

Evolutionary trends in the epithecate scleractinian corals

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Adult stages of wall ontogeny of fossil and Recent scleractinians show that epitheca was the prevailing type of wall in Triassic and Jurassic corals. Since the Late Cretaceous the frequency of epithecal walls during adult stages has decreased. In the ontogeny of Recent epithecate corals, epitheca either persists from the protocorallite to the adult stage, or is replaced in post-initial stages by trabecular walls that are often accompanied by extra-calicular skeletal elements. The former condition means that the polyp initially lacks the edge zone, the latter condition means that the edge zone develops later in coral ontogeny. Five principal patterns in wall ontogeny of fossil and Recent Scleractinia are distinguished and provide the framework for discrimination of the four main stages (grades) of evolutionary development of the edge-zone. The trend of increasing the edge-zone and reduction of the epitheca is particularly well represented in the history of caryophylline corals. We suggest that development of the edge-zone is an evolutionary response to changing environment, mainly to increasing bioerosion in the Mesozoic shallow-water environments. A glossary is given of microstructural and skeletal terms used in this paper.

Key words: Scleractinia, microstructure, thecal structures, epitheca, phylogeny.

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*In Memory of Gabriel A. Gill, an Eminent Student
of Coral Structures, our Colleague and Friend*

Introduction

Recent study of macroevolutionary trends in Scleractinia has focused on the development of coloniality (Coates & Oliver 1974; Coates & Jackson 1985; Rosen 1986), microstructural changes of skeleton in their history (Roniewicz & Morycowa 1993), and phylogenetic differentiation based on molecular data (Romano & Palumbi 1996; Veron *et al.* 1996).

In this paper we focus on some evolutionary aspects of the development of the edge-zone, a feature regarded by Vaughan & Wells (1943) and Wells (1956) as one of

the most important in the evolution of the Scleractinia. These authors remarked that development of the edge-zone led to a reduction of the epitheca and its replacement by other types of outer wall. We attempt to trace this process using changes in wall structures observed in the stratigraphic column and in the ontogeny of some Recent corals. Analysis of paleontological data has also led to the verification of earlier views on the stratigraphic distribution of epitheca.

The majority of pre-Cenomanian genera have epitheca/holotheca developed as a complete wall or at least as epithelial rings (compare Koby 1881–1889, 1905; Frech 1890; Volz 1896; Vaughan & Wells 1943). The Late Triassic – Late Jurassic coral faunas show a great taxonomic diversity of corals with solitary and phaceloid growth forms (compare Vaughan & Wells 1943), nearly all of them being epithecate forms. In the Late Triassic and Late Jurassic, when fine-grained shallow water calcareous sedimentation developed, the phaceloid epithecate corals frequently predominated (Roniewicz & Roniewicz 1971; Stanton & Flügel 1987, 1989; Geister & Lathuilière 1991; Insalaco *et al.* 1997). Questions arise: Whether the success of these corals lacking the edge-zone resulted from their special adaptations to the specific environment of the calcareous sedimentation? Which of the factors: physical, chemical or biological controlled their development? What caused their reduction in the Late Cretaceous and continuation of this trend in the Cenozoic, resulting in their recent limitation to relict cryptic or deep-water solitary forms? Though no definite answers exist, we hope that our speculations will stimulate discussion.

Institutional abbreviations: GBA, Geologische Bundesanstalt, Wien; ZPAL, Institute of Paleobiology, Warsaw; UJ, Jagiellonian University, Cracow; MNHN, Muséum National d'Histoire Naturelle, Paris; MB, Naturhistorisches Museum, Humboldt Universität, Berlin; NHM, Natural History Museum, London; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; MGUWr, Geological Museum, Wrocław University, Wrocław.

Epithelial walls: structure and terminology

The term *epitheca* was used by Milne Edwards & Haime (1848) for a 'skeletal sheath adhering to the external board of costae'. As examples of epitheca-bearing scleractinians they gave: *Montlivaltia* Lamouroux, 1821, *Balanophyllia* Wood, 1844, and *Flabellum* Lesson, 1831 (in the latter case they noticed, however, the 'porcelain' appearance of that wall). In subsequent years, the term epitheca was used for all transversely folded walls of solitary and phaceloid corals, and a wall covering the lower colony surface; for the epitheca of scleractinian colonies, a separate term *holotheca* was later adopted (Alloiteau 1957), a term previously utilized in Rugosa and Tabulata (e.g., Hudson 1929; Hill 1935). Alloiteau (1952) introduced a new term *archaeotheca* to describe the transversely folded 'septo-dissepimental' wall of the stylophyllids, pro-cyclolitids, amphistreids, and thecocyathids. Archaeotheca was, however, imprecisely defined (in fact, none of the above mentioned coral groups have a 'septo-dissepimental' wall) and structurally different walls were later described using this term (see Stolarski 1995). Distinction between epithelial and archaeothecal walls was sup-

ported by Weyer (1975). He considered the walls developed subsequent to the septa to be epithelial, e.g., in scleractinian *Montivaltia caryophyllata* Lamouroux, 1821, or in rugosan *Calostylis cribraria* Lindström, 1868, while the walls developed prior to the septa to be archaeothelial, e.g., *Axosmia* or *Thecocyathus mactrus* (Goldfuss, 1826) among Scleractinia, and *Cyathaxonia cornu* Michelin, 1847 among Rugosa. As we show in this paper, the position of the epitheca may vary in the ontogeny of particular species (it may be formed after or before the septa). Thus, we consider the above-presented distinction between epitheca and archaeotheca unnecessary, and we support the earlier statement that the term archaeotheca should be rejected as imprecisely established and confusing (Stolarski 1995).

Essential for understanding epitheca formation was a paper by Barnes (1972). He studied the epithelial wall in a range of Recent shallow-water zooxanthellate corals [*Isophyllia sinuosa* (Ellis & Solander, 1786), *Manicina areolata* (Linnaeus, 1758), *Montastrea annularis* (Ellis & Solander, 1786), *Porites astreoides* Lamarck, 1816, *Diploria strigosa* (Dana, 1846), *Favia speciosa* (Dana, 1846)] and showed that it is a two-fold, fibrous structure developing in the marginal zone of the polyp body. Barnes (1972) noted also a comparably structured wall in the azooxanthellate *Gardinieria*. Recent studies of the family Flabellidae (Caryophylliina), traditionally considered as epithelial corals, have shown that the wall of most genera is trabecular (marginothelial), and thus essentially different in structure from epitheca (Stolarski 1995). This encouraged us to outline precise criteria for the differentiation between epithelial walls and similar but non-homologous walls in fossil and Recent Scleractinia.

Place of formation

Epitheca is formed in an anatomically specialized soft tissue marginal fold, the lappet cavity (Barnes 1972). The initial, outer layer (primary layer *sensu* Barnes 1972) is formed in the apical part of the lappet cavity. The inner layer may form initially in the lappet or behind it in a secreting zone of the body wall resulting in formation of, respectively, thin (pellicular) or thick (mature) epitheca (see also Stolarski 1995: fig. 1; Stolarski 1996: fig. 1).

Morphology

Epitheca constitutes the external and often the distalmost part of the corallum (Fig. 1A). Generally, it is covered with transverse incremental lines and folds but sometimes also bears longitudinal striations (Fig. 2B, C, F).

During ontogeny, epitheca may differ in rates of development from other skeletal elements (Fig. 3A–D). Growth of epitheca may exceed that of radial elements, thus resulting in the formation of a distal tube of epitheca (Fig. 3B); or it may equal the growth of radial elements (Fig. 3D); or be retarded in comparison with the latter (Figs 3C, 11C), resulting in epitheca coming in contact with septa-derived structures (e.g., septotheca, synapticulotheca) and epicostal dissepiments. Epitheca may be developed as a continuous layer covering the whole corallum or its proximal part (ontogeny of dendrophylliids); it may be reduced to epithelial rings (e.g., in Cretaceous *Montivaltia*, Fig. 10B, or in Recent *Trochocyathus rawsoni* Pourtalès, 1874, Fig. 12E); or it may form 'holothelial rings' (e.g., in *Manicina areolata*, see Fabricius 1964). In corals with continuous epitheca, the living tissue is confined to the narrow zone at the

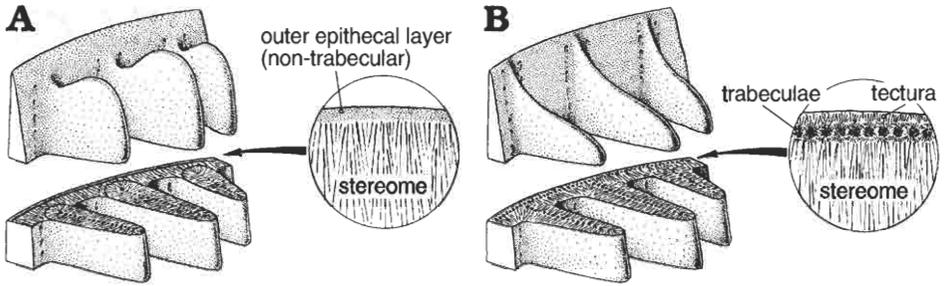


Fig. 1. Epithecal vs. marginothecal wall – transverse sections. **A.** Epitheca in *Gardineria* with thick epithecal stereome. **B.** Marginotheca in *Flabellum* with thick interseptal stereome. Modified from Stolarski (1997).

calicular edge, and the rest of the corallum is bare and exposed to the surroundings. In corals with epithecal rings, the living tissue covers only the corallum surface above the most distal ring.

Some morphological features commonly considered as typical of the epithecal wall may also be observed in other walls. Frequently the contact zone between epitheca and septa is marked by a characteristic notch, but a similar notch may be developed at the contact with trabeculotheca or septotheca e.g., in caryophylliid genera *Conotrochus*, and ‘*Ceratotrochus*’ (Fig. 4A, B). Also, the lines marking the position of the withdrawing edge-zone on the tectura surface (‘*Ceratotrochus magnaghii*’, Fig. 4B), or lines marking periodic incremental growth of trabeculae on the eroded surface of the flabellid marginotheca may resemble epithecal growth lines (see Stolarski 1995: fig. 9I, J). Doubts caused by a lack of precise morphological criteria may be eliminated by the use of microstructural criteria.

Microstructure

Epitheca is built of calcareous fibres not organized into trabeculae. Epitheca often accompanies other wall structures (trabeculotheca, septotheca), but may also form the only corallum wall. It consists of two parts:

(1) Outer epithecal layer. In spite of some variation, the structure of this outer layer is similar in all Scleractinia (Fig. 2B–D, F, G, I). It consists of a layer 1–2 μm thick (Barnes 1972) covered with growth lines, composed of distally oriented fibres (Figs 5C, 8D) sometimes strongly inclined from the vertical position. In some corals, the fibres grow in longitudinal, parallel or subparallel tracts. Within the tracts the fibres may form a fanwise pattern (Fig. 2B).

(2) Inner epithecal layer. This layer, of variable thickness, is built of radially arranged fibres, and it grows centripetally into available intracalicular space (e.g., Figs 3E, F, 5D, 6B, 7D, 11A). It is an epithecal stereome, which in trabecular corals may be continuous structurally with interseptal stereome. In non-trabecular corals (Stylophyllina), the epithecal stereome of fibro-radial structure differs microstructurally from the rest of the stereomal deposit that forms septa, interseptal stereome and adaxial wall stereome, and which is organized into bundles of fibres and scales and grows by

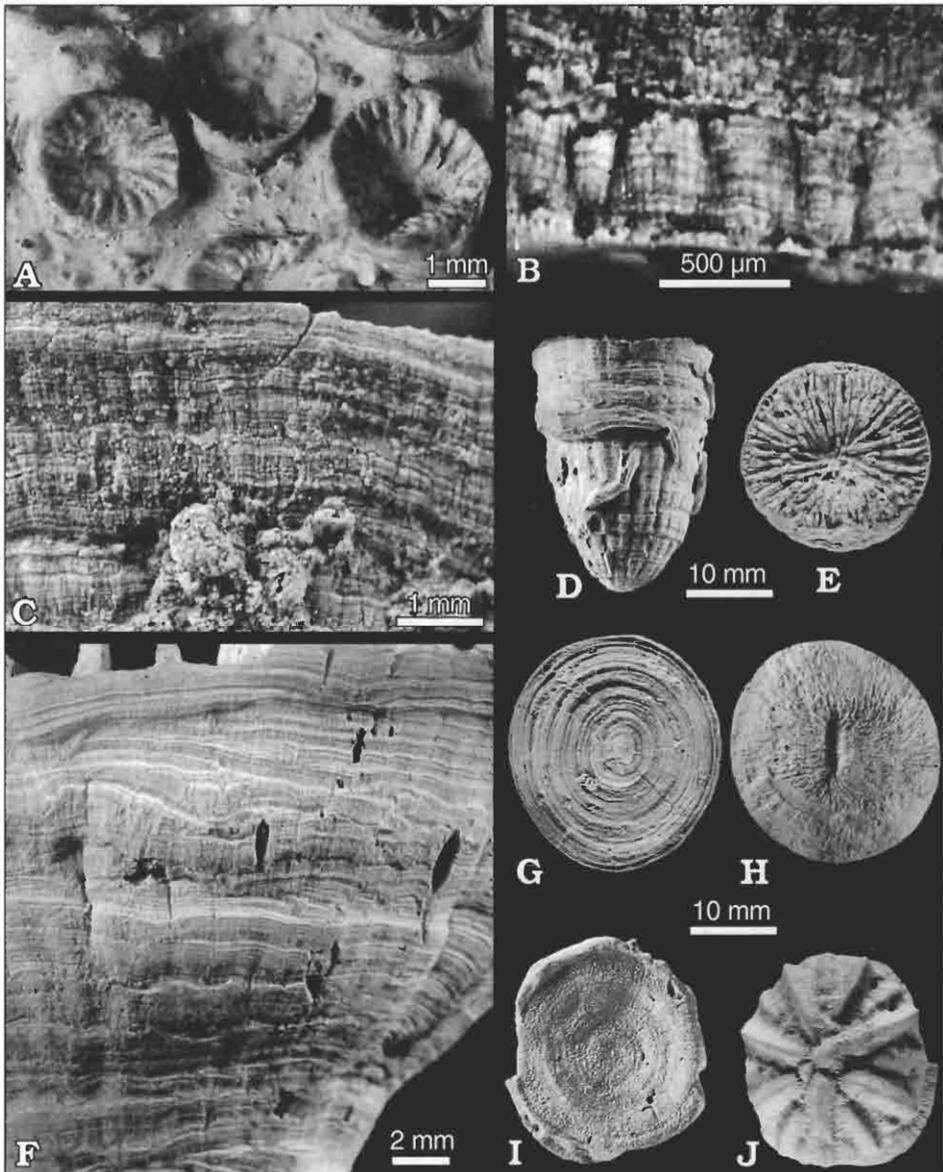


Fig. 2. External surface of the epitheca. **A.** *Cladophyllia minor* Beauvais, 1967, Jurassic (Bathonian), Fairford, Gloucestershire, England, NHM R.9639. Sharp epithecal rims of the calices. **B.** *Cladophyllia* cf. *excelsa* (Koby, 1888), Jurassic (Kimmeridgian), Czarnogłowy (Pomerania, Poland), MB K.351. Epithecal calicular rim with some modular structure of the wall; note minute longitudinal striation. **C–E.** *Stylophyllopsis rugosa* (Duncan, 1868), Early Jurassic, England. **C.** NHM R.13332. A fragment of the corallite surface with the same structural features as above. **D, E.** NHM R.3194. Lateral and distal views of the corallum. Note sharp calicular rim present in **E.** **F.** *Gardineria hawaiiensis* Vaughan, 1907, Recent, 22°15'25''N/159°23'15''W, 497–541 m, holotype, USNM 20731. Note barnacle's borings in epitheca. **G, H.** *Cunnolites* sp., Cretaceous (Senonian), Austria, UJ 82P41. Distal and lower corallum views. Lower surface with concentric epithecal wrinkles. **I, J.** *Aspidiscus* sp., Cretaceous (Cenomanian), Egypt, ZPAL H.XVII/1. Distal (**I**) and lower surface of the colony (**J**), with lower surface slightly concentrically structured.

