sur les Madréporaires du Trias: II — Genres *Montlivaltia* et
　　Thecosmilia. — *Bull. Mus. Nation. Hist. Nat., sér. 3, Sci. Terre*, **40**, 293—400.

— 1975a. Caractères morphologiques, microstructuraux et systématiques des
　　Pachythecalidae, nouvelle famille de Madréporaires triasiques. — *Geobios*, **8**,
　　3, 157—180.

— 1975b. Recherches sur les Madréporaires triasiques: III — Étude des structures
　　pennulaires. — *Bull. Mus. Nation. Hist. Nat., sér. 3, Sci. Terre*, **44**, 45—127.

— 1977a. Caractères et affinités de *Gallitellia*, nouveau genre de Madréporaires
　　triasiques (Ladino-Carnien des Dolomites). 2nd Intern. Symp. Corals and
　　Coral Reefs, Paris 1975. — *Mém. B. R. G. M.*, **89**, 256—263.

— 1977b. Arguments pour une relation phylétique entre les Madréporaires palé-
　　ozoïques et ceux du Trias. — *Mém. Soc. Géol. France, n.s.*, **54**, 129, 1—54.

ELIÁŠOVÁ, H. 1978. La redéfinition de l'ordre des Hexanthiniaria Montanaro-Galli-
　　telli, 1975 (Zoantharia). — *Vest. Ústř. Úst. Geol.*, **53**, 89—101.

FLÜGEL, H. W. 1970. Die Entwicklung der Rugosen Korallen im hohen Perm. —
　　Verh. Geol. B.-A., 146—161.

— 1973. Rugose Korallen aus dem oberen Perm Ost-Grönlands. — *Ibidem*, **1**, 1—
　　57.

GILL, G. et LAFUSTE, J. 1971. Madréporaires simples du Dogger d'Afganistan:
　　étude sur les structures de type "*Montlivaltia*". — *Mém. Soc. Geol. France, n.e.*,
　　50, 115, 1—40.

MELNIKOVA, G. K. and RONIEWICZ, E. 1976. Contribution to the systematics and
　　phylogeny of Amphiastraeina (Scleractinia). — *Acta Palaeont. Polonica*, **21**, 1,
　　97—114.

MONTANARO-GALLITELLI, E. 1973. Microstructure and septal arrangement in a
　　primitive Triassic coral. — *Boll. Soc. Paleont. Italiana*, **12**, 1, 8—82.

— 1974. Morphogenesis and skeletal structure of some primitive Triassic corals:
　　problems of phylogeny. *In*: B. S. Sokolov (ed.), Ancient Cnidaria, 1. — *Trans.
　　Inst. Geol. Geoph. Acad. Sci. USSR, Siberian Branch*, **201**, 220—224.

— 1975. Hexanthiniaria, a new order of Zoantharia (Anthozoa, Coelenterata). —
　　Boll. Soc. Paleont. Italiana, **14**, 1, 8—22.

SCHINDEWOLF, O. H. 1942. Zur Kenntnis der Polycoelien und Plerophyllen. Eine
　　Studie über den Bau der "Tetracorallen" und ihre Beziehungen zu den Ma-
　　dreporarien. — *Abh. R.-A. Bodefor., n.s.*, **204**, 324 pp.

WELLS, J. W. 1956. Scleractinia. *In*: R. C. Moore (ed.), Treatise on Invertebrate Pa-
　　leontology, Part F, 328—477. Geological Society of America and University
　　of Kansas Press, Lawrence.