Ontogenetic development of the thecal structures in caryophylliine scleractinian corals

JAROSŁAW STOLARSKI

Stolarski, J. 1995. Ontogenetic development of the thecal structures in caryophylliine scleractinian corals. *Acta Palaeontologica Polonica* **40**, 1, 19–44.

At the initial stage of ontogeny, in Caryophylliidae (Miocene *Caryophyllia salinaria*, *C. depauperata*, Recent *C. berteriana*) and Flabellidae (Miocene *Flabellum roissyanum*, Recent *Javania cailleti*), wall and septa are formed simultaneously, and their trabecular structure is coalesced (marginothecal wall). At subsequent juvenile stage in Caryophylliidae the presence of the extensive exosarc enables formation of costo-septa and, in consequence, formation of trabeculotheca. Trabeculotheca consists of fragments of primordial wall located between the costosepta. The trabeculothecal segments vanish in the adult stage in the majority of corals when the septothecal wall is formed by thickening of the costo-septa. In others, however, marginotheca can be present throughout the whole ontogenetic sequence (*C. salinaria*). Most Flabellidae are characterized by limited expression of exosarc and the presence of marginothecal wall up to the adult stage. The origin of 'flabellid' organization in Caryophylliina may result from a simple modification of ontogeny — extention of initial morphology to later ontogenetic stages. Such corals could develop several times, and the Flabellidae may be polyphyletic.

K e y   w o r d s : Scleractinia, wall structure, ontogeny, phylogeny.

Jarosław Stolarski, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

Studies on the ontogenetic development of the ahermatypic scleractinian corals have rarely been undertaken. Usually, only some sequences of macrostructural changes used to be documented e.g. appearance of the successive septal cycles, pali and columella. Those data could hardly be compared with microstructural observations traced in the ontogenetic sequence, although some examples can be found in Chevalier (1961), Cuif (1968), and lately in Mori *et al.* (1977), and Mori & Minoura (1980). Except for the two last papers, microstructural data refer only to certain stages of

the corallum growth (usually in the adult stage). Particularly, there are few microstructural observations on the ontogeny of the thecal structures, which are considered by the scleractinian taxonomist as important supra-generic taxonomic criteria (for instance in scleractinian classifications by Vaughan & Wells 1943; Alloiteau 1952, 1957; Wells 1956; Chevalier 1987). In Caryophylliina soft tissue can cover the exterior of the corallum and consequently control formation of extrathecal structures such as costae, and also peculiar for them secondary deposits of extrathecal sclerenchyme (Fig. 1B), called herein 'tectura' (plaster in Latin). In ontogeny, the mor-phological consequences of the presence of skeletogenous exosarc include changes in thecal structures. In the present paper I will describe in microstructural terms some details of the ontogeny of thecal structures in some fossil and extant ahermatypic corals. The results of the studies also allow for some phylogenetic speculations concerning the role of the thecal modifications in the ontogeny.

Specimens abbreviated ZPAL are housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw.

Material

All investigated forms belong to the scleractinian suborder Caryophylliina Vaughan & Wells 1943: a microstructurally uniform group of minitrabe-cular corals having trabeculae varying from ca. 15 to 50 µm in diameter (see Roniewicz 1989; Roniewicz & Morycowa 1993).

Three of the studied species represent the family Caryophylliidae Dana 1846 characterized by a 'septothecal' wall. (1) *Caryophyllia depauperata* (Reuss 1871) from the Miocene (Early Badenian) deposits cropping out in Rudoltice (= Ruditz) in Moravia (Figs 2–3; collection of A.E. Reuss housed at Naturhistorisches Museum Wien; acronym NHMW), (2) *Caryophyllia salinaria* (Reuss 1847) from the Miocene (Upper Badenian; foraminiferal zone *Uvigerina costai*) salt-bearing sediments of the Wieliczka and Bochnia salt mines (Figs 6–7; collection housed at Muzeum Żup Krakowskich Wieliczka, acronym MŻKW, and few at Institute of Paleobiology, ZPAL H.XIII/2–5) and (3) *Caryophyllia berteriana* Duchassaing 1850 extant species from Western Atlantic Ocean (North of Venezuela, 12°46'N, 70°41'W; 201 m; ZPAL H.XIII/6, Fig. 7).

Two other species represent family Flabellidae Bourne 1905: a ca-ryophylliid group consisting of corals with an 'epithecal' wall. (1) *Flabellum roissyanum* Milne Edwards & Haime 1848 from the Miocene (?Early Badenian) clay-deposits of Korytnica (ZPAL H.I/315, ZPAL H.XIII/7–10, Fig. 9; compare Stolarski 1991), and (2) *Javania cailleti* (Duchassaing & Michelotti 1864) Recent species from Western Atlantic Ocean (Bahama, 27°08'N, 77°52'W; 274–302 m; ZPAL H.XIII/11, Fig. 10).

Types of the thecal structures in Caryophylliina

Marginotheca *vs.* archeotheca. — The term marginotheca was introduced by Mori & Minoura (1980) for designation of the wall of *Flabellum pavonicum* Lesson 1831 (= *Flabellum distinctum* Milne Edwards & Haime 1848 of Mori & Minoura 1980). The trabecular structure of marginotheca continues with that of the adjacent septa. It consists of a dark line which accompanies a layer of calcareous fibers only on its inside. Independently, seven years later Chevalier (1987: Fig. 337I) call essentially identical thecal structure of the genus *Flabellum* as archeotheca. However, the primary meaning of the term archeotheca (Alloiteau 1952) was different. It was defined as the wall of a mixed septo-dissepimental origin typical of styllophyllids, procyclolitids, amphiastreids or thecocyathids. In reality, wall structure of the mentioned coral groups have nothing in common with the wall described in *Flabellum* or juvenile ontogenetic stages of Caryophylliidae. Moreover, their thecal structures considerably differ between themselves and cannot be labeled by a collective term (compare Wells 1956; Roniewicz 1989). Being not illustrated by Alloiteau and defined on vague microstructural criteria resulted in subsequent imprecise usage of the term archeotheca in the literature. Among others, Cuif (1972) used it to describe thecal structures of Triassic corals: *Coelocoenia decipiens* (Laube 1865) with a cerioid colony (see Cuif 1972: Fig. 28D, p. 273), and *Cyathocoenia milchi* Volz 1896 (see Cuif 1972: Fig. 29C, p. 274). In *Coelocoenia decipiens* the trabecular wall is a structure common of neighboring corallites. Because the astogeny of the colony remains unknown it could not be excluded that the wall and septa were primarily structurally separated, what in the later growth could be masked by relatively large trabeculae of equal diameter (ca. 70–80 µm). In *Cyathocoenia milchi*, where relationships with corals have been questioned (Montanaro Gallitelli 1980), the theca shows a nontrabecular character.

In this paper I propose to reject the term archeotheca as incorrectly defined. To describe a theca the structure of which continues with that of adjacent septa, we already have a good term — marginotheca. It has priority over the emended definition of archeotheca by Chevalier (1987). I propose also to restrict usage of the term to solitary and these colonial forms which have isolated corallites with their own minitrabecular wall. Minitrabeculae are arranged more or less vertically in the plane of the marginotheca. There is no costo-septa organization of radial elements. All costa-like structures protruding outside the calice should be called 'crests' (see Chevalier 1987: p. 752).

To summarize, a marginothecal wall can be distinguished at early growth stages of most caryophylliids (in solitary but also in some colonial forms like *Euphyllia* — see Chevalier 1971) and oculinids [e.g. *Palaeohelia collignoni* Alloiteau 1958; see Beauvais 1982, or *Galaxea fascicularis* (Linnaeus 1767); see Chevalier 1971]. Similarly, the wall of liassic archeosmilids have a marginothecal nature (see Melnikowa 1975). However, the most

important coral group having in ontogeny almost exclusively marginothecal wall are the flabellids. It is worthy to note that the main reason for introducing the term 'marginotheca' was the observation that the theca of *Flabellum* significantly differs from the epithecal wall encircling the trabe-culothecal ('euthecal') wall of *Trachyphyllia* sp. Mori & Minoura (1980) discovered the trabecular character ('dark line') of the *Flabellum* wall that distinctly contrasted with the generally used term 'epitheca' for description of flabellid wall. In Flabellidae, the term 'epitheca' was used to describe thin rings and sometimes thicker sclerenchymal deposits closely applied to the wall (Vaughan 1900: p. 51). Are then the 'epithecal' wall of flabellids and similarly called wall structure of other scleractinians different?

Epitheca. — The term proposed by Milne Edwards & Haime 1848 as a skeletal sheath adhering to the external board of costae, has been used to describe virtually all nontrabecular skeletal structures covered with growth lines which coated partly or wholly the external parts of the coral skeletons. In this way the wall of some Caryophylliina was described (i.e. Flabellidae, Guyniidae, and also principal thecal structure of Thecocyathi-nae or some Caryophyllinae — *Tethocyathus* as example). By this term also thecal deposits were designated which formed independently of the true wall of some Fungiina (i.e. Cyclolitidae, in *Porites lutea* Milne Edwards & Haime; Jell 1980: Pl. 8: 1–2, 4–6), Faviina (i.e. Stylophyllicae, Montlivalti-dae, some Rhizangiidae and Faviidae like *Manicina* or *Trachyphyllia*), and also Dendrophylliina (i.e. *Thecopsammia, Trochopsammia,* and *Balano-phyllia*).

Studies by Barnes (1972) and Sorauf (1972) show that the thin, covered with growth lines sheet called epitheca, adhering to costae of the colonial coral *Manicina areolata* (Linnaeus 1758) is formed at the perimeter of the skeleton-secreting layer in a lappet cavity and grows centripetally (Fig. 1). Growth lines are formed as a result of daily changes in the shape of the secreting tissue.

