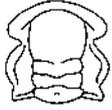


# Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data

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## LETHAIA



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The set of skeletal characters of the Recent azooxanthellate coral *Guynia annulata* Duncan, 1872 is unique among extant scleractinians and encompasses: (a) undifferentiated septal calcification centers (in most extant scleractinians calcification centers are clearly separated); (b) completely smooth septal faces (septa of almost all extant scleractinians bear granular ornamentation); (c) deeply recessed septa in respect to the epithecal rim in the adult coralla (in adults of the majority of extant scleractinians the relationships between septa and wall are the reverse); and (d) an aseptal part of the initial ontogenetic stage, just above the basal plate (almost all known scleractinians have a septate initial coralla). Skeletal features of five other extant traditional guyniids are typical of other caryophylliines (and of Scleractinia). However, the wall types present in different species of traditional guyniids exceed limits traditionally attributed to one caryophylliine family: i.e., *Stenocyathus* and *Truncatoguynia* have a marginothecal wall like the Flabellidae, whereas *Schizocyathus* and *Temnotrochus* usually have an entirely epithecal wall, as in Gardineriidae (Volzeioidea). Moreover, *Pourtalocyathus* and *Schizocyathus* show intraspecific variation in distribution of septal calcification centers (separated vs. non-separated) and in wall types (epithecal vs. consisting of large spherulite-like bodies). These major differences in skeletal architecture form the basis for a new, three-fold taxonomical subdivision of the traditional guyniids: (1) Guyniidae Hickson, 1910, containing only monospecific *Guynia* with an epithecal wall, and septa with non-separated calcification centers; (2) Schizocyathidae fam.n., groups *Microsmilia Schizocyathus*, *Pourtalocyathus*, *Temnotrochus*, which have an epithecal wall and septa with usually well-separated calcification centers; and (3) Stenocyathidae fam.n. with *Stenocyathus* and *Truncatoguynia* which have a marginothecal wall and septa with well-separated calcification centers. Despite differences in the basic architecture of the skeleton, all taxa attributed to these families have 'thecal pores' formed by selective dissolution of the skeleton. I propose two hypotheses for evolutionary relationships among Guyniidae, Schizocyathidae, and Stenocyathidae: (1) Hypothesis A: the three families are not phylogenetically related and 'pores' originated independently in different scleractinian lineages: e.g., Guyniidae may represent distant zardinophyllid or gigantostyliid descendants, Schizocyathidae may be a volzeioid offshoot, whereas Stenocyathidae may be a flabellid descendant; (2) Hypothesis B: the three families are phylogenetically related and 'thecal pores' are synapomorphic for the clade (superfamily Guynioidea). Additional approaches, such as anatomical observations, molecular studies on guyniid DNA sequences, and in-depth studies on scleractinian biomineralization will be necessary to test these hypotheses. □ *Guyniidae*, *microstructures*, *phylogeny*, *Scleractinia*, *taxonomy*.

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Two living scleractinian genera *Guynia* Duncan, 1872 and *Gardineria* Vaughan, 1907 were classified in the nineteenth century as relict taxa of Paleozoic Rugosa (Pourtalès 1868; Poutalès 1871; Duncan 1872). In subsequent revisions, both genera were transferred to the scleractinian suborder Caryophylliina (Turbino-liidae of Duncan 1884). The scleractinian nature of *Gardineria* was confirmed later from the aragonitic mineralogy of the skeleton and cyclic insertion of the septa. However, the presence of an entirely epithecal

wall, an exception for modern corals but dominant among Triassic and Paleozoic corals, argues for setting *Gardineria* apart from extant caryophylliines (Stolarski 1996). Thus, although Duncan's (1872) and Poutalès' (1868, 1871) suggestions concerning rugosan affinity of *Gardineria* have not been confirmed, their initial observations seem to reveal some ancient aspect of that coral. The second extant coral included by Duncan (1872) in Rugosa – *Guynia annulata* – is among the smallest of scleractinian corals. Adult

skeletons attain only a few millimeters in length and about one millimeter in diameter. *G. annulata* is one of the few scleractinian species that has a nearly global distribution (unknown only from Subantarctic and Antarctic regions). The depth range of the species is from 3 to 653 m (Cairns 1989), but the upper bathymetric limit concerns cryptic environments (Zibrowius 1980). Type specimens are from Adventure Bank, the Mediterranean (Recent), and the earliest fossil forms were recorded from the Miocene of the Dominican Republic (Cairns & Wells 1987). In modern classifications, *Guynia* (considered monotypic) is included together with another 11 Recent and fossil genera in the family Guyniidae of the suborder Caryophylliina (Russo 1979; Cairns 1989; Cairns 1994). Most guyniids are monotypic genera with small, scolecoïd or ceratoid coralla; many of them reproduce asexually by transverse or longitudinal division. Other characters are scattered among species: pali or paliform lobes are developed in *Schizocyathus* ( $P_{2-3}$ ), *Stenocyathus* ( $P_2$ ), *Pourtalocyathus* ( $P_2$ ), *Temnotrochus* ( $P_{1-2}$ ), and *Cyathosmilia* ( $P_{1-2}$ ); a columella in *Guynia* (styliiform: 1 twisted lath), *Stenocyathus* (styliiform: 1–2 twisted laths), *Pourtalocyathus*, *Microsmilia*, *Temnotrochus* (fascicular), and *Gillicyathus* (lamellar); (see Cairns 1989, p. 41). The most striking feature of all Recent and putative fossil guyniids are ‘thecal pores’, considered as a synapomorphy for the group. According to Wells (1956, p. F432) and Cairns (1989, p. 40), the guyniid wall, considered an epitheca, is originally pierced by pores that are filled subsequently with stereome. Cairns (1989, p. 42) noted also that the simple morphologic term ‘thecal pores’ encompasses in fact three elements – ‘white spots’ on the outer surface of the wall, thecal depressions on the inner surface of the wall, and pores themselves that may occasionally penetrate the theca. Later, Cairns (1995, p. 92) implied that ‘thecal pores’ are formed in ‘regions of variable calcification’.

So far, only simple morphologic observations of the skeleton of *Guynia* and other traditional Guyniidae are available (the most comprehensive in this respect is the paper by Cairns [1989]). There are no data on their soft tissue, ontogeny, or skeletal microstructure. The evolutionary relationship of the Guyniidae to other Scleractinia is poorly understood, and the only suggestion given by Wells (1956, p. F368) is that they are a neotenic caryophyllian lineage. In this paper I show, for the first time, the results of microstructural investigations of *Guynia* and some other corals traditionally attributed to Guyniidae and propose a new hypothesis concerning the origin of guyniid ‘thecal pores’. I also discuss implications of these studies for the higher classification of Scleractinia.

This study is part of the larger project concerning

microstructural observations of all traditional Flabellidae and Guyniidae, which is to be published separately.

## Methodological remarks

### *Scleractinian microstructures – a conceptual basis*

One of the fundamental distinctions traditionally drawn between microstructures of the scleractinian skeleton is that between trabecular versus non-trabecular calcification (for review, see Roniewicz 1996). The significance of this distinction for scleractinian taxonomy is also a crucial issue in this paper, thus some comments on contemporary understanding of trabecular versus non-trabecular structures are presented here.

The trabecula – the basic unit of the trabecular structures – usually is defined as a rod formed by fibers and provided with an axis (Milne Edwards & Haime 1857; Pratz 1882; Ogilvie 1896; see also Sorauf 1972 and Roniewicz 1996). Depending on the diameter of the trabecular rod and distribution of the calcification centers within it, some authors distinguish several types of trabeculae: (a) mini- (20–50  $\mu\text{m}$  in diameter), medium- (50–100  $\mu\text{m}$ ), and thick trabeculae (100–1000  $\mu\text{m}$ ) (Morycowa & Roniewicz 1995), and (b) simple, compound (or branching), and divergent trabeculae (Ogilvie 1896, Morycowa 1964). Textbook examples of trabecular structures in the skeleton of modern corals are: septa, certain types of septal granulation (‘ornamentation’), pali, paliform lobes, some walls (e.g., marginotheca, trabeculotheca, synapiculotheca), and the columella. Examples of non-trabecular skeletal elements, i.e., with aragonitic fibers not organized around any axis, are: the basal plate, dissepiments, stereome, and the epithecal wall. From a geometric point of view, organization of the fibers in trabecular as well as non-trabecular structures resembles growth patterns of aragonitic marine cements, and thus some authors suggest that its formation is entirely predictable from factors controlling abiotic, physicochemical crystal growth (Bryan & Hill 1941; Constantz 1986). However, recent observations by Cuif *et al.* (1997) and Cuif & Dauphin (1998) support Johnson’s (1980) suggestions of organic matrix mediation for growth of the scleractinian skeleton. In their integrative, ‘biomineralization-based’ approach, Cuif *et al.* (1997) show that the growth of any part of the scleractinian skeleton is mediated by glyco-proteic macromolecules and usually encompasses two main phases: (1) formation of the calcification centers, and (2) formation of the undif-