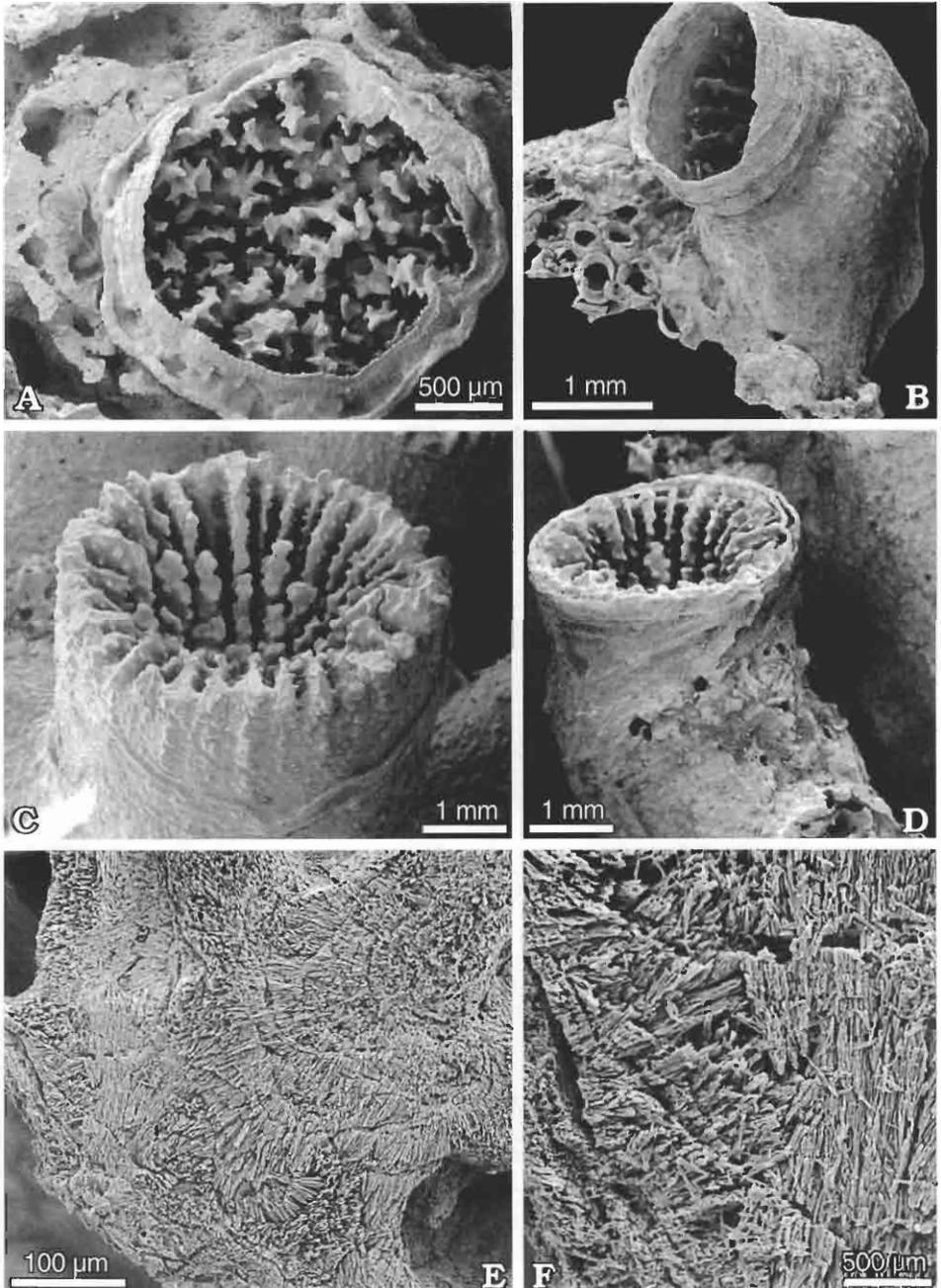


Fig. 3. *Polycyathus muellerae* (Abel, 1959), Recent, Marseille, submarine cave, 'Grotte du Figuier', 12 m. A. ZPAL H.XVII/2. Early juvenile stage with epithecal wall. B. ZPAL H.XVII/3. A calice with tube-like extension of the epitheca. C. ZPAL H.XVII/4. Adult septothecate corallite with epitheca suppressed in its lower part. D. ZPAL H.XVII/5. Adult, septothecate corallite with a thin epitheca reaching the calicular rim. E, F. ZPAL H.XVII/6. Epitheca in transverse section, etched surface. Centripetally oriented fibres (F – enlarged fragment of E).

accretion (Roniewicz 1989a: p. 117). In thin sections of fossil material, only the inner epithelial layer is easily recognizable.

Microstructural and morphological criteria allow for the differentiation of epithelial wall from other wall structures such as tectura and marginotheca (Fig. 1B). It is noteworthy that thin, pellicular epitheca in contact with epicostal dissepiments has been interpreted as a paratheca e.g., in *Montlivaltia* (Vaughan & Wells 1943; Alloiteau 1952, 1957) or in *Thecosmilia*, *Dermosmilia* and *Calamophylliopsis* (Roniewicz 1966, 1976).

Types of epithelial walls

Epitheca may form simple walls or composite walls.

Simple walls. — In simple walls we distinguish *pellicular epitheca* and *mature epitheca*. These descriptive terms have been used to indicate a differences in relative thickness of the inner epithelial layer, i.e. epithelial stereome.

Pellicular epitheca is the most common epithelial wall in the Scleractinia. It is a thin, transparent coating present in early ontogenetic stages, and continues in many corals to be present until adult stages; its inner layer, epithelial stereome, is weakly developed. Pellicular epitheca may be developed as an independent wall or as an element of composite walls (see below). Examples include the wall in phaceloid *Retiophyllia* (Triassic, Fig. 6C), and pellicular holotheca in numerous colonial corals (e.g., *Manicina*, Recent, Fig. 11C, D). Pellicular epithelial structures are developed as epicostal rings in different coral groups from the Middle Jurassic onwards (see below).

Mature epitheca has a thickened inner layer of epithelial stereome that often incorporates external edges of the radial elements. The following examples show the spectrum of mature epithelial structures:

In *Volzeia subdichotoma* (Münster, 1839), Triassic, although the inner layer is relatively thin, it incorporates peripheral edges of radial elements (Fig. 6D). In *V. badiotica* (Volz, 1896), Triassic, the radial elements are deeply embedded in thick epitheca. The internal surface of the epitheca is well separated from the interseptal stereome formed by strongly elongate, centripetally growing fibres.

In *Protoheterastraea leonhardi* (Volz, 1896), Triassic, the inner layer is formed from fibres generally oriented centripetally with some distal declination. At the perimeter are numerous and well defined centres of centripetally radiating fibres. In transverse sections of the wall, a complicated picture is seen, with more than one generation of radiating fibres. Septa are deeply embedded in the wall (Fig. 7A, B). Recent *Gardineria* has essentially a similar wall (Fig. 7E, F; see also Stolarski 1996: figs 4H, I, 5A–G).

In *Craspedophyllia alpina* (Loretz, 1875), Triassic, the epithelial wall incorporating the peripheral parts of radial elements is much more folded than in *Protoheterastraea* (Fig. 6A, B). A similar style of folding has been observed in some Recent Guyniidae (Stolarski 1997) and *Madracis* (Fig. 5A, B).

In post-Triassic corals, mature epitheca with embedded septa is known in *Cladophyllia* (Jurassic–Cretaceous, Morycowa & Roniewicz 1990: pl. 15: 1e, pl. 16: 1a).

Genera of the *Cuifia* group (Triassic) represent a different structural specialization from those discussed above. The epithelial wall does not incorporate septa at all. Longitudinal structures of equal size are formed on the internal wall surface. They are tri-

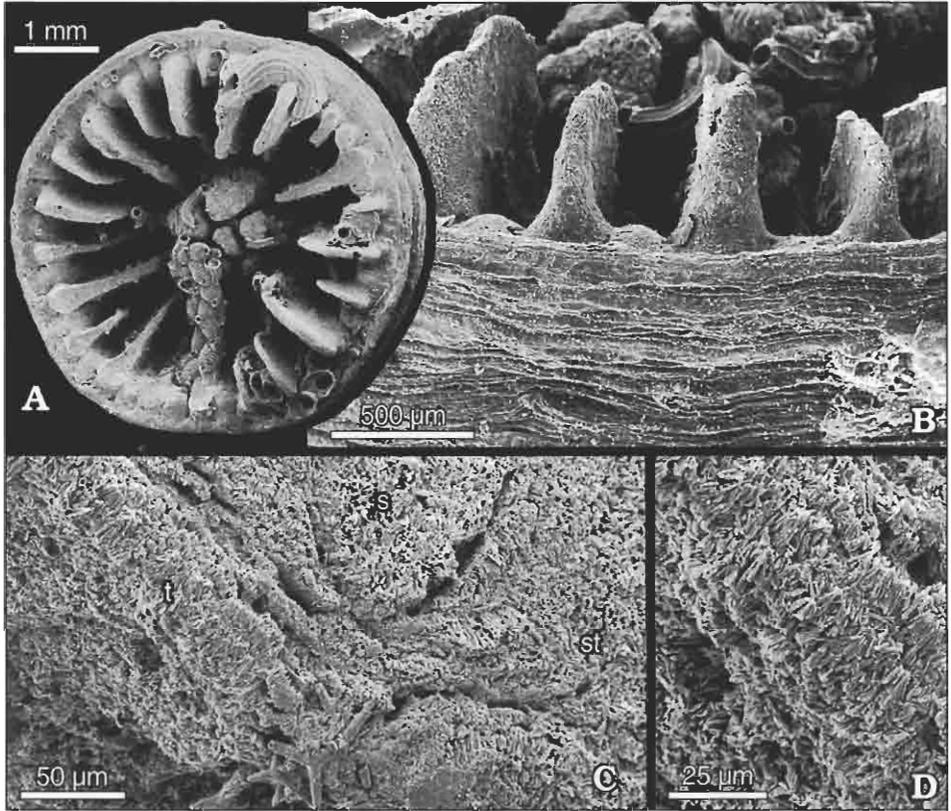


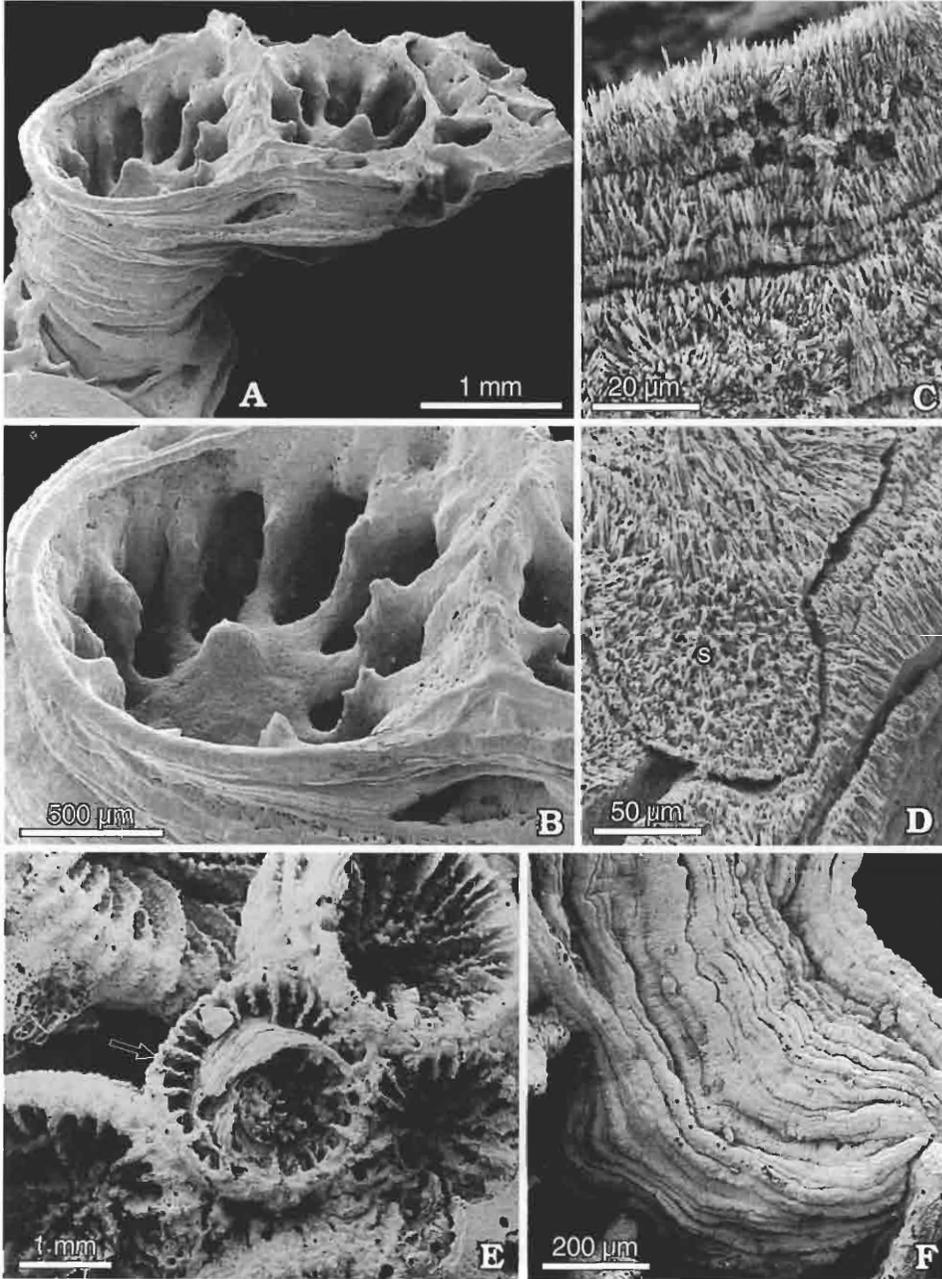
Fig. 4. '*Ceratotrochus*' *magnaghii* Cecchini, 1914, Recent, Marseille, submarine cave, 13 m – species resembling an epithecal *Gardinieria* but covered with thick, wrinkled tectura. **A.** ZPAL H. XVII/7, distal view. **B.** Magnified fragment of the same specimen in lateral view. **C, D.** ZPAL H.XVII/8, etched, transverse sections. Explanations: s – septum incorporated into interseptal stereome (st), t – centrifugally oriented fibres of tectura.

angular in transverse section, and may terminate on the calicular rim as tubercles. These structures remain opposite the septa and form a type of architectural 'support'.