Let us consider these thecal structures of a nontrabecular nature which grow centripetally as being homologous and call them true epitheca. In early stages of formation of epitheca its tube-like edge may precede the formation of radial elements (for example in *Culicia*; see Chevalier 1971). In the later growth, epitheca is separated from the costosepta by a distinct notch. In corals the epithecal wall of which formed only in early growth stages, the border between epithecate stage and the later one, non-epithe-cate, might be sharp and distinct (*Balanophyllia*). Very thick, nontrabecu-lar skeletal structure of centripetal growth, which formed the only wall structure of Triassic protoheterastreids or volzeids (see Cuif 1980) suggest a significant similarity if not a homology with true epitheca. Although there is unknown wall microstructure of Mesozoic Thecocyathidae its separation from costosepta suggests an epithecal character. Also in the Rugosa a wall structure named epitheca, at least in the Polycoeliidae and Timorphylli-dae, shows centripetal growth (Iljina 1984; Kato 1963: Fig. 19; Schouppe & Stacul 1966; Fedorowski 1974; Sorauf 1983).
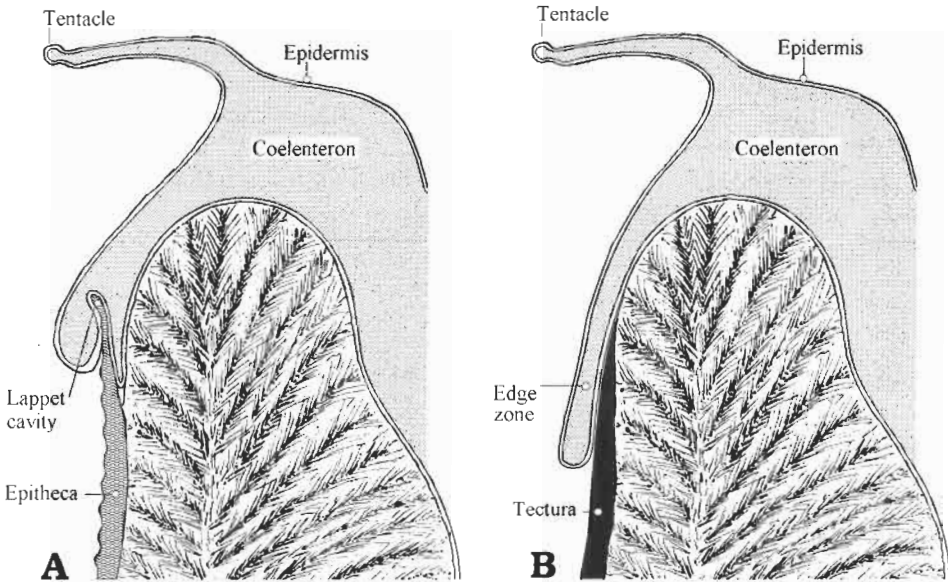
Fig. 1. Comparison between modes of formation of the true epitheca (A) and tectura (= extrathecal sclerenchyme) (B).

However, structures previously described in the here investigated fla-bellids as epitheca have a fundamentally different structure. Their smooth ('porcelaneous') or covered with growth ridges walls grows centrifugally (Fig. 9I–J, E). This growth direction is the same as in tectural deposits common for representatives of Caryophylliidae (compare Figs 4F, 5C, 6D) — this is an argument to reject homology with true epitheca. In Caryo-phylliinae aragonitic fibers of tectura may differentiate into the trabeculae (expressed externally as costal granulations; Fig. 8E), or nontrabecular fascicles forming successive, smooth skeletal coatings. Tectura of Flabel-lidae is nontrabecular. In the proximal part of corallum it can be thin (*Flabellum*; Fig. 9B, G) or considerably extended (*Javania*; Fig. 10B, F), in distal part it is strongly reduced, what can be caused by a limited expression of exosarc in adults (Zibrowius 1974). The surface of tectura can be covered with growth ridges what suggests similar periodic growth as in the case of true epitheca (Fig. 9I). The structure probably responsible of formation of the tectura is the edge zone (Fig. 1). The presence of the extensive tectura appears to be an adaptation helping juveniles in attach-ment to the substrate.

Because of the lack of a true epitheca in Flabellidae, their diagnosis (*sensu* Wells 1956) should be emended. I propose to consider a margino-thecal wall as a peculiar neotenic flabellid character. Commonly there develop marginothecal invaginations — in the form of crests, but there can be formed costosepta (*Javania*) as a result of reduction of marginothecal arches (interseptal interruption of marginotheca) or sometimes by the interruption of highly reduced marginothecal arches.

Trabeculotheca (Chevalier 1987). — Trabeculotheca is composed of very small vertical or strongly inclined trabeculae, generally of a small diameter and crowded closely to each other ('fused'); the wall located between septal blades (interseptally) is formed by so-called 'euthecal pieces' (= trabeculothecal segments).

Septotheca [Vaughan & Wells 1943 (= pseudotheca *sensu* von Heider (1886)]. — The wall is developed by thickening of the outer part of septa.

Paratheca (Vaughan & Wells 1943). — The wall consisted of dissepiments.

Ontogeny of thecal structures in Caryophylliina

In the ontogeny of solitary Caryophylliina three main stages can be distinguished: (1) initial stage which starts with basal plate, and ends with distinct constriction of the corallum diameter, (2) juvenile stage which starts with enlargement of the corallum diameter and continues up to the (3) adult stage in which the ultimate septal number (for particular species) and also other taxonomically important structures (pali, columella) are fully developed (see Fig. 11). Observations dealing with ontogeny of thecal structures are preceded by shorten description of development of other skeletal structures.

Following abbreviations are used:

C (1–n)   costae of a cycle indicated by a number,
CD   calicular diameter,
GCD   greater calicular diameter,
LCD   lesser calicular diameter,
P (1–n)   pali of a cycle indicated by a number,
S (1–n)   septa of a cycle indicated by a number,
SC (1–n)   septal crests of a cycle indicated by a number.

Suborder Caryophylliina Vaughan & Wells 1943
Family Caryophylliidae Dana 1846
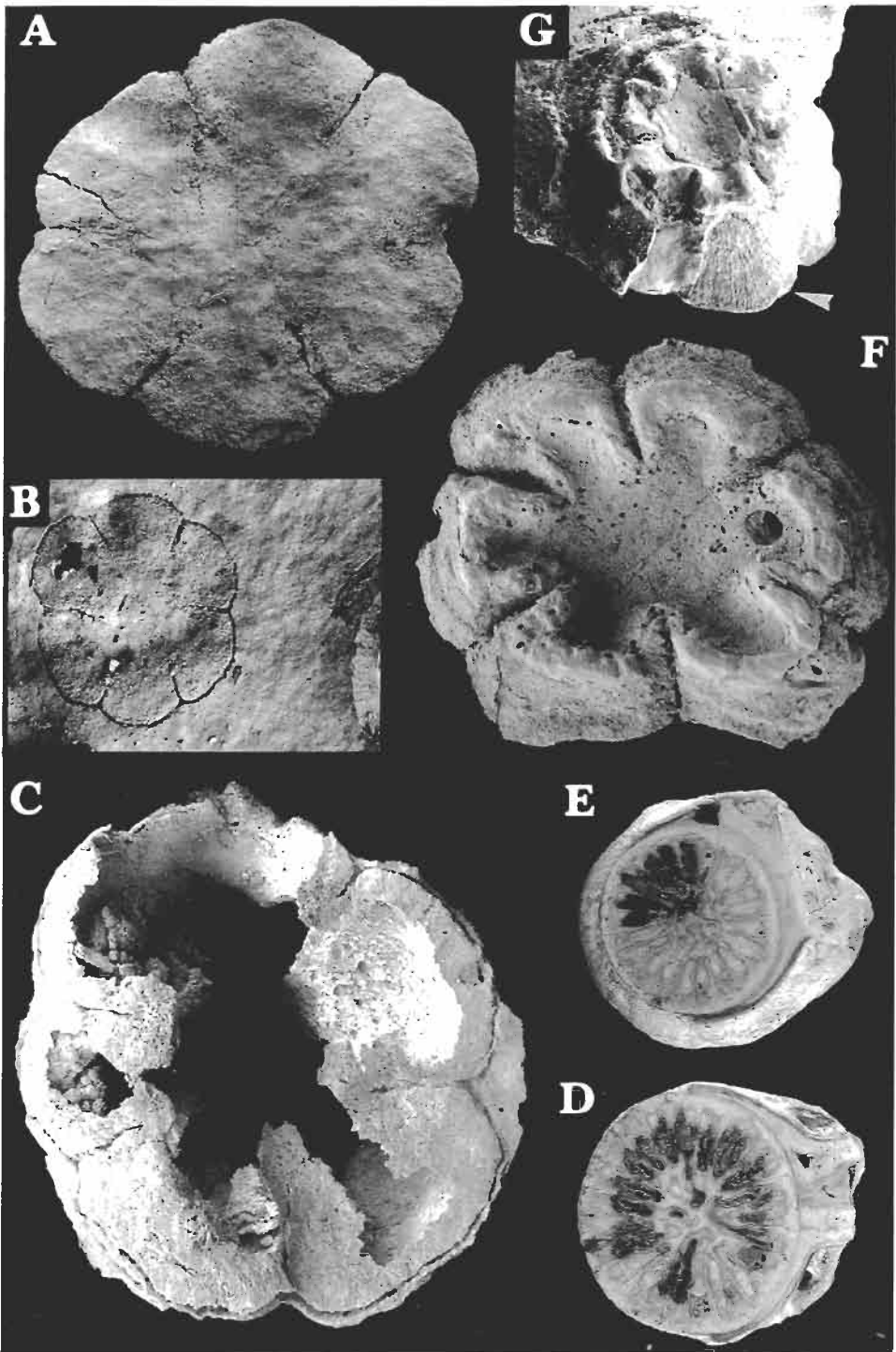Genus *Caryophyllia* Lamarck 1801

Caryophyllia depauperata (Reuss 1871)
Figs 2–3.
Coenocyathus depauperatus sp. n.; Reuss 1871: p. 15–16, Pl. 3: 7–9.
Caryophyllia cladaxis sp. n.; Reuss 1871: p. 13–14, Pl. 1: 7.

───   →

Fig. 2. *Caryophyllia depauperata* (Reuss 1871), Miocene, Rudoltice (Moravia). A–C. Proximal sides of the initial coralla NHMW 1994/262/1n, i, j with marginothecal wall; × 50, × 31, × 53 respectively. D–E. Specimen (NHMW 1994/262/2a) cut transversely to show juveniles attached to their skeletons and covered by thick tectural deposits; × 30, × 34 respectively. F. Specimen NHMW 1994/262/1k in distal view. Note peculiar sclerenchymal infilling; × 47. G. Distal-lateral view of specimen NHMW 1994/262/1l. Note vertically arranged trabeculae (arrow) in the plain of marginotheca, and sclerenchymal deposits infilling calice; × 37.

Initial stage. — Initial skeleton consists of 6 protosepta and margino-theca (Fig. 2A–C, F–G). Diameter of the base is ca. 1.3 mm. There is no columella or pali. Marginotheca and septa are composed of a vertical minitrabecular palisade (Fig. 2B–C, G). In later growth the corallum diameter decreases to ca. 0.7 mm (Fig. 3D). Initial part of corallum encircled by thick layers of tectura which is developed in the next growth stages.

Juvenile stage. — It starts with enlargement of corallum diameter (Fig. 2D–E) and with the appearance of S2 septa and columella that is formed by the fusion of the inner septal edges. In the later growth, S3–S4 septa appear and relatively long P3 pali develop in front of S3 septa. Most specimens have hexameral, rarely octameral, symmetry. The lumen of the calice is gradually (from the initial stage) infilled by fibrous sclerenchyme (Figs 2E, 3C).

The wall is trabeculothecal. Minitrabeculae forming midline of the wall and septa are ca. 15 μm in diameter. Costal parts of septa are weakly developed. Initial trabeculothecal segments are long and straight, and when the next septal cycles arise (S3–4), they become shorter and more undulated (Fig. 4C, G). Septa of the successive cycles originate from the interseptally situated trabeculothecal segments ('midline' of newly formed septa is a continuation of the 'midline' of theca). Thecal ring and costae are coated by sclerenchymal tissue, the bundled crystallites of which disclose centrifugal accretion (Fig. 4D, F). In the subsequent corallum growth the succeeding sclerenchymal rings cover the earlier ones, resulting in forma-tion of the thickest sclerenchymal deposits at the proximal end of larger specimens (monocyclic development of Durham 1949). Proximal tectura consists of bundles of aragonitic crystals and sub-horizontal trabeculae (Fig. 4D) which correspond to the minute granulations on the corallum surface. Non-trabecular tectura dominates in the next growth phases.