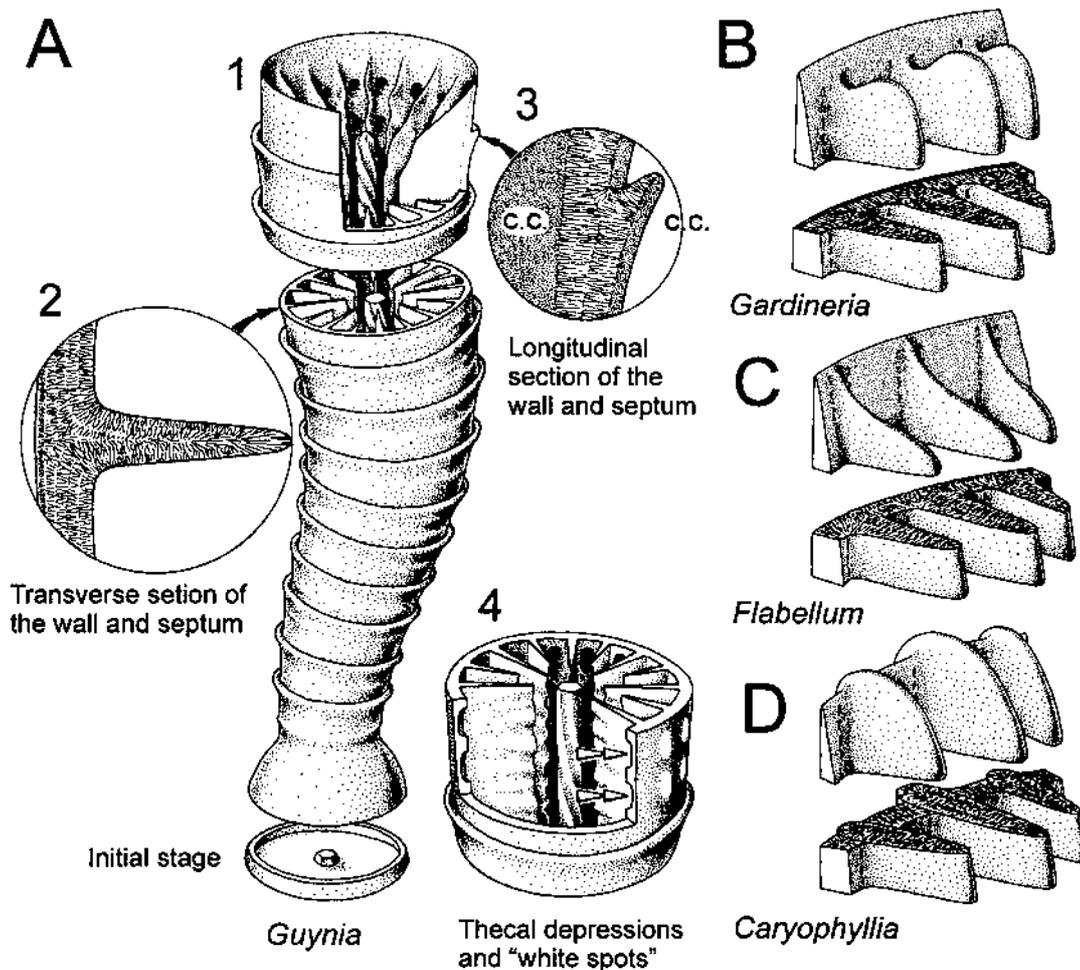


Fig. 1. Diagrammatic picture of the major morphological and microstructural characters of *Guynia* and some other extant caryophyllines. □A. *Guynia* with epithelial wall and septa with non-separated calcification centers (abbreviated c.c.) in transverse (A<sub>2</sub>), and longitudinal (A<sub>3</sub>) section. 'White spots' on the outer part of the wall correspond with thecal depressions on the inner part of the wall (A<sub>4</sub>). □B. Entirely epithelial wall (calcification centers non-separated) and septa with separated calcification centers in *Gardineria*. □C. Marginothecal wall (separated calcification centers) and septa with separated calcification centers in *Flabellum*. □D. Trabeculothecal wall (separated calcification centers) and septa with separated calcification centers in *Caryophyllia* (juvenile stage).

ferentiated fibrous tissue (see comments of Cuif & Dauphin [1998] about difficulties in distinguishing these two successive secretory steps in *Madracis pharensis* and *Phyllangia mouchezi*). Calcification centers consist of tiny isodiametric aragonite crystals and/or organic components. On the growing edge of 'trabecular' parts of the skeleton they form round patches, which are well separated one from the other (often by a distance of 10–100 μm). Spaces between separated calcification centers are filled with fibrous tissue in the next growth phase. Calcification centers most likely play the function of scaffolding the growth of fibrous tissue and are not centers of crystallization/calcification in the crystallographic sense (Cuif *et al.* 1997). In transverse section of the septum, microcrystalline patches forming the so-called mid-septal

zone (or 'Urseptum' of Volz 1896) are well separated and surrounded by concentric fibrous layers, while in longitudinal section (along the mid-septal zone) they are separated horizontally but almost perfectly superimposed vertically. On the growing edge of 'non-trabecular' structures, calcification centers are indistinguishable as individual units. Fibrous tissue is formed only outside their concentrations. In transverse section of 'non-trabecular' structures, the zone of homogeneous concentration of calcification centers is surrounded by (or bordered by in the case of the epitheca) successive layers of fibrous tissue (Figs 1A:2, 3F). In longitudinal section made along the zone of concentrations of calcification centers, only microcrystalline skeletal tissue is observed (Figs 1A:3, 2H, 3D).

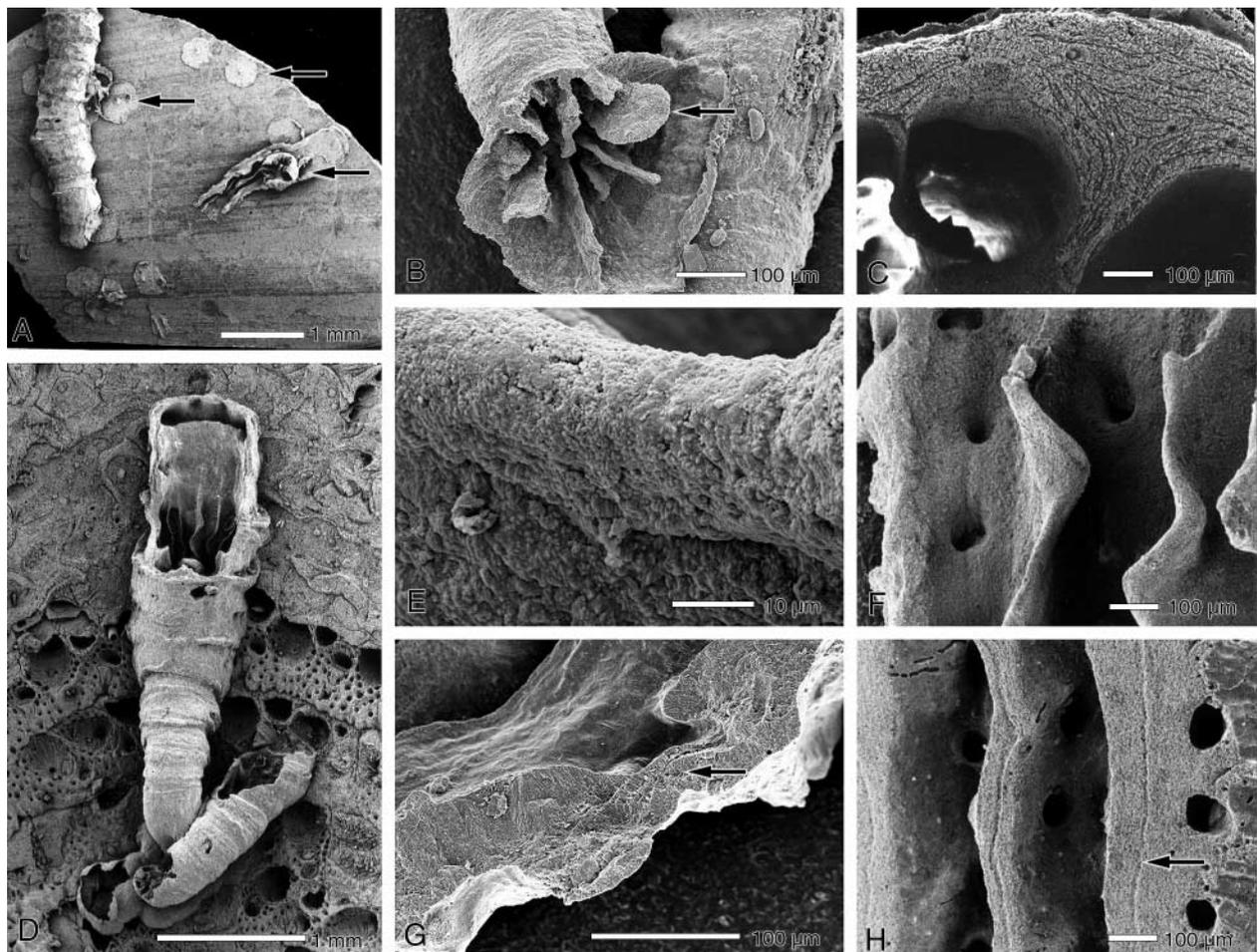


Fig. 2. *Guynia annulata* Duncan, 1872. □A. Adult specimen (left) and the earliest initial growth stages consisting of basal plate, styliform columella, and occasionally incipient wall incrusting a bivalve shell (ZPAL H.XIV/1). □B. Initial part of the corallum with removed basal plate and part of the wall. Some protosepta that appeared at initial constriction (arrow) have strongly arched proximal edges indicating bipolar growth (USNM 94723). □C. Transverse, etched section of the wall and  $S_1$  of ZPAL H.XIV/2 with superimposed layers of fibrous tissue. □D. Specimen (ZPAL H.IV/3) incrusting substrate (bryozoan colony) with partially broken calice to show deeply recessed septa. Note also juvenile and aseptate initial stage attached in the same part of substratum (bottom of the picture). □E. Smooth growing edge of the septum (ZPAL H.IV/4) with homogeneously distributed calcification centers. □F. Intercalicular surface of the wall with prominent thecal depressions, and wavy septa (USNM 87620). □G. Wall fractured in position of thecal depression. Skeleton in that region is less compact than in remaining part of the wall (USNM 94723). □H. Longitudinal section of septa (etched surface) showing their non-separated calcification centers (arrow) – USNM 87620. All Recent. A–B, D–E, G. Mediterranean, submarine caves, few meters depth. C. Indian Ocean, MD08, Sta. 6 – DC43, 33°12.0'S/43°58.2'E, 200–360 m. F, H. Atlantic Ocean, Caribbean Sea, Barbados, Holetown (1.6 km off). Sta. 1443, 200 m.

In traditional higher-level scleractinian classifications, septal microstructure is considered diagnostic at the subordinal level, whereas wall type is diagnostic at the familial level (Vaughan & Wells 1943; Wells 1956; see also Stolarski 1995, 1996). Other skeletal elements like columella, pali, paliform lobes, and dissepiments are considered diagnostic usually at generic/species levels. In this paper, morphological and microstructural characteristics of septa and wall are presented in reference to *Guynia*, other traditional guyniid taxa, and other scleractinians. Attention is paid to substantial differences between their skeletons, thus descriptions of shared features are omitted.

