Gardineria — a scleractinian living fossil

JAROSŁAW STOLARSKI

Stolarski, J. 1996. *Gardineria* — a scleractinian living fossil. *Acta Palaeontologica Polonica* **41**, 4, 339–367.

The basic architecture (Bauplan) and microstructure of the skeleton of Recent *Gardineria* are noticeably different from those of most other modern scleractinians. The wall of the *Gardineria* skeleton is entirely epithecate (non-trabecular), while in the majority of modern Scleractinia the epitheca is either absent or added to the main wall which usually is of trabecular nature. These different patterns of theca formation reflect significant anatomical differences in the peripheral parts of the polyp. The Bauplan of *Gardineria* pattern, exceptional in the modern scleractinian fauna, was widespread among early Mesozoic corals, particularly among the Triassic protoheterastraeids. Similar skeletons also occur in some late Palaeozoic rugosans (e.g., polycoeliids). *Zardinophyllum zardini*, an aberrant Triassic scleractinian coral, with a supposed rugosan septal insertion, supports the hypothesis of the rugosan origin of the Scleractinia.

Key words: Anthozoa, Scleractinia, Rugosa, microstructure, biomineralization, taxonomy, phylogeny.

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

Introduction

Since Vaughan & Wells' (1943) revision of scleractinian families and genera, only few major changes have been made in the taxonomy of Recent higher taxa (see Wells 1956; Chevalier 1987; Veron 1995). Vaughan & Wells' taxonomic system, giving a key role to easily recognizable macroscopic features of the skeleton, is still used by most zoologists and paleontologists. Introduction of modern analytical methods, e.g., molecular phylogenetics, in the near future may cause an extensive reevaluation of scleractinian phylogeny (Romano & Palumbi 1996). Techniques commonly used by paleontologists, i.e. serial sectioning and microstructural observations of the skeletons embedded in rocks, are reluctantly employed by zoologists. But it was just the development of these techniques, particularly intensive during the last 30 years, that resulted in important changes in the taxo-

nomy of extinct groups of the Scleractinia (Gill 1970; Cuif 1977; Cuif & Gautret 1993; Roniewicz & Morycowa 1993; Morycowa & Roniewicz 1995).

Application of paleontologic techniques for studying the skeletons of Recent scleractinians may provide unexpected results. During the last few years I examined the microstructure of Caryophylliina, focusing on the flabellid branch. In a previous report I suggested the polyphyletic nature of the Flabellidae (Stolarski 1995). In the present paper I take the opportunity to show the microstructural disparity between *Gardineria* Vaughan, 1907 and the typical Flabellidae. The Bauplan of *Gardineria* is exceptional not only among the flabellids as conventionally understood, but also among the Caryophylliina and Recent Scleractinia in general. This necessitates a broader comparison with extinct members of the Scleractinia. I will discuss possible relationships of *Gardineria* with early Mesozoic corals and reevaluate arguments for the rugosan ancestry of the Scleractinia.

Materials and methods

This study is based on the examination of Recent and fossil Caryophylliina. Thin sections have been studied with a light microscope and with a scanning electron microscope (SEM). After polishing, samples prepared for SEM were treated for 15–30 seconds in 5% acetic acid. Trabecular centres built of submicron sized crystals are subject to more intensive dissolution than the rest of the skeleton (Sorauf 1972; James 1974). In consequence they are visible on etched transverse sections as series of pits (i.e. on Fig. 3C, G–I).

The main representative of the family Caryophylliidae studied here is the Recent *Caryophyllia cyathus* (Ellis & Solander, 1786), type species of the genus *Caryophyllia*; the main representative of the Flabellidae is the Recent *Flabellum (Flabellum) chunii* Marenzeller, 1904, which is close to the type species *F. (F.) pavoninum* Lesson, 1831 (see Zibrowius 1980). These have been compared to some other species of Caryophylliina (housed at the Institute of Paleobiology, Warsaw). The study of *Gardineria* is based on two Recent species: *G. hawaiiensis* Vaughan, 1907 (type of the genus) and *G. paradoxa* (Pourtalès, 1874). In addition still undescribed corals from the New Caledonia area (obtained from H. Zibrowius) have been examined (herein under Gen. n. A).

Examined fossil corals comprise: Cretaceous *Adkinsella edwardsensis* Wells, 1933, considered as the oldest flabellid (Wells 1933), and Triassic *Protoheterastraea leonhardi* (Volz, 1896), *Protoheterastraea* sp. and *Zardinophyllum zardini* Montanaro-Gallitelli, 1975.

Institutional abbreviations: MGUWr — Geological Museum of the Wroclaw University, TMM — Texas Memorial Museum, Austin, Texas, USNM — National Museum of Natural History (formerly United States National Museum), Washington, D.C., ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.
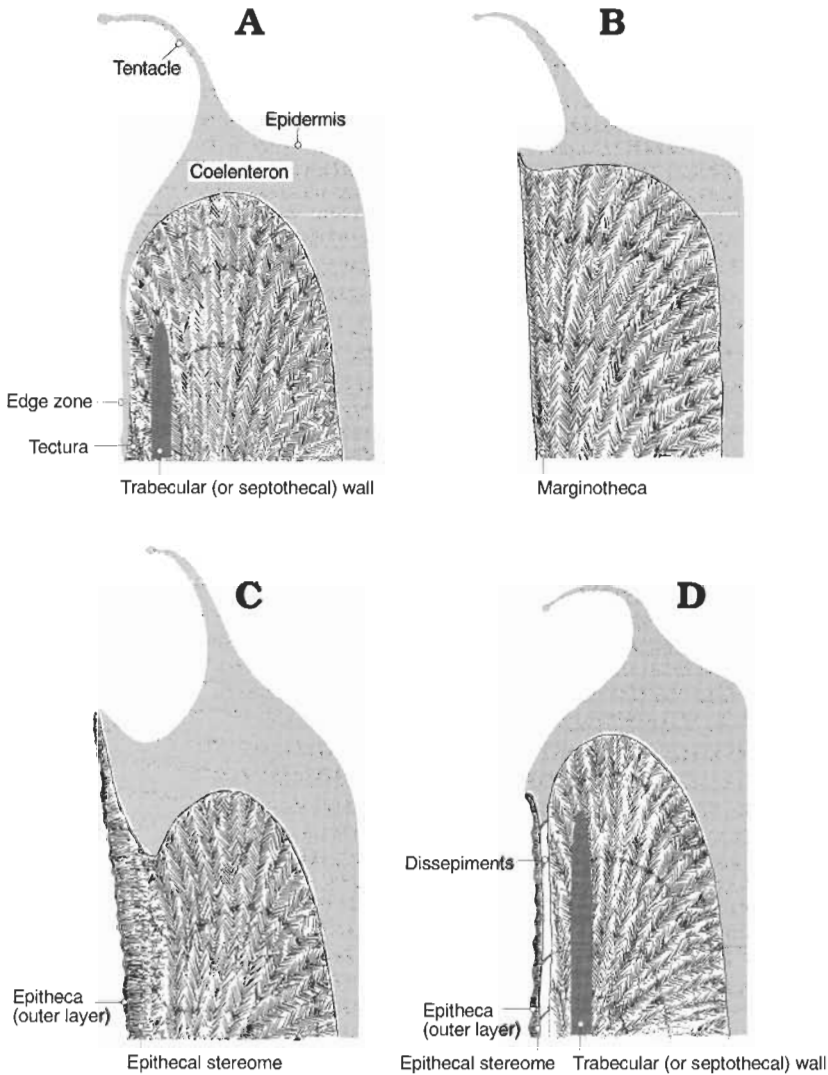
Fig. 1. Reconstruction of the marginal parts of coralla having different wall structures. **A**. Trabecular wall with tectural deposits (Caryophylliidae: *Caryophyllia*). **B**. Marginothecal wall (Flabellidae, e.g., *Flabellum*). **C**. Entirely epithecate wall (Gardineriidae fam. n., e.g., *Gardineria*). **D**. Trabecular wall with epitheca (Caryophylliidae, e.g., some *Trochocyathus*). Not to scale (modified after Stolarski 1995).

Terminology

Epitheca (Milne Edwards & Haime 1848, emended Barnes 1972, and herein) — wall formed by the marginal part of the polyp, growing in thickness only from the inner side of the calice. An epitheca is built of calcareous fibres not organized into trabeculae. Its outer part (outer or

primary layer *sensu* Barnes 1972) is formed in the apical part of the soft tissue fold (lappet cavity). The calcareous fibres of the outer part are oriented distally, rarely centripetally. The inner part of the epitheca consists of stereome showing centripetal organization of fibres; called herein epithecal stereome (structurally indistinguishable from the inter-septal stereome of various scleractinians). The epitheca often accompanies other wall structures (i.e. trabeculotheca, septotheca) but may also form the only corallum wall (in the latter case the original, strictly surficially topographically meant name epitheca is somewhat misleading since it does not cover any other structure); Fig. 1C–D.

Marginotheca (Mori & Minoura 1980) — wall built of the palisade of small-sized, distally oriented trabeculae that are continuous with those of mid-septal line (Figs 1B, 3G–H, 7A). The trabecular core of the margino-theca is formed in the apical part of the fold (edge-zone) of the basal ectoderm. Usually, it is thickened from both sides by secondary calcareous deposits. The deposits laid down outside the calice are called tectura, whereas those secreted inside the calice are the stereome.

Septotheca (Vaughan & Wells 1943, = pseudotheca *sensu* von Heider 1886) — wall built of the thickened outer parts of radial elements.

Tectura (Stolarski 1995) — skeletal deposits laid down by the edge-zone (Figs 1A, 3D, 7A). Its calcareous fibres are usually not arranged into trabeculae and its surface is smooth (porcellaneous); sometimes however, the fibres form short trabeculae and then its surface has a grainy texture. Occasionally, the surface of the tectura is corrugated and at the first glance is similar to that of an epitheca covered with growth lines. Most probably, individual corrugations mark successive steps of the edge-zone withdrawal. Tectura is easily distinguishable from epitheca by the cen-trifugal organization of its calcareous fibres.

Trabecular walls — thecal structures having their own trabeculae. I include here the marginotheca and the trabeculotheca.

Trabeculotheca (Chevalier 1987) — wall composed of a discontinuous trabecular palisade (trabeculothecal segments) which is interrupted by radial elements. In ontogeny it is formed by splitting of the marginotheca by developing costae (Stolarski 1995). Formation of the new septa and thickening of their costal parts often result in narrowing and finally vanishing of trabeculothecal segments (septotheca); Fig. 7A.