Adult stage. — There are four septal cycles at this stage, P3 pali, and a fascicular columella (Fig. 4H). The largest specimens reach ca. 40 mm in height (GCD ca. 25 mm; LCD ca. 20 mm).

The wall is trabeculothecal, occasionally (between some septa) septo-thecal (Fig. 4H). Sclerenchymal cover is thin or absent; in the later case there are visible broad costae covered by numerous granulae (Fig. 4B).
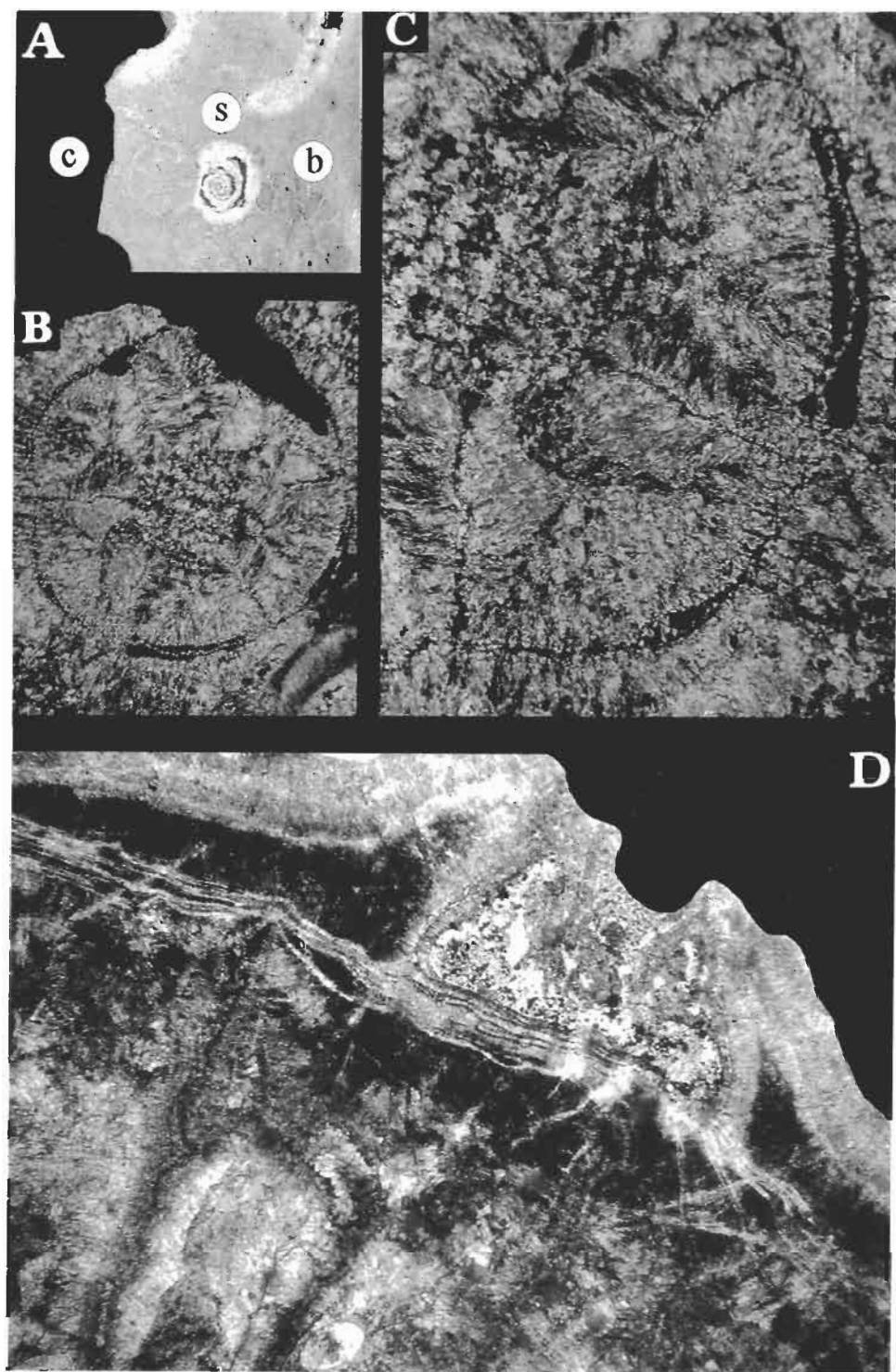
Caryophyllia salinaria (Reuss 1847)
Figs 5–6.

Caryophyllia salinaria Reuss; Morycowa & Roniewicz 1987: pp. 110–112, Figs 3–4, Pls 41–
    42 (with synonymy).
Vielicyathus zejszneri sp. n. Morycowa & Roniewicz 1987: pp. 112–115: Figs 5–6, Pls 44–48.

Fig. 3. *Caryophyllia depauperata* (Reuss 1871), Miocene, Rudoltice (Moravia). A. Incrusting organisms visible on the inner part of the detached tectural layer: juvenile coral (c) — NHMW 1994/262/1m, serpulid (s) and bryozoan (b); × 8. B–C. Thin sections of the specimen NHMW 1994/262/1m; × 36, × 90 respectively. D. Longitudinal section of juvenile form attached to older one and covered by tectural tissue (NHMW 1994/262/2b); × 38.
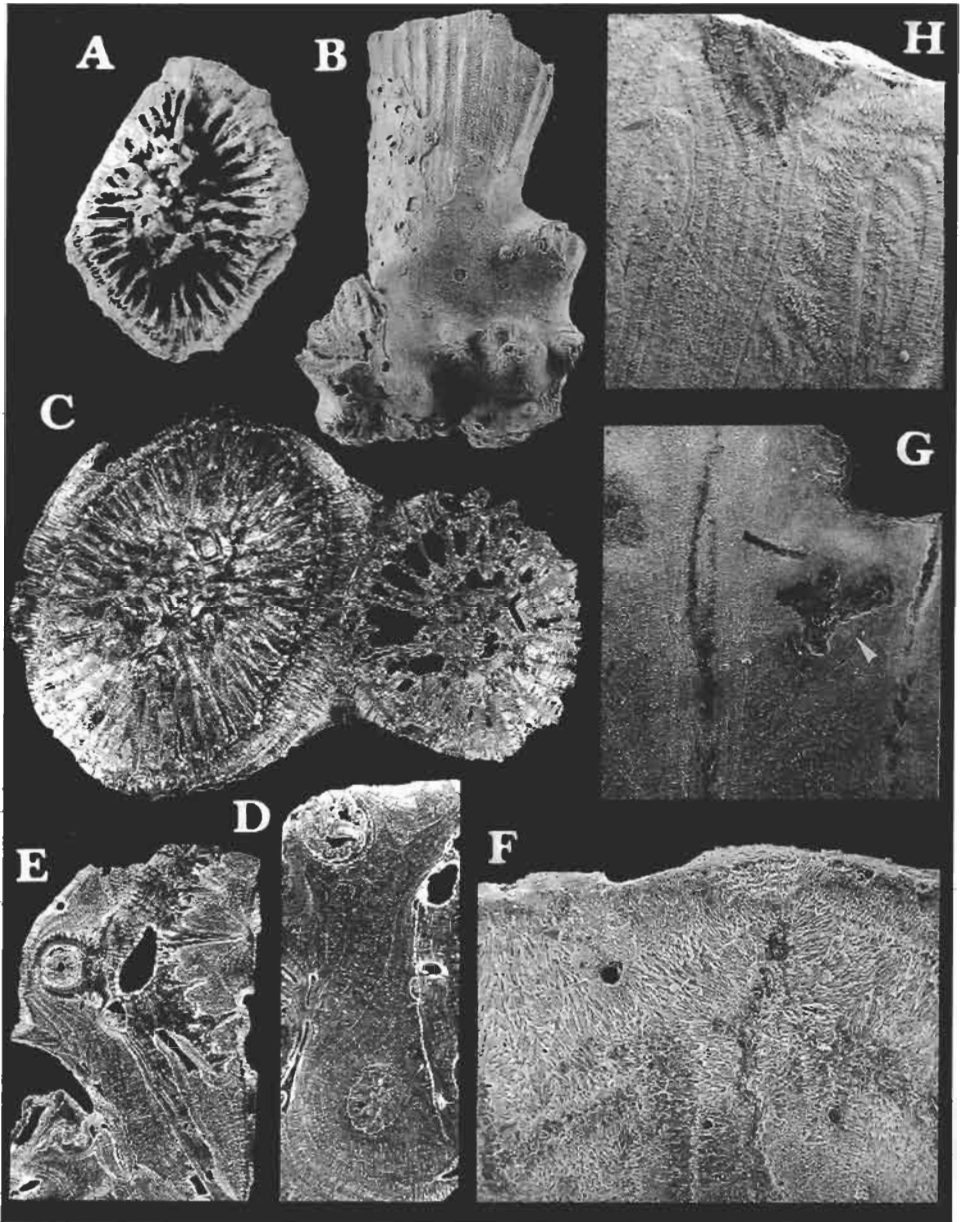
Fig. 4. *Caryophyllia depauperata* (Reuss 1871), Miocene, Rudoltice (Moravia). A–B. Specimen NHMW 1994/262/1a in distal (A) and lateral (B) views; × 1.3. C–E. Transverse sections of the specimen NHMW 1994/262/1b, c, d; × 3.7. F. Early trabeculothecal stage NHMW 1994/262/1e; × 40. G. Late trabeculothecal stage (NHMW 1994/262/1f); note strongly reduced and undulated trabeculothecal segment (arrow); × 40. H. Septothecal stage (NHMW 1994/262/1g); × 36.

Initial stage. — At this stage the initial skeleton (Fig. 5A–F) does not differ significantly from that of *C. depauperata* (6 protosepta, lack of pali

and columella) — but the diameter of the base is smaller (ca. 0.7 mm). Corallum diameter in the subsequent growth apparently decreases to ca. 0.4 mm. The wall is of marginothecal type with vertically arranged mini-trabeculae (Fig. 5C–D). Initial skeleton is encircled by thick sclerenchymal deposits developed in succeeding growth stages.

Juvenile stage. — The stage begins with increasing of the corallum diameter and formation of columella by the fusion of the inner septal edges (Fig. 5B). Then S2–S3 septa appear (Fig. 6E–F). Coralla usually have septameral symmetry, rarely hexameral.

Wall is marginothecal (Fig. 6C, E), exceptionally trabeculothecal (Fig. 7E). Diameter of the minitrabeculae in the wall and septa is ca. 17–20 µm. Costae are usually absent. Layers of centrifugally growing tectura are deposited outside of the thecal ring (Fig. 6C). The surface of tectura is smooth, rarely bearing minute granulations. Sometimes, however, in the proximal part of corallum, tectural rings are separated by a costa-like ornamentation (polycyclic development of Durham 1949). Tectura is of mostly non-trabecular, fascicular nature. However, the presence of granu-lations on the surface of some specimens suggests its occasional trabecu-lar character (see Morycowa & Roniewicz 1987: Pl. 45: 2, 46: 4).