#### *Techniques and redepository institutions*

SEM observations were made on specimens polished with carborund powder (800–1200 grain size) and etched with 5% acetic acid for 15–30 sec. Specimens figured here are in the collection of the Institute of Paleobiology, Poland (ZPAL); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); the Natural History Museum, London (NHM); Museum of the Institute of Geological Sciences, Kraków (MING); Instituto di Paleontologia, Università di Modena (IPM); and Naturhistorisches Museum Basel, Switzerland

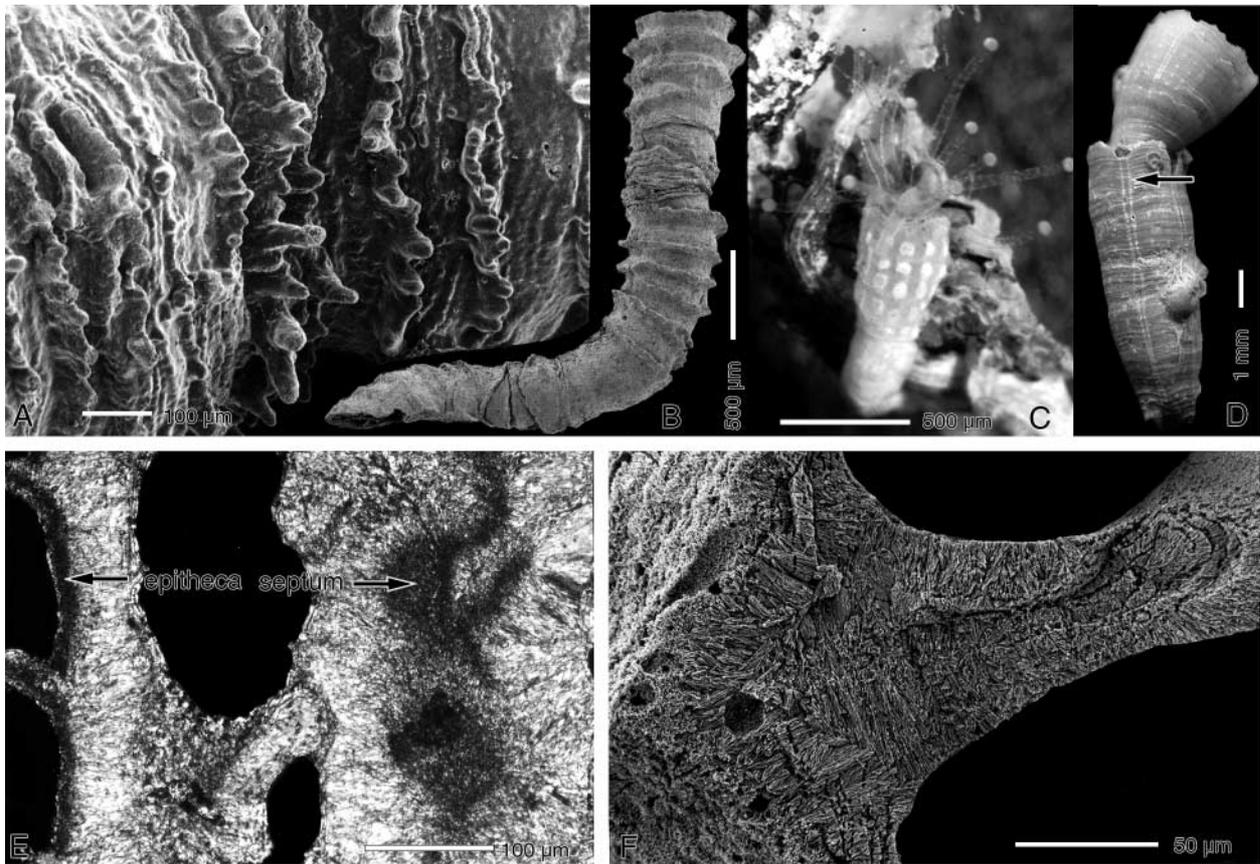


Fig. 3. A–C. *Guynia annulata* Duncan, 1872. □A. External part of the wall of USNM 87620 with edges of annulations forking into numerous spines (horizontal orientation). □B. Specimens ZPAL H.XIV/5 with regularly distributed smooth annulations. □C. Fully expanded polyp photographed in laboratory a few hours after dive in submarine cave near Marseille (November 1997). After several hours polyp retracted to the skeleton and did not expand again (tissue of this specimen was sent to Sandra Romano for genetic analysis). □D. *Schizocyathus fissilis* Pourtales, 1874 – lateral view of specimen USNM 61473 with ‘white spots’ and ‘white stripes’ (arrow). E–F. *Guynia annulata* Duncan, 1872. □E. Longitudinal thin-section of the epithelial wall (left) and septum (right) of the ZPAL H.XIV/6 (nicole crossed). Zones of non-separated calcification centers (arrow) have the same optical characteristics (‘dark line’) for septa and epitheca. □F. Transverse section of the specimen (ZPAL H.XIV/7) with well-developed external ridges and linear concentrations of non-separated calcification centers. All Recent. A, D. Atlantic Ocean, Caribbean Sea, Barbados, Holetown (1.6 km off). Sta. 1443, 200 m. B–C. Mediterranean, Marseille, submarine caves, few meters depth. E–F. Indian Ocean, MARION DUFRESNE, MD08, Sta. 6-DC43, 33°12.0'S/43°58.2'E, 200–360 m.

(NHMB). A list of all investigated type specimens is given in the Appendix.

## Recent Scleractinia – skeletal characteristics

*Septa*. The distal septal edge (often highly arched) is the fastest growing region of the skeleton of most scleractinians. The theca is usually formed with some delay after the septa. Septal faces of virtually all modern Scleractinia are covered with more or less prominent granulations with separated calcification centers.

Until recently, it was assumed that the septa and pali of all extant Scleractinia have separated calcification

centers (‘trabecular microstructure’, see Wells 1956; Sorauf 1972, 1993, and in this paper in the section Discussion: Skeletal Microstructure). Based on the arrangement of trabeculae, Vaughan & Wells (1943) and Wells (1956) distinguished five principal types of septa that define the limits of scleractinian suborders: (1) laminar or as simple spines composed of a few simple or compound trabeculae (i.e., *Astrocoeniina*); (2) fenestrate, formed by numerous simple or compound trabeculae, united by synaptoculae (i.e., *Fungiina*); (3) laminar or as isolated spines formed by one or more fan systems of numerous simple or compound trabeculae (i.e., *Faviina*); (4) laminar composed of one fan of numerous, simple trabeculae (i.e., *Caryophylliina*); (5) laminar, irregularly perforated composed of one fan of numerous simple trabeculae (i.e., *Dendrophylliina*). Roniewicz & Morycowa