Historical background

Peculiar features of the skeleton of *Gardineria* were first noticed by Pour-talès (1868, 1871). His *Haplophyllia paradoxa* (in fact a *Gardineria*) differed so markedly from his other scleractinians that he attributed it to the Rugosa. In his taxonomic decision Pourtalès (1871) was impressed by the coral 'general appearance' and its 'smooth ungranulated septa not resolv-able into the regular hexameral arrangement'. He considered the Permian
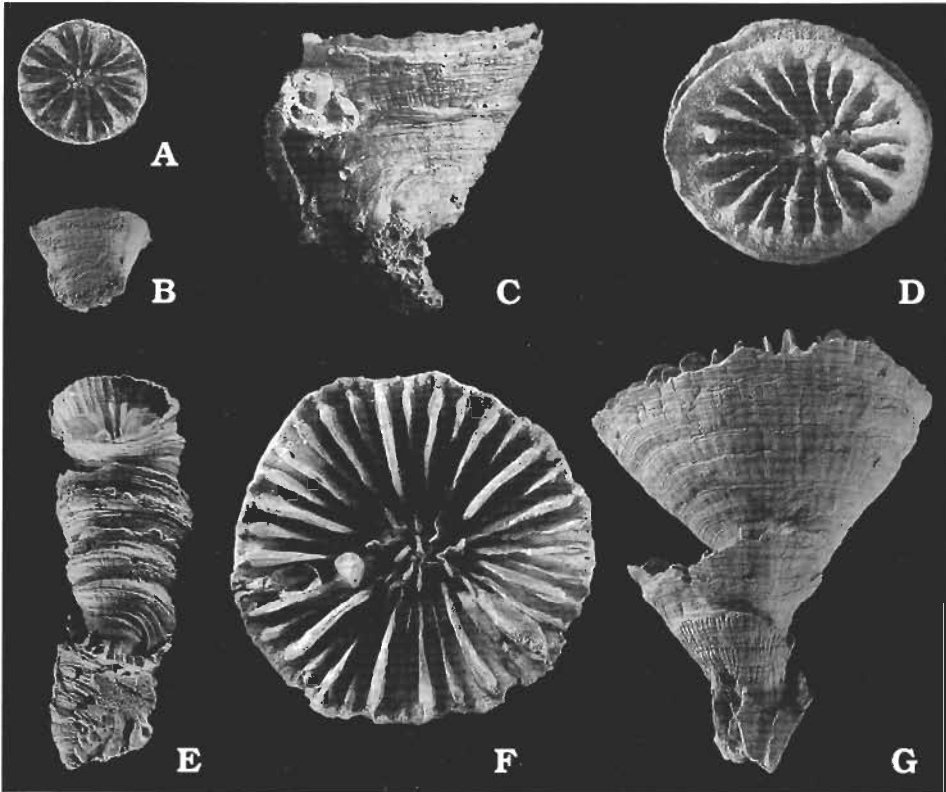
Fig. 2. Representatives of the genus *Gardineria*. **A–B**. *Gardineria philippinensis* Cairns, 1989, paratype USNM 82003, × 1.5. Recent, ALB-5217, 13°20'N/123°14'E, 192 m. **C–E**. *Gardineria paradoxa* (Pourtalès, 1868), ZPAL H.XV/3–4 respectively, **C–D** × 2, **E** × 1.5. Recent, S.W. of Jamaica, GOS-59A, Stat. 112/78, 17°21'N/78°19'W, 700 m. **F–G**. *Gardineria hawaiiensis* Vaughan, 1907, holotype USNM 20731, × 1.5. Recent, 22°15.25'N/159°23.15'W, 497–541 m.

rugosan *Calophyllum profundum* [= *Polycoelia profunda* (Geinitz, 1842)] as most similar to his *Haplophyllia*. The taxonomic position of Pourtalès' *Haplophyllia* within the Rugosa was accepted by Duncan (1872), who assigned it, together with *Guynia*, to the rugosan family Cyathaxonidae. *Duncania barbadensis* Pourtalès, 1874 has also been classified among the Rugosa (Pourtalès 1874). However, Lindström (1877) recognized the originally hexameral organization of the septal apparatus in the proximal part of *D. barbadensis*, thus questioning its rugosan status. Subsequently, Duncan (1883, 1885) admitted that *Haplophyllia*, *Duncania* and *Guynia* were lacking essential rugosan features (i.e. septal fossula) and concluded that they should be classed as Haplophyllioida within scleractinian family Turbinoliidae (i.e. Caryophylliidae). Remarkable dissimilarity between these corals and other Recent scleractinians has no longer been discussed in the biological literature. Schindewolf (1942) was probably the last who presented a broad historical panorama of these investigations.

In the 20th century literature, these generic names were mentioned in grouping species and genera within the Scleractinia. Vaughan (1907) described the new *Gardineria hawaiiensis* with an extensive epitheca, and linked it with the just established scleractinian family Flabellidae Bourne, 1905. Vaughan & Wells (1943) synonymized the genera *Gardineria*, *Haplophyllia* and *Duncania* (similarity of *Haplophyllia* and *Duncania* was previously noticed by Gardiner 1904). The valid generic name is *Gardineria*, *Duncania* Pourtalès and *Haplophyllia* Pourtalès having been recognized as homonyms but not available, being preoccupied (see also Lindström 1877; Vaughan 1907). Until now, the taxonomic position of *Gardineria* within the Flabellidae has not been questioned (Alloiteau 1952; Cairns 1979, 1984, 1989, 1995; Chevalier 1987; Wells 1956, 1973).

The skeleton of the typical Caryophylliina

In order to show the unusual position of *Gardineria* among the Recent Caryophylliina, I will compare its skeleton with that of typical Flabellidae and Caryophylliidae.

Initial stage. — In Flabellidae and Caryophylliidae the initial stage begins with a basal plate associated with protosepta (usually 6 or 12) and a prototheca (marginotheca) — Fig. 3C, G–I; see also Stolarski 1995. At least in some flabellids the protosepta are secreted on the basal plate prior to the wall (Gardiner 1902; Squires 1963: pl. 2: 1–3). Wall and septal trabeculae (15–50 µm in diameter) are closely packed forming a trabecular palisade.

In both the Caryophylliidae and Flabellidae, during the subsequent growth, the corallum diameter first decreases compared to the diameter of the basal plate (Stolarski 1995).

Juvenile stage. — This stage begins with increasing of the diameter of the trabecular-walled corallum (in monocyclic development) or surrounding the initial prototheca by a peripheral new wall/walls (in polycyclic development); see Durham (1949), Zibrowius (1984).

In caryophylliids with a monocyclic development, the initial marginotheca is continuous in the juvenile stage. However, at the very beginning of that stage, the marginotheca may be interrupted by costosepta and a trabeculothecal wall begins to develop. Although the interruption of a uniform marginotheca is the start of a trabeculotheca, septa of the higher cycles which appear later in ontogeny have always a marginothecal beginning. Their mid-septal trabeculae coalesce with those of the trabeculothecal segments. In the subsequent development, new septa are formed and thickened, and the trabeculothecal segments become narrower. Usually, by the end of the stage, the vestiges of the trabeculothecal segments disappear and a uniform septotheca is developed (Fig. 7A; see also Stolarski 1995).
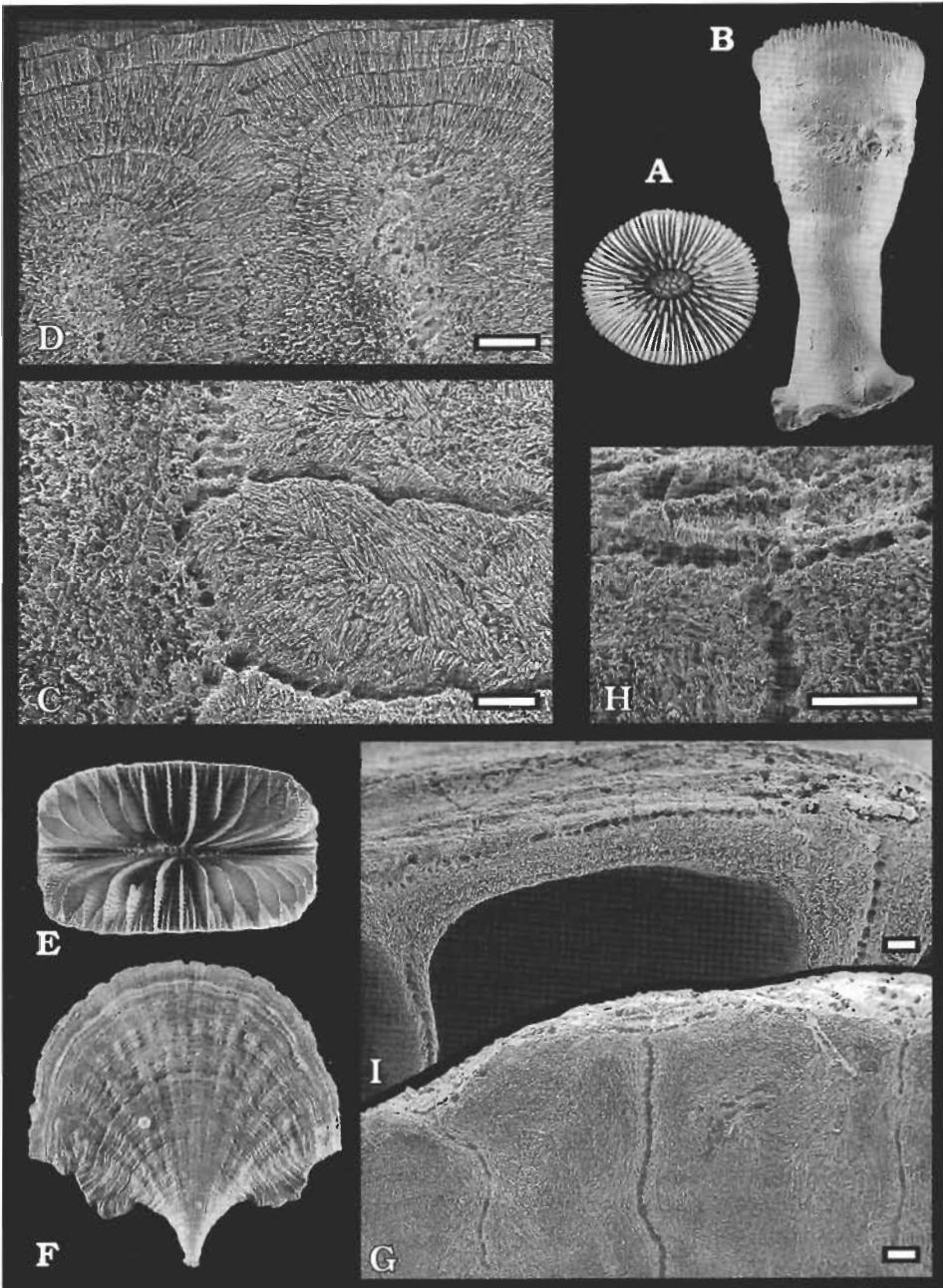
Fig. 3. Microstructural characteristics of Recent, 'typical' caryophylliine corals. **A–D**. *Caryophyllia cyathus* (Ellis & Solander, 1786), ZPAL H.XV/1, distal (**A**) and lateral (**B**) views. × 1.5. **C**. Early juvenile stage with marginothecal wall. **D**. Adult stage with septothecal wall. 'Calypso' SME 1293, SW Alboran, 35°49'N/03°14.4'W, 80–84 m. **E–I**. *Flabellum chunii* Marenzeller, 1904, ZPAL H.XV/2, distal (**E**) and lateral (**F**) views, × 1.5. **G–I**. Early juvenile stage with marginothecal wall (**G–H**), which is continued in adult stage (**I**). Great Meteor Seamount, SEAMOUNT 2, DW 167, 30°04.6'N/42°1'W, 520 m. Scale bars equal 50 μm.

In caryophylliids with a polycyclic development (e.g., *Concentrotheca*, *Tethocyathus*, many species of *Paracyathus*, *Trochocyathus*, some *Caryophyllia*) juvenile walls are formed as concentric thecal rings. Usually, there are 2–3 thecal rings, but occasionally multiple juvenile walls may be formed, e.g., up to 7 thecal rings in the Miocene *Tethocyathus microphyllus* (Reuss, 1871) as shown by Stolarski (1991). Successive walls typically are marginothecal, rarely trabeculothecal. Cylindrical coralla with many thecal rings show septotheca just above the basis of the last thecal ring.

Most flabellids grow monocyclically and have the marginothecal wall continuous along the juvenile stage. However, in the late juvenile stage of *Javania* (*J. insignis*, *J. cailleti*), the marginotheca often is split at an interseptal position into marginothecal arches (Stolarski 1995). I also observed trabeculotheca in the late juvenile stage of *Javania pachytheca* Cairns, 1995 and *Placotrochus laevis* Milne Edwards & Haime, 1848. In both forms the marginotheca was interrupted in septal position. A peculiar type of polycyclic development is shown by *Polymyces*. Its second wall is formed by development and fusion of several rootlets (Cairns 1994; Stolarski in preparation). The rootlets develop far above the juvenile expansion of the corallum diameter, and the juvenile wall is marginothecal. The related *Monomyces* develops only one lateral rootlet as an asymmetrical attachment to the substrate.

Most caryophylliid and flabellid genera have their initial and juvenile parts covered with tectural deposits (Fig. 7; see also Stolarski 1995, 1996).

Adult stage. — This stage is characterized by the appearance of the last cycle septa and other skeletal features considered as adult for particular species.