Adult stage. — At this stage four septal cycles are present, long P3 pali and fascicular columella (Fig. 6A–D). The height of the largest forms reaches over 85 mm (GCD up to 33 mm; LCD 30).

Types of the wall vary from marginotheca to septotheca. There are specimens with calicular diameter over 30 mm and with marginothecal wall (see Morycowa & Roniewicz 1987: Pl. 44: 1) and another form with diameter of ca. 17 mm and a septothecal wall (Fig. 6A–B). Forms with marginothecal wall are usually cylindrical with constant calicular diameter or have characteristic transverse narrowings (Morycowa & Ro-niewicz 1987: Pl. 43: 4A, 6). Forms with septothecal wall are often trochoidal with costosepta covered by layers of non-trabecular tectura (Fig. 7D), or exposed on the corallum surface (Fig. 7A–C).

Remarks on larval ecology and taphonomy. — On the surface of the adult coralla of *Caryophyllia depauperata* and *C. salinaria* numerous juvenile forms were observed (Figs 2, 3B; 6, 7F). Their growth usually terminates at the protoseptal stage; only some of them could grow longer (see Figs 4B–C, 7A, F). Juvenile coralla were found also between successive tectural layers (Figs 2E, G, 3D; 5E). Dimensions and morphological characters of the juvenile specimens are identical with the youngest ontogenetical stages of larger forms to which they were attached, so they are regarded as conspecific.

One of the possible cause of formation of juveniles' assemblage could be the benthic character of the larvae (planulae) of the species. Such larvae could attach to the substrate — particularly parent individuals — almost immediately after planulation. Benthic planulae observed so far are large, in *Balanophyllia elegans* ca. 1–2 mm in diameter and ca. 3–5 mm in length (Fadlallah & Pearse 1982), in *Flabellum thouarsii* benthic planulae are ca.

2.1–2.6 mm in diameter, and 2.8–4.5 mm in length (Squires 1962). According to Cairns (1982) pedicel diameter of the latter species is ca. 2.5–3.2 mm. The diameter of the protoseptal stage of ca. 0.5 mm in *C. salinaria* and ca. 1 mm in *C. depauperata* suggest much smaller dimensions of their planulae in comparison with Recent examples.

Another possible explanation of the assemblage of the juveniles of *C. salinaria* and *C. depauperata* is an increase by coenosarcal budding, as discussed by Morycowa & Roniewicz (1987: p. 110). In longitudinal sections of attached forms there is visible a horizontal structure, interpreted here as a basal plate (*Caryophyllia depauperata* — Fig. 3D; *Caryophyllia salinaria* — Fig. 6B). The presence of the basal plate can be used as a criterion to discriminate the pseudocolonial aggregations of solitary forms from colonies formed as a result of budding (in this case criterion allowing determination of the genera *Caryophyllia* and *Coenocyathus* Milne Edwards & Haime 1848).

It should be noted that in both species many juvenile individuals (Figs 2F–G, 4A) are very similar to the structures described in Early Silurian tabulates as 'fossilized polyps' (Copper 1985; Copper & Plusquellec 1993). However, in the here described specimens all 'soft'-looking calcareous deposits strictly adhere to the radial elements (Fig. 2B–C, G–F) even if some trabecular centres are dissolved. So, these deposits could be considered as intrathecal sclerenchyme secreted by juveniles (see also Kaźmierczak 1993: p. 29). On the other hand, it is plausible that these deposits were secreted by the individuals to which juveniles were attached. Soft tissue of the adults must cover juveniles killing them as many of them were disclosed within the tectural layers.
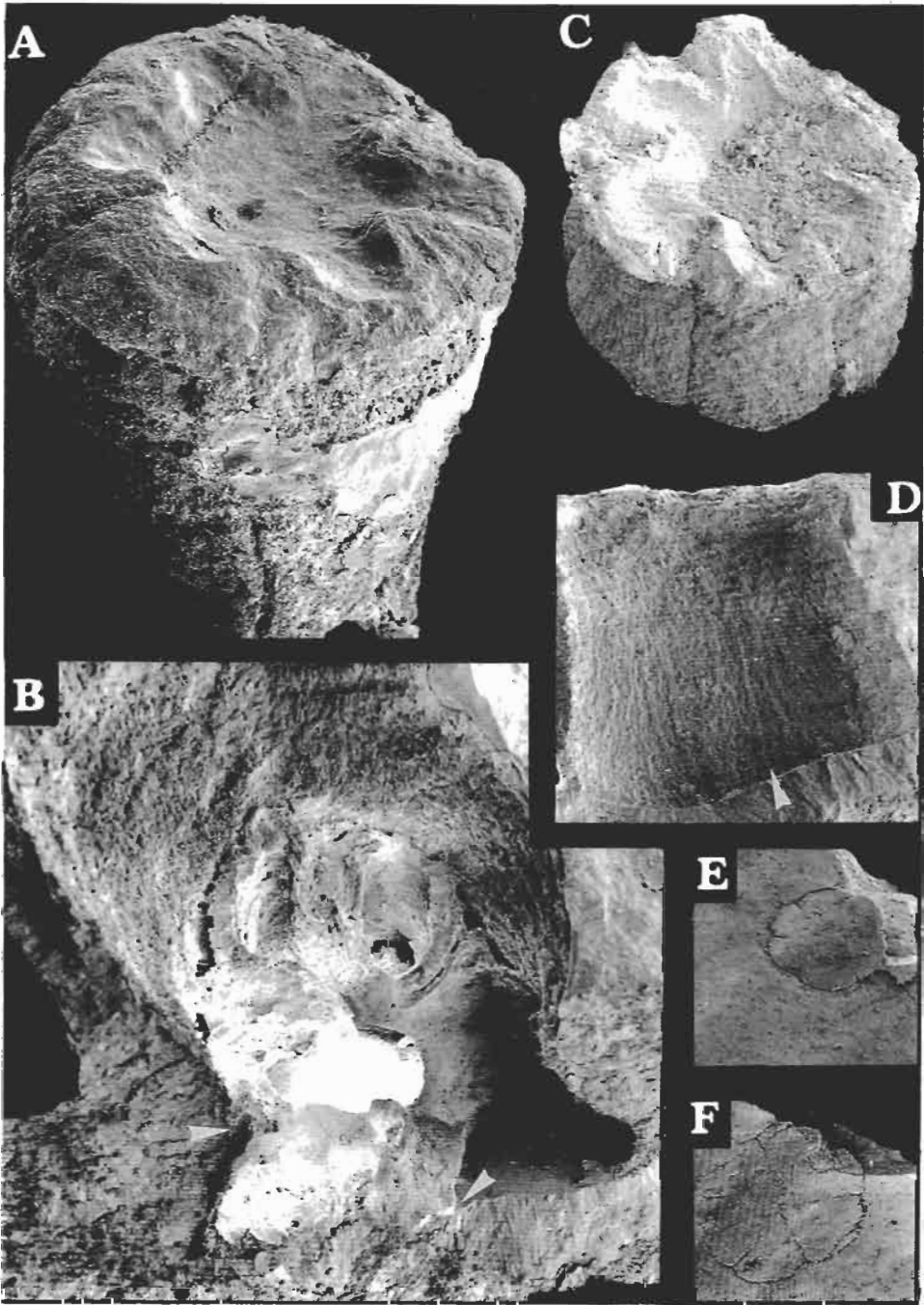
Caryophyllia berteriana Duchassing 1850
Fig. 8.

Caryophyllia berteriana Duchassing; Cairns 1979: pp. 47–49, Pl. 6: 4–8, Pl. 7: 1. (with synonymy).

Initial stage. — The structure of the initial skeleton is the same as in two above described *Caryophyllia* species (skeleton consists of 6 protosepta and marginotheca). The diameter at the base is ca. 1.4–1.5 mm. Pali and columella absent. Minitrabeculae of theca and septa arranged vertically. Corallum diameter in the later growth decreases to ca. 1.2 mm. Initial skeleton is covered by thick tectural deposits which are developed in succeeding growth stages.

Juvenile stage. — The stage begins with an increase of the corallum diameter and formation of columella by fusion of septal projections (Fig.

Fig. 5. *Caryophyllia salinaria* (Reuss 1847), Miocene, Wieliczka (Poland). A. Distal-lateral view of the juvenile corallum ZPAL H.XIII/1 filled with intrathecal sclerenchyme; × 93. B. Proximal part of the specimen ZPAL H.XIII/1 attached to the tectural layer detached from the specimen MŻKW III/413/12. Basal plate (arrow), initial constriction of corallum (arrow) and juvenile

increasing of its diameter are visible; × 93. C. Distal-lateral view of the mould of initial corallum ZPAL H.XIII/2; × 98. D. Impression of the initial corallum ZPAL H.XIII/2. Note the longitudinal traces of marginothecal trabeculae (arrow); × 98. E–F. Proximal views of the specimens ZPAL H.XIII/3; × 24 and ZPAL H.XIII/4; × 34.
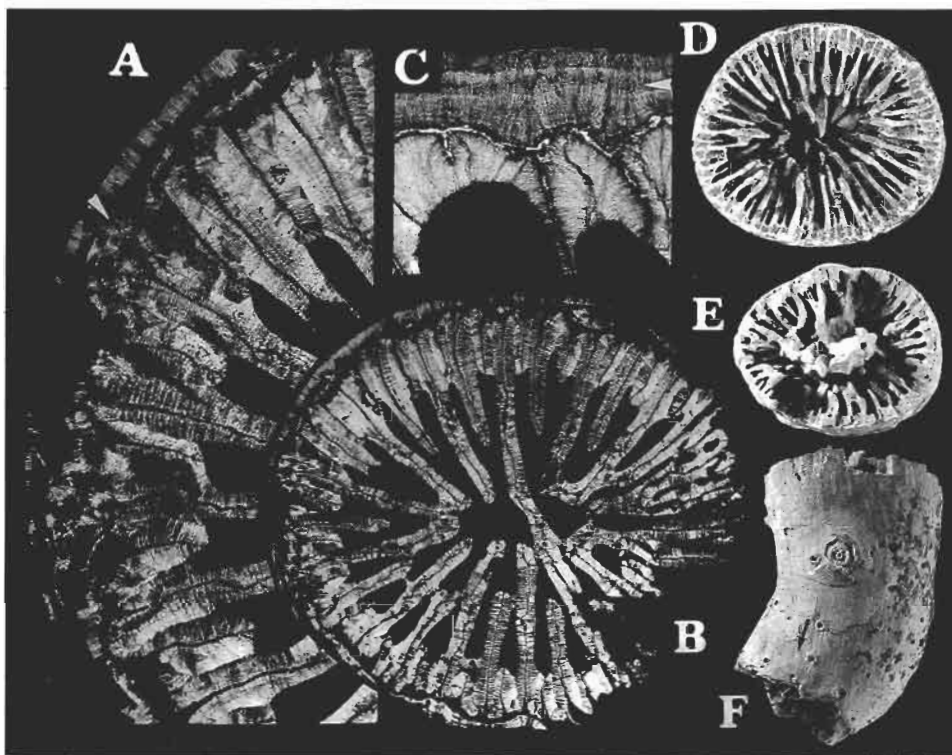
Fig. 6. *Caryophyllia salinaria* (Reuss 1847), Miocene, Wieliczka (Poland). A–B. Corallum ZPAL H.XIII/5 with partially destroyed septothecal wall (arrow) at the adult stage; × 9.6, × 3.8 respectively. C. Late-juvenile corallum MŻKW III-985/16 with marginothecal wall. Note thick deposits of tectura (arrow); × 30. D. Transverse broken section of the corallum MŻKW 413/7; × 1.8. E–F. Distal and lateral views (respectively) of the late-juvenile corallum MŻKW III/413/12 with marginothecal type of wall (E) and numerous initial and juvenile coralla (arrow) attached to its surface (F); × 1.3.