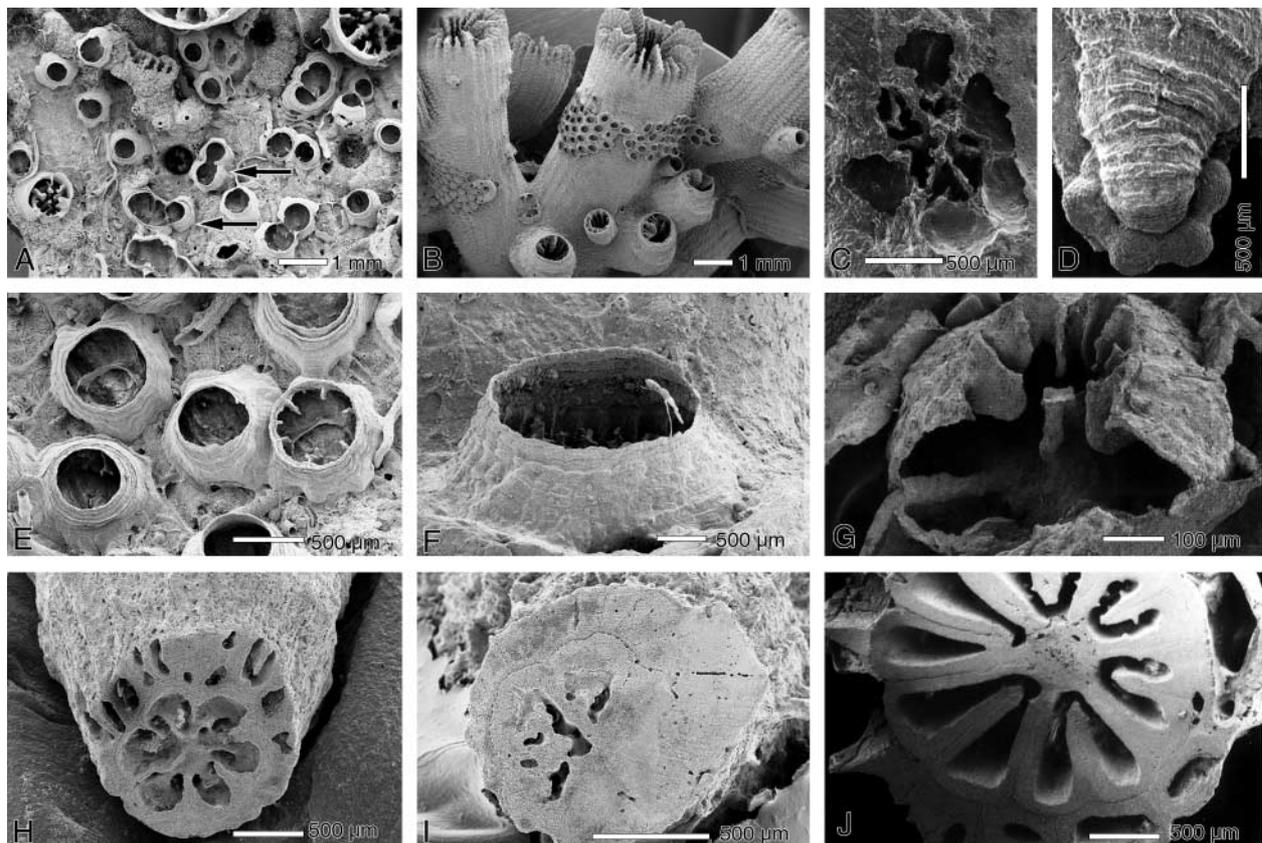


Fig. 4. Initial stages of Recent corals. □A, E. Aseptate and septate initial and early juvenile stages of *Gardineria minor* Well, 1973 (note that in some instances common epithecae wall encircles two or three individuals (arrow)); USNM 53503 (paratype), Recent, North Atlantic Ocean; Caribbean Sea; Jamaica; Blue Hole, Sta. DBL5, 12.2 m. □B. *Hoplangia durotrix* Gosse, 1860 – detached fragment of the colony USNM 94721. Coralla located within intracolony cavity show sudden change from ‘septothecate’ to ‘epithecae’ appearance in comparison with constantly septothecate marginal coralla. Recent, Mediterranean, France, Marseille, between Riou and Grand Congloue Islands, 50 m. □C. *Stenocyathus vermiformis* Pourtalès, 1868 – septate initial stage (ZPAL H.XIV/8). Recent, Atlantic Ocean, JEAN CHARCOT, Sta. 150, 37°37’N/25°53’W, 550–600 m. □D. *Guynia annulata* Duncan, 1872 – specimen USNM 87620 with relatively flat initial corallum with distinct initial lobes of the prototheca and wall ridges. Recent, Atlantic Ocean, Caribbean Sea, Barbados, Holetown (1.6 km off). Sta. 1443, 200 m. □E. *Polycyathus muelleriae* (Abel, 1959) – specimen USNM 48354 with upper part of the corallum formed entirely by epithecal wall. Recent, Mediterranean, France, Marseille, submarine caves, few meters depth. □F. *Guynia annulata* Duncan, 1872. Early juvenile stage (ZPAL H.XIV/1) with septa simultaneously appearing around initial constriction. Folded basal plate (in septal manner) of this specimen results from attachment to the septum of adult, dead corallum. Recent, Mediterranean, France, Marseille, submarine caves, few meters depth. □G. *Schizocyathus fissilis* Pourtalès, 1874 – initial septate stage (etched section of the base of adult corallum) of hispid anthocaulus USNM 61743. Recent, Atlantic Ocean, off Venezuela, 11°30’N/62°29’W, 329 m. □H. *Pourtalocyathus hispidus* (Pourtalès, 1878) – initial septate stage (etched section of the base of adult skeleton) of hispid morphotype with marginothecal wall (USNM 61928). Recent, Atlantic Ocean, 18°32.18’N/65°46.12’W, 329–512 m. □I. *Pedicellocyathus keyesi* Cairns, 1995 – polished and etched base of adult specimen showing septate initial part and juvenile ‘chambers’ of polycyclic development, ZPAL H.XIV/9, Recent; Pacific Ocean, New Zealand, Sta. BS833(0578), 37°38.5’S/178°56.4’E, 153–143 m.

(1993) distinguished two major microstructural groups among Recent Scleractinia, which, they supposed, might range from the Triassic: (1) ‘thick-trabecular’ (i.e., with widely-spaced calcification centers – e.g., Siderastreaeidae), and (2) ‘thin-trabecular’ (i.e., with closely-spaced calcification centers – e.g., Caryophylliina). In contrast to Recent corals, some extinct scleractinians may have had, in the opinion of these authors, non-trabecular septa – for example stylophyllids. Cuif (1977) and Sorauf (1996) implied that some Triassic corals (i.e., zardinophylliids = pachythealids) did not have tabecular septa. However, quite recently, Roniewicz (1996) suggested that

Recent acroporids may also have non-trabecular septa, and Cuif *et al.* (1997) showed that acroporid septa, built of ‘scaly’ skeletal units, are indeed different from other known extant scleractinians. Cuif & Dauphin (1998) were the first to point out that the distinction between ‘thin-trabecular’ and ‘non-trabecular’ septal microstructure is sometimes misleading. They showed that in some specimens of *Lophelia pertusa* (Linnaeus, 1758) septal calcification centers are densely packed, forming a continuous line in transverse section, whereas in other specimens they are well separated (Cuif & Dauphin 1998, figs 3.7–3.8). Different patterns in distribution of calcification centers were

also observable on a single septum of *Mussa angulosa* (Pallas, 1766) – they were closely packed in the region of ‘mussoid tooth’ calcification centers, whereas in other parts of the septum they were clearly separated (Cuif & Dauphin 1998, Fig. 3.4).

*Wall.* The main types of scleractinian wall have well-separated calcification centers (e.g., marginotheca and trabeculotheca – Fig. 1C–D; the septotheca is a structure formed by thickening of the outer part of the septa and does not have its own calcification centers). Only the epitheca has, as a rule, non-separated calcification centers. Epitheca exceptionally forms the only wall of extant scleractinians (i.e., in Gardineriidae – Fig. 1B), and generally it accompanies walls with well-separated calcification centers, e.g., trabeculotheca in *Manicina areolata* or in some other faviines (Stolarski 1996; Roniewicz & Stolarski 1999). In addition to the epitheca and septa of some scleractinians, the basal plate and dissepiments also lack separated calcification centers (e.g., Sorauf 1970, Jell 1980).

*Early ontogeny.* Nearly all Recent scleractinians have septate initial coralla. An initial corallum usually consists of the basal plate, incipient septa, and the wall (Lacaze-Duthiers 1873, 1897; Duerden 1902, 1904; Boschma 1929; Atoda 1947a, b, 1951a, b; 1953; Durham 1949; Vandermeulen & Watabe 1973; Jell 1980; Chevalier 1987; Stolarski 1995). Aseptate initial coralla have been described so far only for *Gardineria minor* Wells, 1973; however, only a part of the juvenile ‘spat’ of *G. minor* described by Wells (1973) was represented by truly aseptate forms (Wells 1973, Fig. 36d and herein Fig. 4A, E). These aseptate coralla are devoid of the basal plate, their epithecal wall cemented directly to the unobscured substrate. In some cases the common epithecal wall encircles two or three individuals that can be judged by the size and shape of the theca (Fig. 4A). Other initial coralla of the same ‘spat’ have from two to six spinose septa (Fig. 4E); see also section entitled Discussion: Taxonomic significance of early ontogeny.

## Skeleton of *Guynia*

The skeleton of *G. annulata* differs in the following ways from the characteristics described above for the typical scleractinian.

*Septa.* Septa are, as a rule, located deeply inside the calice and their growing edge is directed towards the fossa (Figs 1A, 2D). Septal faces are completely smooth and devoid of any ornamentation (Figs 2F, 3E). In transverse, etched sections they consist of several

clearly distinguished, superimposed layers of fibrous tissue (Fig. 2C). Each layer consists of bundles of fibers oriented more or less perpendicularly to the surface layer. Usually, there is no sharp border between layered fibrous tissue of the septum and wall, although occasionally, in forms having a slightly convex distal septal edge, a clear distinction between septa and the thecal part of layered tissue can be observed (Fig. 3E). Concentrations of microcrystalline material (calcification centers) are observed on the growing septal edge (Fig. 2E) and in longitudinal sections as a homogeneous mid-septal line (Figs 2H, 3D). Rarely, also in transverse section, linear concentrations are visible (Fig. 3E). It is worthy of mention that the columella, attaining about 1/4 of the calicular diameter, also has non-separated calcification centers.

*Wall.* The wall is entirely epithecal; concentrations of non-separated calcification centers occur peripherally and the wall is centripetally thickened by fibrous tissue (‘epithecal stereome’); (Fig. 3E). Typically, smooth and cylindrical parts of the wall alternate with regular annulations that are formed by regular inflations of the calicular edge (Fig. 3B, E). Exceptionally, the edge of the annulations may fork in numerous spines (Fig. 3A). In some specimens longitudinal ridges are developed in addition to annulations. These ridges are not continuous along the wall, but are interrupted by annulations (Fig. 4D). In some specimens, neither annulations nor costae are developed, and only delicate growth lines, or sudden growth irregularities are visible.

Depressions about 0.1 mm in diameter occur on the inner surface of the wall (Fig. 2F, G). They are usually visible in juvenile and mature skeletons, starting from the initial constriction (i.e. from the first enlargement of corallum diameter – see terminology in Stolarski [1995]). Thecal depressions are usually equally distributed in every interseptal space, forming rows, and have a rounded though slightly irregular outline. The ‘white spots’ appear on the external part of the wall, in places corresponding to the position of thecal depressions (Figs 1A, 3C). These spots are either unmarked in relief on the theca or form shallow pits. The skeleton in areas of ‘white spots’ is pulverized, i.e., composed of poorly organized, loose fibers in contrast to other parts of the skeleton that are composed of densely packed aragonite fibers (Fig. 2G; see also Discussion: ‘Thecal Pores’). Occasionally, the skeleton corresponding to ‘white spots’ is perforated (‘thecal pores’). Specimens with particularly dense annulations or with growth irregularities may lack or have ‘white spots’ developed only in some places, whereas internal thecal depressions are present in all specimens.