Usually adult caryophylliids have septothecal walls (Figs 3D, 7A), but forms with weakly developed costae may have trabeculothecal walls up to the end of their growth (e.g., in *Caryophyllia alaskensis* Vaughan, 1941). Some caryophylliids have the costae covered with a thin epitheca (e.g. some *Trochocyathus*). In all these epithecate forms however, the epitheca is developed as rudimentary epithecal rings covering the costae locally (Roniewicz & Stolarski in preparation).

Most flabellids have a marginothecal wall up to the end of growth. However, *Javania* and *Placotrochus* have trabeculothecal or even septothecal walls in the adult stage. I did not find any epitheca in flabellids.

In the majority of caryophylliids and in some flabellid genera (*Javania* and *Placotrochus*) septa are exsert above the calicular edge. Only rarely (e.g., in the caryophylliid genus *Conotrochus*) the outer edges of the septa form a notch where they join the trabecular theca. In this case, the theca

→

Fig. 4. *Gardineria hawaiiensis* Vaughan, 1907. **A–D**. Distal (**A**) and lateral (**B**) views of ZPAL H.XV/5, × 1.5. **C**. Longitudial section in midseptal plane. At distal edge note trabecular 'tracts' arranged in fan-like pattern. **D**. Septum of last cycle (S_4) with fringe-like axial margin, foreground; on background S_1 with typical low-granular ornamentation. Recent, New Caledonia, MUSORSTOM 5, DW 255, 25°15.40'S/159°54.80'E, 280–295 m. **E**. Transverse section of
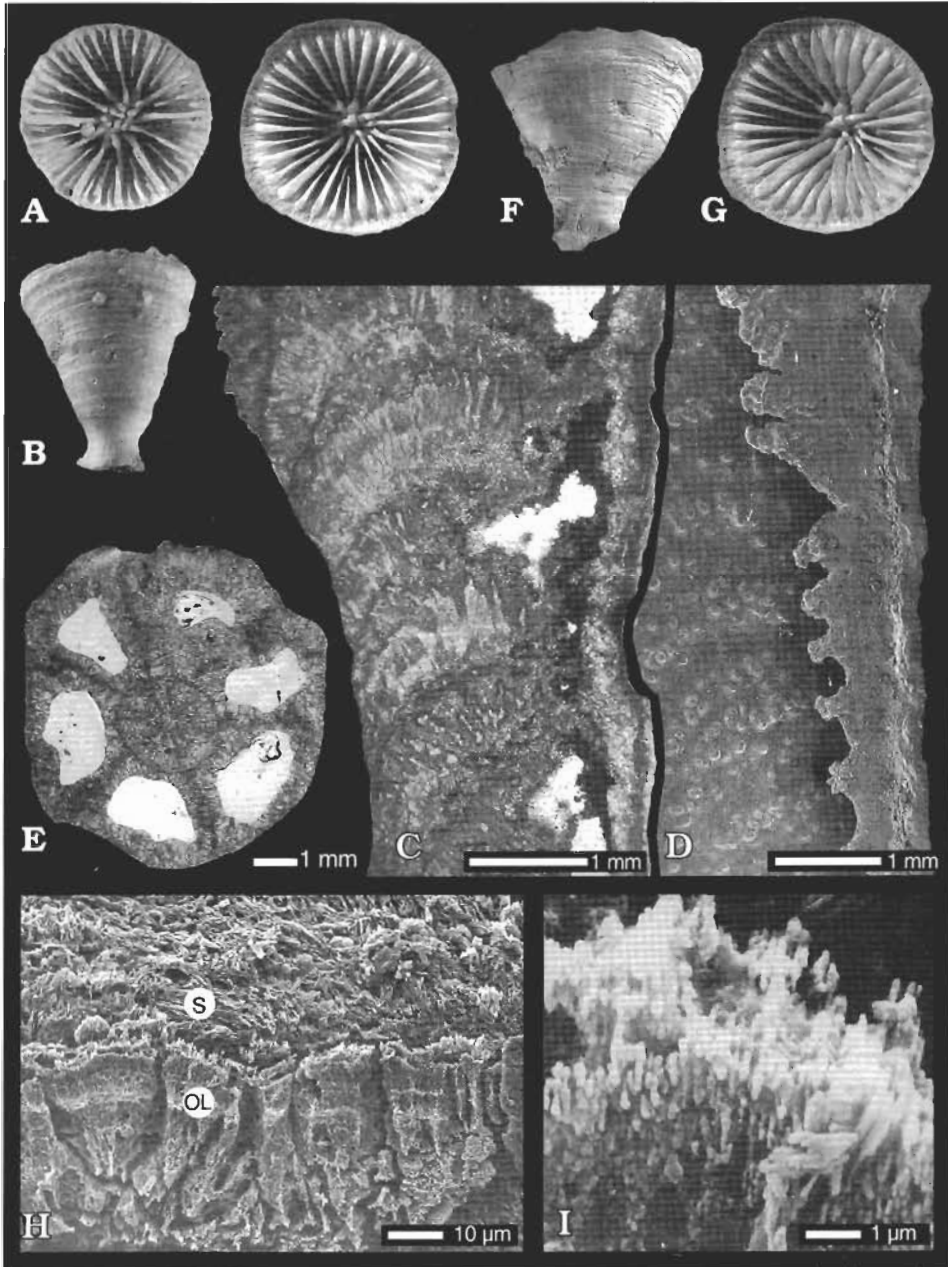
the base of ZPAL H.XV/6 with two thecal rings corresponding to initial and juvenile stage. Recent, New Caledonia, MUSORSTOM 5, DW 273, 24°43.02'S/159°43.26'E, 290 m. **F–G**. Calicular (stereo) and lateral views of ZPAL H.XV/7, × 1. Recent, New Caledonia, CHALCAL 2, DW 73. 24°39.90'S/168°38.10'E, 573 m. **H–I**. Oblique view on etched trasverse section and surface of epitheca in juvenile stage (OL — outer layer buit of distally oriented cristallites, S — epithecal stereome). ZPAL H.XV/8, Recent, New Caledonia, CHALCAL 2, DW 21, 22°54.2'S/167°19'E, 525 m.

forms an exsert calicular rim (Cairns 1994: p. 58). Flabellidae usually have the outer septal edges attenuate, joining the theca in a smooth concave or slightly notched curve.

Axial structures (various types of columella), paliform lobes or pali are widely distributed among the Caryophylliidae, whereas the Flabelliidae (*sensu* Stolarski 1995) have neither pali nor paliform lobes.

Representatives of all families of the Caryophylliina have septal faces covered with a dense, prominent granulation. Granules usually form by regular lateral expansions of trabeculae. In some Caryophylliidae the septal faces are ornamented with conspicuous flange-like structures (Zibrowius 1980, 1984; Morycowa & Roniewicz 1995). They do not occur in the Flabellidae. It is rare that Caryophylliina have nearly smooth septal faces, e.g., adult *Desmophyllum*, some species of *Conotrochus*, *Stephanocyathus*. The inner wall surface in the Caryophylliina is usually smooth, often (especially in Flabellidae) with desmocyte attachment scars (Wise 1970; Roniewicz & Morycowa 1987).

The skeleton of *Gardineria*

Initial stage. — This stage starts with a basal plate associated with protosepta and a prototheca. The initial corallum of sectioned *G. hawaiiensis* and *G. paradoxa* has 6 protosepta. The mid-septal zone of the protosepta consists of trabeculae (about 50 µm in diameter) and approaches closely to the prototheca. The prototheca is entirely epithecate (Fig. 5A–B).

Juvenile stage. — This stage begins with increasing of the corallum diameter and almost simultaneous formation of the polycyclic base. *G. hawaiiensis* develops usually 2 thecal rings whereas *G. paradoxa* forms 2–4 thecal rings (Figs 4–5; see also Cairns 1995: pl. 36c). The corallum of *G. paradoxa* is often laterally attached to the substrate and its polycyclic base is asymmetrical (Fig. 5A, C–D). In both species the successive thecal rings are epithecate. In the subsequent development, the space between neighbouring walls is filled with stereome (Fig. 5A–B). From the beginning of this stage the septa are deeply recessed and have no contact with the outer part of the epithecate wall. Septa are incorporated as independent structures into the stereomal part of the epitheca (Figs 4C, E; 5D–F). Newly-formed septa originate on the stereomal part of the wall, at some distance below the calicular rim.

Adult stage. — The pattern of the skeleton development remains unchanged: the wall is epithecate and septa are incorporated into its stereomal part.

In the mature corallum of *G. hawaiiensis* (up to 32.6 mm in calicular diameter — holotype, and 26 mm in height — here figured specimen, Fig. 4F) septa are exsert and have a peripheral notch (Figs 3–4). In *G. hawaiiensis* septa are organized hexamerally ($6S_1 > 6S_2 > 12S_3 > nS_4$). The fourth cycle is incomplete and the largest coralla have only $12–20S_4$. S_4 septal
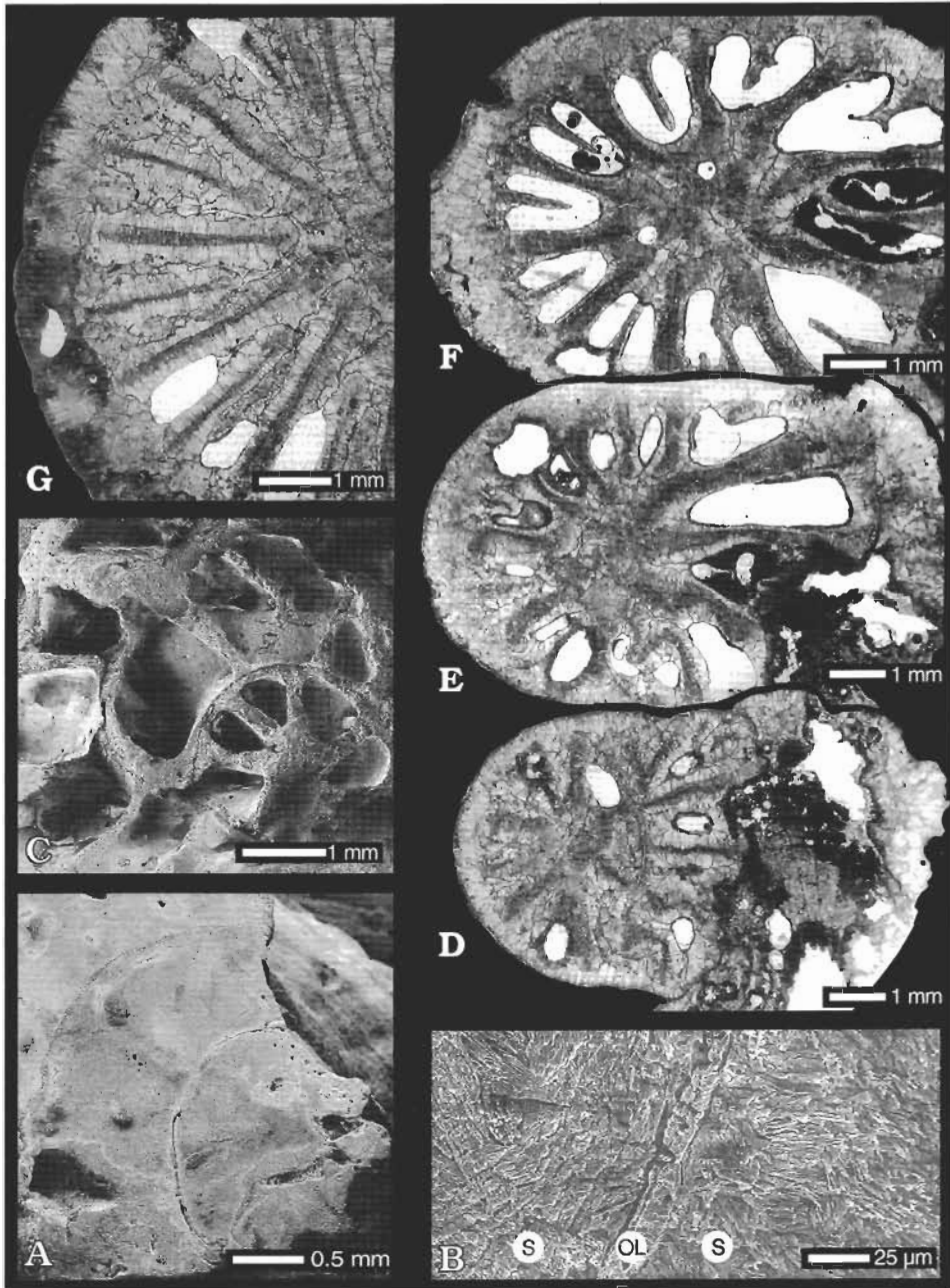
Fig. 5. *Gardineria paradoxa* (Pourtals, 1868). **A–B**. Polished and etched basal part of ZPAL H.XV/9 with three thecal rings (last ring is outside the photograph). **B**. First thecal ring (OL — epithecal outer layer). Space between adjacent walls is filled with stereome (S). **C**. Juvenile specimen ZPAL H.XV/10 with three thecal rings. **D–F**. Serial transverse section of ZPAL H.XV/3. **G**. Transverse section of the ZPAL H.XV/11. All specimens Recent, SW of Jamaica, GOS-59A, Stat. 112/78, 17°21' N/78°19' W, 700 m.

blades are occasionally split into tooth-like elements (Fig. 4A, E). Trabeculae of the mid-septal zone of lower cycles septa are arranged in a fan-like pattern (Fig. 4D). Some coralla show an apparent bilateral symmetry (Fig. 4F). The columella is composed of a few papillae of septal origin (paliform lobes) or is not developed at all.