In guyniid genera *Schizocyathus* (Recent) and *Pourtalocyathus* (Miocene–Recent), epithecal wall may be replaced during ontogeny by a trabecular wall with trabeculae more than 100 µm in diameter, initiating in the epitheca, diverging at an acute angle from the vertical direction and protruding on the corallite surface as a hispid ornamentation (Stolarski 1997).

The wall of the pachythecline corals (Zardinophyllidae and related Amphistraeidae; Montanaro-Gallitelli 1975; Cuif 1975; Melnikova & Roniewicz 1976), here named pachytheca, differs from the epitheca of other corals in the organization of the internal stereomal layer. In the Zardinophyllidae (Triassic), the external wall surface bears incremental folds and a longitudinal microstriation (Fig. 8A, E). The

Fig. 5. **A–D.** *Madracis pharensis* (Heller, 1868), Recent, Marseille, submarine cave 'Grotte du Figuier', 22 m. **A.** ZPAL H.XVII/9. An incipient colony formed by parietal budding with strongly folded epitheca. **B.** Enlargement of the same specimen with epithecal infolding at the calicular rim. **C.** ZPAL H.XVII/10.



Outer epithelial layer – distally oriented fibres at the calicular rim, lateral view. Etched surface. **D.** ZPAL H.XVII/11. Epithelial stereome – centripetally oriented fibres, transverse section, etched surface. Note septum (s) that is embedded in succeeding layers of epithelial stereome. **E, F.** *Hoplania durotrix* Gosse, 1860, Recent, Sagres (Portugal, Algarve), caves in the cliff south of Ponta da Baleeira, 1–6 m, ZPAL H.XVII/12. **E.** Calicular view of the colony. Some of the adult, septothecate coralla rejuvenate (arrowed) and form epithelial calices. **F.** Centripetally growing epithelial diaphragm reducing calicular lumen ('rejuvenescence').

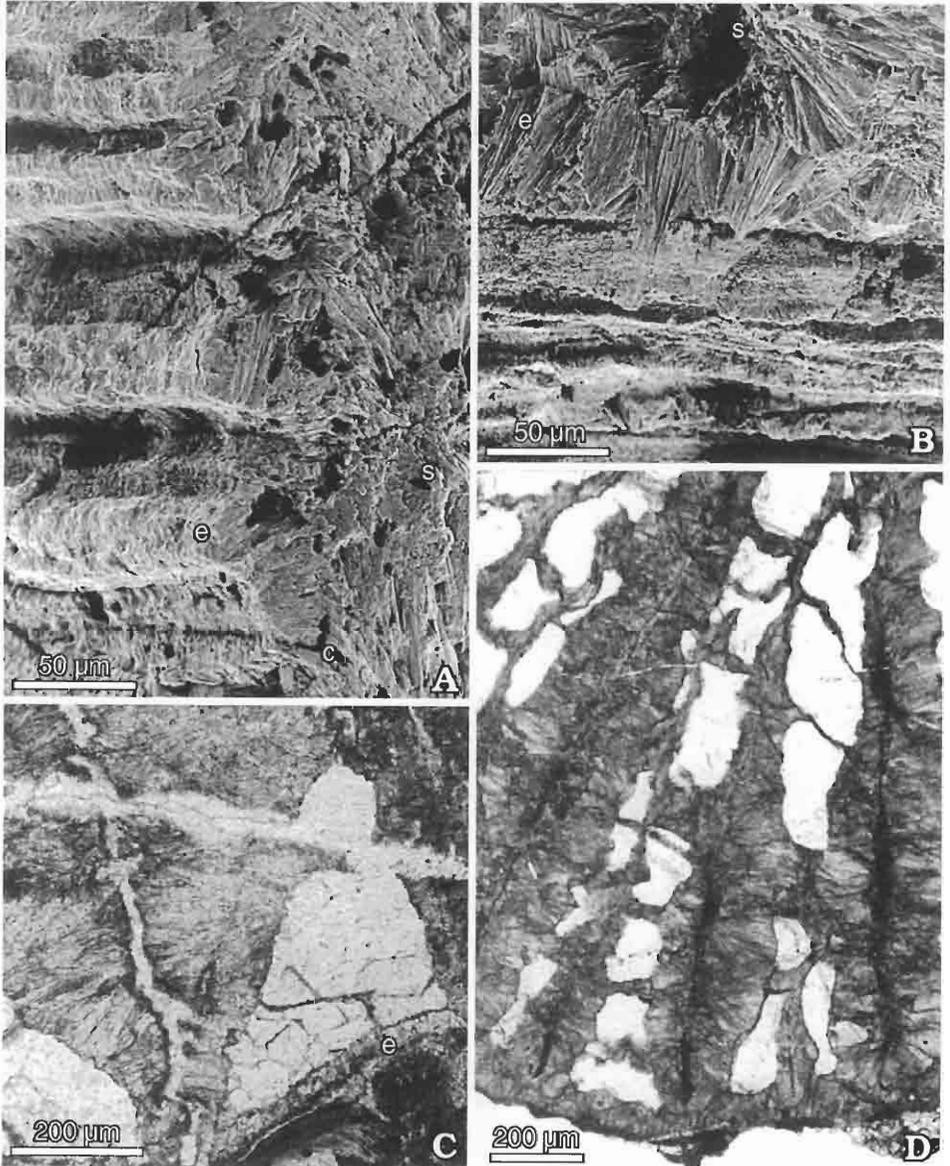


Fig. 6. **A, B.** Mature epitheca in *Craspedophyllia alpina* (Loretz, 1875), Carnian, Italy, GBA Volz collection 4402. **A.** Lateral view of the epithecal corallite wall, its longitudinal broken section showing successive growth wrinkles (at right), and a contact of the epitheca and septa. **B.** Transverse broken section with centripetally oriented fibres of epithecal stereome which incorporates peripheral ends of septa. Note wrinkled epithecal surface at the lower part of the picture. **C.** Pellicular epitheca in *Retiophyllia norica* (Frech, 1890), Rhaetian, Austria, GBA 1982/12/113. Transverse thin section of the wall region with epitheca (e) covering radial elements. **D.** Mature epitheca in *Volzeia subdichotoma* (Münster, 1839), Triassic (Carnian), Dolomites, Italy, MGUWr/75sz-a. Transverse thin section showing an epitheca incorporating peripheral ends of radial elements. Explanations: c – contact of the epitheca and septa; e – epithecal stereome; s – septa.

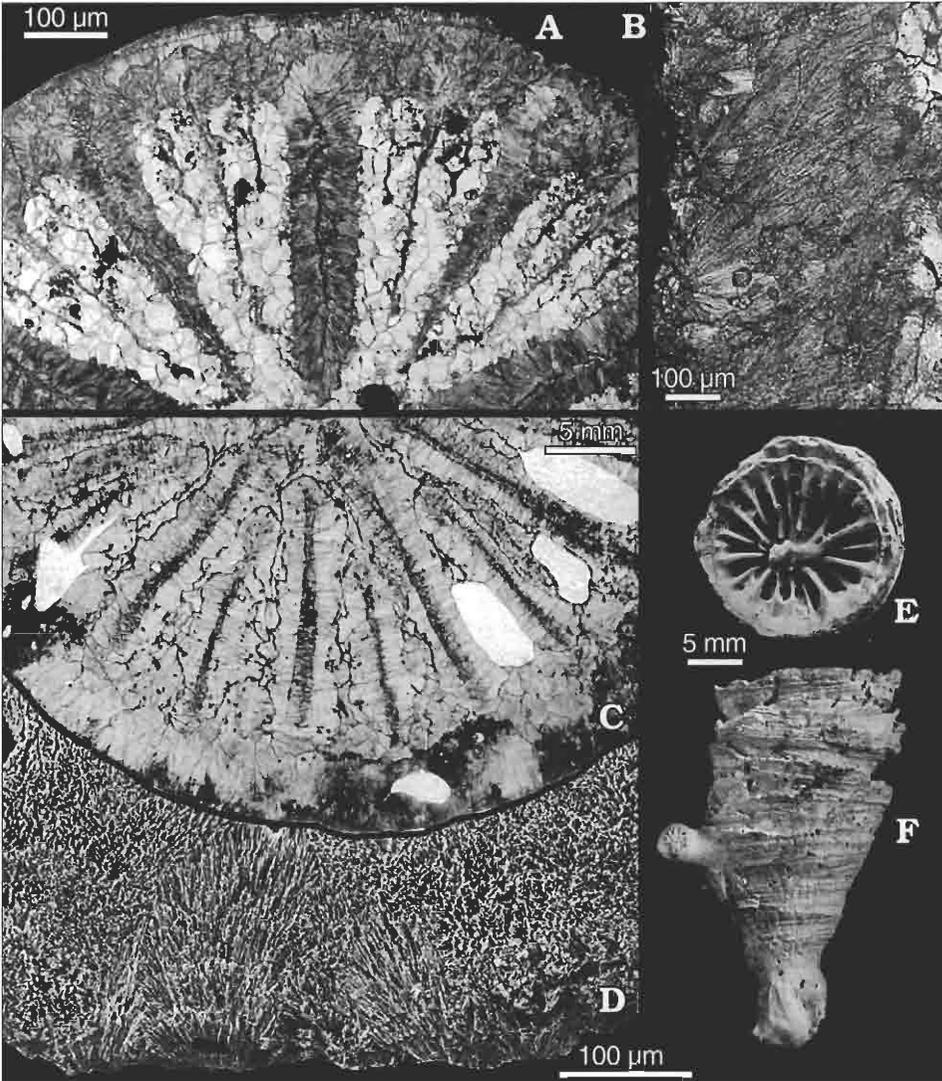


Fig. 7. Mature epitheca in Triassic *Protoheterastraea* (A, B) and Recent *Gardineria* (C–F). A. *Protoheterastraea leonhardi* (Volz, 1896), Triassic (Ladinian), San Cassiano Beds, Forcella di Sett Sass, Dolomites, Italy, MGUWr/Sc2. Transverse thin section showing thick epithecal sterome which incorporates peripheral ends of radial elements. B. Longitudinal thin section showing external wrinkling of the wall (at left) and centripetally oriented fibres of epithecal sterome. C–F. *Gardineria paradoxa* (Pourtalès, 1868), Recent, SW of Jamaica, GOS-59A, Stat. 112/78, 17°21'N/78°19'W, 700 m, ZPAL H.XV/11. C. Transverse thin section showing a thick epithecal sterome with peripheral septal ends embedded. D. Transverse section showing centripetally oriented fibers, etched surface. E, F. Distal (E) and lateral (F) views of the corallum.

outer layer consists of very thin, distally oriented fibres (Fig. 8E). The very thick inner layer reveals a modular structure (especially well seen when slightly altered diagenetically, Fig. 9B, C). The modules represent equal and large bundles of fibres