X-ray analysis of samples taken from the septum

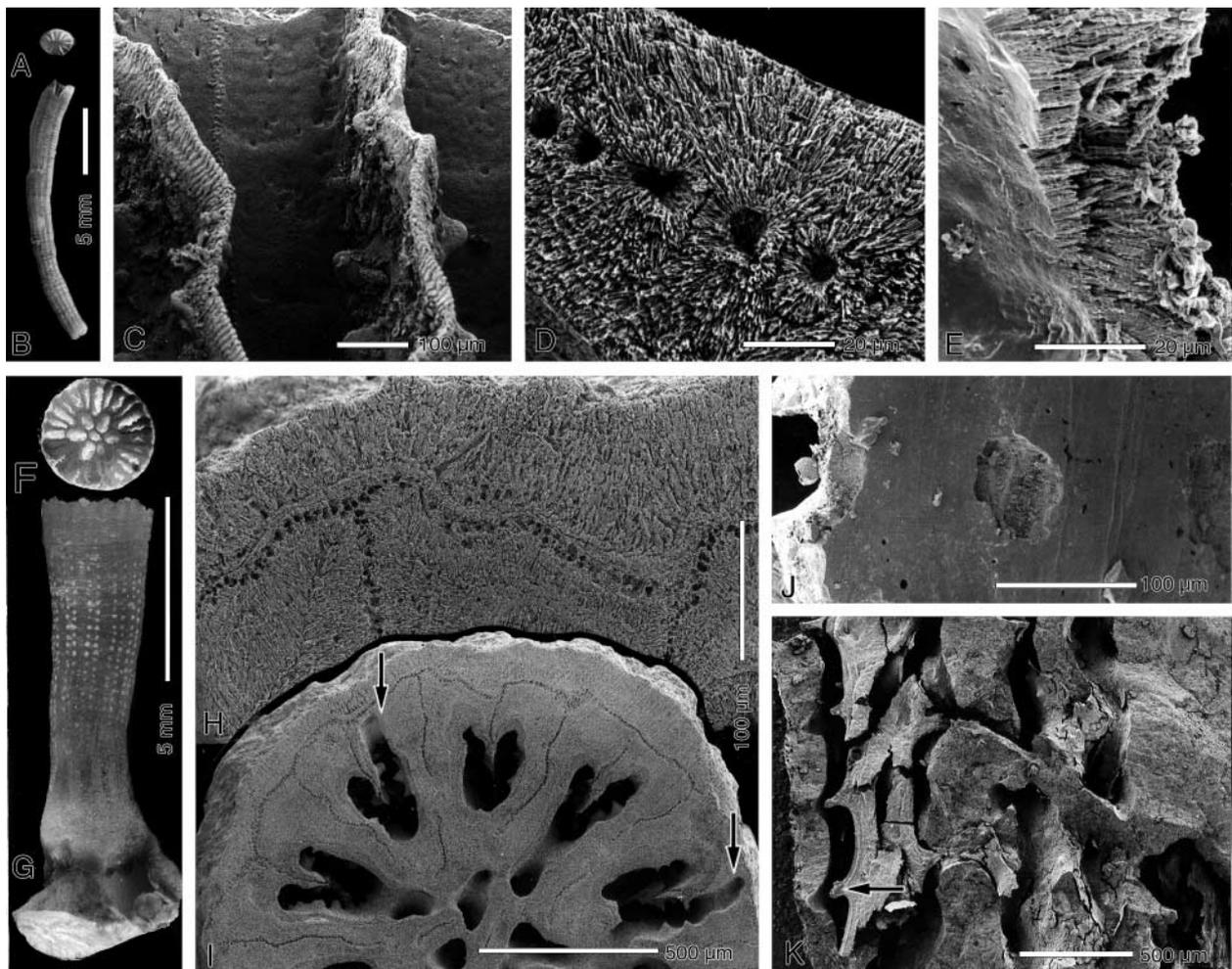


Fig. 5. A–E. *Truncatoguyonia irregularis* Cairns, 1989. □A–B. Specimen ZPAL H.XIV/10, in distal (A) and lateral (B) view. Recent, Pacific Ocean, Loyalty Islands, MUSORSTOM 6, Sta. DW399, 20°41.80'S/167°00.20'E, 282 m. □C. Inner part of the corallum (ZPAL H.XIV/11) having  $S_{1-2}$  with distal dentations representing trabecular tips (separated calcification centers) and rudimentary  $S_3$  as rows of small granulae projecting towards corallum center. Recent; New Zealand, 3.9 km off Nugent and Raoul Islands, 146–165 m. □D. Separated septal calcification centers (transverse section, etched surface) – ZPAL H.XIV/12, Recent, MUSORSTOM 6, Pacific Ocean, Loyalty Islands, Sta. DW485, 21°23.48'S/167°59.33'E, 350 m. □E. Wall fractured in position of thecal depression – skeleton is less compact than in remaining part of the wall (ZPAL H.XIV/13). Recent, Pacific Ocean, Loyalty Island, MUSORSTOM 6, Sta. DW 417, 20°41.80'S/167°03.65'E, 283 m. F–I. *Stenocyathus vermiformis* Pourtalès, 1868. □F–G. Calicular (F) and lateral (G) views (ZPAL H.XIV/14). Recent, Pacific Ocean, MARION DUFRESNE, Sta. 22, 38°48.68'S/77°36.14'E, 410–450 m. H–I. Specimen ZPAL H.XIV/15, etched, transverse section. □H. Enlargement of marginothecal wall. □I. Interseptal spaces filled with stereome, except for 'channels' ending with thecal depressions (arrows). Recent, Indian Ocean, MARION DUFRESNE, MD50, Sta. 21 (DC99), 38°47.81'S/77°34.61'E, 320–450 m. □J. *Truncatoguyonia irregularis* Cairns, 1989 – external part of the wall with detached part of the skeleton in place of the 'white spot' (ZPAL H.XIV/13). Recent, MUSORSTOM 6, Pacific Ocean, Loyalty Island, Stac. DW 417, 20°41.80'S/167°03.65'E, 283 m. □K. *Stenocyathus vermiformis* Pourtalès, 1868. Longitudinal fracture through corallum with dry soft tissue (ZPAL H.XIV/16). Originally soft tissue projections reached the base of thecal depression (arrow), but due to dehydration it has become detached. Recent; Atlantic Ocean (Morocco), CRYOS, Stac. DR 40, 35°49.54'N/06°08.36'W, 362 m.

and from parts of the theca with white spots did not indicate any mineralogical difference between regions.

**Early ontogeny.** Some of the specimens investigated, especially from the Mediterranean, have a prominent bubble-shaped initial skeleton (ca. 0.5 mm in diameter and ca. 0.2 mm in height) (Figs 2B, D, 4G). Specimens with a much flatter initial coralla, having five very distinct initial prototheca lobes, also occur (Fig. 4D).

The earliest coralla yet observed are attached to a single fragment of bivalve shell (Fig. 2A). They consist of the basal plate, central columella, and initial wall, but bear no traces of septa. In specimens with an aseptate basal part of the initial corallum, six proto-septa and septa of the second (last) cycle appeared at the end of this stage, i.e., slightly below or at the initial constriction (Fig. 4G). By removing part of the prototheca I traced aseptate basal parts also in some early juveniles, as well as in adult specimens. In such

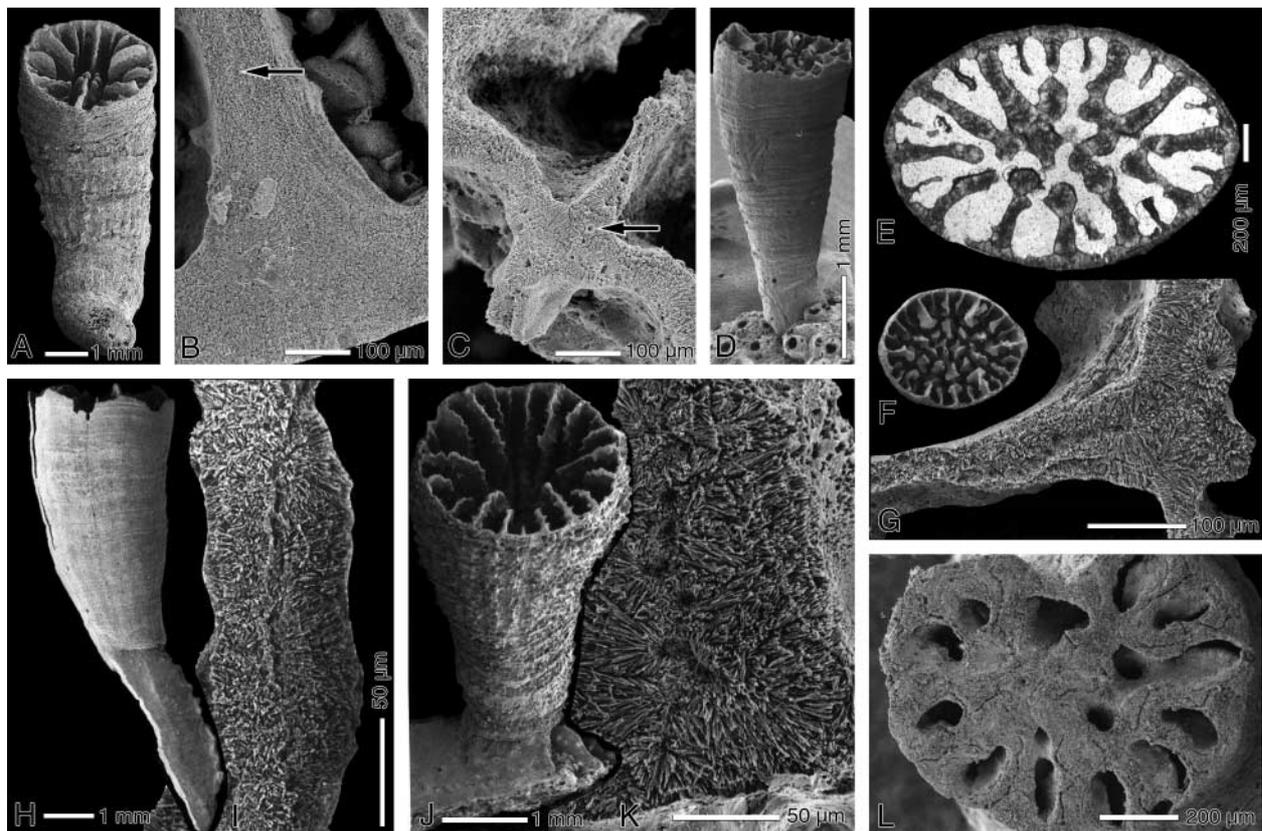


Fig. 6. A–C. *Portalocyathus hispidus* (Pourtalès, 1878). □A. Oblique view of the specimen ZPAL H.XIV/17 with different types of the wall in ontogeny – hispidotheca through most of the juvenile stage and wrinkled epitheca in adult stage. Recent, Atlantic Ocean, off Puerto Rico, CAROLINE, Sta. 67, 18°32.18'N/65°46.12'W, 329–512 m. □B. Epithecal morphotype USNM 61929 with poorly separated septal calcification centers (arrow). Recent, Atlantic Ocean, off Grand Bahama Island, 27°28.2'N/78°57.8'W, 450 m. □C. Hispidothecate morphotype USNM 61928 with well-separated septal calcification centers. Recent, Atlantic Ocean, off Puerto Rico, 18°32.18'N/65°46.12'W, 329–512 m. □D–F, L. *Temnotrochus kermadecensis* Cairns, 1995. D, F. *Anthocaulus* ZPAL H.XIV/18, lateral (D), and calicular (F) views. L. Transverse, etched section of the base (ZPAL H.XIV/18) with 12  $S_{1-2}$  with separated calcification centers. Recent, Pacific Ocean, New Caledonia, MUSORSTOM 6, Sta. DW 459, 21°01.39'S/167°31.47'E, 425 m. □E. Transverse section of the anthocyathus ZPAL H.XIV/19 with epithecal wall (paratype – previously USNM 94287). Recent, Pacific Ocean, Kermadec Islands (3.7 km off Raoul Island), Sta. BS441. H–K, G. *Schizocyathus fissilis* Pourtalès, 1874. □H. Epithecal morphotype (USNM 61728) regenerated from 3-septal parental module with smooth wall. Recent, Atlantic Ocean, Caribbean Sea, EXPLORER, 16°35.4'N/82°47.2'W, 183–335 m. □I. Transverse, etched section of the septum of epithecal morphotype (USNM 61728) with non-separated calcification centers. G, J–K. Hispid morphotype (ZPAL H.XIV/20) regenerated from hispid parental septal module, oblique view (J). □G, K. Transverse etched sections of septum and wall with separated septal calcification centers and large spherulites of the wall (G). Recent, Atlantic Ocean, off Madeira, JEAN CHARCOT JC49, 32°27.8'N/16°25.9'W, 450–500 m.