Adults of *G. paradoxa* (up to 16 mm in calicular diameter and 41 mm in height) commonly have deeply recessed septa and a highly exsert epithecal rim. They have 19–22 (usually 20) septa more or less differentiated into two size classes. The columella is composed of 2–35 papillae of septal origin (paliform lobes) or is not developed at all.

In *G. hawaiiensis* and in *G. paradoxa*, the septal faces are covered with a dense and random granulation. The inner surface of the wall is also granulated. Sometimes, thecal granules are aligned into a linear pattern (Fig. 8B). The granules are apparently associated only with the stereomal cover, and not with trabeculae of the mid-septal zone (Fig. 5G). Rejuvenescence is common. The calice diameter of rejuvenated specimens decreases but at short distance returns to the normal size (Figs 2E, G; 8B). Some larger specimens, especially of *G. paradoxa*, rejuvenate several times (Cairns 1979). The corallum wall is epithecate before and after rejuvenescence.

Occurrence of a *Gardineria*-like skeleton in Recent scleractinians

I found the *Gardineria*-like structures in some other Recent Scleractinia. When examining the collection of deep-water scleractinians from the New Caledonia region, studied by H. Zibrowius, my attention was attracted by specimens labelled 'Flabellidae with columella' — herein designated as gardineriid Gen. n. (see Taxonomy). In this form the corrugated, intriguingly porcellaneous wall forms an exsert calicular rim. Thin sections and SEM observations confirmed the assumption of the epithecate nature of this wall. The outer part of the epitheca shows a centripetal organization of the fibres and is strongly bioeroded (Fig. 6C). Similar to *Gardineria*, the septa are deeply incorporated into the stereomal part of the wall (Fig. 6C, F–K). However in contrast to *Gardineria*, the septal faces bear distinct granulae (Fig. 6B, D, K). Also unlike *Gardineria*, the inner wall surface is relatively smooth with distinct desmocytes attachment scars (Fig. 6B). Coralla show monocyclic growth, some undergoing rejuvenescence.

I further traced an entirely epithecate wall in the ontogeny of some Guyniidae (Stolarski in preparation). *Culicia*, which is grouped with rhizangiids (Faviina), also appears to have an entirely epithecate wall (Cheva-

---

Fig. 6. Gardineriidae fam. n., Gen. n. A. **A–B**. Side (**A**) and calicular (**B**) views of specimen (ZPAL H.XV/12) with 'columella elements more independent', **A** × 7.3. Recent, New Caledonia, MUSORSTOM 6, DW 468, Loyalty Island, 21°05.86'S/167°32.98'E, 600 m. **C**. Transverse
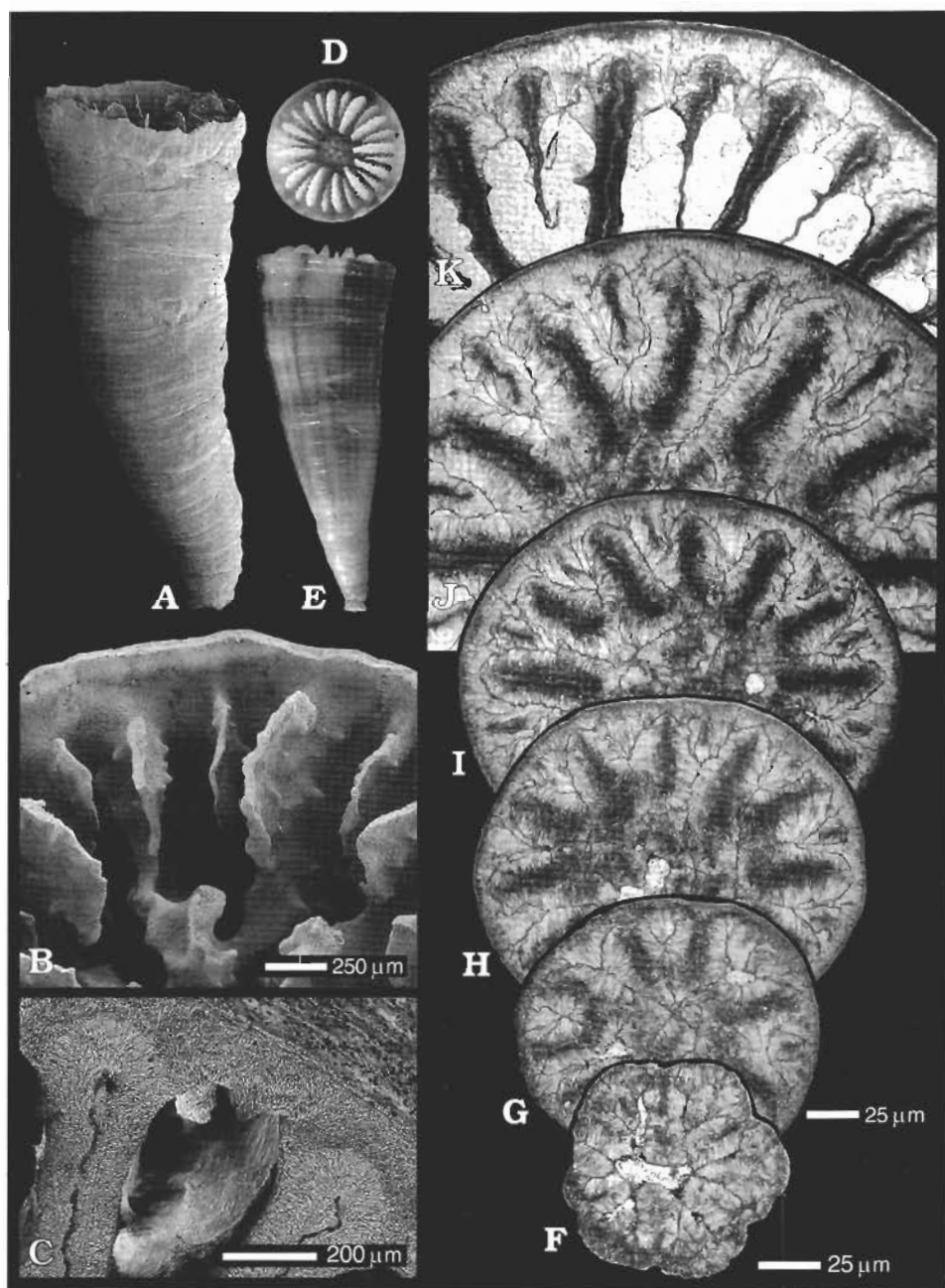
section of juvenile part of specimen (ZPAL H.XV/13) with 'columella elements more independent'. Thin, outer part of epitheca is bioeroded (upper-right corner). Recent, New Caledonia, MUSORSTOM 6, DW 468, Loyalty Island, 21°05.86'S/167°32.98'E, 600 m. **D–K**. Specimen ZPAL H.XV/14 with 'columella elements fused'. Calicular (**D**) and side (**E**) views, × 3.3. Serial transverse sections (**F–K**); scale bar for **H–K** sections same as showed for **G**. Recent, New Caledonia, MUSORSTOM 6, DW 335, Loyalty Island, 20°03.24'S/158°45.35'E, 315 m.

lier 1971: fig. 65). The latter observation, however, needs to be confirmed by serial sections. An epithecate prototheca is probably present in some Fungiidae (*Fungia*; see Vaughan & Wells 1943) and Poritidae (*Porites*; see Jell 1980).

The Recent scleractian fauna is dominated by forms having no epitheca at any stage of growth (e.g., most Caryophylliina) or having an epithecate wall developed as an additional structure to the main wall. Such an additional epitheca is common among the Faviina (e.g., *Manicina*, *Myceto-phyllia*), and also occurs in some Astrocoeniina (e.g., *Montipora*, *Madracis*) and Dendrophylliina (e.g., *Thecopsammia*). Here the epitheca is added to the main trabecular, septothecal, parathecal or synapticulothecal wall (Roniewicz & Stolarski 1995; Roniewicz & Stolarski in preparation).

Caryophylliid *versus* gardineriid Bauplan

Skeleton (Figs 1, 7). — Bauplan and microstructural features of *Gardineria* and allied forms (gardineriids; see taxonomy) differ significant-ly from those observed in other extant groups of Caryophylliina. These differences concern particularly the type of the wall and its relation to the septa.

In the Caryophylliidae and Flabellidae the theca and septa have trabe-cular foundations. These two families differ in growth rates of wall and septa observable in ontogenetic development (Bourne 1905). In Ca-ryophylliidae, at the initial stage, the growth rates of septa and wall are similar, but later the septa grow faster than the trabecular wall (the septa increase in thickness and height, and the costae develop). As a result, the trabecular wall is progressively reduced and disappears in adult stage, giving way to the development of a septotheca. Usually, in caryophylliid ontogeny the following succession is observed: marginotheca (initial and early juvenile stage) trabeculotheca (juvenile stage) septotheca (adult stage). In most flabellids instead, the growth rates of wall and septa are similar during the whole corallum growth, and a marginotheca is present at all growth stages (exceptions are *Javania* and *Placotrochus*). The outer surface of the caryophylliid and flabellid corallum is covered with tectural deposits. In caryophylliids and in some flabellids (e.g., *Javania*) tectural deposits are usually very thick, especially in the proximal parts. However, most flabellids have a thin (often one-layered) tectural cover.

During ontogeny, gardineriids have an exclusively epithecate wall. At the initial stage, septa and epitheca have similar growth rates. Marginal parts of the protosepta are in touch with the thin epitheca at its distal part. At the juvenile stage, the epitheca is developed in advance of the septal apparatus. The margin of the epitheca is often separated from the distal parts of the septa by a distance of a few millimeters (Fig. 2E). The epitheca is thickened only on its inner side by centripetally growing stereome. In the subsequent development, the epithecal stereome enwraps costae and
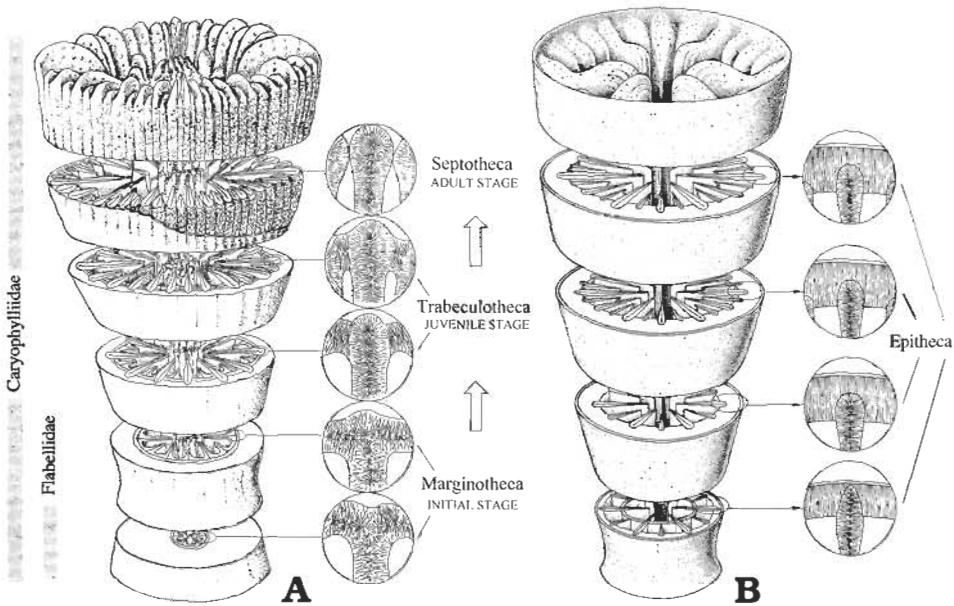
Fig. 7. Model of the ontogeny of thecal structures in Caryophylliidae and Flabellidae (**A**) *versus* Gardineriinae (**B**).

infills the interseptal space. As there is no structural barrier to stereome expansion (e.g., additional thecal structures or dissepiments), the stereome may fill the entire lumen of the calice. At the adult stage, the septa are often exsert, but their junction with the wall is always below its margin. In rejuvenated coralla of *Gardineria*, constrictions of the corallum diameter are particularly conspicuous, since they are not masked by extrathecal deposits (e.g., tectura).