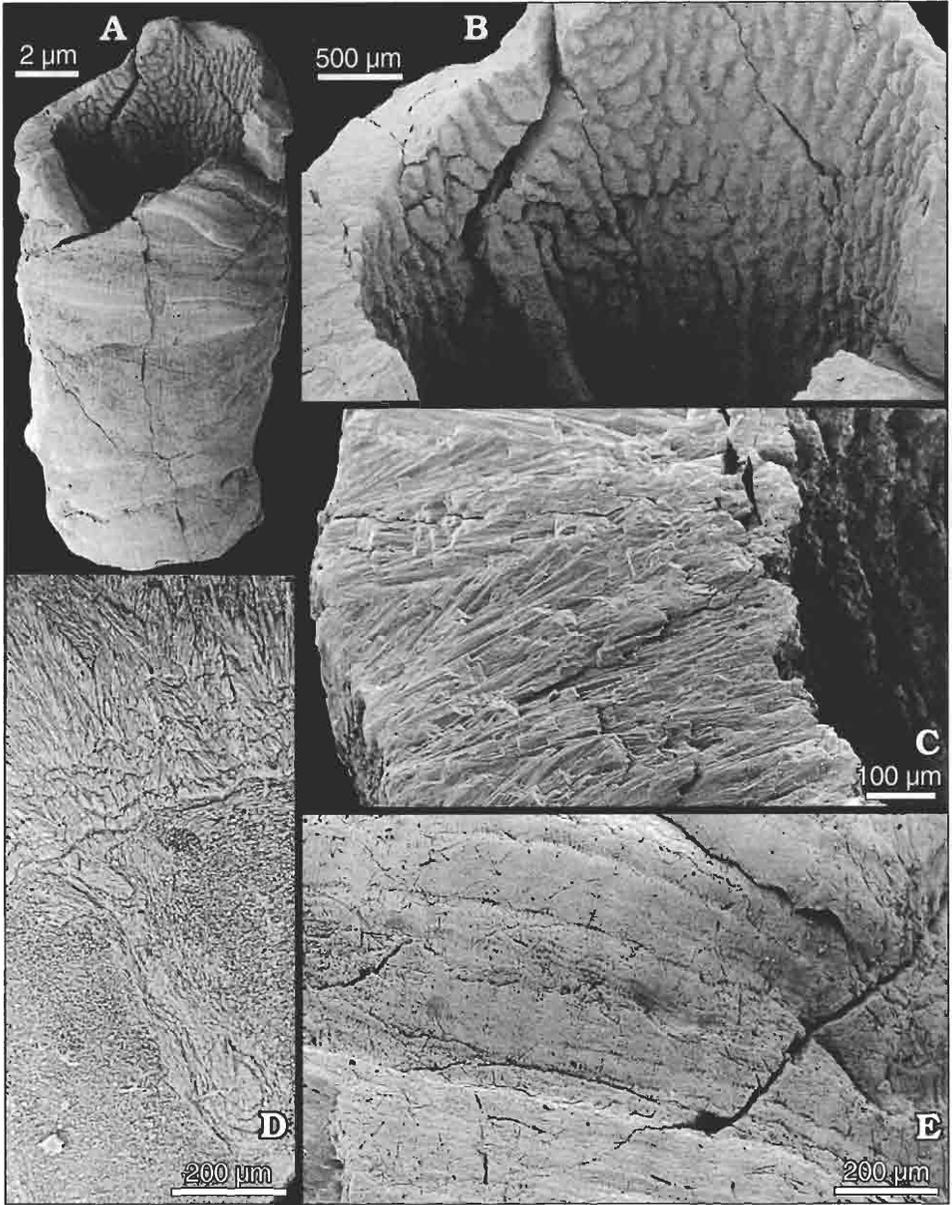


Fig. 8. Epithecal wall of a pachythechal type in *Zardinophyllum zardinii* Montanaro-Gallitelli, 1975, Triassic (Carnian), San Cassiano Beds, Alpe di Specie (Dolomites, Italy). **A.** ZPAL H.XV/17. Side view of a fragmentary corallum with slightly wrinkled surface and longitudinal microstriation. **B.** Fragment of the same specimen showing internal wall surface with irregular pattern formed by extremities of fascicles of fibres. **C, D.** ZPAL H.XV/17 and ZPAL H.XVII/13, respectively. Modular structure of the wall composed of fascicles of fibres of centripetal orientation. **E.** ZPAL H.XVII/14. Longitudinal microstriation on the outer layer of the wall.

growing centripetally (Fig. 8C, D). These bundles display a tendency to form a centered structure (as in *Pachydendron*, see Cuif 1975; *Zardinophyllum*, Fig. 8C, D, or

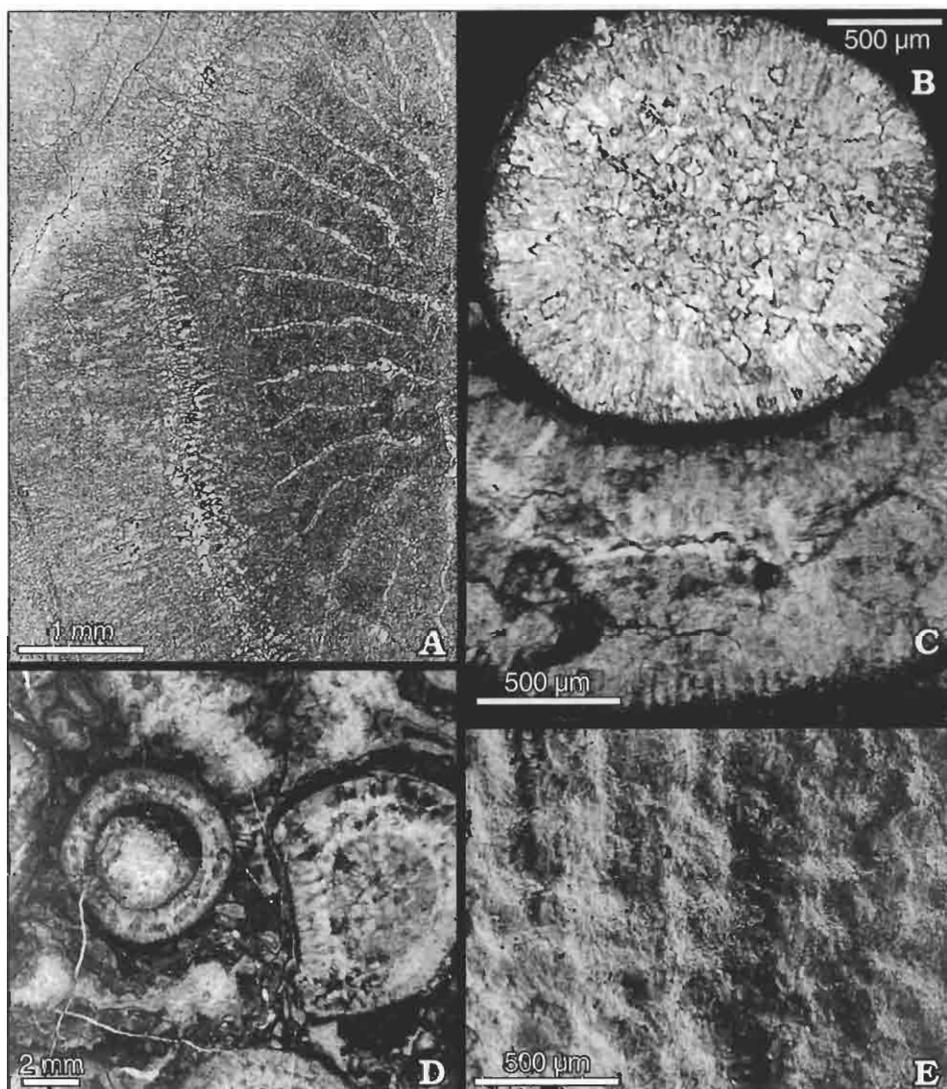


Fig. 9. Epithelial wall of a pachythechal type (continued). **A.** *Amphiaulastraea rarauensis* (Morycowa, 1971), Cretaceous (Lower Aptian), Valea Izvorul Alb (Romania), IGB 120. Thick wall with thin structural modules in the middle, and numerous septa at right; polished and etched surface. **B–D.** *Pachysolenia* sp., Triassic (Lower Norian), Austria, GBA 1987/01/14. **B, C.** Modular organization of the pachythecha discernible in diagenetically altered corallites; thin sections. **D.** General view of pachythechal corallites in transverse thin section. **E.** *Mitrodendron ogilviae* Roniewicz, 1966, Jurassic (Oxfordian), Poland, ZPAL H.III/110. Internal surface of the pachythecha with regularly arranged extremities of its modular elements; SEM.

Pachysolenia, see Cuif 1975 and herein Fig. 9B, C). Tips of bundles form granulations emerging on the internal wall surface, which are arranged in vertical rows or dispersed chaotically (Fig. 8A–C). Septa are in structural continuation with wall bundles of fibres, or may be separated from the wall by a suture (Fig. 8D).

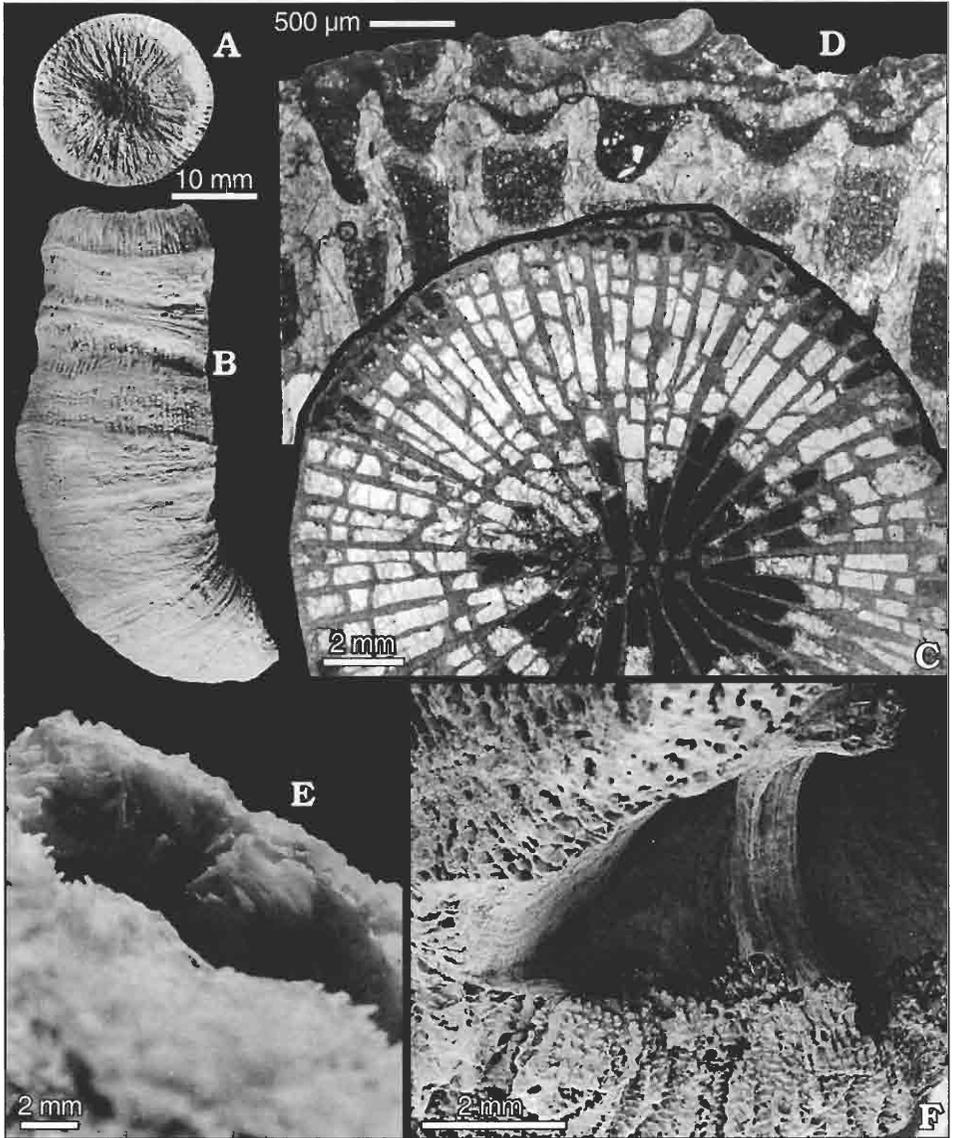


Fig. 10. A–D. Composite epithecal wall in *Montlivaltia multiformis* Toula, 1889, Cretaceous (Aptian), Bulgaria, ZPAL H.XVII/15. Distal (A) and lateral (B) views of the corallum; epithecal cover interrupted. C, D. Transverse thin section showing thin epitheca lying on the peripheral septal edges. E. *Mycetophyllia reesi* Wells, 1973, Recent, ZPAL H.XVII/16. Growing edge of the epitheca with distally oriented fibres of the outer epithecal layer. F. *Thamnasteria concinna* (Goldfuss, 1826), Jurassic (Oxfordian), Poland, ZPAL H.IV/17. Epitheca in the 'caverns' situated on the sides of the colony.

In the Amphistraeidae (Jurassic–Cretaceous) the external and internal wall structures resemble those in some zardinophyllids (Cretaceous *Amphistraea* recte *Amphiaulastraea rarauensis*, Morycowa 1971: pl. 26: 1g, herein Fig. 9A). In comparison with the Triassic pachythechal wall, the amphistraeid wall is built of well arranged

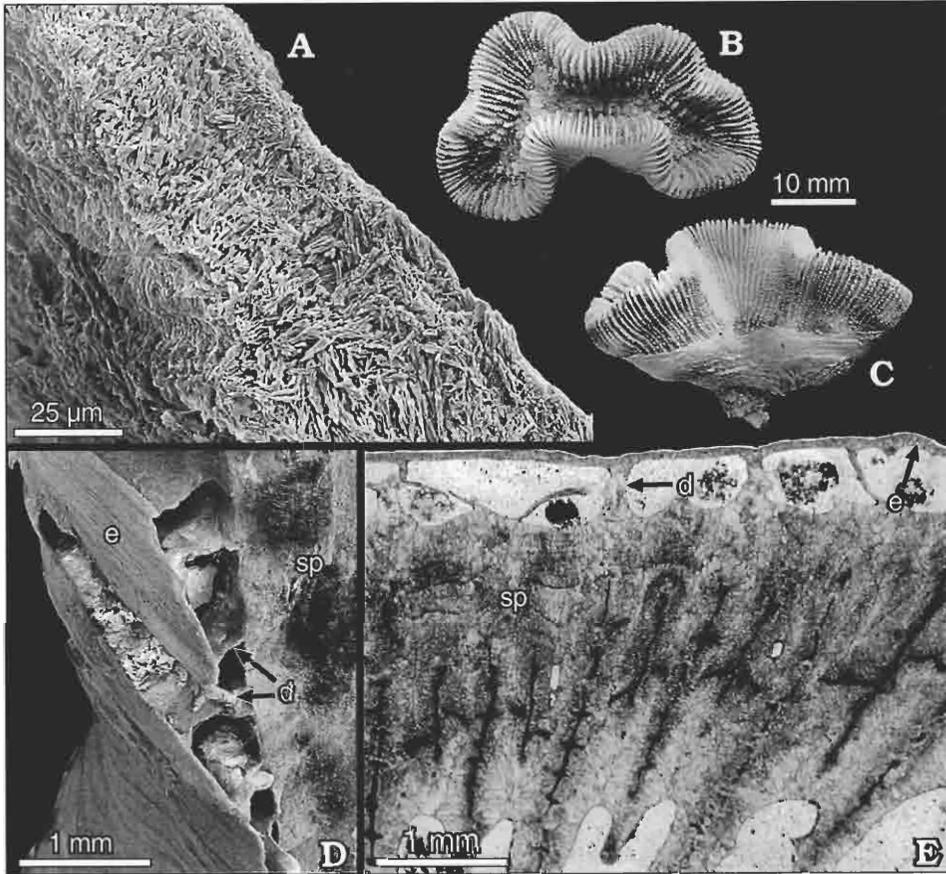


Fig. 11. A–E. Composite epithelial wall in *Manicina areolata* (Linnaeus, 1758), Recent, Bahamas. A, D. ZPAL H.XVII/18, broken and etched longitudinal section in SEM (A – enlargement of the inner epithelial layer); explanations as in E. B, C. ZPAL H. XVII/19. Colony in upper (B) and side (C) views. Epithea covers proximal half of the corallum, $\times 1.5$. E. ZPAL H.XVII/19. Transverse thin section showing a thick septotheca (sp), pellicular epitheca (e), and dissepiments developed between these two walls (d).

modules of the shape of horizontal spines (Septaldorn of Ogilvie 1896) and arranged in vertical rows (*Mitrodendron*, Fig. 9E; *Amphiastrea*, Morycowa 1964: pl. 22: 1b, c; Eliášová 1975: pl. 1: 2, 3; Kołodziej 1995: fig. 4: A–F). The microstructure of all septa continues into the wall structure. If one can judge from various patterns of diagenetically altered walls, the wall structure varies considerably in the Jurassic–Cretaceous *Amphiastrea* (compare Eliášová 1976b).