cases, however, septa that entered the initial chamber from the side of the initial constriction often had strongly arched edges (Fig. 2B). In some specimens, protosepta were attached directly to the basal plate.

The prototheca of the initial coralla is devoid of perforations, white spots, and thecal depressions.

## Mesozoic Guyniidae

Upper Jurassic (Oxfordian) *Microsmilia erguelensis* (Thurmann, 1851) from Switzerland (the type of the genus) is considered to be the oldest guyniid (Fig. 7B, J). The other two species of '*Microsmilia*' described by Koby (1888) i.e., *M. delemontana* (Thurmann, 1851)

and *M. matheyi* Koby, 1888 apparently belong to other genera, since none exhibits characteristic 'thecal pores' (white spots or thecal depressions). Most likely, *M. delemontana* (Thurmann, 1851), with well-developed costae, is a caryophylliid (perhaps from the *Trochocyathus* group), whereas *M. matheyi* Koby, 1888, with an epithecal wall and discoidal corallites, is thecoyathid (perhaps from the *Thecoyathus* group). The skeleton of *M. erguelensis* is completely recrystallized (Fig. 7J) and characters important for the present discussion are not preserved. In addition, all specimens originated by longitudinal division (Fig. 7B) and initial stages of sexually reproduced forms have not been found. In the earliest part of the skeleton of these asexually reproduced forms (just above the regenerated fragment of the parental corallum) three cycles of

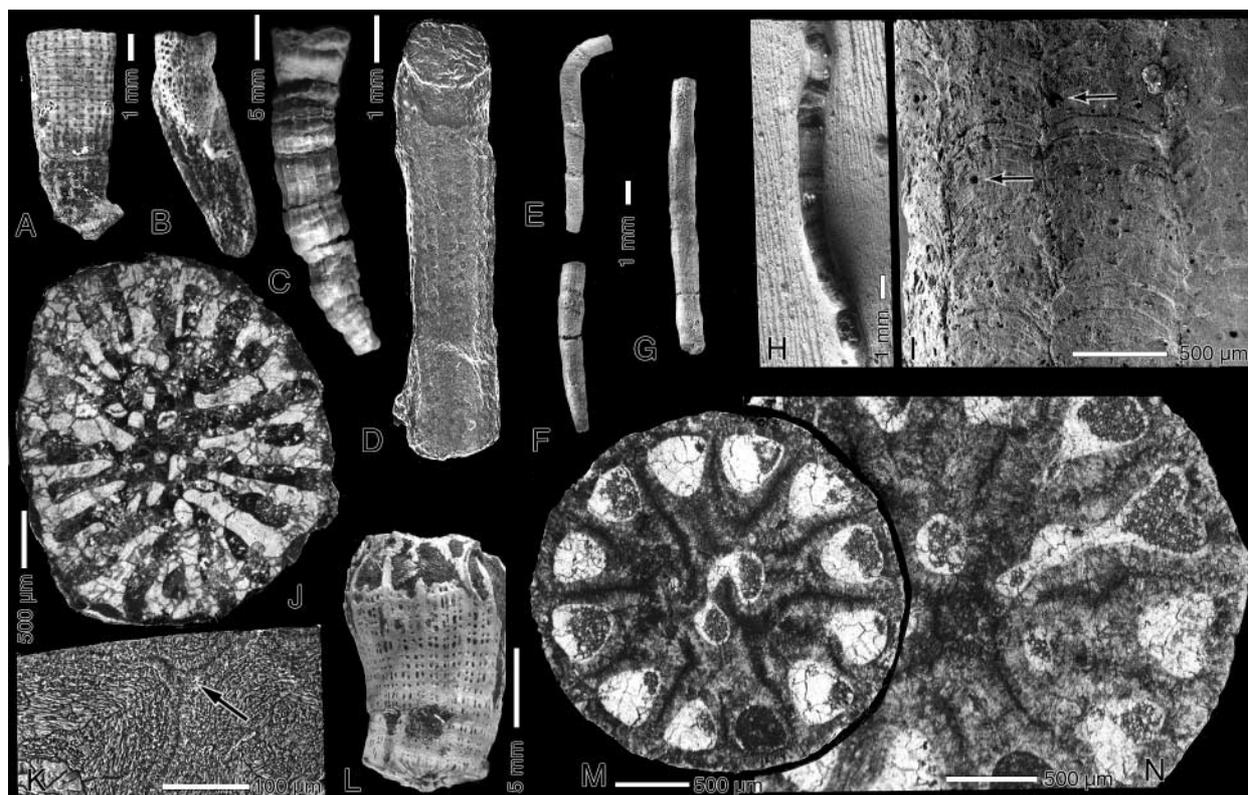


Fig. 7. Some fossil taxa traditionally attributed to Guyniidae. A–B. *Microsmilia erguelensis* (Thurmann, 1851). □A. Lateral view of NHMB D3098/1 with rows of darker spots indicating position of thecal depressions on the inner part of the wall. Late Jurassic (Oxfordian), region of Baden (Kandern, clay pit), Switzerland. □B. Specimen NHMB D4874 (see also Koby 1888: p. 415: 112/11–11b) regenerated from the broken part of parental specimen. Epitheca is eroded and granulae visible on the corallum surface represent sediment infillings of intracalicular thecal depressions. Late Jurassic (Oxfordian), Châtillon, Switzerland. □C. ‘*Stenocyathus*’ *alabamiensis* Wells, 1947. Lateral view of the paratype USNM I04178(b). Cretaceous, United States, Alabama, Marengo County, Linden. □D. *Stenocyathus hoffmeisteri* Wells, 1977. Lateral view of the paratype USNM 208319 – note clearly visible ‘thecal pores’. E–I. *Onchotrochus* cf. *serpentinus* Duncan, 1870. □E. Lateral view of MING/Onch/8, Senonian, Poland, Kraków (Bonarka). □F. Lateral view of MING/Onch/5, Senonian, Poland, Pychowice near Kraków. □G. Lateral view of specimen MING/Onch/7, Senonian, Poland, Kraków (Bonarka). □H. Lateral view of NMNH 155444, Senonian, England (Sussex). □I. Enlargement of the outer part of the wall covered with dense growth lines (MING/Onch/3). Longitudinal fissures are in position of mid-septal line. Senonian, Poland, Kraków (Bonarka). □J. *Microsmilia erguelensis* (Thurmann, 1851). Transverse section of the proximal part of regenerated specimen NHMB D12/1-26/2. Late Jurassic (Oxfordian), Liesberg, Switzerland. K, L. *Gillicyathus alpinus* (d’Archiardi, 1868). □K. Transverse, etched section of ZPAL H.XIV/21 – marginotheca in the region of S2 (arrow). □L. Lateral view of the lectotype (IPM; coll. d’Archiardi, n. 610). Tertiary (Eocene, Priabonian), Cava Cunial, region Possagno, northern Italy. □M, N. *Onchotrochus* cf. *serpentinus* Duncan, 1870. Transverse thin-sections of specimen MING/Onch/7 – though skeleton is recrystallized still recognizable are traces of the original microstructure (‘dark mid-septal line’ of former position of calcification centers).

septa are already developed. Since external features of the skeleton are very well preserved, it is possible to make some judgements concerning the possible original microstructure:

**Septa.** Septa of *M. erguelensis* are not exsert, but their more or less arched distal edges reach the calicular rim. Septal faces are covered with distinct granules, thus resembling those of ‘typical’ Caryophylliina with trabecular septa.

**Wall.** The corallum wall, generally smooth, resembles an epitheca in bearing delicate transverse wrinkles (Fig. 7A). Owing to recrystallization of the skeleton it

is not possible to affirm that the ‘thecal pores’ are fully comparable to those of *Guynia* (they are formed in places of previously pulverized skeleton). In well-preserved specimens the wall is not perforated in a position corresponding to intracalicular thecal depressions. The position of these depressions is, however, easily traceable from the outside, since dark sediment infilling the calice shines through the thin and semi-transparent wall in these places (Fig. 7A). Depressions have rounded, though not perfectly circular, outlines. In more poorly preserved specimens, the wall is either perforated or completely removed, and the position of the internal thecal depressions is marked by sediment protrusions (Fig. 7B).

Table 1. Comparison of traditional guyniid genera.