All Caryophylliina (gardineriids included) here investigated have a similar septal microstructure. The straight or zigzag mid-septal zone consists of small trabeculae (diameter 15 to 50 µm, exceptionally up to 100 µm). The septal faces are composed of fibrous stereome. In terms of septal ontogeny, this microstructure pattern reflects gradual thickening of the incipient, thin septal blade.

When tested by X-ray diffraction, the skeleton of *Caryophyllia cyathus*, *Flabellum chunii*, *Gardineria hawaiiensis* and *G. paradoxa*) proved to be fully aragonitic.

Soft tissue (Fig. 1). — While basic data on the anatomy and polyp behaviour are now available for many species of shallow-water, hermatypic scleractinians, such data are still very rare for deep-water, ahermatypic species. For gardineriids there is no detailed anatomical description at all. The only available information for this group is a general description of the polyp of *G. paradoxa* by Pourtalès (1868, 1874). The polyp is said to have 'about 16 rather long tentacles, blunty tuberculated at the tip. Outside the

ring of tentacles extends a membranous disk with radiating and concentric folds' (Pourtalès 1868: pp. 140–141).

In the absence of sufficiently detailed anatomical observations, it is possible to infer the general organization of the polyp's soft tissues by analyzing microstructural traits of the skeleton.

The formation of the extrathecal parts of the caryophylliid and flabellid skeleton is controlled by the edge-zone (Vaughan & Wells 1943). Many caryophylliids have a well developed edge-zone which may even cover the whole corallum (e.g., *Deltocyathus*, *Heterocyathus*). In some forms the edge-zone periodically migrates downwards and upwards, thereby covering and disclosing the corallum. Encrusting organisms, which settled on the temporarily exposed skeleton surface, are killed when the edge-zone re-expands. Tubes or shells of various encrusters, and also juvenile coralla, are thus embedded between successive tectural layers (Stolarski 1995). Flabellidae generally have the edge-zone reduced to a small tissue fold which enwraps only the distalmost part of the skeleton. It migrates upwards with corallum growth. Extrathecal deposits (e.g., tectura) are usually very thin. However in some flabellids, the edge-zone can cover a considerable part of the juvenile skeleton, thus resulting in the formation of a thick tectura (*Javania* and anthocaulus of *Placotrochides*; see Zibrowius 1974, 1980).

In gardineriids (and also in other Recent epithecate scleractinians) soft tissues enwrap the external part of the skeleton within a narrow lappet cavity (over a distance of about 0.1 mm; see Barnes 1972: p. 347). In *Gardineria*, only the early juvenile stage has the soft tissues expanding outside the epithecate wall and producing polycyclic base. This early juvenile period excepted, the soft tissues are kept away from the wall outer surface. Thus epitheca is not covered by tectural deposits and is often encrusted and strongly bioeroded while the polyp is still alive (Figs 2E, 8C; see also Cairns 1989: p. 82).

Apparently, the tissue/skeleton relationships in gardineriids is similar to that in flabellids. However, trabecular (flabellids) versus non-trabecular (gardineriids) microstructure of the wall suggests a dissimilarity of organization of the marginal parts of the calicoblastic ectoderm. It seems that the most significant difference consists in the distribution of calicoblastic cells which initialize the deposition of seed nuclei packages. These seed crystals (possibly calcitic according to Gladfelter 1983, Constantz & Meike 1990, and Sorauf 1993) are centres of calcification around which aragonite fibres nucleate (Constantz 1986a, 1986b; Sorauf 1993). The entirely trabecular organization of the flabellid marginotheca involves continuous deposition of seed crystals within spatially separated pathways. This mirrors concentration of calicoblasts within distinctly bordered ectodermal regions ('active centres' of Bryan & Hill 1940). On the contrary, the lack of trabeculae in the outer epithecal layer of gardineriids reflects the random arrangement of calicoblasts within the marginal ectoderm.

Epithecal growth-ridges in zooxanthellate, hermatypic corals (e.g., *Manicina, Montastraea*, etc.) represent daily growth increments and are formed as a result of the diel cycle of expansion and contraction of the polyp. The mechanism of the epithecal growth in azooxanthellate ahermatypic corals (e.g., gardineriids) is probably the same, yet precise data correlating their growth-ridges with the polyp's daily cycle are still missing (see arguments by Barnes 1972: pp. 347–349).

Gardineria evolutionary lineage

The Bauplan of the gardineriid skeleton is exceptional among extant scleractinians. Fossil evidence suggests however that the gardineriid evolutionary lineage may be deeply rooted in the scleractinian history.

Tertiary. — Though many genera of Recent Caryophylliina have an extensive Cenozoic fossil record, *Gardineria* is known only from deep-water environments of the modern seas (see taxonomy). Most probably, this lack of fossil documentation reflects sampling bias of Tertiary deep-water deposits and poor representation of the genus in Cenozoic scleractinian faunas. Eocene scleractinian assemblages from southeastern Australia (Dennant 1902) contain two taxa that resemble the still undescribed Recent gardineriid genus from New Caledonia (Gen. n. A) briefly presented herein. *Cyathosmilia velata* Dennant, 1902 and *Ceratotrochus exilis* Dennant, 1902 have transversely ridged walls (epithecate according to Dennant 1902), and organization of the septal apparatus close to that of Gen. n. A. (but *C. exilis* has paliferous S_2). Microstructural investigation of the wall can show whether they are part of the gardineriid evolutionary lineage.

Cretaceous. — The Early Creataceous (Albian) *Adkinsella edwardsensis* Wells, 1933 seems to be closely related to gardineriids (as suggested by Wells 1933). Its large corallum (up to 31 mm in calicular diameter and 40 mm in height) with at least two cycles of septa is fully recrystallized. Thus, the original structure can be inferred only on the basis of microarchitectural details. The wall appears to be entirely epithecate with the outer surface covered with fine growth ridges (Fig. 8D). The septal faces and inner surface of the wall bear low granules aligned into longitudinal rows and are sometimes fused into small ridges. The same type of ornamentation continues exactly between septa and theca. The same arrangement also occurs in some juvenile *Gardineria*, where it results from the thickening of intracalicular elements by the same type of granular stereome (Fig. 8C, F). The paratype of *A. edwardsensis* shows evidence of rejuvenescence (Fig. 8D). The epithecate wall continues between succesive, rejuvenate coralla.

The Early Cretaceous coral described as *Tiarasmilia zangbeiensis* Liao & Xia, 1985 from Berriasian-Valanginian strata of Tibet shows gardineriid features of skeletal organization (Liao & Xia 1994). The wall is entirely
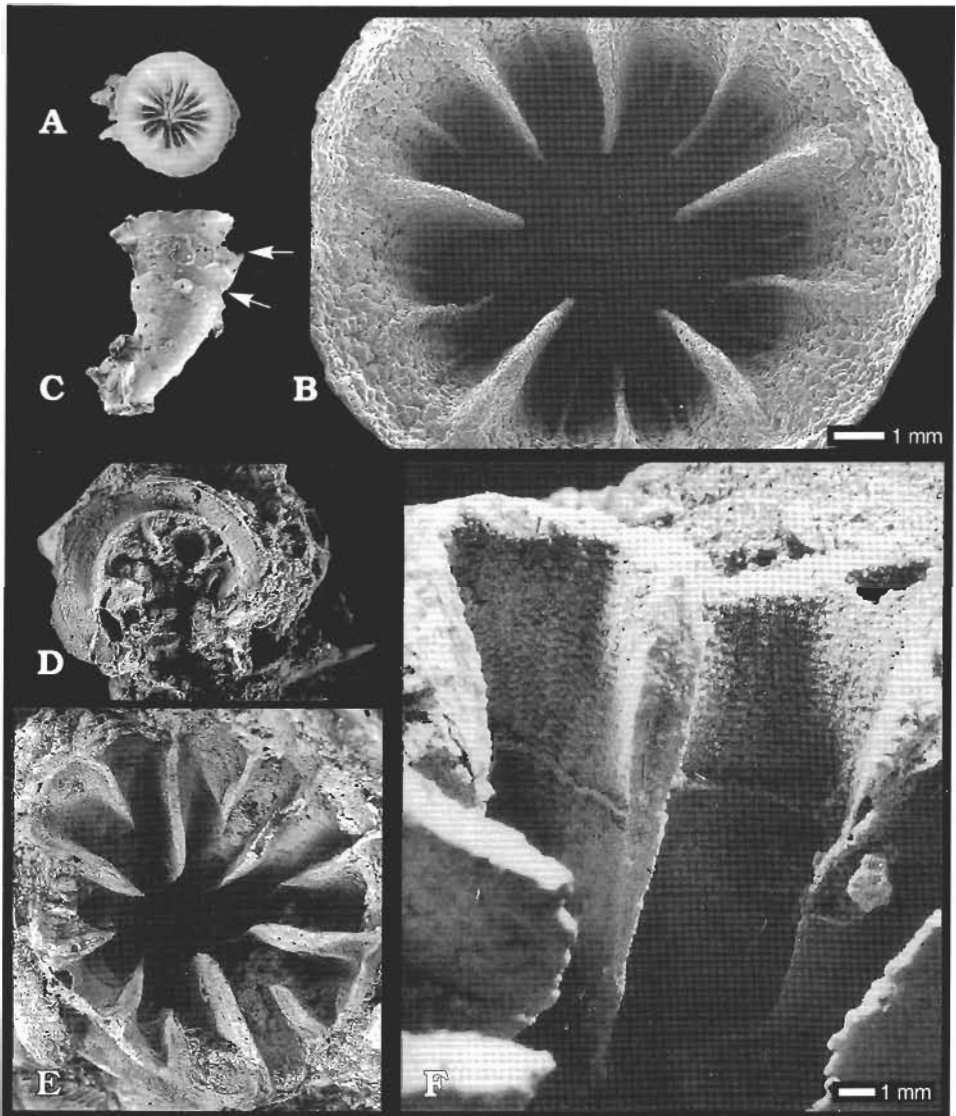
Fig. 8. **A–C.** *Gardineria hawaiensis* Vaughan, 1907. Calicular (**A–B**) and side (**C**) views of the specimen ZPAL H.XV/15. Note three episodes of rejuvenescence (arrows), **A–B** × 1.5. Recent, New Caledonia, CHALCAL 2, 1986, DW 81, 23°19.60'S/168°03.40'E, 311 m. **D–F.** *Adkinsella edwardsensis* Wells, 1933, Early Cretaceous (Albian), Edwards limestone, Crow Ranch, Bell County (Texas, USA). **D.** Paratype TMM/21343 in distal view, × 1.5. **E–F.** Holotype TMM/34690. Calicular view (**E** × 1.6) and enlargement of inner part of corallum showing granular ornamentation of wall and septa (**F**).

epithecate, developed in advance to the septa and the calice is not filled with dissepiments.