Composite walls. — Pellicular epitheca may join structurally with various skeletal elements, as in the following examples:

(a) Epithelial-stereomal wall. In stylophylline corals (Triassic–Lias), the wall is composed of microstructurally discontinuous parts: the epithelial inner layer contacts with a stereome deposit built of multidirectionally oriented bundles and scaly fibre aggregates (see Glossary: non-trabecular or fascicular corals).

(b) Epithecal-dissepimental wall. This wall results from the development of dissepiments within a free space between costae and the pellicular epitheca situated below the calicular rim. It develops alternately with an intercostal paratheca. Example: *Montlivaltiidae* (Jurassic–Cretaceous; Fig. 10D).

(c) Epithecal-trabeculothecal or epithecal-septothecal wall. In the *Dermosmiliidae* (Jurassic–Cretaceous) the calicular rim is trabeculothecal and segmented by costosepta (*Calamophylliopsis*, Roniewicz 1976: pl. 18: 2a, trabeculotheca determined as eutheca). The trabeculotheca may be replaced by septotheca. Pellicular epitheca is in contact with exothecal dissepiments (*Dermosmilia* and *Calamophylliopsis*, Roniewicz 1976: pl. 17: 5d and pl. 18: 5b, respectively). Epithecal wall is developed here as a discontinuous structure, often rudimentary, in the form of rings (*Calamophylliopsis*, Roniewicz 1976: pl. 19: 3). Similar is the wall in the *Smilostyliidae* (Roniewicz 1976: pl. 19: 2a, b; abundant in the Jurassic but possibly existing from the Triassic, see *Protoheterastrea razorensis* in Ramovš & Turnsek 1991, showing calicular structure resembling that of *Smilostylia*). Identical structural elements may be found in the composite structure of the holotheca in *Manicina* (Faviidae; Miocene–Recent, Fig. 11D, E).

(d) Epithecal-synapticulothecal wall. Within the *Dendrophylliina* (Late Cretaceous–Recent), as seen in solitary and dendroid corals, the pellicular epitheca may be developed within post-initial ontogenetic stages and combined with synapticulotheca and septotheca, as in *Thecopsammia* and *Balanophyllia*.

It is worthy of notice, that thin epithecal coatings occurring in types (b) (*Montlivaltia*) and (d) (*Balanophyllia*) of composite walls were used by Milne-Edwards & Haime (1857) as examples of epitheca, while the epithecal coating in the type (c) (*Manicina*) was analysed by Barnes (1972).

Epithecal Scleractinia in stratigraphical succession

Triassic

The earliest (Anisian) Scleractinia were highly diverse, taxonomically and morphologically. Four microstructural/morphological patterns of coral skeleton characterized four main phylogenetical stems, three of which are of a subordinal rank and traceable from the Triassic onwards. These are: (1) the pachythecaliid (*Pachythecaliina*); (2) non-trabecular or fascicular (*Stylophyllina*); (3) minitrabecular (*Caryophylliina*); and (4) thick-trabecular microstructural groups (Roniewicz & Morycowa 1993). Triassic corals showed diverse growth forms, i.e., solitary, phaceloid (see Glossary), and various colonial forms representing diverse integration levels (cerioid, thamnasterioid, meandroid, plocoid), but invariably possessed epithecal walls.

Simple epitheca/holotheca. — Pellicular epitheca was the most common wall, microstructurally documented in about ten families of corals of minitrabecular, thick-trabecular and non-trabecular, fascicular septal microstructure (e.g., *Reimaniphylliidae*, *Margarophylliidae*, *Procycolitidae*, *Omphalophylliidae*, *Tropiastraecidae*, *Ara-iophyllum*-group, *Stylophyllidae*, and *Thamnasteriidae*). Mature epitheca is known chiefly in the families: *Volzeidae*, *Protoheterastraecidae*, *Procycolitidae*, *Cycliphyllidae*, *Reimaniphylliidae* (*Cuifta*), i.e., in minitrabecular corals. Pachytheca is known in *Zardinophyllidae*.

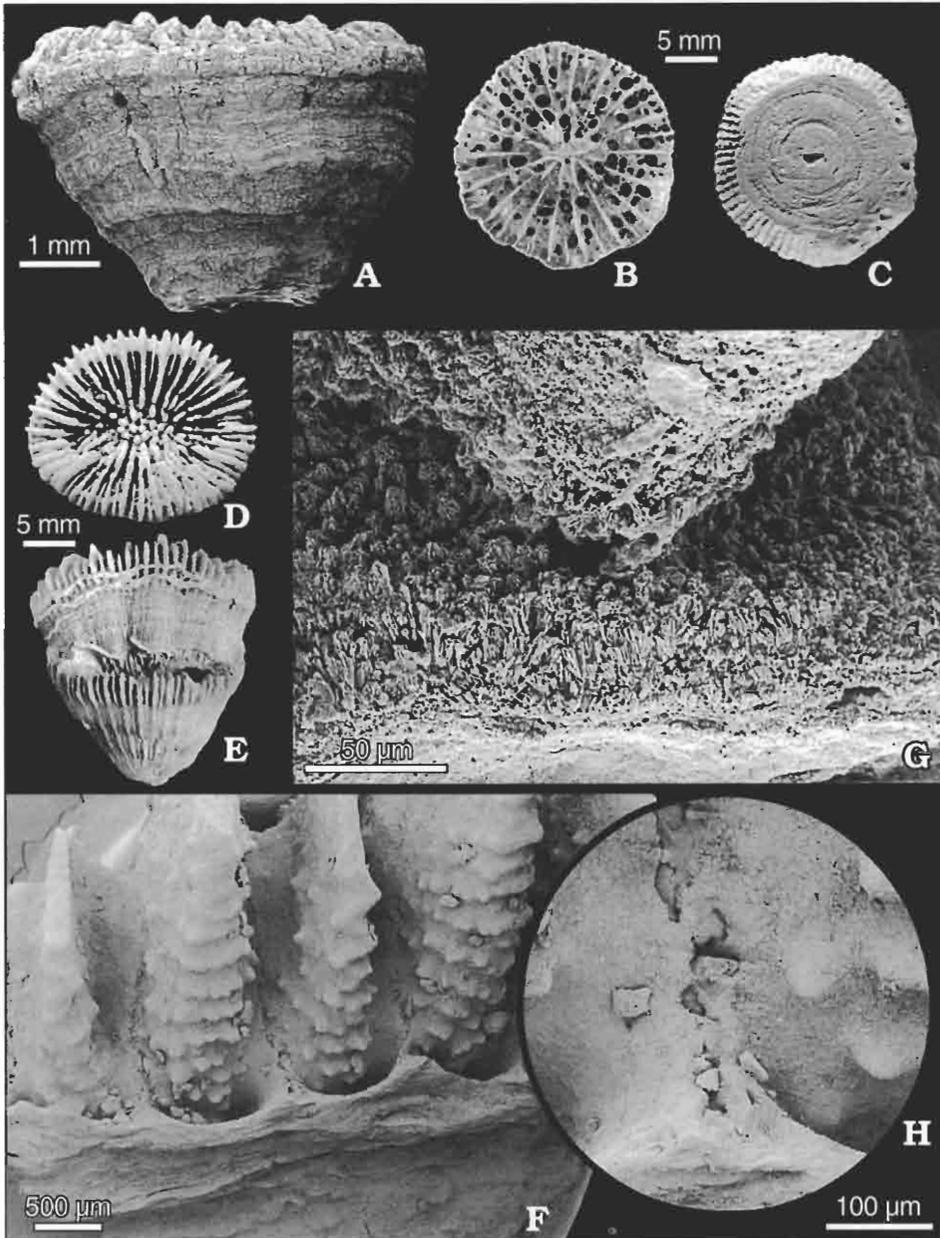


Fig. 12. **A.** *Thecocyathus mactrus* (Goldfuss, 1826), Jurassic (Toarcian), France, MNHN M.01263. Epithecally corallum in lateral view. **B.** **C.** *Discocyathus eudesii* (Michelin, 1840), Jurassic (Bajocian), Croisille, Calvados, France, MNHN M.00086. Distal (**B**) and proximal (**C**) views; epitheca in concentric folds. **D–H.** *Trochocyathus rawsoni* Pourtalès, 1874, Recent, off Venezuela, 12°46'N/70°41'W, 201 m, ZPAL H.XVII/20. Distal (**D**) and lateral (**E**) views, epithecal cover incomplete. **F.** A fragment of the calicular rim to show a contact zone between the wall and septa (see the text); note a sharp rim of the epitheca. **G.** A fragment magnified showing centripetally oriented fascicles of fibres of the epitheca; etched surface. **H.** Interseptal extensions of the epithecal stereome with desmocyte attachment scars on the surface.

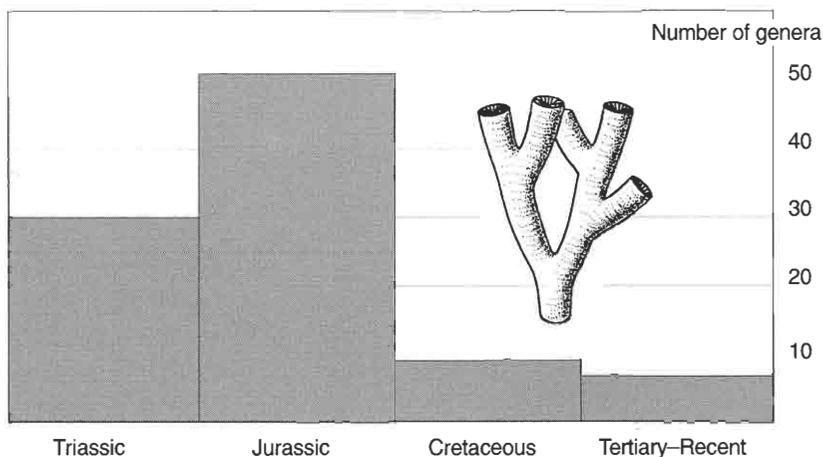


Fig. 13. Total number of phaceloid shallow-water scleractinian genera in the Mesozoic and Cenozoic (after Vaughan & Wells 1943, completed with data from Alloiteau 1957, 1958; Alloiteau & Dercourt 1966; Alloiteau & Tissier 1958; Barta-Calmus 1973; Beauvais 1986; Cuif 1977; Deng & Kong 1984; Eliášová 1975, 1976a–b, 1978; Floris 1972; Geyer 1969; Melnikova 1985; Melnikova & Roniewicz 1976; Morycowa & Roniewicz 1990; Roniewicz 1976; Russo 1979; Siharulidze 1977; Wells 1961, 1973).

Composite epithecal wall. — The only wall of this category known in the Triassic is an epithecal-stereomal wall in solitary and phaceloid stylophyllines.

Early Jurassic–Early Cretaceous

At the Triassic–Jurassic boundary the majority of the then dominant epithecate scleractinians became extinct except for the stylophyllids, and were replaced by new coral groups that comprised faunas of different morphology and microstructure (Roniewicz & Morycowa 1989, 1993).

The replacement faunas contained numerous solitary corals (cylindrical, ceratoid, trochoid or discoid; see Duncan 1867–1868; Beauvais 1986); phaceloid corals became relatively rare, although well differentiated taxonomically (compare Beauvais 1986). The phaceloid epithecate corals re-appeared as an important faunal component not earlier than the Late Jurassic. In microstructural plan, the change at the Triassic–Jurassic boundary was even more dramatic, as practically all known earlier microstructural groups at the family level disappeared (Roniewicz & Morycowa 1989, 1993). It led to a great taxonomic change in the coral faunas. The impact of the mid-Cretaceous faunistic crisis upon corals, expressed as a taxonomic impoverishment of a fauna still Late Jurassic in character, resulted in a conspicuous reduction of epithecate solitary and phaceloid corals (Fig. 13).

In the Early Jurassic–Early Cretaceous interval the following types of epithecal wall were common:

Simple epitheca/holotheca. — This type of wall was common in holothecal corals. These corals belonged to the families that range to the Early Cretaceous e.g., thamnasteriids, microsolenids, stylinids, haplaraeids. Since the Aptian, discoid corals developed with concentrically wrinkled undersurfaces (morphological features of epitheca).