8B). Then S2–S3 septa appear (coralla have mostly hexameral, sometimes septameral or octameral symmetry).

The wall is trabeculothecal (Fig. 8C–F). Diameter of the wall and septal minitrabeculae is ca. 17–20 μm. Tectura have mostly trabecular foundation with trabeculae situated sub-horizontally in the proximal part of corallum (Fig. 8A) and almost vertically in the distal part (Fig. 8E–F). Tectural surface is ornamented with granulations of ca. 0.125 mm in diameter.

Adult stage. — Four septal cycles are present, relatively long P3 pali in the front of third cycle septa and columella composed of small, tightly twisted, pointed ribbons arranged in an elliptical field (Fig. 8G–H). Largest specimens reach ca. 22 mm in height (GCD 17.5 mm; LCD 16.5 mm).

The wall is septothecal, sometimes with vestiges (interseptal segments) of trabeculothecal wall (Fig. 8G).

Family Flabellidae Bourne 1905
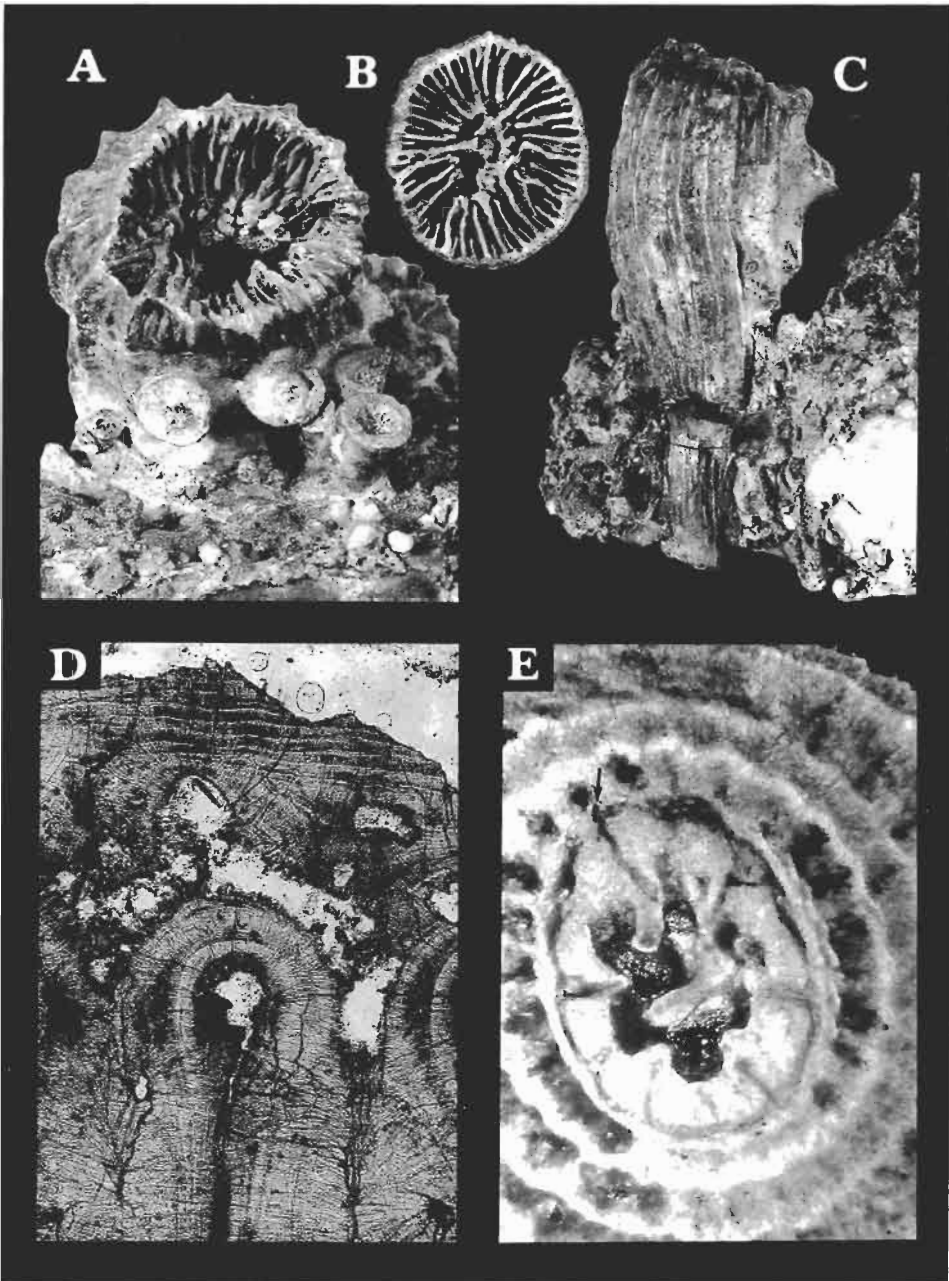Genus *Flabellum* Lesson 1831

Fig. 7. *Caryophyllia salinaria* (Reuss 1847), Miocene, Wieliczka (Poland). A–C. Proximally broken corallum MŻKW III/410/11 with septothecal wall at adult stage in distal (A), proximal (B) and lateral (C) views; × 2.6. D. Transverse section of the corallum MŻKW III-985/1 with septotheca at adult stage; × 30. E. Sligtly oblique transverse section of the juvenile corallum MŻKW III-985/25 with marginothecal and partially trabeculothecal wall (arrow). Note traces of the succesive tectural rings (I–IV) separated by costa-like structures; × 27.

Flabellum roissyanum Milne Edwards & Haime 1848
Fig. 9A–K.

Flabellum roissyaum Milne Edwards & Haime; Stolarski 1991: pp. 55–57, Pl. 9: 1–5, Pl. 12: 1 (with synonymy).

Initial stage. — The initial skeleton consists of 6 protosepta and marginotheca (Fig. 9G). Calice is circular in outline. Diameter of the base is ca. 1.5–1.6 mm. The shape of basal disc varies from completely flat to tube-like (algae is then inferred as possible cylindrical substrate). In subsequent growth, corallum diameter decreases to ca. 1.3 mm. Wall marginothecal with minitrabeculae arranged vertically. Initial skeleton is covered by one layer of thin tectura.

Juvenile stage. — The stage begins with an increase of corallum diameter, appearance of S2 septa and with slight compression of the calice (Fig. 9D–F, H). Axial structure develops by fusion of lower, inner edges and projections of the major septa (primary of S1 than S2–S3 septa). Symmetry hexameral. Septa of higher cycles and septal crests SC1 (particularly expressed lateral SC1) and SC2 appear in later growth. Calice becomes more compressed and its interior is infilled by intrathecal sclerenchyme.

The wall is marginothecal. Minitrabeculae of marginotheca and septa are ca. 15–20 µm in diameter. Crests are formed outside the ellipsoidal calice outline as a convexity of marginotheca. Outside the thecal ring a one layer (sometimes preserved as isolated slices) of thin tectura is deposited (see Fig. 9G, K). Surface of tectura is usually covered with growth lines (Fig. 9I) but sometimes it looks completely smooth and 'porcelaneous'. Aragonite crystal clusters of non-trabecular tectura show centrifugal growth (Fig. 9J).

Adult stage. — At this stage septal apparatus of complete five cycles and usually rare S6 septa (about 110–130 septa) may be developed (Fig. 9A–C). Septa S6 are present mostly in lateral sectors. Largest specimens may reach ca. 30 mm in height (GDC up to 45 mm; LCD up to 22 mm)

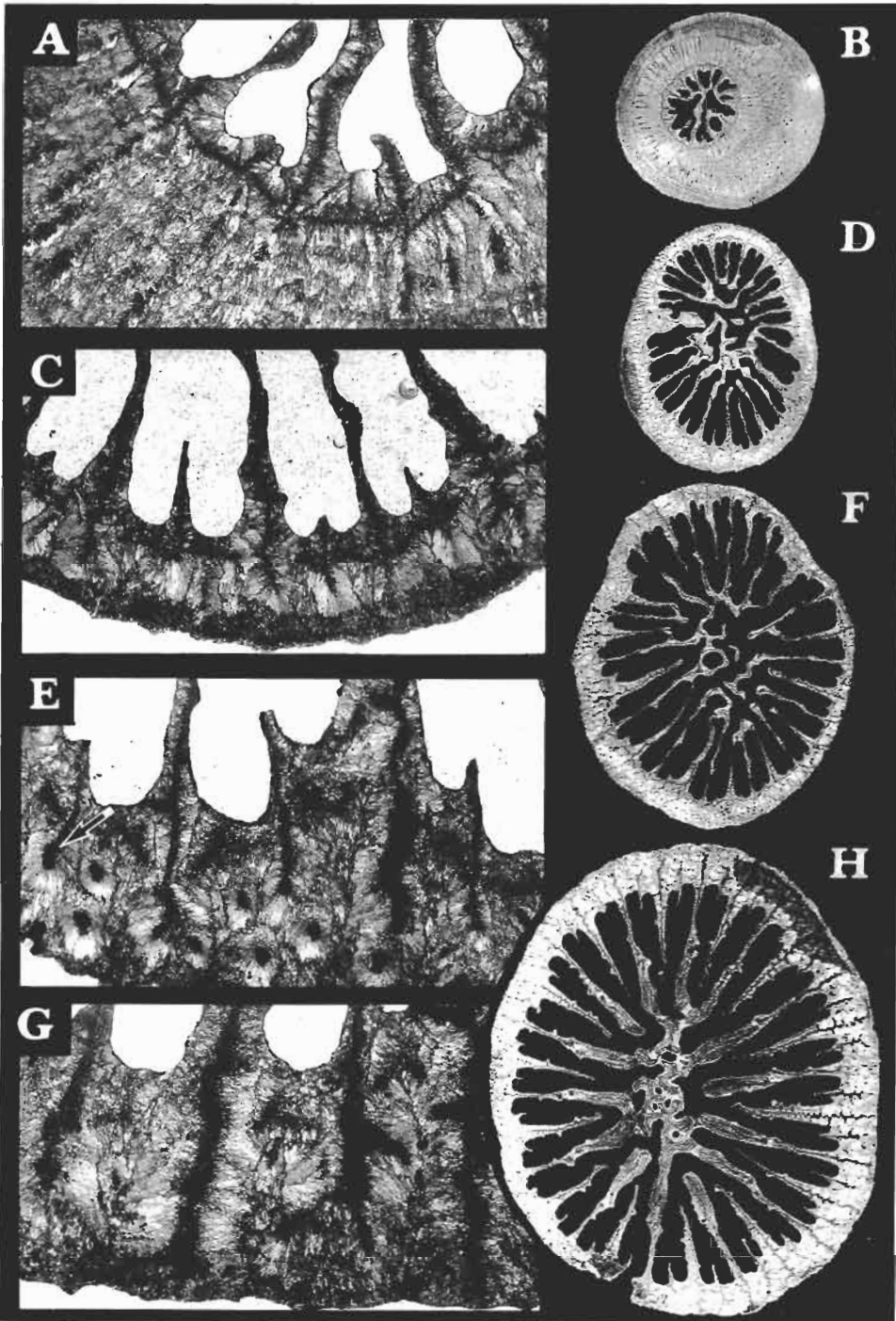Wall is marginothecal of identical character as in juvenile stage.