Jurassic. — Among Early Jurassic scleractinians, the Moroccan *Rodinosmilia elegantula* Beauvais, 1986 is presumably close to the gardineriid

evolutionary lineage (Fig. 11). Although the skeleton is strongly altered by diagenesis, the microarchitecture remained well preserved. The surface of the wall is covered with many growth ridges. The septa bear very low, randomly arranged granules. The septal apparatus also resembles that of morphotypes of *Gardineria* (Fig. 4A, D), except for the higher number of cycles (up to 6). The holotype illustrated by Beauvais (1986: pl. 4: 2) has prominent primary septa with a smooth distal margin while many septa of the higher cycles have dentate inner margins. The holotype shows evidence of rejuvenescence as well (Beauvais probably interpreted the young rejuvenate calice as a ring of endotheca associated with lonsdaleoid septa).

The Bajocian *Kraterostrobilos bathys* Crickmay, 1930 from the British Columbia also shows a very simple corallum morphology resembling that of the gardineriids (Crickmay 1930). Unfortunately, the poor illustration does not allow a closer comparison.

Triassic. — Triassic protoheterastraeids have virtually the same skeletal Bauplan as gardineriids. The structure of the wall and septa in both groups is almost identical. In aragonitic, excellently preserved specimens of *Protoheterastraea* from the San Cassiano Beds, the wall is entirely epithecate with septa deeply incorporated into the epithecal stereome. The hexamerally arranged septa have a mid-septal line built of small trabeculae (about 50 μm in diameter) arranged in a fan-like pattern (Fig. 9C; see also Roniewicz & Morycowa 1993: figs 1–3). The solitary or phaceloid *Protoheterastraea* differs from *Gardineria* in smaller size of calices (about 4–5 mm in diamater), tabular endotheca and a lack of axial structure (albeit internal edges of septa may bear sharp, horizontal outgrowths; Roniewicz & Morycowa 1993: fig. 2). Lately, solitary protoheterastraeids have been found with a corallum size similar to Recent *Gardineria* (Roniewicz personal communication 1996).

Diverse solitary and phaceloid Triassic corals have an almost exclusively epithecate wall throughout ontogeny (Roniewicz & Stolarski 1995; Roniewicz & Stolarski in preparation). In addition, some develop a septothecal wall by simple thickening of the peripheral parts of the septa (e.g. *Retiophyllia*, see Cuif 1975: fig. 41). The septotheca formed this way does not substitute the trabecular wall as it is absent in Triassic solitary scleractinians (the trabecular wall between corallites in cerioid colonies has a different origin). The epithecate wall is developed as a pellicular calcareous sheet adhering to costae (e.g., Reimaniphylliidae Melnikova, 1974; Margarophylliidae Cuif, 1977) or as a thick structure incorporating the costae into a thick epithecal stereome (e.g. Volzeiidae Melnikova, 1974; Protoheterastreidae Cuif, 1977; Cycliphylliidae Roniewicz, 1991). In Zardinophylliidae Montanaro-Gallitelli, 1975 (= Pachythecalidae Cuif, 1975) epithecal stereome with penicillate organization of fibres (terminology by Cuif & Gautret 1993) is particularly well developed. Newly formed septa, strongly suppressed in respect to the epithecal rim, abut against the already formed wall. Thus, the septa are almost not incorporated into the stereomal structure (Cuif 1975: pls 13–14).
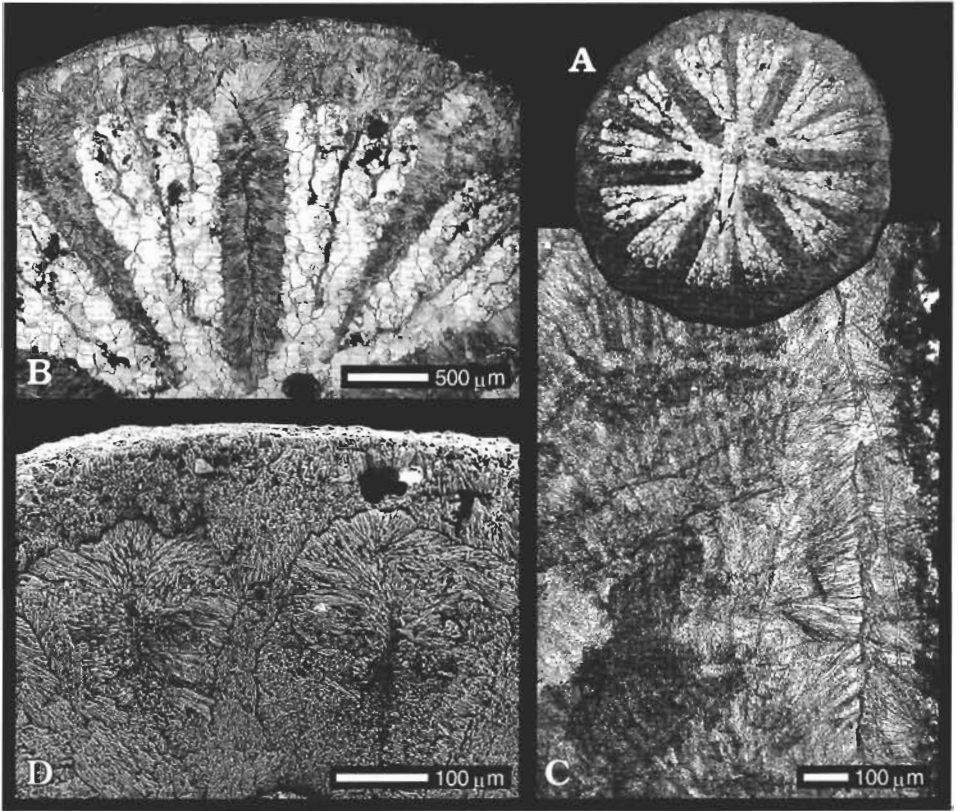
Fig. 9. **A–C**. Solitary *Protoheterastraea leonhardi* (Volz, 1896), lectotype, Volz's original thin section, MGUWr. Transverse section of the corallum with hexamerally arranged septa (**A**, × 7.5) and detail (**B**) showing structure of epithecate wall. Costae deeply incorporated into epithecal stereome. **C**. Longitudial section in midseptal plane with trabeculae arranged into fan-like pattern. Contact between fibres of epithecal stereome and costae has competitive nature (arrows). Middle Triassic (Ladinian), San Cassiano Beds, Forcella di Sett Sass (Dolomites, Italy). **D**. Phaceloid *Protoheterastraea* sp., ZPAL H.XV/16. Etched transverse section of corallite in wall region. Investigated specimen somewhat weathered, hence outer epithecal layer possibly not preserved. Late Triassic (Carnian), San Cassiano Beds, Alpe di Specie (Dolomites, Italy).

How ancient is the *Gardineria* Bauplan?

When comparing various Triassic and Recent Caryophylliina, the most evident difference refers to the prevailing Bauplan. Among old Caryophylliina the gardineriid Bauplan predominates, while modern Caryophylliina almost exclusively follow the caryophylliid Bauplan. It appears however, that the ancient, gardineriid type of corallum construction predominates also among Rugosa.

Similarity of late Permian Polycoeliidae (suborder Plerophyllina Soko-lov, 1960 of the Rugosa) to early Triassic scleractinians has attracted attention of a number of paleontologists. They emphasized the bilateral septal insertion and profound similarities of earliest ontogenetic stages in both groups. Mainly these arguments were the core of the hypothesis on direct rugosan-scleractinian descent (Schindewolf 1942; Ilina 1965, 1974, 1984; Cuif 1974, 1975, 1977, 1980; Montanaro-Gallitelli 1974a, b, 1975; Melnikova & Roniewicz 1976).

Advocates of the opposing hypothesis — independent origin of Scleractinia — argued that bilateral symmetry is fundamental in anthozoans, but that Rugosa invariably have serial septal insertion whereas it is cyclic in Scleractinia. Other arguments for the independent origin are differences in skeleton mineralogy (aragonite in Scleractinia, calcite in Rugosa) and the Early Triassic gap in fossil documentation of skeletal anthozoans (Oliver 1980a, b; Ezaki 1989; Scrutton & Clarkson 1991).

The main argument against direct evolutionary relationships between Rugosa and Scleractinia remains the difference in septal insertion. The two groups would thus originate by independent skeletonization of some sea anemones: corallimorpharian-like (Scleractinia) and zoanthiniarian-like (Rugosa) (Oliver & Coates 1987; Scrutton & Clarkson 1991). In fact, almost all rugosans investigated so far show serial metaseptal insertion, whereas in scleractinians it is cyclic. The intriguing fact remains that teratological Rugosa (septal insertion deviating from strictly serial one) and aberrant Scleractinia (septal insertion neither serial nor cyclic) are known from the fossil record just around the critical moment of evolution for both groups — the Permian/Triassic boundary (Oliver 1980a, b). *Zardino-phyllum zardinii* Montanaro-Gallitelli, 1975 from the San Cassiano Beds (Ladinian–Carnian) in the Italian Alps has a special position among those aberrant Scleractinia. The aberrations of its septal insertion (metasepta appearing randomly in sextants) have already been claimed to be of great importance (Montanaro-Gallitelli 1974, 1975). The so far illustrated spe-cimens of *Zardinophyllum* show a rather broad range of intraspecific variability with respect to metaseptal insertion. However, none shows the typical rugosan septal pattern. The here illustrated corallum of *Z. zardinii* has its metasepta inserted in quadrants, as in Rugosa (Fig. 10). Even if such an insertion occurs only in few individuals of a large population, this new data together with the previous ones indicate instability of this important feature generally accepted as an important character (Montana-ro-Gallitelli 1975).

Wendt's (1990a) arguments convincingly dispel the concept of min-eralogical disparity between Rugosa and Scleractinia. He concludes that the late Permian rugosan *Numidiaphyllum gillianum* Flügel, 1976 (Poly-coeliidae) was aragonitic. Although all so far investigated modern scleractinians are fully aragonitic (see also Filkorn 1994; Cairns 1995), it cannot be excluded that some fossil scleractinans might have been calcitic (Bøggild 1930; Constantz 1986a; Wendt 1990a, b).
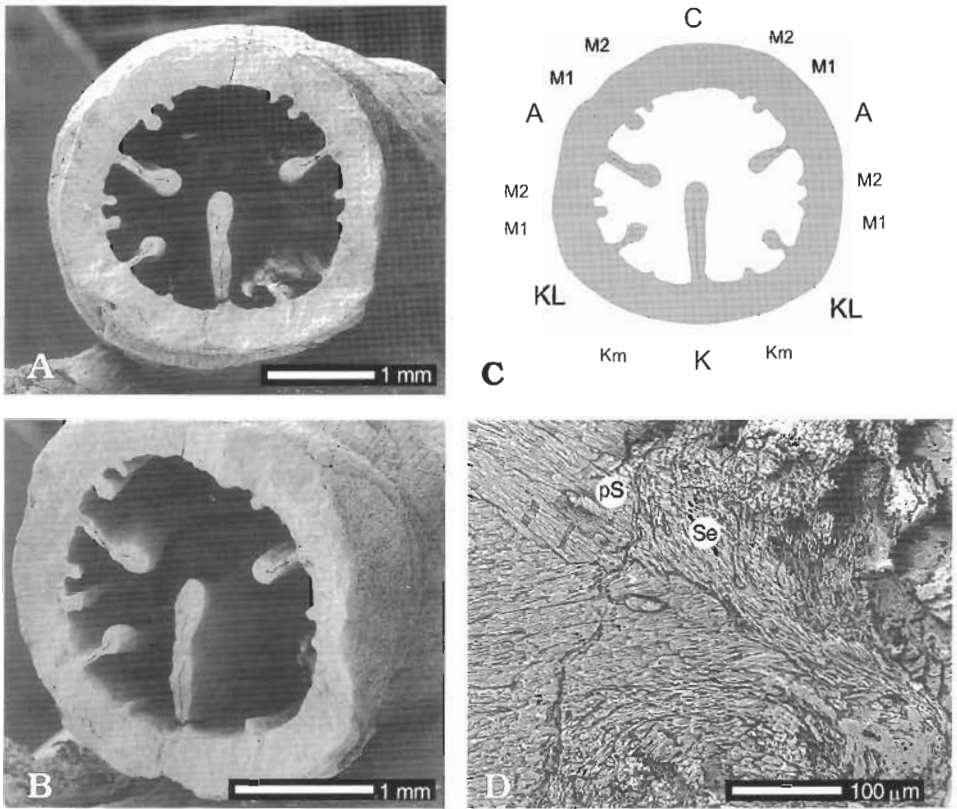
Fig. 10. **A–B**. Juvenile part of *Zardinophyllum zardini* Montanaro-Gallitelli, 1975 (ZPAL H.XV/17). Late Triassic (Carnian), San Cassiano Beds, Alpe di Specie (Dolomites, Italy). **C**. Interpretation of septal arrangement: K — counter septum, KL — counter-lateral septa, C — cardinal septum region, A — alar septa, Km — minor septa in loculi between K and KL septa, M1 — first major septa, M2 — second major septa. **D**. Transverse section of the ZPAL H.XV/18. Septum (Se) is not incorporated into epithecal stereome which shows penicillate organization of fibres (pS).