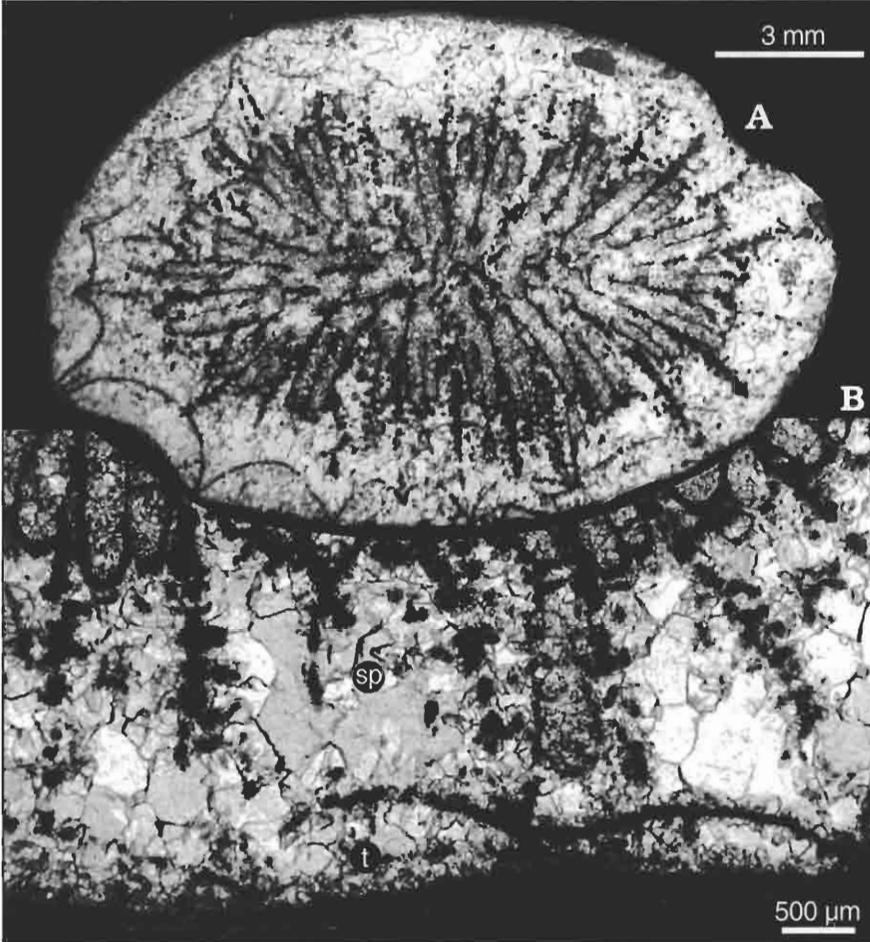


Fig. 14. *Aplosmilia* sp., Jurassic (Oxfordian), France, ZPAL H.XVII/21. A. General view. B. Enlarged fragment. Septothecal wall (sp) covered with thick tectura (t). Thin section.

Here also belong the Aptian faviine corals *Cyclophyllopsis* (Alloiteau 1957) and *Dimorphocoeniopsis* (Zlatařski 1967), and the Aptian–Cenomanian *Cyclastraea* (Alloiteau 1957; Zlatařski 1970; Gill & Lafuste 1971). Mature epitheca is observed in the Intersmiliidae, Donacosmiliidae, and Cladophylliidae. Typical pachythea is observed only in the Amphistraeidae.

Composite epithecal walls. — Epitheca combined with epicostal dissepiments appeared for the first time in the Early Jurassic (Montlivaltiidae) and became common in the Late Jurassic (Montlivaltiidae, Fig. 10A–D; Misistellidae and *Placophyllia*: a wall determined as epicostal paratheca in Eliášová 1976a: figs 1, 2; pl. 1: 1–3; pl. 5: 1; pl. 7: 1). Beginning in the Middle Jurassic, there are common composite walls with thin epitheca and trabeculotheca or septotheca (Dermosmiliidae, Smilostyliidae). Epitheca (identified morphologically) covered skeletons of the earliest caryophylliids: e.g., the

trochoid corallum of Toarcian *Thecocyathus*, or the lower surface of discoid Bajocian *Discocyathus* (Fig. 12A, E).

The walls of some Jurassic–Cretaceous corals, considered up to now to be epithecal, differ essentially in structure. Here we place a wrinkled, probably trabecular wall (with a peripheral line made of dissolved centres of calcification joined to the midline of septa, as in the Flabellidae) of the archaeosmiliids (Early Jurassic; Melnikova 1975: pl. 1: 1v; Beauvais 1986: pl. 2: 3d), and septothecal wall with thick tectura in the rhipidogyrids (Fig. 14).

Late Cretaceous–Recent

Since the Late Cretaceous, a difference in morphology of corallites has been marked between shallow-water and deep-water corals.

Beginning with the Turonian, corals in deep-water environments (Type C. Middle Shelf, see Droser *et al.* 1993) became a conspicuous element in the faunal spectrum. These were caryophylliine corals (Late Cretaceous, see Alloiteau 1957; Turnšek 1978; Nielsen 1922), and later, dendrophylliine corals (Paleogene, see Wanner 1902; Nielsen 1922; Floris 1972). However, among these corals, epithecal walls are no longer common (less than 5% of caryophylliine genera). The most progressive groups of the Caryophylliina (i.e., the Flabellidae, Turbinoliidae, and Caryophylliidae) developing in the Cenozoic, nearly completely lack epitheca. Their walls are trabecular or septothecal, and often covered with tectura (Stolarski 1995).

The Late Cretaceous shallow-water coral assemblages closely resembled those of the Early Cretaceous in their taxonomic composition (see Eliášová 1991, 1992; Löser 1989, 1994; Baron-Szabo 1997; Baron-Szabo & Fernandez-Mendiola 1997). Colonial corals dominated; some of them had holotheca. Epithecate phaceloid and solitary corals became rare with the exception of various discoid forms with epithecal lower surfaces (e.g., the large group of cunulitid corals ranging from the Coniacian to Maastriichtian, see Alloiteau 1957; Turnšek 1978; Beauvais 1982).

Also during the Tertiary, epithecate solitary and phaceloid corals were rare in shallow-water environments. Some of them had epithecal walls (judging from their morphology), e.g., Paleogene faviid *Rhabdophylliopsis* (Alloiteau & Tissier 1958) or *Liptodendron* (Eliášová 1991). In the Cenozoic, the following types of epithecal walls have been recognized:

Simple epitheca/holotheca. — Pellicular epitheca is known in protocorallites of Gardineriidae, some Guyniidae and Rhizangiidae (*Culicia*), some Poritidae (*Porites*: Jell 1981: pl. 8: 4–6), some Caryophylliidae (*Polycyathus*, Fig. 3A). Epitheca apparently is also developed in early ontogenetic stages of Fungiidae (*Fungia* anthocaulus, see Vaughan & Wells 1943). Mature epitheca has been noted only in adult stages of Recent *Culicia* (see Chevalier 1971: fig. 65) and in some caryophylliines: in Recent *Gardineria* (see Barnes 1972; Stolarski 1996; herein Fig. 7C–D), and three guyniids: *Guynia*, *Schizocyathus* and *Temnotrochus* (see Stolarski 1997).

Composite epithecal walls. — These walls are common in shallow water corals that retain epithecal prototheca. Their holotheca or epitheca are combined with synapticulotheca, trabeculotheca and/or septotheca; Miocene mussiid *Syzygophyllia* has an epithecal-parathecal wall. Recent *Manicina areolata* shows that the holotheca may

cover more or less completely the colony lower surface depending on the shape of the colony; in conical colonies the holotheca may cover nearly the whole lower colony surface (Barnes 1972: fig. 1a), or may form rings, or be developed only proximally (Fig. 11), whereas in colonies with a convex calicular surface and flat lower surface, the holotheca is developed as a horizontal sheath (Fabricius 1964). Composite epithelial walls are known also in some caryophylliids (epithelial rings on the septothecal wall in some species of *Trochocyathus*, e.g., Eocene *T. hyatti* Vaughan, 1900 and *T. uber* Vaughan & Popenoe, 1935, and Recent *T. rawsoni*, see Fig. 12D–H, and in *Paracyathus*, e.g., in Eocene *P. bellus* Vaughan, 1900).

Epitheca in ontogeny

A primary epithelial prototheca sometimes extends into postlarval stages as an epitheca. In some corals, the epitheca continues as a thin lamella from the basal plate to the upper corallum part (e.g., some Rhizangiidae), but more frequently it is discontinuous, or lacking in adult stages (Chevalier 1987). On the assumption that the ontogeny of the wall in *Gardineria* and some other corals (zardinophylliids, guyniids) is typical of most epithecate corals, and considering Chevalier's remarks on extension of protothecal epithelial structure into the adult stages, we regard a purely epithelial wall in post-protothecal stages in fossil corals (with inaccessible proximal portion) to be indicative of their having epithelial prototheca.

In the bulk of caryophylliids, a marginothecal prototheca develops. During trabecular wall ontogeny two modes of development have been observed: (1) in some taxa the marginotheca extends into the adult stage, whereas in others (2) the marginotheca is replaced successively by trabeculotheca and septotheca (Stolarski 1995). In some taxa the trabecular wall is combined in the adult stage with the epitheca interpreted here as a rudimentary element transferred from the juvenile to the adult stage.

Generally speaking, the wall structure at the post-juvenile stage manifests the main features of its early ontogenetic stage, i.e., the presence of either fibrous or trabecular prototheca. This allows discrimination of a number of patterns of wall ontogeny typical of some Recent and also of some important groups of fossil Scleractinia (Fig. 15). The following review chiefly concerns phaceloid and solitary corals, as data on colonial corals are scarce.

Pattern A. — The prototheca is epithelial. In the adult stage, the wall is purely fibrous; the epithelial calicular rim may form a distal tube of various length. In the adult stage, apart from pellicular epitheca (especially common in the Triassic Reimaniphylliidae, Margarophylliidae, and some Procyclolitidae), there is a tendency to form thick walls. These include various types of mature epitheca, pachytheca, and epithelial-stereomal wall. The distal septal margin often has a peripheral depression. The pattern is common in the Mesozoic, chiefly in the Triassic (Protoheterastreaeidae, Volzeiidae, some Reimaniphylliidae, some Procyclolitidae, Stylophyllina, Zardinophyllidae) and in the Jurassic (Cladophylliidae, Placophylliidae, Intersmiliidae, Donacosmiliidae, Amphistraeidae, and others). In the Recent, this feature is observed in a few genera (*Culicia*, *Gardineria*, *Guynia*, *Schizocyathus* and *Temnotrochus*).

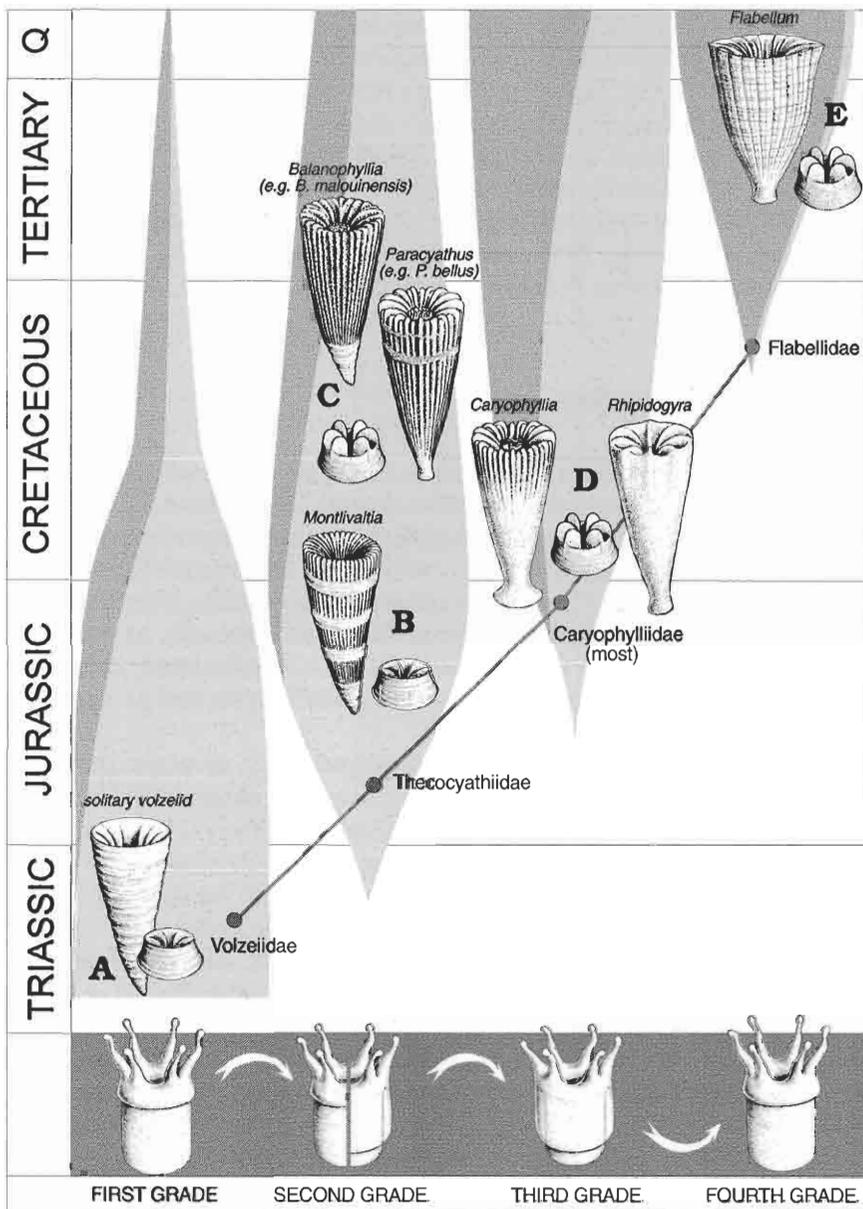


Fig. 15. Evolution of the scleractinian edge-zone (four grades) expressed in terms of wall development (five ontogenetic patterns A–E). The grades are shown as spindle-diagrams which illustrate the relative spread of corals in shallow- (bright portion of the spindle) and deep-water environments (dark portion); not to scale. First grade: edge-zone originally lacking, epithecal wall throughout ontogeny. Second grade: variable range of the edge-zone; epithecal or trabecular prototheca, and adult walls of different types (parathecal, trabeculo-septothecal, synapticulothecal) combined with epitheca. Third grade: edge-zone fully developed, often investing the whole corallum and producing tectura; trabecular prototheca and adult walls. Fourth grade: edge-zone reduced in range, producing tectura; marginothecal wall. The line linking Volzeiidae–Thecocyathiidae–Caryophylliidae–Flabellidae represents an evolution of the structural plan of the Caryophylliina and at the same time illustrates a stratigraphical sequence of presumed steps in phylogeny of the suborder.

Pattern B. — The prototheca is epithelial. The post-protothecal stage shows a pellicular epitheca, in places reduced to epithelial rings, but generally occurring in composite epithelial structures. The septa are exsert, and the calicular rim is marked by the peripheral elevation of endotheca. It is common in the Jurassic–Cretaceous family *Montlivaltiidae* and occurs also in Recent colonial corals with epithelial prototheca, e.g., *Poritidae* (*Porites*, see Jell 1981: pl. 8).

Pattern C. — The prototheca is trabecular (marginotheca). In post-protothecal stage, the wall is trabecular (either trabeculothecal or trabeculo-septothecal) or synapticulothecal. Pellicular epitheca occurs in post-juvenile stages and epithelial rings tend to be reduced.