Javania cailleti (Duchassaing & Michelotti 1864)
Fig. 10A–J.

Javania cailleti (Duchassaing & Michelotti); Cairns 1991: p. 21, Pl. 8c–e (with synonymy).

Initial stage. — The initial skeleton consists of 6 protosepta and a marginotheca (Fig. 10D–E). Calice circular in outline. Diameter of the base about 1.4 mm. In subsequent growth the corallum diameter decreases to ca 1.2 mm. Wall of marginothecal nature with arranged vertically minitrabeculae. The initial part of skeleton is covered by a very thick (5 and more mm), multilayered tectura developed in succeeding growth stages.

Fig. 8. Serial thin-sections of Recent *Caryophyllia berteriana* Duchassaing 1850, Atlantic Ocean (North of Venezuela); ZPAL H.XIII/6. A–B. Early-juvenile stage with trabeculothecal wall and thick deposits of tectura. C–D. Juvenile stage with trabeculothecal wall. E–F. Late-

-juvenile stage with trabeculothecal wall. Tectural deposits have trabecular nature (arrow). G–H. Adult stage. Note vestiges of the trabeculothecal segments vanishing on the inner part of forming septotheca ('endoseptothecally'). A, C, E, G × 30; B, D, F, H × 4.

Juvenile stage. — At this stage corallum diameter increases and there appear S2 septa and rudimetary columella developed by fusion of inner edges of the S1 septa (Fig. 10F–G). In the later growth, the axial structure vanishes, as the septa no longer remain fused. Symmetry hexameral. Simultaneously with the development of S2 and, particularly S3 septa, the calicular outline changes to more elliptical. On the corallum surface there may appear C1–C3 costal ridges. Interior of the calice is partially infilled by intrathecal sclerenchyme.

Wall marginothecal, however, in subsequent growth in some interseptal places (between S1–S2 septa) the trabecular palisade of the wall may interrupt and 'marginothecal arches' appear (Fig. 10H). With the increase of number of septa marginothecal arches become more and more narrower. Minitrabeculae of peripheral parts of the arches are inclined toward neighboring marginothecal arches. Diameter of septal and thecal minitrabeculae ca. 15 μm. Outside the trabecular thecal ring there appears a thick, externally smooth and 'porcelaneous' tectural cover of a non-trabecular nature. Arrangement of aragonite crystal clusters indicate its centrifugal growth. In the later growth the tectural deposits become more thinner.
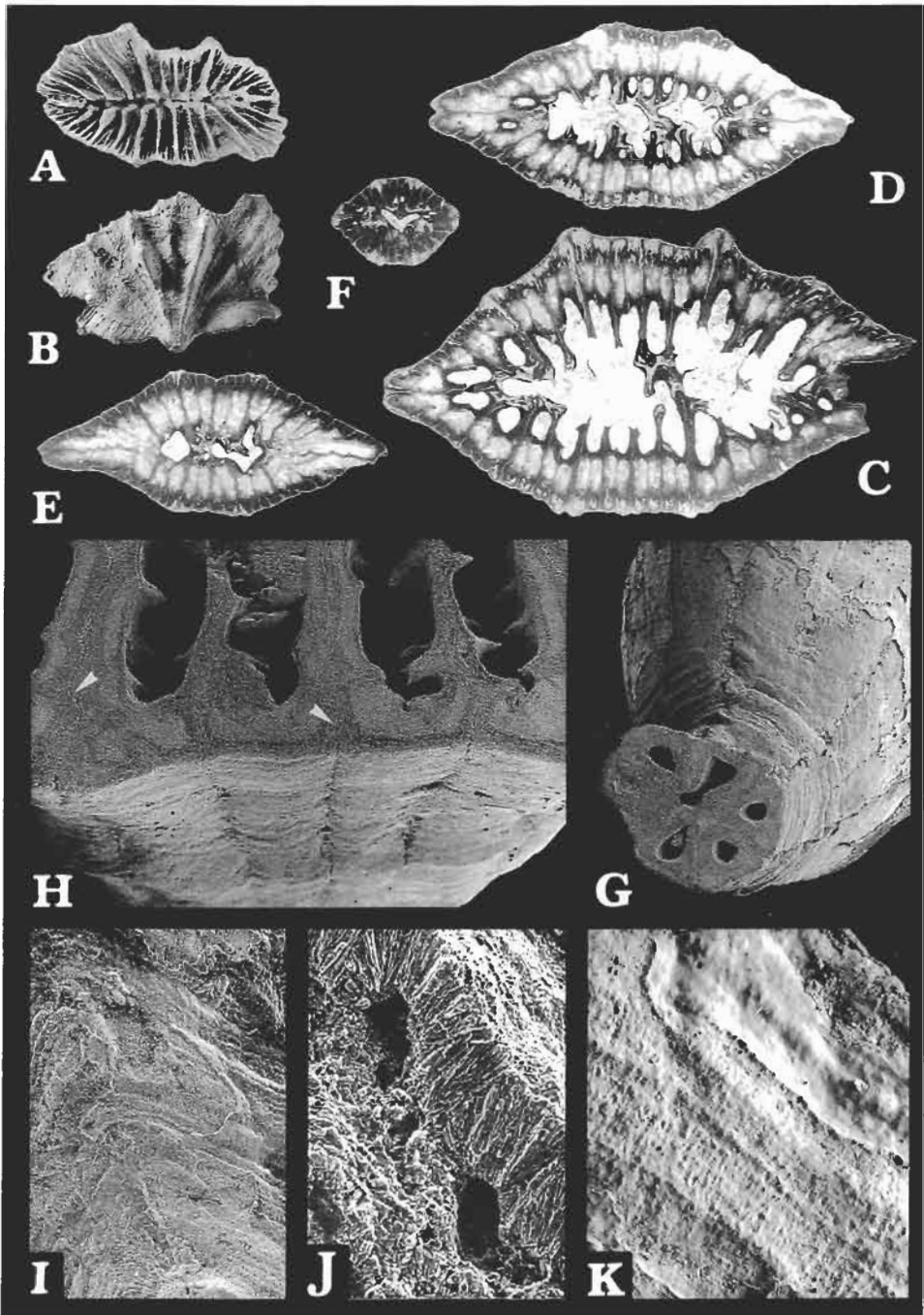
Adult stage. — The septal apparatus consists of complete four septal cycles. Height of the largest specimen reaches ca. 70 mm (GCD up to 65 mm; LCD up to 45 mm).

The wall may be partially marginothecal in character (as marginothecal arches) or it is septothecal (Fig. 10C). Septotheca develops by gradual reduction of marginothecal arches and thickening of septa (Fig. 10I). Creation of the septothecal wall corresponds to development of costosepta which sometimes may be prominent (Fig. 10C and Zibrowius 1980: Pl. 82A, K). Costosepta which grow larger may interrupt relics of marginothecal arches causing development of a peculiar trabeculotheca consisting of a fragment of a marginothecal arch (Fig. 10J).

Patterns of the ontogenetical thecal modifications

Initial stage. — In all investigated forms the prototheca is developed always as marginotheca. It seems to be a rule in the Caryophylliinae (at least in *Acanthocyathus, Desmophyllum, Labyrintocyathus, Paracyathus, Parasmilia, Paraconotrochus, Trochocyathus*) and Flabellidae. For this

Fig. 9. *Flabellum roissyanum* Milne Edwards & Haime 1848, Miocene, Korytnica (Poland). A–B. Adult corallum ZPAL H.I/315 with large septal crests; × 1. C–F. Serial thin-sections of the specimen ZPAL H.I/285 with marginothecal wall continuing up to the adult stage; × 4. G. Initial (6 protosepta) and juvenile parts of the corallum ZPAL H.XIII/7 skeleton; × 16. H. Etched surface of the juvenile corallum ZPAL H.XIII/8. Note minitrabeculae of the septum

crowded closely to each other (arrow); × 33. I–J. Deposits of tectura on the surface of ZPAL H.XIII/9 corallum. Aragonite crystal clusters show centrifugal growth; × 33, × 1000 respectively. K. Vertically arranged wall minitrabeculae, partially covered by thin tectura ZPAL H.XIII/10; × 100.
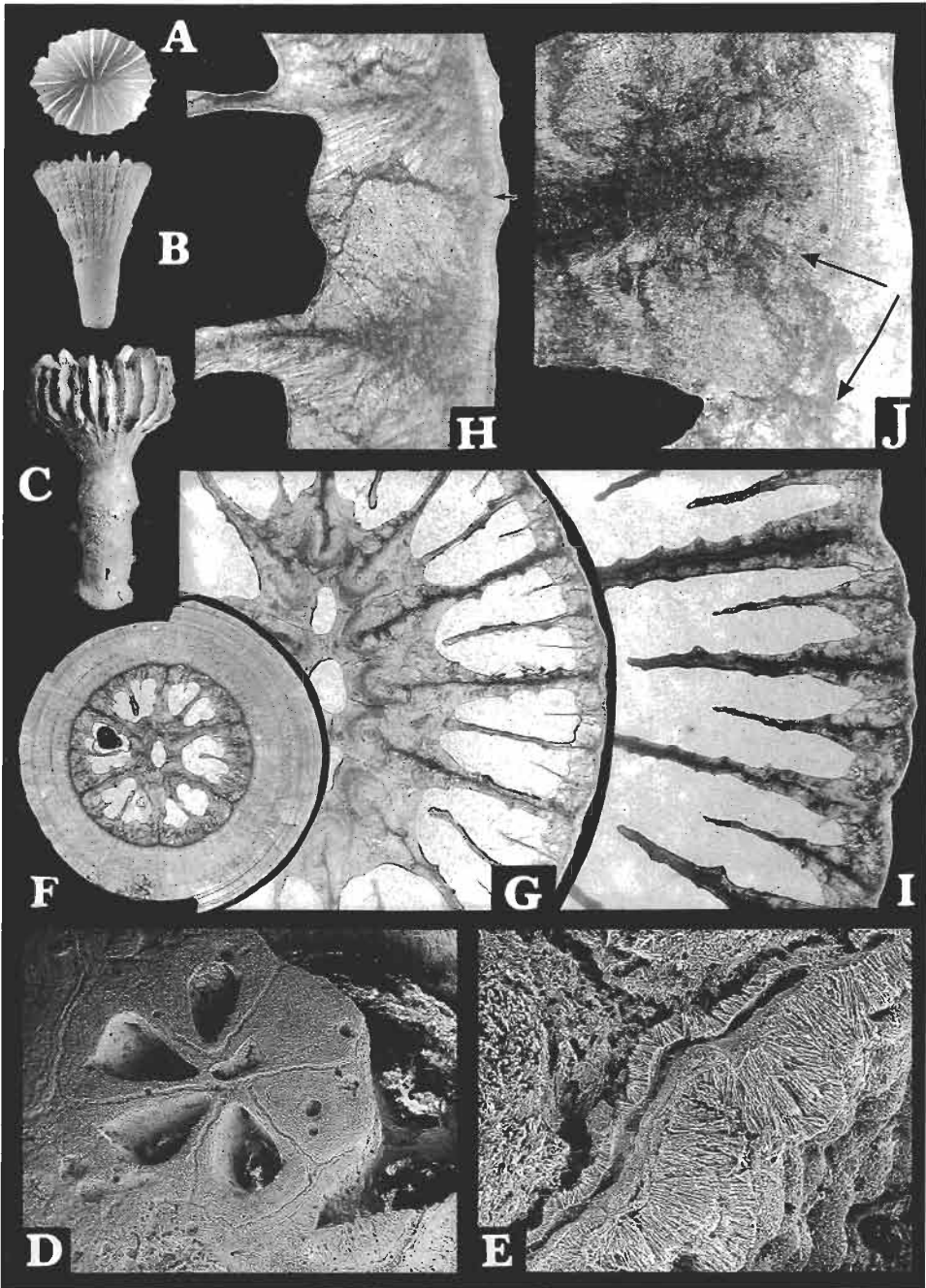
reason it is important to review available information on different types of protothecal walls.