Transitions between different body plans are extremely rare in the fossil record. Most probably a major modification of a Bauplan would occur in a small, isolated population. Textbook examples of transitional forms never represent ideal transitional stages between the groups in question, but display a mosaic of features which are specific to both groups. It is difficult to expect then that documentation of the presumed rugosan/scleractinian transition will be more abundant. Thus, contrary to Oliver (1980a, b), I think that the available examples of unorthodox rugosans and scleractinians near the P/T boundary are of great importance. They show the potential of both groups to produce essential modifications, including features like skeleton mineralogy and septal insertion. In light of these facts only the early Triassic gap in documenting

skeleton possessing anthozoans is troubling. Rugosans, decimated by extinctions in the Late Permian (see Fedorowski 1989) could however survive the P/T boundary in small refuges, which hitherto have not been discovered. We can expect that in these refuges also some coralline sponges were able to survive, the fossil documentation of which has the gap in the Early Triassic (Wendt 1990a) similar to that of the skeletonized anthozoans.

The possible ancestral position of Rugosa to Scleractinia may contribute to an explanation of the inertness in the architectonical style of anthozoan coralla observable across P/T boundary. This inertness would be more difficult to explain by advocating only the hypothesis of skeletonization of sea anemone-like organisms, which, as the advocates of their independent origin claim, were not related to a rugosan stock.

If Rugosa survived the P/T boundary and gave rise to Scleractinia, the latter should be accepted as their descendants. Thus, Recent *Gardineria*, as a living fossil, with a skeleton typical rather of its alleged Triassic ancestors, would also be a distant relative of rugosans.

Taxonomy

In modern skeleton-based scleractinian taxonomy, septal structure is considered as a main subordinal discriminant character (Vaughan & Wells 1943; Wells 1956). Accordingly, the Caryophylliina differ from other suborders by the presence of laminar septa with smooth or nearly smooth margins composed of one fan system of small, simple trabeculae (Vaughan & Wells 1943; Roniewicz 1989). This broad taxonomical concept of the Caryophylliina includes both Triassic and post-Triassic forms (see also Roniewicz 1989).

The principal type of wall is here proposed as a discriminating character of the division of the Caryophylliina at the superfamily level. Volzeioidea have an exclusively non-trabecular, epithecate wall whereas Caryophyllioidea have a trabecular wall. In the latter, an epitheca may be added to the main trabecular wall. Criteria for division of the Volzeioidea at the family level include: development of endotheca and microstructure of the septal apparatus. In contrast to other volzeoiidean families, Gardineriidae have no endotheca (?rudimentary in fossil representatives) and exclusively have a solitary, often large corallum.

Thecocyathidae are considered here as a transitional stage between Volzeioidea and Caryophyllioidea. Thecocyathids were probably the first Caryophylliina to develop a trabecular wall.

Within the Caryophyllioidea decisive diagnostic features include: edge-zone development (family rank), presence of endotheca and type of budding (subfamily rank).

Suborder Caryophylliina Vaughan & Wells, 1943
Superfamily Volzeioidea Melnikova, 1974
Family Protoheterastreidae Cuif, 1977
Family Gardineriidae fam. n.
Family Volzeiidae Melnikova, 1974
Family Cycliphylliidae Roniewicz, 1991
Family Reimaniphylliidae Melnikova, 1974
Family Margarophylliidae Cuif, 1977
Superfamily Caryophyllioidea Dana, 1846
Family Thecocyathidae Vaughan & Wells, 1943
Family Caryophylliidae Dana, 1846
Subfamily Caryophylliinae Dana, 1846
Subfamily Desmophyllinae Vaughan & Wells, 1943
Subfamily Parasmiliinae Vaughan & Wells, 1943
Subfamily Eusmiliinae M. Edwards & Haime, 1857
Family Flabellidae Bourne, 1905
Family Turbinoliidae M. Edwards & Haime, 1857
Caryophylliina incertae sedis: Guyniidae Hickson, 1910.

Gardineriidae fam. n.

Diagnosis. — Volzeioidea with an endotheca rudimentary or absent.

Genera included: *Gardineria* Vaughan, 1907, Gen. n. A briefly presented herein, *Adkinsella* Wells, 1933 (*A. edwardsensis* Wells, 1933; Albian, Edwards limestone, Texas, United States), ?*Kraterostrobilos* Crickmay, 1930 (*K. bathys* Crickmay, 1930; Bajocian, Ashcroft, British Columbia, Canada), and *Rodinosmilia* Beauvais, 1986 (*R. elegantula* Beauvais, 1986; Pliensbachian, Bou Dahar, Beni Tadjit, Morroco).

Genus *Gardineria* Vaughan, 1907

Type species: *Gardineria hawaiiensis* Vaughan, 1907, by original designation.

Species included: *Gardineria* is represented by five Recent species: *G. hawaiiensis* Vaughan, 1907; New Zealand region, Hawaiian Islands (type locality), Philippines; 192–541 m, *G. paradoxa* (Pourtalès, 1868); Caribbean (Antilles), Gulf of Mexico (Yucatan, Florida); 91–700 m, *G. simplex* (Pourtalès, 1878); Caribbean (Cuba); 183 m, *G. minor* Wells, 1973; Caribbean, Bahamas; 2–241 m and *G. philippinensis* Cairns, 1989; Philippines; 192–494 m.

Cairns (1989) excluded from the genus the septothecal species *G. antarctica* Gardiner, 1929, and *Duncania capensis* Gardiner, 1904. He tentatively included them into the caryophylliid genus *Paraconotrochus* Cairns & Parker, 1992. Early Miocene *G. simojovelensis* Frost & Langenheim, 1974 from Mexico with trabecular wall and costae (Frost & Langenheim 1974: pl. 119: 5), should probably also be grouped with the caryophylliids.

Gen. n. A

Remarks. — Specimens studied by me (originally labeled 'Flabellidae with columella') come from a large collection of deep-water ahermatypes from the New Caledonia region (H. Zibrowius in preparation). They have exclusively epithecate walls but are distinguished from *Gardineria* by the
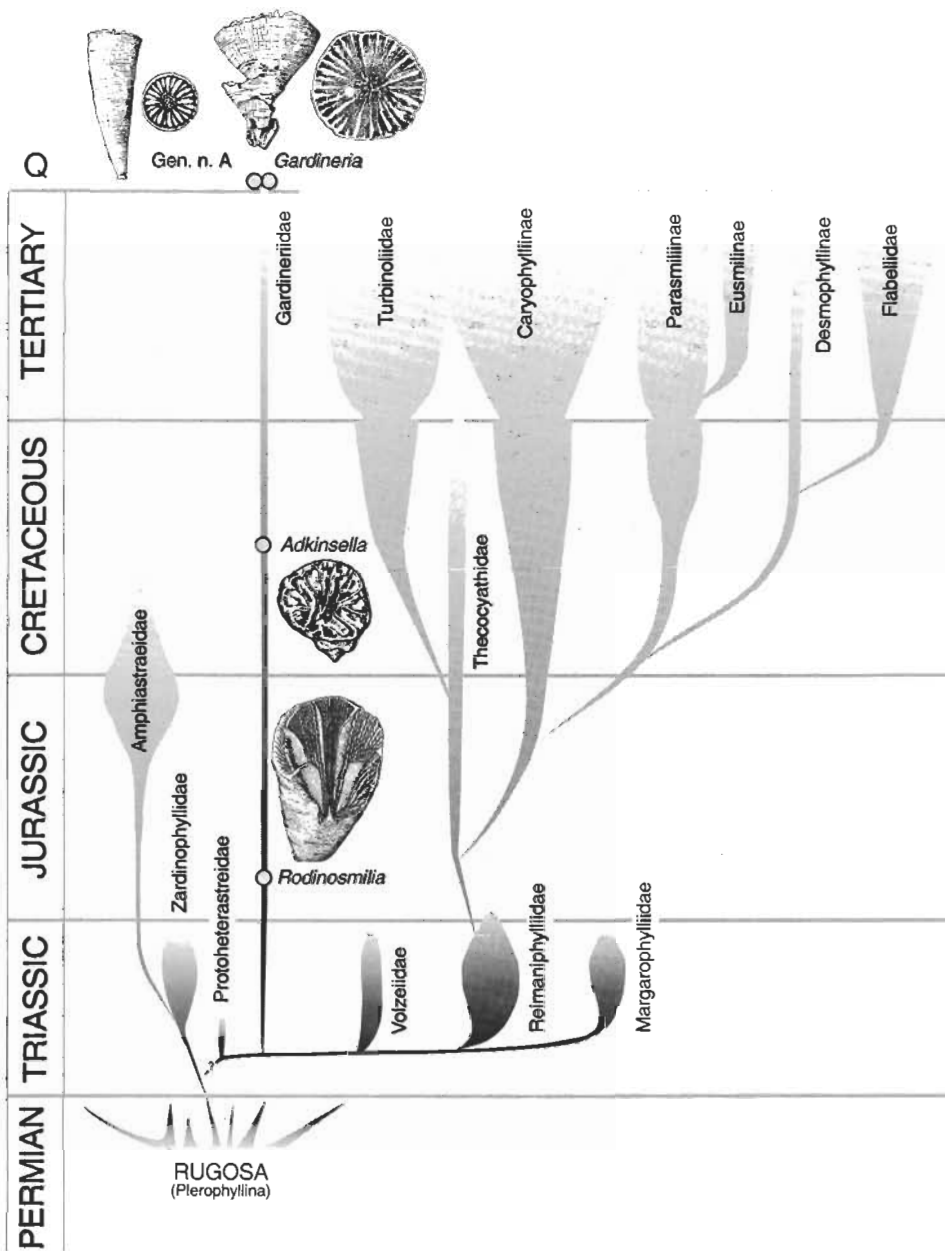
Fig. 11. Possible phylogenetic relationships and stratigraphic distribution of higher taxa discussed in the text.

presence of a well developed axial structure (columella consisting of more or less fused papillar elements) and septal faces ornamented with pointed granules on trabecular foundations. Ornamentation not continued on the

inner surface of the wall. Desmocyte attachment scars distinct. Some specimens show the detached initial corallum (?transverse division; compare Sieg & Zibrowius 1989).

Acknowledgements

References

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

Beauvais, L. 1986. Monographie des madréporaires du Jurassique inférieur du Maroc. — *Palaeontographica Abhandlungen A* **194**, 1–68.

Bourne, G.C. 1905. Report on the solitary corals collected by professor Herdman, at Ceylon, in 1902. — *Ceylon Pearl Oyster Fisheries. Supplementary Reports* **29**, 187–242.

Bøggild, O.B. 1930. The shell structure of the molluscs. — *Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark, Section des Sciences* **9**, 231–326.

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. 1984. New records of ahermatypic corals (Scleractinia) from the Hawaiian and Line Islands. — *Occasional papers of the Bernice Pauahi Bishop Museum, Honolulu* **25**, 1–30.

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

Cairns, S.D. 1994. Scleractinia of the temperate North Pacific. — *Smithsonian Contributions to Zoology* **557**, 1–108.