In the Mesozoic, the pattern is common in the *Dermosmiliidae*, *Smilostyliidae*, *Archeosmiliidae* and supposedly in *Thecocyathidae* (protothecal stages not examined directly due to recrystallization); in the Mesozoic–Recent interval it is known in the *Faviina* and *Dendrophylliina* and some *Caryophylliidae* (*Paracyathus*, *Trochocyathus*).

Pattern D. — The prototheca is trabecular (marginotheca). The post-initial trabeculothecal wall may be replaced in the adult stage by a septotheca. The wall is often covered with tectura. Generally, epitheca is lacking, but sometimes relict rings may be present.

The pattern is dominant in the Cenozoic *Caryophylliina*. At least some *Rhipidogyrina* (Jurassic–Cretaceous) probably also had this ontogenetical pattern; however, the microstructure of their protothecal stages has not been examined directly. The indirect evidence is the presence of the epithelial wall in the phaceloid genus *Placophyllia* (family *Placophylliidae* Eliášová, 1990) exhibiting the neorhipidacanth type of the septal microstructure (Eliášová 1976: pl. 2: 2; 1990: pl. 2: 1) typical of the suborder.

Pattern E. — The prototheca is trabecular (marginotheca). The adult wall is marginothecal or, rarely, trabeculothecal. Tectura may develop.

This pattern is known exclusively in *Flabellidae sensu* Stolarski (1995). A similar pattern (wall constructed of a palisade of vertical spines in initial stage and trabeculae in adult skeletons) is known in the *Pocilloporidae* and *Acroporidae*.

Wall patterns versus edge-zone development

Vaughan & Wells (1943) and Wells (1956) noted that enlarging the edge-zone causes reduction of the epithelial wall. Wells (1956) defined the edge-zone as a column wall outfold extending over the calicular rim, and containing a continuation of the gastrovascular cavity. The edge-zone is developed in some solitary and phaceloid corals, whereas in colonial corals it is transformed into coenosarc. The calicoblastic layer of the edge-zone has potentially the same secreting capacity as the column wall of the polyp, and produces the extra-calicular prolongation of septa (costae), dissepiments and sclerenchyme.

The edge zone's ability to develop external sclerenchyme is highly differentiated. In some coral groups the edge zone covers the skeleton and does not produce the extracalicular sclerenchyme at all, in some groups it produces sclerenchymal thickening of extracalicular prolongation of skeletal elements, and in a few coral groups, the

edge zone of a high skeletogenic potential forms a particular structure covering the wall, i.e., tectura. In this section, we present the stratigraphic distribution of corals developing an edge-zone and their ability to form extra-calicular sclerenchyme.

Paleontological data and information on wall patterns in Recent corals allows the following gradation in the development of edge-zone within the Scleractinia to be traced (Fig. 15).

First grade. — Polyp entirely surrounded by an epitheca, edge-zone absent. Pattern A of skeletal ontogeny. Mainly Triassic and Jurassic genera, some reaching the Albian; occurrence in shallow water deposits. In the Recent known as relict faunas in deep water or cryptic environments.

Second grade. — Temporary covering of the distal portion of corallum with edge-zone, alternating with its withdrawal up to the calicular rim. This results in the formation of an incomplete epithelial wall or epithelial rings alternating with paratheca, trabeculotheca, synapticulotheca or septotheca. Generally, the edge-zone lacks or has only a small ability to form extra-calicular sclerenchyme. Patterns B and C of skeletal ontogeny. Mainly Jurassic and Early Cretaceous; shallow water environments, from Late Cretaceous deep-water environments. Colonial (holothecal) forms known in the Recent.

Third grade. — The edge-zone covering the distal skeletal portions or enveloping the entire skeleton, depending on the ontogenetic stage. It deposits sclerenchyme that results in thickening of existing elements and/or formation of tectura. Pattern D of skeletal ontogeny. Mesozoic–Recent; shallow-water and deep-water environments.

Fourth grade. — Polyp entirely surrounded by a trabecular wall. Edge-zone is developed as a narrow marginal fold encircling the calice, which may produce tectura. The skeletal ontogeny follows pattern E. Cenozoic, deep-water.

Development and decline of scleractinian epithecate corals

Transformations of scleractinian faunas

The extinction event at the Permian–Triassic boundary eliminated the last remnants of the Permian rugosan fauna. Some cryptogenic coral groups (pachythecal, minitrabecular, thick-trabecular, and non-trabecular groups, see Roniewicz & Morycowa 1993) soon entered abandoned niches and in a span of about five million years became a significant element of shallow-water benthic communities. These groups constituted the framework for the Mesozoic scleractinian fauna. Among the earliest scleractinians there is a considerable percentage of solitary forms but frequent are also colonial, highly integrated corals.

In the Triassic, scleractinians with simple epitheca (including holotheca) prevailed. This fauna resembled coral faunas of the Paleozoic due to common occurrence of epithecate taxa and thus similar polyp/corallum relationships. The presence of the epitheca as a main structural element in subsequent coral faunas supports the hypothesis of a continuation of the same architectural style across the P-T boundary (Stolarski 1996).

The crisis at the Triassic–Jurassic boundary eliminated the majority of the early scleractinian genera with a Paleozoic type of polyp/corallum relationship. In the Jurassic, some survivors from the Triassic (stylophyllids) and descendants of zardino-phyllids (amphiastraeids, intersmiliids, donacosmiliids) retained their primary morphology and microstructure. In addition to these successful coral groups without edge-zone (First grade), there were some new groups (montlivalitiids, dermosmiliids), which exhibited an enlargement of the edge-zone (decline of epitheca). This edge-zone had limited ability to produce extra-calcular sclerenchyme (Second grade), and co-existed with an epithelial wall. The families mentioned flourished in Jurassic–Early Cretaceous shallow-water environments.

The Second grade in edge-zone development was attained by corals of many Mesozoic groups, which differ from each other in their ontogeny. In these corals, epitheca, if developed, was rudimentary; in some groups it was confined to protothecal stages, while in others it remained as a relict element in post-initial ontogenetic stages. This epitheca was retained by Cenozoic shallow-water corals and a larger group of deep-water corals (*Dendrophylliina*) that began in the Late Cretaceous.

The Third grade in edge-zone development started as early as the Jurassic (*Rhipidogyridae*). In rhipidogyrids, an edge-zone covering large portions of the corallum was highly active in the production of extra-calcular sclerenchyme. Other groups having an extended edge-zone were represented by the *Caryophylliina*, with their expansion to deeper waters beginning as early as the Late Jurassic.

Noteworthy is the evolutionary trend initiated in the Late Cretaceous by the *Flabellidae*, which involved some reduction of the edge-zone co-occurring with a complete loss of epitheca (Fourth grade).

Mesozoic environments that were on the one hand favourable to survival of conservative faunas, on the other hand induced important changes in the ontogeny and polyp anatomy of various phylogenetic lines. The appearance of composite epithelial walls and non-epithelial walls (trabecular walls, tectura), testifies to ontogenetic evolution and the loss of the Triassic pattern (Pattern A). In the Jurassic genus *Chomatoseris* (appearing in the Lias, Beauvais 1986), a complete investment of the skeleton with a living tissue may be observed for the first time (see Gill & Coates 1977). These transformations in the wall structure and/or polyp-skeleton relationships through geological time testify to the growing importance of the polypal edge-zone. The great number of phylogenetic lines experiencing structural transformation of walls suggests directional selective stresses in Triassic and Jurassic coral environments.

Early in the Cenozoic time, phaceloid and solitary epithecate forms almost completely disappeared. At the same time, the role of colonial corals increased in shallow water assemblages, especially fast-growing zooxanthellate forms. However, epitheca remained important in some colonial corals, either as prototheca, or as a more or less complete holothecal coating of adult colonies.

Shallow-water colonial corals, which appeared at the beginning of Cenozoic time and achieved an unprecedented evolutionary success (e.g., the *Acropora* Emergence of Rosen 1993), displayed adaptations confined to agitated water conditions (acroporids, pocilloporids, poritids, fungiids). The resulting colonies are characterized by the highest degree of integration of polyps, thus producing strong, porous, quickly built skeleton which is totally covered by zooxanthellate living tissue having a high regeneration potential.

Mesozoic success of epithecate corals

The successes of corals with simple epitheca observed in Late Triassic and Late Jurassic apparently were ecologically controlled. The impressive and intriguing history of epithecate corals was connected above all with the temporal flourishing of solitary and phaceloid growth forms (Fig. 13).

The paleontological record suggests that a direct relationship existed between the radiation of phaceloid corals and the expansion of shallow-water environments of fine-grained, muddy and sandy limestone deposition on carbonate platforms (especially those of Late Triassic and Late Jurassic age). Conversely, their disappearance correlated with the decline of these environments. Fine-grained sedimentation led to the prevalence, on a global-scale, of relatively unstable sediment bottom. Sedimentological data indicate that, as a rule, calcareous sediments rather quickly consolidated. However, taking into consideration that micritic limestones were deposited as loose micritic particles (Gruszczynski 1986), we assume that bottom surfaces remained rather unstable causing temporary turbidity of water during storms. Thus, abundant limy sedimentation, unstable substrates and turbid waters resulted in the development of a unique coral environment. The analysis of some Upper Jurassic West European reefs by Insalaco *et al.* (1997) indicates that phaceloid coral thickets (built of non-epithecate *Aplosmilia*) developed in a depositional environment of pure micritic limestone showing no traces of early cementation. Other examples of phaceloid coral assemblages within environments of fine-grained micritic sedimentation origin are from the Upper Triassic of the Alps (epithecate *Retiophyllia* assemblages, see Stanton & Flügel 1989, 1989), from the Upper Jurassic of Poland (epithecate *Calamophyllia* assemblages, Roniewicz & Roniewicz 1971), Portugal, Spain, Switzerland and France (bibliographical data summarized by Leinfelder 1993).

Given the deficiency of hard substrates suitable for settlement of planulae, and the continuous race with sedimentation, growth forms may have played an important role in the survival and propagation of species. Phaceloid growth forms assumed this role in Mesozoic carbonate platform environments (Roniewicz 1989b). In those environments, two extreme coral life-strategies may be differentiated that are analogous to the soft-bottom strategies of bivalves, i.e. 'mudstickers' and 'recliners' (Seilacher 1984; Machalski 1998). Phaceloid epithecal and solitary non-discoid corals adopted the soft-bottom strategy of 'mudstickers' where sedimentation rates increased, whereas colonial lamellate and/or massive corals and discoid solitary and colonial corals, the 'recliners', where sedimentation rates lowered. In coral 'recliners', one may consider the possible adaptive significance of their epitheca/holotheca. In juvenile colonies and at the perimeter of adult lamellate colonies in different suborders, the holotheca is the most external element of the colony and serves as a 'bedplate' for the development of newly formed septa. Thus, its development might be important for corals laying on the sedimentary bottom (snow-shoe effect).

The decline of epithecate corals – possible causes

Major ecological changes at the Triassic–Jurassic boundary resulted in the extinction of a majority of corals having a primary wall structure. The number of taxa having a polyp initially enclosed in epithecal wall (First grade) declined, especially the representatives of the Zardinophyllidae, Volzeiidae, Reimaniphylliidae, Cycliphylliidae,

and others. Free niches soon became occupied by corals with new types of ontogeny and a new mutual relation between the polyp and skeleton, i.e. corals that have developed an edge-zone (Second and Third grades). In turn, these successors as well as some relict but abundant coral groups with an epithelial wall similarly, adversely reacted in response to the environmental crises at the end of the Jurassic, and later during the middle of the Cretaceous period. These were, among others, the epismiliids, amphistraeids, and dermosmiliids (Roniewicz & Morycowa 1993). As a consequence of these environmental changes, phaceloid and solitary shallow-water epithelial corals never flourished after the mid-Cretaceous crisis.

Adverse responses to environmental changes were not observed in colonial holothecal corals originating in the Mesozoic (e.g., Faviidae), which exist today in shallow waters, though Recent coral environments, confined to the near-shore zones and, at most, to the hard substrate, differ from those of the Mesozoic, which developed mostly on sediment bottom, and presumably at greater depths (Geister & Lathuilière 1991). This suggests the high adaptability of their colonial mode of life to survival in shallow waters.

A general decline of epithelial forms in modern seas can be seen in both shallow water and deep water environments. It has been caused by two parallel processes during the Cenozoic, influencing the growth-forms exhibited in modern fauna:

(1) in shallow waters, the process of elimination of solitary and phaceloid corals other than the expansive *Fungia* which has a skeleton fully covered with living tissue, and a few phaceloid genera living in sheltered conditions, all of which lack epitheca; domination by colonial highly integrated colonies.

(2) in deep waters, the process of taxonomic increase of solitary forms which, with rare exceptions (gardineriids, some guyniids), have skeletons covered by living tissue, either completely devoid of epitheca or retaining it in a relict form in late ontogenetic stages (ontogeny of Pattern E and D, respectively); colonies are represented by zig-zag-branch forms (uniserial erect forms of Coates & Jackson 1985).

It may be inferred that Triassic and Jurassic epithelial solitary and phaceloid forms developed in environments with low rates of mechanical destruction. This conclusion is based on the fact that regeneration potential of epithelial corals is relatively low due to a lack of an edge-zone, i.e., the tissue which could cover the external surface of the corallum and repair injuries, or to build the strengthening layer, i.e., tectura. It is worthy of notice, that the ability to repair injuries in phaceloid corals is incomparable to that of colonial branching corals having the total surface covered with small polyps. In epithelial phaceloid corals, only the tips of branches (corallites) bear the living tissue, i.e., the polyps; the death of the polyp means inevitable destruction of the naked skeleton. For the reason of the low regeneration potential of Mesozoic phaceloid epithelial corals, their life conditions can hardly be compared with those of easily regenerating Recent branching corals (e.g., Triassic *Retiophyllia* vs. Recent *Porites*, see Bernecker *et al.* 1999). Perhaps the ability to form a thick tectura by the Rhipidogyrina (phaceloid *Aplosmilia*, solitary *Rhipidogyra* and colonial forms homeomorphic with Recent shallow-water Eusmiliinae) could explain the rapid expansion of those corals in the latest Jurassic and in early Late Cretaceous environments (Eliášová 1973 and 1991, respectively), and their colonization of waters of higher energy.