Mori *et al.* (1977), in showing ontogeny of thecal structures in *Acrohelia horrescens* (Dana 1846) and *Galaxea fascicularis* (Linnaeus 1767), acknowledged that trabeculotheca is the first thecal structure (prototheca) formed directly on the basal plate. However, the documentation included in the paper suggested that they studied specimens isolated from the colony and formed trough budding and not representing the first astogenetical stages (types of budding see in Chevalier 1971: p. 57). According to Chevalier (1971: p. 70, Fig. 54) the first thecal structure of *Galaxea fascicularis* forms an epithecal ring(?), and after that there develops marginotheca followed by other trabecular thecal structures. Information about non-marginothecal protothecal wall of *Manicina* was given by Chevalier (1987: p. 530); however, lack of any illustration doesn't allow a check of this data. It should be pointed out that data hitherto available does not confirm that scleractinian prototheca can be formed as a solitary trabecular ring (eutheca *sensu* Heider). Mori & Minoura (1980: Fig. 6) deduced that a trabecular ring precedes formation of radial elements in *Flabellum pavonicum* (= *F. distinctum*). My own observations of initial coralla and also data from literature (Gardiner 1904; Squires 1963) show a marginothecal character of flabellid primordial trabecular wall.

Subsequent growth of the initial skeleton in all investigated forms is combined with decreasing of a corallum diameter (in comparison with the diameter of the basal plate). This phenomenon was observed also, e.g. in *Paracyathus stearnsii* Verrill (see Durham 1949: Fig. 9) or in *Monomyces rubrum* (Quoy & Gaimard 1833) (see Squires 1963). According to Squires (1963: p. 19) 'the period of contraction of diameter may represent that time during which the polyp is not feeding, but utilizing stored food'.

Juvenile and adult stages. — Studies on caryophylliid corals reveal that particular wall types can change during their ontogeny (Fig. 11). The sequence is as follows: marginotheca → trabeculotheca → septotheca. A part of this sequence — a change from marginotheca to trabeculotheca — has been documented in *Galaxea fascicularis* by Mori *et al.* (1977), and also observed in *Desmophyllum cristagalli* Milne Edwards & Haime 1848 (Sorauf & Jell 1977). Marginotheca-trabeculotheca replacement can be connected with different degree of the edge-zone development in the succesive growth stages. Edge-zone that contains extensions of the mesenteries is the only coral tissue which can control secretion of the extrathecal skeletal deposits (particularly the formation of costae). The change considered can be an outcome of increasing number and thickness of septa. In most cases vanishing of interseptal, trabeculothecal segments take place on the inner part of forming septotheca ('endoseptothecally'). Cuif

Fig. 10. *Javania cailleti* (Duchassaing & Michelotti 1864), Recent, Atlantic Ocean (Bahama). A–B. ZPAL H.XIII/11 in distal (A) and lateral (B) views; × 0.9. C. Lateral view of the peculiar specimen USNM 80964 with very long cylindrical juvenile stage and strongly septothecate

adult stage; × 0.5. D–E. Initial corallum ZPAL H.XIII/11 covered by thick tectural deposits consisting of centrifugally oriented aragonite crystal clusters (E at right); × 33, × 250 respectively, F–J. Serial transverse thin-sections of the specimen ZPAL H.XIII/11. F. Juvenile stage with marginothecal wall and thick tectural deposits; × 6.6. G–H. Late-juvenile stage with interseptally interrupted trabecular palisade of the wall (arrow); × 6.6, × 40 respectively. I–J. Septothecate adult stage with fragments of marginothecal arches (arrow); × 6.6, × 40.
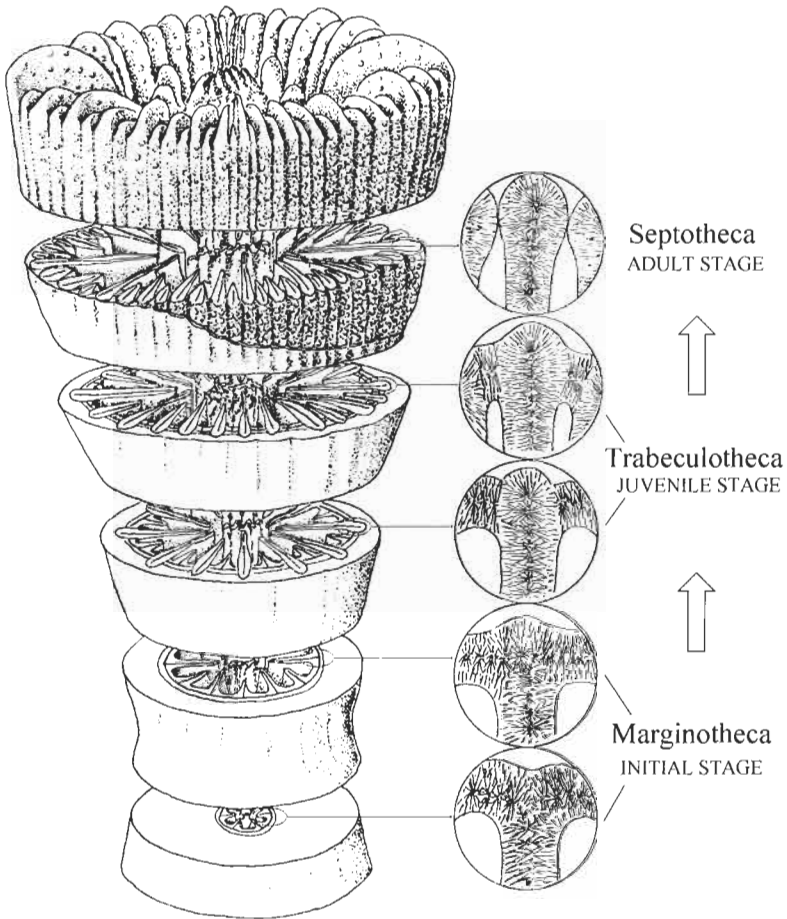
Fig. 11. Model of the ontogeny of thecal structures in Caryophylliina.

(1968) showed the example of *C. clavus* in which trabecular segments vanished outside of the forming septotheca ('exoseptothecally'). In all investigated Caryophylliidae, the marginotheca is interrupted by radial elements. The rests of the primordial marginotheca formed interseptally located trabeculothecal segments. Septa of the successive cycles are formed begining from the trabecular palisade of the wall, i.e. from the trabeculothecal segments (in this way, similarly as in marginotheca, the midline of the newly-formed septa coalesces with the midline of theca).

In Flabellidae (*Flabellum*, *Polymyces*, *Rhizotrochus*), the development of thecal structures concludes with the marginothecal stage. Example of *Javania* shows however, that also in that family original thecal structure (marginotheca) can be replaced.

Situations in which thecal succession is disordered or does not take place in particular concerns: (1) anthocyathi of forms reproduced by transverse division. To show the full thecal sequence it is necessary to

examine both anthocaulus and anthocyathus, (2) corals which undergo a rejuvenescence in the ontogeny (thecal sequence can be reversed, see Lang 1909; Fedorowski 1991: Fig. 6), and (3) corals which retain protothecal wall (marginotheca) up to the adult stage due to neoteny (e.g., Flabelliidae)

In some coral groups septotheca is replaced in ontogeny by paratheca (Vaughan & Wells 1943: p. 38), for example in *Mussa*, *Acanthophyllia* and *Thecosmilia*.

Phylogeny

Microstructural and morphological data argue for close phylogenetic relationships between two groups of minitrabecular corals, Caryophylliidae and Flabellidae.

'Epitheca', which was considered characteristic of Flabellidae, turns out to be a structure homologous to tectura of the Caryophylliidae. Marginotheca typical of the initial stages of caryophylliids is retained in flabellids up to the end (or almost to the end) of their growth. The marginothecal nature of the flabellid wall coincides with the presence of other juvenile caryophylliid characters in their adult skeletons: weakly developed axial structure, lack of pali, relatively rare and not differentiated ornamentation of the septal flanks. Wells (1956: p. F386) also noticed the neotenic character of the skeleton of Flabellidae. Marginothecal walls, few septa, lack of pali and columella, and circular or slightly elliptical outline of calices are characteristic of forms considered as ancestral to Flabellidae, i.e. middle Jurassic ?*Kraterostrobilos* Crickmay 1930 (specimens preserved as moulds) and early Cretaceous *Adkinsella* Wells 1933 (Wells 1933: Pl. 1: 3–4). The first representatives of the genus *Flabellum* (i.e. *F. fresnoense* Durham 1943 from the Late Cretaceous of California, *F. groenlandicum* Floris 1972 from the Paleocene of Greenland, *F. primitivum* Kuhn 1967 from the Paleocene of Austria) are also characterized by relatively simple morphology of its corallum (see Gaździcki & Stolarski 1992). Originally simple and not differentiated flabellids underwent a very intensive processes of speciation: more than 263 fossil and Recent species in 12 genera have been described (see Cairns 1989).

Examples of the Miocene *Caryophyllia salinaria* show that ontogenetic shifts in appearance of the particular wall types can take place also in other than Flabellidae caryophylliine group. It suggests that fixation of this character in the ontogeny of minitrabecular corals could take place independently in the different groups. Flabellidae is considered in contemporancous systematics as a monophyletic group (clade), but may, in reality, be a polyphyletic group consisting of neotenically organized forms. However, it is possible to choose within flabellids several genera forming morphologically consistent group in which monophyly ('true' Flabellidae) is unquestionable i.e. *Flabellum, Truncatoflabellum, Polymyces, Monomyces, Rhizotrochus,* and possibly *Blastotrochus, Javania, Placotrochus,*

Placotrochides, and *?Tortoflabellum*. Remaining genera classified as flabellids i.e. *Gardineria, Conosmilia,* and previously mentioned Mesozoic *?Kraterostrobilos* and *Adkinsella* seem to be superficially similar to 'true' Flabellidae only by their neotenic nature. The groups of corals which may be ancestral to the flabellid organization of skeleton could be, in particular, two subfamilies of Caryophylliidae: Desmophyllinae and Parasmilinae, both containing relatively non-specialized representatives.