Genus	Septal calcification centers	Wall	Asexual reproduction	Columella	Pali	Stratigraphic range
a. Recent genera with thecal depressions and 'white spots' of pulverized skeleton on the external wall surface.						
<i>Guynia</i>	Not separated	Epitheca	Occasionally by 'extratentacular offsets' (Wells 1973)	Styliform	None	Miocene-Recent
<i>Pourtalescyathus</i>	Poorly separated or not separated	Epitheca/hispidotheca	None	Fascicular	P <sub>2</sub>	Miocene-Recent
<i>Schizocyathus</i>	Poorly separated or not separated	Epitheca/hispidotheca	Longitudinal fission	Rudimentary	None	Recent
<i>Stenocyathus</i>	Well separated	Marginotheca	Common transverse breakage resulting in bipolar growth	Styliform	P <sub>2</sub>	?Eocene, Miocene-Recent
<i>Tennotrochus</i>	Well separated	Epitheca	Transverse division	Fascicular	P <sub>1-2</sub>	Recent
<i>Truncatogynia</i>	Well separated	Marginotheca	Transverse division	Rudimentary	None	Recent
b. Recent and fossil genera referred to Guyniidae having deep thecal depressions but without (or not preserved) traces of wall pulverization.						
<i>Cyathosmia</i>	?	? Epitheca	None	?	P <sub>1-2</sub>	Miocene
<i>Gillicyathus</i>	Closely spaced (?Separated)	? Marginotheca	None	Lamellar	None	Eocene
<i>Microsmilia</i>	?Separated	? Epitheca	Longitudinal fission	Fascicular	None	Late Jurassic (Oxfordian)
<i>Pedicolocyathus</i>	Separated	Marginotheca	None	None	None	Recent
c. Other genera referred to in the literature to Guyniidae (apparently without thecal depressions, pores or traces of wall pulverization).						
<i>Onchotrochus</i>	?Separated	?Marginotheca	None	None	None	Early-Late Cretaceous: Albian-(Senonina)
<i>Sakalavicyathus</i>	?(recrystallized)	Synapticulotheca	None	None	None	Late Cretaceous (Mastrichtian)

## Cenozoic (Tertiary and Recent) Guyniidae

In addition to *Guynia*, the following five Cenozoic taxa bear similar thecal ‘pores’: *Pourtalocyathus* Cairns, 1979 (monotypic *Pourtalocyathus hispidus* (Pourtalès, 1878)); *Stenocyathus* Poursalès, 1871 (*S. hoffmeisteri* Wells, 1977; *S. vermiformis* (Pourtalès, 1868) – see Discussion: Evolutionary relationships among traditional guyniids); *Schizocyathus* Poursalès, 1874 (monotypic *S. fissilis* Poursalès, 1874); *Temnotrochus* Cairns, 1995 (monotypic *T. kermadecensis* Cairns, 1995); and *Truncatoguynia* Cairns, 1989 (monotypic *T. irregularis* Cairns 1989). Presence of the thecal depressions and ‘white spots’ is the unifying character for all these taxa and other skeletal features are distributed in a mosaic pattern (cf. Table 1). A synthesis of microstructural observations is presented below.

**Septa.** Septa of *Stenocyathus*, *Temnotrochus*, and *Truncatoguynia* have, in contrast to *Guynia*, closely spaced and distinctly separated calcification centers that are similar to those known from various caryophylline species; septal faces bear prominent granulae (Figs 5C, D, H–I; 6E). *Schizocyathus* and *Pourtalocyathus* have septal faces also covered with granulae but calcification centers are not so clearly separated as in the above-mentioned taxa. Typically, in specimens of *S. fissilis* and *P. hispidus* with a smooth wall, septal calcification centers are very closely spaced, without distinct borders between them (Fig. 6C, I), whereas in forms with hispid thecal ornamentation, septal calcification centers are also closely spaced though clearly separated (Fig. 6B, G, K).

**Wall.** The main difference between *Temnotrochus*, *Truncatoguynia*, and *Stenocyathus* is in the wall structure. In *Temnotrochus* the wall is epithelial (Fig. 6E), whereas in *Stenocyathus* and *Truncatoguynia* it is marginothecal with clearly separated calcification centers and, in *Stenocyathus*, a thick layer of tectura (Fig. 5H, I). In smooth morphotypes of *Schizocyathus* and *Pourtalocyathus* the wall meets the definition of an epitheca – the microstructural picture is much more complex in the case of morphotypes with hispid ornamentation. In early juvenile stages of the ontogeny of hispid morphotypes of *S. fissilis* and *P. hispidus*, the wall consists of very closely spaced though separated calcification centers – in transverse section a ‘chain’ of calcification centers is continuous with that of the adjacent septa resembling marginotheca (Fig. 4H, I). However, later in ontogeny the epitheca-like wall appears in places with hispid ornamentation consisting of large spherulite-like

bodies (Fig. 6G). This type of wall is here named *hispidotheca* (new term). In the ontogeny of *P. hispidus*, phases of development of a smooth, epithelial wall may alternate with phases when the hispidotheca is formed (e.g., Cairns 1979, pl. 33:8 and herein Fig. 6A). Asexually originated specimens of *S. fissilis* inherit their wall type (epitheca versus hispidotheca) from the parental form (Fig. 6H, J).

Rows of thecal depressions are equally distributed in every interseptal space in *Pourtalocyathus*, *Stenocyathus*, *Temnotrochus*, and *Truncatoguynia*. The position of thecal depressions corresponds usually to the position of ‘white spots’ on the thecal surface. The skeleton just beneath the ‘white spots’ in all considered taxa is pulverized in the same manner as in *Guynia* (Fig. 5E, J). Depressions and ‘white spots’ usually have rounded, more or less circular outlines, but in some heavily calcified, hispid morphotypes of *Pourtalocyathus* they are very narrow and elongate along intercostal spaces. In the heavily calcified *Pourtalocyathus*, ‘white spots’ may not be distinguishable at all, although thecal depressions are consistently present (all other characters match the species diagnosis). In forms where calcular diameter changes during ontogeny (particularly frequent in very long specimens of *Stenocyathus*, *Truncatoguynia*, and *Pourtalocyathus*), ‘white spots’ and thecal depressions occur in some places, whereas in other coralla there are only internal thecal depressions. In *Temnotrochus* ‘white spots’ have been noticed only in a few specimens, but in all specimens the inner part of the theca is covered with small depressions about 20–30 µm in diameter (see also Cairns 1995, p. 96). Thecal depressions and corresponding ‘white spots’ usually do not occur near the calcular rim of traditional guyniids. Typically, thecal depressions are the shallowest in the distal part, and deepest in the proximal part of the corallum (especially conspicuous in *S. vermiformis* – Fig. 5I); however, their progressive deepening may not necessarily correlate with stronger skeleton pulverization of the proximal skeleton (e.g., Cairns 1989, pl. 23a; Cairns & Keller 1993, fig. 12e; Cairns 1994, pl. 29c; Cairns 1999, fig. 18c). In the few available alcohol-preserved specimens of *S. vermiformis*, protrusions of soft tissue were attached to the base of thecal depressions (Fig. 5K). In juveniles of *S. fissilis* thecal depressions are regularly distributed in every interseptal space; however, in adult forms with advanced stages of longitudinal fission, depressions flanking small  $S_2$  form a sort of continuous gutter. In such specimens, viewed from the exterior, rows of regularly distributed ‘white spots’ are separated in the vicinity of  $S_2$  by longitudinal ‘white strips’ (Fig. 3D). The skeleton in areas of ‘white strips’ and ‘white spots’ is identically colored and pulverized in the same way but ultimately breaks only along the weakened

parts of 'white strips', producing up to six potentially regenerable offshoots (most likely, six very slender wedges with short  $S_2$  resulting from corallum fragmentation do not regenerate).

X-ray analysis of samples taken from the septum and from parts of the theca with white spots of *S. vermiformis* and *S. fissilis* did not indicate any mineralogical difference between regions.

*Early ontogeny.* Presence of septate initial coralla has been confirmed in *P. hispidus*, *S. vermiformis*, and *S. fissilis*, and the presumed anthocaulus of *Temnotrochus* (Figs 4C, H, I; 6L). Initial stages of *T. irregularis* are unknown since the anthocauli of this asexually reproduced species are not yet known (Cairns 1989).

## Taxa of uncertain position

### Mesozoic

Apart from *Microsmilia*, two other Mesozoic genera have been attributed to traditional guyniids: Cretaceous *Onchotrochus* Duncan 1870, and *Sakalavicyathus* Alloiteau, 1958. In *Sakalavicyathus collignoni* (type species – see Appendix) costae covered with granulae extend almost to the corallum basis, and regular depressions occur on external as well on internal sides of theca. This last character suggests a turbinoliid affiliation of this species (see also Discussion: Origin and homology of 'thecal pores').

*Onchotrochus.* – *Onchotrochus* affiliation with guyniids with thecal 'pores' was first proposed by Vaughan & Wells (1943) and later affirmed by Alloiteau (1952), Wells (1956), Chevalier (1987), and Cairns (1989). Long, scolecoïd coralla of *Onchotrochus* are, at a glance, very similar to those of *Stenocyathus* (Fig. 7E–H, Table 1); however, none of the specimens illustrated by various authors or herein investigated of Late Cretaceous (Senonian) *Onchotrochus serpentinus* Duncan, 1870 (type species) bore 'thecal pores' (thecal depressions/'white spots') comparable to those of *Guynia* (see Duncan 1870; Hillmer & Scholz 1991; see also Cairns 1989). Nor have thecal 'pores' been observed in *O. cartei* Duncan, 1870, recorded from the Albian (Upper Greensand) of England (Duncan 1870) and Cenomanian of Crimea (Kuz'mičeva 1987), nor in *O. hatifnatus* Stolarski & Eliášová, 1997 from the early Turonian of Bohemia (Eliášová 1997). Occasionally, I observed small pores (ca. 35  $\mu\text{m}$  in diameter) piercing the wall of *Onchotrochus* cf. *serpentinus* from the Senonian of Poland (Fig. 7I) and *O. hatifnatus* (see Eliášová 1997, pl. 7:3, 5), but since they were irregularly distributed (including parts of the wall in septal position), had a very small diameter, and did

not correspond to thecal depressions inside the calice, they were most likely a bioerosional artifact. Coralla of *Onchotrochus* cf. *serpentinus* from Poland are entirely calcitized though they still bear some traces of the original microstructure: regularly distributed 'points' within septal 'dark line' (?separated calcification centers). On the thin-section of the wall no 'dark-line' nor traces of calcification centers are recognized (Fig. 7M, N). From exterior, the wall bears delicate transverse wrinkles resembling those in epitheca (Fig. 7I). However, presence of distinct septal grooves on the wall surface suggests that the wall could originally be marginothecal with very thin, wrinkled tectura that subsequently eroded. Very similar wall morphology also exists in eroded specimens of *Flabellum* and *Stenocyathus* (e.g., Stolarski 1995: fig. 9G, H; see also comments in Roniewicz & Stolarski 1999, p. 134). Further discussion about possible phylogenetic relationships of this genus is provided in Discussion: Evolutionary relationships among traditional guyniids.