Cairns, S.D. 1995. The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). — *New Zealand Oceanographic Institute Memoir* **103**, 1–210.

Cairns, S.D. & Parker, S. A. 1992. Review of the Recent Scleractinia (stony corals) of South Australia, Victoria and Tasmania. — *Records of the South Australian Museum, Monograph series* **3**, 1–61.

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

Chevalier, J.P. 1987. Ordre des Scléractiniaires. *In:* P. Grassé (ed.), *Traité de Zoologie 3*, 405–764. Masson, Paris.

Constantz, B.R. 1986a. Coral skeleton construction: a physiochemically dominated process. — *Palaios* **1**, 152–157.

Constantz, B.R. 1986b. The primary surface area of corals and variations in their susceptibility to diagenesis. *In:* J.H. Schroeder & B.H. Purser (eds), *Reef Diagenesis*, 53–76. Springer-Verlag, Berlin.

Constantz, B.R. & Meike, A. 1990. Calcite centers of calcification in *Mussa angulosa* (Scleractinia). *In:* R.E. Crick (ed.), *Origin, Evolution, and Modern Aspects of Biomineralization in Plants and Animals*, 201–207. Plenum Press, New York.

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

Cuif, J.P. 1974. Indices d'affinités paléozoques chez des Madréporaires du Trias supérieur. — *Comptes rendus hébdomadaires des séances de l'Académie des Sciences* **279D**, 1753–1756.

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

Cuif, J.P. 1977. Arguments pour une relation phylétique entre les madréporaires paléozoques et ceux du Trias. Implications systématiques de l'analyse microstructurale des Madréporaires triasiques. — *Mémoires de la Société Geologique de France* **129**, 1–54.

Cuif, J.P. 1980. Microstructure *versus* morphology in the skeleton of Triassic scleractinian corals. — *Acta Palaeontologica Polonica* **25**, 361–374.

Cuif, J.P. & Gautret, P. 1993. Microstructural features of fibrous tissues in the skeletons of some chaetetid sponges. — *Courier Forschungs-Institut Senckenberg* **164**, 309–315.

Dennant, F.G.S. 1902. Description of new species of corals from the Australian Tertiaries. Part V. — *Transactions of the Royal Society of South Australia* **26**, 255–264.

Duncan, M. 1872. On the structure and affinities of *Guynia annulata*, Dunc., with remarks upon the persistence of palaeozoic type of Madreporaria. — *Philosophical transactions of the Royal Society of London* **162**, 29–40.

Duncan, M. 1883. Remarks on an essay by Prof. G. Lindström, entitled 'Contribution to the actinology of the Atlantic Ocean', and a reply to some of his criticisms. — *Annals and Magazine of Natural History* **12**, 361–369.

Duncan, P.M. 1885. A revision of the families and genera of the Sclerodermic Zoantharia, Ed. & H., or Madreporaria (M. Rugosa excepted). — *Journal of the Linnean Society, zoology.* **18**, 1–204.

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

Ezaki, Y. 1989. Morphological and phylogenetic characteristics of Late Permian rugose corals in Iran. — *Memoirs of the Association of Australian Palaeontologist* **8**, 275–281.

Fedorowski, J. 1989. Extinction of Rugosa and Tabulata near the Permian/Triassic boundary. — *Acta Palaeontologica Polonica* **34**, 47–70.

Filkorn, H.F. 1994. Fossil scleractinian corals from James Ross Basin, Antarctica. — *Antarctic Research Series* **65**, 1–96.

Frost, S.H. & Langenheim, R.L. 1974. *Cenozoic reef biofacies. Tertiary larger foraminifera and scleractinian corals from Chiapas, Mexico.* 388 pp. Northern Illinois University Press, De Kalb, Illinois.

Gardiner, J.S. 1902. South African corals of the genus *Flabellum*, with an account of their anatomy and development. — *Marine Investigations of South Africa* **2**, 115–154.

Gardiner, J.S. 1904. The turbinolid corals of South Africa, with notes on their anatomy and variation. — *Marine investigations in South Africa* **3**, 93–129.

Gill, G. 1970. La structure et microstructure septale de *Montlivaltia* Lmx.: critres nouveaux pour la systématique des Hexacoralliaires. — *Comptes rendus hébdomadaires des séances de l'Académie des Sciences* **274D**, 2459–2462.

Gladfelter, E.H. 1983. Skeletal development in *Acropora cervicornis*. II. Diel patterns of calcium carbonate accretion. — *Coral Reefs* **2**, 91–100.

Ilina, T.G. (Il'ina, T.G.) 1965. Tetracorals from the Upper Permian and Lower Triassic of Transcaucasia [in Russian]. — *Trudy Paleontologičeskogo Instituta* **107**, 1–104.

Ilina, T.G. (Il'ina, T.G.). 1974. Morphology and important evolutionary stages of development of the suborder Polycoeliina [in Russian]. *In:* B.S. Sokolov (ed.), Ancient Cnidaria 1. — *Trudy Instituta Geologii i Geofiziki* **201**, 211–219.

Ilina, T.G. (Il'ina, T.G.) 1984. Historical development of anthozoa. Suborder Polycoeliina [in Russian]. — *Trudy Paleontologičeskogo Instituta* **198**, 1–183.

James, N.P. 1974. Diagenesis of scleractinian corals in the subaerial vadose environment. — *Journal of Paleontology* **48**, 785–799.

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

Liao Weihua & Xia Jinbao. 1994. Mesozoic and Cenozoic scleractinian corals from Xizang. — *Palaeontologia Sinica* **31**, 1–252.

Lindström, G. 1877. Contributions to the actinology of the Atlantic Ocean. *Kongliga svenska vetenskaps-akademiens handlingar* **14**, 1–26.

Melnikova, G.H. & Roniewicz, E. 1976. Contribution to the systematics and phylogeny of Amphiastraeina (Scleractinia). — *Acta Palaeontologica Polonica* **21**, 97–114.

Milne Edwards, H. & Haime, J. 1848. Recherches sur les polypiers. Premier mémoire. Structure et développement des polypiers en général. — *Annales des sciences naturelles, zoologie. ser. 3,* **9**, 37–89.

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

Montanaro-Gallitelli, E. 1974b. Morphogenesis and skeletal structure of some primitive Triassic corals: problems of phylogeny. *In:* B.S. Sokolov (ed.), Ancient Cnidaria 1. — *Trudy Instituta Geologii i Geofiziki* **201**, 220–224.

Montanaro-Gallitelli, E. 1975. Hexanthiniaria a new ordo of Zoantharia (Anthozoa, Coelenterata). — *Bollettino della Societ Paleontologica Italiana* **14**, 21–25.

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

Morycowa, E. & Roniewicz, E. 1995. Microstructural disparity between Recent fungiine and Mesozoic microsolenine scleractinians. — *Acta Palaeontologica Polonica* **40**, 361–385.

Oliver, W.A. 1980a. On the relationship between Rugosa and Scleractinia (Summary). — *Acta Palaeontologica Polonica* **25**, 395–402.

Oliver, W.A. 1980b. The relationship of the scleractinian corals to the rugose corals. — *Paleobiology* **6**, 146–160.

Oliver, W.A. & Coates, 1987. Phyllum Cnidaria. *In:* R.S. Boardman, A.H. Cheetham, & A.J. Rowell, (eds), *Fossil Invertebrates,* 140–193. Blackwell Scientific Publishers, Palo Alto, Oxford.

Pourtalès, L.F. de 1868. Contributions to the fauna of the Gulf Stream at great depths (2d series). — *Bulletin of the Museum of comparative zoology* **1**, 121–142.

Pourtalès, L.F. de 1871. Deep-sea corals. — *Illustrated catalogue of the Museum of comparative zoology* **4**, 1–93.

Pourtalès, L.F. de 1874. Zoological results of the Hassler expedition. Deep-sea corals. — *Illustrated catalogue of the Museum of comparative zoology* **8**, 33–49.

Romano, S.L. & Palumbi. S.R. 1996. Evolution of scleractinian corals inferred from molecular systematics. — *Science* **271**, 640–642.

Roniewicz, E. & Morycowa, E. 1987. Development and variability of Tertiary *Flabellum rariseptatum* (Scleractinia), King George Island, West Antarctica. — *Palaeontologia Polonica* **49**, 83–103.

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

Roniewicz, E. & Stolarski, J. 1995. Epithecate scleractinians: burst and decline. — *Abstracts of the Seventh International Symposium on Fossil Cnidaria and Porifera, Madrid 1995,* 78.

Schindewolf, O. 1942. Zur Kenntnis der Polycoelien und Plerophyllen. Eine Studie über den Bau der 'Tetrakorallen' und ihre Beziehungen zu den Madreporarien. — *Abhandlungen des Reichsamts für Bodenforschung. N.F.* **204**, 1–324.

Scrutton, C.T. & Clarkson, E.N.K. 1991. A new scleractinian-like coral from the Ordovician of the Southern Uplands. Scotland. — *Palaeontology* **34**, 179–194.

Sieg, J. & Zibrowius, H. 1989. Association of a tube inhabiting tanaidacean, *Bifidia scleractinicola* gen. n., sp. n., with bathyal scleractinians of New Caledonia (Crustacea Tanaidacea — Cnidaria Scleractinia). — *Mésogée* **48**, 189–199.

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

Sorauf, J.E. 1993. The coral skeleton: analogy and comparisons, Scleractinia, Rugosa and Tabulata. — *Courier Forschungs-Institut Senckenberg* **164**, 63–70.

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.

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

Stolarski, J. 1996. Paleogene corals from Seymour Island, Antarctic Peninsula. — *Palaeontologia Polonica* **55**, 51–63.

Vaughan, T.W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. — *Bulletin of the United States National Museum*, **59**, 1–427.

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.

Veron, J.E.N. 1995. *Corals in space and time: biogeography and evolution of the Scleractinia.* 321 pp. Cornell University Press, Ithaca, N.Y.

Wendt, J. 1990a. The first aragonitic rugose coral. — *Journal of Paleontology* **64**, 335–340.

Wendt, J. 1990b. Corals and coralline sponges. *In:* J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Vol. 1*, 45–66. Van Nostrand Reinhold, New York.

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**, 85–288.

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

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

Zibrowius, H. 1984. Taxonomy in ahermatypic scleractinian corals. — *Palaeontographica Americana* **54**, 80–85.

Gardineria — „żyjąca skamieniałość" wśród koralowców sześciopromiennych

JAROSŁAW STOLARSKI

Streszczenie

Podstawowy plan budowy (Bauplan) i mikrostruktura szkieletu przedstawicieli współczesnego rodzaju *Gardineria* różni się zasadniczo nie tylko od Flabellidae do których rodzaj ten był zaliczany, ale od większości współczesnych Scleractinia. *Gardineria* ma wyłącznie epitekalną (nietrabekularną) ścianę, gdy u większości współczesnych koralowców sześciopromiennych epiteka nie występuje, albo rozwinięta jest obok podstawowej ściany, która ma budowę trabekularną. Różnice w budowie ściany u tych korali odzwierciedlają odmienną budowę brzeżnej, szkieletotwórczej części polipów. Koralowce wczesnomezozoiczne, w szczególności triasowe protoheterastreidy, powszechnie tworzyły szkielety o planie budowy podobnym do występującego u *Gardineria*. Rodzaj ten uznany został za formę reliktową uważanej za wymarłą nadrodziny Volzeioidea. Linię rozwojową *Gardineria* (Gardineriidae fam. n.) reprezentują w stanie kopalnym: wczesnokredowy rodzaj *Adkinsella*, wczesnojurajski *Rodinosmilia*, a być może również środkowojurajski *Kraterostrobilos*. Szkielety o podobnej budowie tworzyły również niektóre późnopaleozoiczne rugozy, m.in. z rodziny Polycoeliidae. Znalezisko triasowego *Zardinophyllum zardini*, uważanego za aberantnego koralowca sześciopromiennego, o podobnym planie budowy co *Gardineria*, jednak o przypuszczalnie seryjnym (a nie cyklicznym jak u Scleractinia) sposobie przyrastania septów, przemawia za hipotezą o rugozowych korzeniach Scleractinia.