Acknowledgments

References

Alloiteau, J. 1952. Madréporaires Post-Paléozoiques. In: J. Pivetau (ed.) *Traité de Paléontologie* **1**, 539–684.

Alloiteau, J. 1957. Contribution a la systématique des madréporaires fossiles. Tome I. 426 pp. C.N.R.S.

Barnes, D.J. 1972. The structure and formation of growth-ridges in scleractinian coral skeletons. *Proceedings of the Royal Society London B* **182**, 331–350.

Beauvais, L. 1982. Révision du genre *Palaeohelia* Alloiteau (Scleractiniaire méso-crétacé). *Eclogae geologicae Helvetiae* **75**, 669–687.

Cairns, S.D. 1979. The deep-water Scleractinia of the Caribbean Sea and adjacent waters. *Studies on the fauna of Curaçao and other Caribbean Islands* **180**, 1–341.

Cairns, S.D. 1982. Antarctic and Subantarctic Scleractinia. *Biology of the Antarctic Seas XI, Antarctic Research Series* **34**, 1–74.

Cairns, S.D. 1989. A revision of the ahermatypic Scleractinia of the Philippine Islands and adjacent waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae. *Smithsonian Contributions to Zoology* **486**, 1–136.

Cairns, S.D. 1991. A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands. *Smithsonian Contributions to Zoology* **504**, 1–32.

Chevalier, J.P. 1961. Recherches sur les Madréporaires et les formations récifales miocenes de la Mediterranée occidentale. *Mémoires de la Société Géologique de France* **93**, 1–562.

Chevalier, J.P. 1971. Les Scléractiniaires de la Mélanésie Francaise (Nouvelle-Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). *Expédition Francaise sur les récifs coralliens de la Nouvelle-Calédonie* **5**. 3–307.

Chevalier, J.P. 1987. Ordre des Scléractiniaires. In: P. Grassè (ed.) *Traité de Zoologie* **3** (3), 679–753.

Copper, P. 1985. Fossilized polyps in 430-Myr old *Favosites* corals. *Nature* **316**, 142–144.

Copper, P. & Plusquellec, Y. 1993. Ultrastructure of the walls, tabulae and 'polyps' in Early Silurian *Favosites* from Anticosti Island, Canada. *Courier Forschungsinstitut Senckenberg* **164**, 301–308.

Crickmay, C.H. 1930. The Jurassic rocks of Ashcroft, British Columbia. *University of California Publications, Bulletin of the Geological Sciences* **19**, 23–74.

Cuif, J.P. 1968. Étude ontogénique de quelques madréporaires Caryophyllidae actuels et fossiles. *Mémoires du Muséum National d'Historie Naturelle* **16**, 101–156.

Cuif, J.P. 1972. Recherches sur les Madréporaires du Trias. I. Famille des Stylophyllidae. *Bulletin du Muséum National d'Histoire Naturelle* **97**, 211–291.

Cuif, J.P. 1975. Caractéres morphologiques microstructuraux et systématiques des Pachythecalidae nouvelle familie de Madréporaires Triasiques. *Geobios* **8**, 157–180.

Cuif, J.P. 1977. Arguments pour une relation phyletique entre les madreporaires paleozoiques et ceux du trias. Implications systematiques de l'analyse microstructurale des Madreporaires triasiques. *Mémoires de la Societe Geologique de France* **129**, 1–54.

Durham, J.W. 1949. Ontogenetic stages of some simple corals. *University of California Publications, Bulletin of the Department of Geological Sciences* **28**, 137–172.

Fadlallah, Y.H. & Pearse, J.S. 1982. Sexual reproduction in solitary corals: overlapping oogenic and brooding cycles, and benthic planulas in *Balanophyllia elegans*. *Marine Biology* **71**, 223–231.

Fedorowski, J. 1974. The Upper Palaeozoic tetracoral genera *Lophophyllidium* and *Timorphyllum*. *Palaeontology* **17**, 441–473.

Fedorowski, J. 1991. Principles of early ontogeny in the rugose corals: a critical review. *Hydrobiologia* **216/217**, 413–418.

Gardiner, J.S. 1904. South African corals of the genus *Flabellum*, with an account of their development. *Marine Investigations of South Africa* **3**, 97–129.

Gaździcki, A. & Stolarski, J. 1992. An Oligocene record of the coral *Flabellum* from Antarctica. *Polish Polar Research* **13**, 265–272.

Heider, A.R. von 1886. Korallenstudien. *Zeitschrift für wissenschaflische Zoologie* **44**, 507–535.

Iljina, T. (Ильина, Т.Г) 1984. Историческое развитие кораллов (Подотряд Polycoeliina). *Труды Палеонтологического Института* **198**, 1–184.

Jell, J.S. 1980. Skeletogenesis of newly settled planulae of the hermatypic coral *Porites lutea*. *Acta Palaeontologica Polonica* **25**, 311–320.

Kato, M. 1963. Fine skeletal structures in Rugosa. *Journal of the Faculty of Science, Hokkaido University* **11**, 571–630.

Kaźmierczak, J. 1993. Sclerite-bearing alveolitid favositids from the Devonian of central Poland. *Paläontologische Zeitschrift* **67**, 27–44.

Lang, W.D. 1909. Growth-stages in the British species of the coral genus *Parasmilia*. *Zoological Society London, Proceeding*, 285–307.

Melnikowa, G. (Мелникова, Г) 1975. Новые раннерские представители Amphiastraeina (склерактины) юго-восточного Памира. *Вопросы палеонтологии Таджикистана*, 108–118.

Milne Edwards, H. & Haime, J. 1848. *Recherches sur les polypiers. Mém. 1. Structure et développement des polypiers en général 9*, 37–89.

Montanaro-Gallitelli, E. 1974. Microstructure and septal arrangement in a primitive triassic coral. *Bollettino della Societa Paleontologica Italiana* **12**, 8–22.

Montanaro-Gallitelli, E. 1979. Lemniscasterina, a new order, related to Hydrozoa (Coelenterata). *Memorie della Accademia Nazionale di Scienze, Lettere e Arti di Modena* **6** (21), 1–80.

Mori, K., Omura, A., & Minoura, K. 1977. Ontogeny of euthecal and metaseptal structures in colonial scleractinian corals. *Lethaia* **10**, 327–336.

Mori, K. & Minoura, K. 1980. Ontogeny of 'epithecal' and septal structures in scleractinian corals. *Lethaia* **13**, 321–326.

Morycowa, E. & Roniewicz, E. 1987. Scleractinian corals from the Middle Miocene salt deposits in Carpathian Foredeep, Poland. *Acta Palaeontologica Polonica* **32**, 105–119.

Roniewicz, E. 1989. Triassic scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. *Österreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse Denkschriften* **126**, 1–152.

Roniewicz, E. & Morycowa, E. 1993. Evolution of the Scleractinia in the light of microstructural data. *Courier Forschungs-Institut Senckenberg* **164**, 233–240.

Schouppé, A. & Stacul, P. 1966. Morphogenese und Bau des Skelettes der Pterocorallia. *Palaeontographica* **11**, 1–186.

Sorauf, J.E. 1972. Skeletal microstructure and microarchitecture in Scleractinia (Coelenterata). *Palaeontology* **15**, 88–107.

Sorauf, J.E. 1983. Primary biogenic structures and diagenetic history of *Timorphyllum wanneri* (Rugosa), Permian, Timor, Indonesia. *Memoirs of the Association of Australian Palaeontologist* **5**, 275–288.

Sorauf, J.E. & Jell, J.S. 1977. Structure and incremental growth in the ahermatypic coral *Desmophyllum cristagalli* from the North Atlantic. *Palaeontology* **20**, 1–19.

Squires, D.F. 1962. Deep sea corals collected by the Lamont Geological Observatory. 3. Larvae of the Argentine scleractinian coral *Flabellum curvatum* Moseley. *American Museum Novitates* **2078**, 1–11.

Squires, D.F. 1963. *Flabellum rubrum*. *Bulletin of the New Zealand Department of Scientific and Industrial Research* **154**, 1–44.

Stolarski, J. 1991. Miocene Scleractinia from the Holy Cross Mountains, Poland; Part 1 — Caryophylliidae, Flabellidae, Dendrophylliidae, and Micrabaciidae. *Acta Geologica Polonica* **41**, 37–67.

Vaughan, T.W. 1900. The Eocene and Lower Oligocene coral faunas of the United States with description of a few doubtfully Cretaceous species. *United States Geological Survey Monographs* **39**, 1–205.

Vaughan, T.W. & Wells, J.W. 1943. Revision of the suborders, families, and genera of the Scleractinia. *Geological Society of America Special Papers* **44**, 1–363.

Wells, J.W. 1933. Corals of the Cretaceous of the Atlantic and Gulf Coastal Plains and Western Interior of the United States. *Bulletins of American Paleontology* **18**, 1–212.

Wells, J.W. 1956. Scleractinia. In: R.C. Moore (ed.) *Treatise on Invertebrate Paleontology, part F (Coelenterata)*, F328–F444. Geological Society of America and Kansas Press.

Zibrowius, H. 1974. Révision du genre *Javania* et considérations générales sur Flabellidae (Scléractiniaires). *Bulletin de l'Institut Océanographique* **71**, 1–48.

Zibrowius, H. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Océanographique, Monaco* **11**, 1–284.

Streszczenie

U sześciopromiennych korali z rodzin Caryophylliidae oraz Flabellidae ściana i septa tworzą się jednocześnie na płytce podstawowej i wykazują ciągłość budowy mikrostrukturalnej (ściana typu marginotekalnego). U Caryophylliidae obecność tkanek pokrywających szkielet od zewnątrz (egzosark) umożliwia, w następnej fazie wzrostu, tworzenie kostoseptów.

Wzrost kostoseptów powoduje przerwanie pierwotnej ściany — resztki marginoteki oraz kostosepta formują ścianę typu mieszanego — trabekulotekę. W wyniku pogrubiania kostoseptów trabekuloteka ustępuje w ontogenezie miejsca septotece. Większość Flabellidae charakteryzuje się ograniczonym rozwojem egzosarku i obecnością marginoteki aż do stadium dorosłego. Młodociane cechy szkieletu dorosłych flabelidów obejmują również słabo rozwiniętą strukturę osiową, brak pali, rzadką i nie zróżnicowaną ornamentację bocznych powierzchni septów. Pochodzenie flabellidowej organizacji szkieletu w podrzędzie Caryophylliina mogło być rezultatem rozciągnięcia młodocianej morfologii na późniejsze stadia rozwojowe. Do powstania tego typu modyfikacji ontogenetycznej mogło dojść w historii Caryophylliina kilkakrotnie, a Flabellidae w dotychczasowym rozumieniu mogą być grupę polifiletyczną.