In modern shallow-water environments, solitary and phaceloid epithecate corals could not survive due to high rates of bioerosion accomplished by various organisms, i.e., microborers harmful to their bare skeletons and, especially, grazing molluscs or fish predators which could easily kill their isolated polyps. In Mesozoic material we observed microborings (endolithic algae) in surficial skeletal parts, boring bivalves and polychaetes in massive colonies, but have never discerned the traces of grazing organisms on any coral skeletons. This observation agrees with the statement of Stanton & Flügel (1987) that various organisms from the destroyer guild (Fagerstrom 1984) expanded no earlier than late in the Mesozoic and in the Cenozoic. Two factors may cause the level of bioerosion on the sea bottom to be low: lack or unimportance of bioeroders (cause of evolutionary or ecological nature) or high rate of sedimentation and quick burial of exposed skeletons (cause of sedimentological nature). Bertling (1997) has shown an inverse proportion of intensity of bioerosion to sedimentation rates in Jurassic coral environments. We assume that a bulk of Triassic and Jurassic phaceloid and elongated solitary epithecate corals lived in environments of high-rate sedimentation. Apart from their growth form, it is supported also by low bioerosion of their skeletons.

In shallow water, the main factor causing edge-zone extension may be a bioerosion, whereas in deep water environments below the calcium compensation depth (CCD) a factor of chemical corrosion of calcareous skeleton must be considered. Thus, an escape from the epithecal state observed in many coral groups might be caused by the environmental stress leading to the elimination of epithecate corals and the development of corals provided with an evolutionary novelty, a protective edge-zone. Naturally, an extended edge-zone may be an effective protection only against endolithic microborers, but ineffective as a protection against mollusk, echinoderm and fish predators, which are important destroyers in modern shallow-water coral environments (compare Hutchings 1986). The role of animal bioeroders in the post-Mesozoic red algae evolution has been a matter of discussion by Steneck (1983). The decline of Mesozoic solenoporacean red algae is analogous to the decline of the epithecate corals. Thus, bioerosion, increasing significantly since Late Jurassic (Bromley 1994), appears to be a powerful factor in the turnover and evolution of some Mesozoic/Cenozoic organisms.

The success of Cenozoic corals

The most successful corals in the Cenozoic belong to the acroporids, pocilloporids, poritids, fungiid and dendrophylliid corals, as well as multidirectionally radiating caryophylliine corals. The first four groups are shallow-water and colonial except for the solitary *Fungia*, the latter two are predominantly deep-water, mostly solitary corals. In the acroporids and pocilloporids, any epithecal wall seems to be lacking. In the other groups, the epitheca is rudimentary and edge-zone evolution resulted in a maximum covering of the skeleton by living tissue. Judging from its morphology, in fungiids a relict epitheca has been retained in the protothecal stage (see Vaughan & Wells 1943). In the dendrophylliids, the prototheca is trabecular, and the epitheca initiated during the early post-larval stage may also extend into adult stages in some solitary forms (e.g., *Thecopsammia*), but the majority of corals have skeleton completely devoid of epitheca, and covered with living tissue, up to a complete envelopment of the corallum (*Heteropsammia*).

In the caryophylliine phylogenetic stem, development of this tendency is observed throughout its history (Fig. 15) and is illustrated by the following stratigraphical distribution of successive forms: Triassic – epitheca well developed (Volzeiidae); Toaracian – epitheca well developed (*Thecocyathus*); Bajocian–?Paleocene – reduced epitheca (*Discocyathus*); ?Oxfordian–Recent – rudimentary (*Trochocyathus*) or lacking epitheca. The turbinoliids represent the final stage of the edge-zone expression (?Albian, Maastrichtian – Recent). Their coralla are fully covered with living tissue and lack epitheca, although traces of it can be seen in some Paleocene forms that probably represent a separate evolutionary line (see Alloiteau & Tissier 1958). Covering of the corallum by living tissue resulted in developing of automobility (see Fabricius 1964; Gill & Coates 1977).

The expansion of living tissue beyond the thecal rim increased the skeletogenic polyp surface, and this, supposedly, was responsible for an unparalleled evolutionary plasticity within the Recent Caryophyllioidea. This is a group of corals that now occupies most Cenozoic environments available to corals. Thus, it includes shallow- and deep-water azooxanthellate species, as well as zooxanthellate, hermatypic forms. It is also the most taxonomically diverse group of Scleractinia, represented today by about 70 genera and more than 400 species (Cairns 1997). Differentiation of ontogenetical types within the traditional Caryophylliina (Pattern A, C–E) is also greater than that within other suborders (Faviina: Pattern A, B, and C; Dendrophylliina: Pattern C). Similarly, there is a highly differentiated development of the edge-zone, as the suborder contains forms without an edge-zone, and some with an edge-zone of varying skeletogenic potential (First to Fourth grades), showing various edge-zone-derived skeletal adaptations to soft as well as hard substrates.

Conclusions

- In the history of the Scleractinia there are changes in wall structure, that show a trend of modification of the polyp anatomy, i.e., expansion of the edge-zone (First to Fourth grades). Triassic corals with complete epitheca and lacking the edge-zone (First grade) represent the starting point for further development of the coral polyp. Extension of a simple edge-zone lacking skeletogenic potential led to the formation of epithelial compound walls (Second grade). The secreting ability achieved by the edge-zone created a new condition: the capability of forming of extra-calcicular skeletal deposits, e.g., tectura (Third and Fourth grades). The trend of edge-zone enlargement is expressed in the phylogeny of some coral groups (e.g., Caryophylliina) and is reinforced by general faunistic turnovers caused by biotic crises which eliminated taxa (sometimes of higher ranks) with underdeveloped edge-zone.
- This trend was probably accomplished by a transformation of ontogeny with the reduction or elimination of epithecate stages. This process may be reconstructed based on the ontogenetic sequence exhibited by the Caryophylliina. This group has retained the most primitive ontogenetic pattern (Pattern A) with epithelial prototheca which survived until the Recent together with a series of progressively transforming patterns (Pattern C, D, E). Most post-Triassic Caryophyllioidea lost epitheca gradually during the Jurassic, and entered the Cretaceous practically devoid of

epitheca. Radiation of the Cretaceous caryophylliines generated new phyletic lines, each of which was characterized by its unique skeletal organization. Along with this development, there persisted relict epithecate lineages ranging from the Triassic to the Recent represented by dwarf forms.

- The fact that most deep-water caryophylliid lines are devoid of epitheca suggests that their migration from shallow water to deeper water took place after they lost the ability to form epitheca.
- Modification of polyp anatomy and development of the edge-zone with transformation of the wall structure occurred dramatically in corals confined to shallow water. In these environments, older lineages of epithecate phaceloid and solitary forms were eliminated during successive environmental crises (Triassic–Jurassic, Jurassic–Cretaceous, Early Cretaceous–Late Cretaceous), which accelerated faunal turnover and resulted in selection of polyp organization. In contrast, colonial corals having a poorly-developed edge-zone persist up to the present and retain epitheca in their ontogeny. Modern shallow-water faunas also comprise corals with a well developed edge-zone (from the Second to Fourth grades).
- In the Mesozoic, the environments of corals with simple polyp organization were carbonate platforms; their development in the Late Triassic, Late Jurassic and in the Early Cretaceous prolonged the survival of forms which lacked an edge-zone, and thus continued existence of an ancient Paleozoic anatomical pattern. Even new post-Triassic corals that diversified during Late Jurassic and Early Cretaceous time, having relatively well developed edge-zone (Second grade), retained epitheca as an addition to trabeculotheca and/or septotheca. The ecological driving force for evolution of non-epithecate corals in the Mesozoic was probably the increasing role of bioerosion in the coral environments. The edge-zone developed as a protective feature, which in the Cenozoic became a subject of intensive evolution. Today, the corals with purely epithelial walls are known exclusively in deep-water or cryptic environments where the stress caused by bioeroders is negligible.

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Glossary

Colonial corals. — Corals in which polyps are integrated to various degree (Coates & Oliver 1974). Corallites of colonial Scleractinia may form cerioid, plocoid, dendroid, thamnasterioid, and meandroid colonies.

Epitheca (Milne Edwards & Haime 1848). — Wall built of calcareous fibres not organized into trabeculae. Its outer part is formed in the apical part of the soft tissue fold (lappet cavity). The calcareous fibres of the outer part are oriented distally. The inner part of the epitheca, i.e., epithecal stereome, shows centripetal organization of fibres. Epitheca often accompanies other skeletal structures in forming composite walls (i.e., epithecal-dissepimental; epithecal-trabeculothecal, epithecal-septothecal; epithecal-stereomal in → non-trabecular corals) but may also form the only corallum wall.

Holotheca (Hudson 1929). — Epithecal wall common to peripheral corallites of a colonial corallum.

Marginotheca (Mori & Minoura 1980; Stolarski 1995). — A wall consisting of distally growing minitrabeculae (→ trabeculae), continuing into a median line of radial elements.

Non-trabecular or fascicular corals (Roniewicz 1989a). — The term describing microstructural features of corals in which septa as well as the whole skeleton are organized into bundles of fibres that emerge on the surface as minute granulations about 30 μm in diameter. Excluding the epitheca, the skeletal parts (septa, dissepiments, adaxial wall portions) are in structural continuity with each other. In septal spines, the bundles are elongate and diverge laterally from the axial part of the septal spine. The elongated bundles resemble minitrabeculae in dimension but differ in lacking the trabecular arrangement of fibres; their fibres are parallel to each other. The adaxial wall portion is built of multidirectionally oriented bundles and scaly fibre aggregates. This microstructure is known only in the suborder Stylophyllina (Cuif 1973; Roniewicz 1989a).

Pachytheca (new term). — A type of epitheca with a very thick inner layer showing characteristic modular structure. The modules are large and equal-sized bundles of fibres that tend to form centred structures (penicillate organization of fibres of Cuif & Gautret 1993).

Paratheca (Vaughan & Wells 1943). — Wall consisting of intercostal or epicostal dissepiments.

Phaceloid corals. — Corals in which polyps are not integrated, although developed from single planula. Because of their lack of integration, phaceloid corals are considered as pseudocolonies (Coates & Jackson 1985).

Septotheca (Vaughan & Wells 1943 = pseudotheca of von Heider 1886). — Wall developed by thickening of the outer part of septa.

Solitary corals. — Corals with single polyps, whose most common condition is monostomodeal.

Tectura (Stolarski 1995). — Extra-calicular sclerenchyme adhering to the outer corallum surface; deposited by edge-zone; growing centrifugally; fibrous or organized in trabeculae; surface smooth (porcellaneous), or corrugated, or covered by granulations.

Trabeculae (Trabekeln of Pratz 1882 = poutrelles of Milne Edwards & Haime 1848; modified after Bryan & Hill 1942). — Continuously growing rods formed by fibres (aggregated in tufts, Jell 1974), provided with an axis, and not divided into sclerodermites. For descriptive purposes, it is useful to distinguish two main size classes of trabeculae: minitrabeculae from 10 to 50 μm in diameter, and large (thick) trabeculae which are more than 50 μm in diameter. Septal trabeculae may be arranged in a fan-like pattern or uniserially. Most Scleractinia have trabeculate septa, except Stylophyllina (→ non-trabecular or fascicular corals).

Trabeculotheca (Chevalier 1987; Stolarski 1995). — Wall consisting of a trabecular palisade, interrupted by radial elements.

Tendencje ewolucyjne w rozwoju fałdu brzeżnego wśród epitekalnych Scleractinia

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Streszczenie

Zmiany w budowie ściany szkieletu Scleractinia, jakie obserwować można od triasu do dziś (Fig. 1–14), są wyrazem modyfikacji anatomicznych w budowie dystalnej części ich polipów. Pierwotnym typem ściany u skleraktinii, który występował niemal u wszystkich osobniczych i faceloidalnych koralu triasowych była epiteka tworząca zewnętrzną część szkieletu (Fig. 1A, 6). Ciało polipa nie wykraczało poza granice epiteki, co w przypadku wielu rodzajów oznaczało, że zawarte ono było w obrębie niewielkiej przestrzeni wewnątrzkielichowej. Epiteka powstaje w bruzdzie epitekalnej dystalnego zafałdowania ścianki polipa, które można uważać za zaczątkowy fałd brzeżny. Epiteka odróżnia się od innych ścian koralu (1) miejscem tworzenia, (2) mikrostrukturą i (3) morfologią. Obecność epiteki u koralu kopalnych i dzisiejszych stwierdza się na podstawie włóknistej (nietrabekularnej) struktury o wroście dośrodkowym, lub morfologii jej zewnętrznej powierzchni pokrytej liniami przyrostowymi (Fig. 2–12). W ewolucji Scleractinia widoczny jest trend do otaczania szkieletu fałdem ciała miękkiego, tzw. fałdem brzeżnym (edge-zone), czego efektem jest redukcja, a następnie eliminacja pierwotnej ściany epitekalnej. Epiteka jest zastępowana przez ściany trabekularne, którym towarzyszą pozakielichowe złogi szkieletowe (np. tynk ścienny = tectura, patrz Fig. 1B i 4), bądź wchodzi w skład ścian złożonych, np. jako ściany epitekalno-paratekalne, epitekalno-septotekalne (Fig. 3, 11). Wydzielono pięć podstawowych modeli ontogenezy szkieletu kopalnych i współczesnych skleraktinii i rozpatrzono na ich tle gradacje w rozwoju fałdu brzeżnego (Fig. 15). Wyróżniono cztery stopnie w rozwoju fałdu brzeżnego: (I) preformacja fałdu brzeżnego w postaci dystalnego fałdu ściany; (II) uformowanie się fałdu brzeżnego o zmiennym zasięgu i braku/ograniczonej zdolności do tworzenia pozaściennych złogów szkieletowych; (III) pokrycie szkieletu przez fałd brzeżny posiadający zdolność wytwarzania tynku ściennego; (IV) redukcja zasięgu fałdu brzeżnego do strefy dystalnej szkieletu, z zachowaniem zdolności do wytwarzania tynku ściennego. Przemiany związane z wykształceniem się fałdu brzeżnego, a następnie jego rolę w tworzeniu szkieletu widać najlepiej w ewolucji Caryophylliina: od wyłącznie epitekalnych Volzeioidea (trias-dziś) do posiadających szkielet całkowicie otoczony fałdem ciała miękkiego Turbinoliidae (kreda-dziś). Rozwój fałdu brzeżnego mógł stanowić ewolucyjną odpowiedź koralu na zmieniające się warunki środowiska, głównie na nasilenie bioerozji w mezozoicznych środowiskach płytkowodnych. Dziś koralu o wyłącznie epitekalnych ścianach występują jedynie w wodach głębokich bądź w środowiskach kryptycznych (np. *Gardineria* i niektóre Guyniidae).