### Cenozoic

Tertiary *Cyathosmilia* Tenison Woods, 1878, *Gillicyathus* Russo, 1979, and Recent *Pedicellocyathus* Cairns, 1995, have been attributed by various authors to Guyniidae (see Vaughan & Wells 1943; Alloiteau 1952; Russo 1979; Cairns 1995). Thecal depressions, and occasionally wall perforations, regularly distributed in every interseptal space, have been described in all these taxa. Thecal perforations, however, were present only in specimens with a worn corallum surface and thus it seems possible these are only post-mortem artifacts, not homologous with 'pores' as in *Guynia*. For purposes of discussion of the possible evolutionary relationships of traditional guyniids, a brief description of these three taxa is provided below.

*Cyathosmilia.* – Type specimens of *Cyathosmilia laticostata* Tenison Woods, 1878 (type of the genus) and *C. tenuicostata* Tenison Woods, 1878 from the Miocene of Aldinga (southeast Australia) are lost (according to Stuart Norrington, Macleay Museum, Sydney, personal communication). According to the original description, *C. laticostata* has an epithecal wall that is longitudinally folded and covered with dense growth lines. Ridges correspond with position of  $S_{1-2}$ , and furrows with position of  $S_3$ . Initially narrow and very distinct furrows become wider and shallower later in ontogeny. Tenison-Woods observed thecal depressions ('pits' only in 'worn specimens where the epitheca is absent'). Primary and secondary septa are paliferous, and faces of all septa are granular.

Without microstructural examination it is impossible to prove the epithelial character of the theca, but wide and very distinct furrows are not typical of that type of wall. Most characters of *Cyathosmilia* listed by Tenison-Wood (1878) can also be found outside traditional Guyniidae, e.g., among turbinoliids (pali, thecal depressions) or caryophylliids (pali, endotheca). Among turbinoliids, *Bothrophoria*, *Idiotrochus*, *Tropidocyathus* have  $P_{1-2}$ , and *Endocyathophora* Cairns, 1989 have regularly distributed depressions on internal parts of the wall. Continuation of furrows from the base to the calicular margin in *C. laticostata* is also typical of turbinoliids, but no turbinoliid taxa possess that unusual *Cyathosmilia* character that only some septa correspond to costae whereas some others to furrows (however, turbinoliid *Idiotrochus* and *Dunocyathus* belong to those few scleractinian genera in which the position of all septa alternates with that of costae; see Cairns 1997).

*Gillicyathus*. – Syntypes of *G. alpinus* (type species: *Lophosmilia alpina* d'Achiardi, 1868 from the Eocene [Priabonian] of Possagno, Italy) have a generally well-preserved aragonite skeleton, though in places slightly diagenetically altered (Fig. 7K, L). In wall and in septa (with faces covered with granulae), calcification centers are closely spaced and poorly separated. In transverse section, calcification centers form a continuous zone between septa and wall (marginotheca); (Fig. 7K). Skeletal layers outside the calcification centers of the wall (tectura) are thin. Except for deep thecal depressions, *Gillicyathus* is very similar to the caryophylliid *Asterosmilia* [Oligocene-Recent] – see Russo 1979, Fig. 19, pl. 15:2–3). Representatives of both genera have elongate, ceratoid/cylindrical coralla, endothecal dissepiments, and lamellar columella (see Cairns & Wells 1987).

*Pedicellocyathus*. – Extant *Pedicellocyathus* Cairns, 1995 (known only from a few specimens of the type *P. keyesi* Cairns, 1995 from the northeast coast of New Zealand) is very similar to the flabellid *Polymyces* Cairns, 1979 (type species: *Rhizotrochus fragilis* Pourtalès, 1871). Specimens of the type species of both genera have similar turbinate coralla without columella and pali, and a unique mode of polycyclic development in early ontogenetic stages (Fig. 4J). Both taxa have septa with faces covered with distinct granulae, and closely spaced but separated calcification centers that are continuous with that of the wall (marginotheca). Tectura is very thin. *Pedicellocyathus* differs from *Polymyces* in having very deep and regularly distributed thecal depressions (ca. 0.2 mm in diameter). Depressions aligned in longitudinal rows are separated by thickened parts of the wall. The bottom of these depressions is very thin, the wall is not

whitened from the exterior, but occasionally may be pierced. In *Polymyces fragilis* the wall in every interseptal space is also covered with small, circular depressions; however, they are about a magnitude smaller (ca. 0.03 mm in diameter), much shallower, and not as regularly distributed as in *Pedicellocyathus*. Also noteworthy is the great similarity of thecal depressions between *P. keyesi* and fossil *Flabellum rariseptatum* Roniewicz & Morycowa, 1987, described from the Early Miocene of King George Island. Thecal depressions in *F. rariseptatum* are large and deep (ca. 0.2 mm in diameter and depth), fully comparable to those in *Pedicellocyathus* and, in worn specimens, visible from the outside as a series of pores (Roniewicz & Morycowa 1987, pl. 24:2).

## Discussion

### *Taxonomic significance of the distinction between separated and non-separated calcification centers*

Differences in distribution of septal calcification centers in septa and wall mirror differences in the earliest phase of skeletal biocalcification. In this phase the calcicoblastic cells that initiate formation of calcification centers expel an organic and/or crystalline agent at the most distal margin of the septum or wall that forms the framework for skeletal growth. There are a limited number of observations of ectoderm calcicoblastic cells expelling crystal-bearing vesicles (Hayes & Goreau 1977) or vacuoles with calcium-enriched fluids (Johnston 1980; Isa 1986). As there are no detailed 'maps' of the cytophysiologic activity of the ectoderm, it is not clear exactly how its organization/function translates into microstructural patterns of the skeleton. One may suppose, however, that organic (or crystalline) agents are expelled either along well-defined 'tracts' resulting in the formation of separated calcification centers, or are dispersed within the zone of extrusion resulting in a more or less homogeneous zone of calcification centers. If these 'tracts' are poorly defined, the resulting microstructural pattern may also be 'transitional'. In some coral groups this pattern is very consistent, e.g., most flabellids have predominantly closely spaced and distinctly separated septal and wall calcification centers (at least in many *Flabellum* species since the Miocene – see Roniewicz 1984; Stolarski 1995). Another example of stability of microstructural characters is *G. annulata*, whose specimens from different parts of the world consistently have an epithelial wall and septa with calcification centers that are not separated. Principally, the only differences

between specimens from different populations consist of slightly different growth dynamics of the wall and septa, resulting in a different pattern of thecal annulations (however, some may have a spinous edge of thecal annulations similar to spines in the hispidotheca), and the presence of longitudinal thecal ridges. On the other hand, hispid and smooth morphotypes of *S. fissilis* or *P. hispidus* have a different pattern of distribution of septal and thecal calcification centers. The above observations clearly indicate also that microstructural features, like other characters, are subject to inter- and intraspecific variability, and a large number of observations are necessary to estimate the range of this variation. Variability in distribution of septal and wall calcification centers in *P. hispidus* and *S. fissilis* decreases the value of the traditional distinction between trabecular (separated calcification centers) and non-trabecular structures. What is the expected impact of these observations for phylogenetic studies or high-level scleractinian classification based on microstructural characters? Are microstructural criteria still reliable?

Observations of possible transitions between these two kinds of skeletal organization will surely stimulate discussion about evolutionary relationships between corals having similar but, considered until now, non-homologous skeletal structures – such as between Volzeioidea with an epithecal wall and Flabellidae with a marginothecal wall (see Stolarski 1996). On the other hand, molecular analyses are providing phylogenetic hypotheses independently of skeletal data, thus making it possible to test morphological hypotheses. Recent molecular analyses of zooxanthellate scleractinians demonstrate that the unity of traditional, morphologically based scleractinian families is generally maintained (Veron *et al.* 1996; Romano & Palumbi 1996). There are exceptions, however, and corals with similar septal microstructures may be grouped in different clades. For example, Caryophylliidae and Oculinidae were put in the microstructurally coherent group of ‘minitrabecular corals’ (Roniewicz & Morycowa 1993), whereas molecular data suggest their assignation to two major scleractinian clades (‘robust’ and ‘complex’ corals), differing in their mitochondrial 16S ribosomal DNA sequences by an average of 29.4% (Romano & Palumbi 1996). Also, the forthcoming analysis of a larger array of molecular data including azooxanthellate corals suggests that the taxonomic status of a majority of traditional families seems to be justified, but some very large families (e.g., Caryophylliidae or Faviidae) appear to be polyphyletic (Romano & Cairns, submitted). Characteristically, traditional scleractinian families with the most generic diagnoses (e.g., the Caryophylliidae groups all corals with a smooth septal

margin) appear heterogeneous in molecular hypotheses, whereas families with more detailed diagnoses (e.g., the Dendrophylliidae, which includes taxa with a synapticulothecal wall, usually with septa arranged according to Pourtales’s plan) retain their monophyletic status. Another example demonstrating that taxonomic decisions based on a wider spectrum of morphological data may also be supported by molecular data is that of *Psammocora*. According to Veron & Pichon (1976) this genus should be transferred from the Thamnasteriidae (Astrocoeniina) to the Siderastreaeidae on the basis of the wall structure (example cited also by Romano 1996). Similarly, wall structure was the decisive character for Chevalier (1987) to remove *Fungiacyathus* from Fungiidae to the new family Fungiacyathidae, a decision subsequently supported by molecular data (Romano & Palumbi 1996). It therefore seems reasonable to assume that diagnoses of families based on detailed microstructural observations of basic parts of the scleractinian skeleton may define natural scleractinian groups that persist in the course of coming years of extensive molecular studies, whereas generic diagnoses of the largest families may have to be redefined. This reasoning is used in this paper to distinguish three microstructural groups within the traditional Guyniidae as the basis for taxonomic reorganization of this family (see section: Taxonomy). To understand evolutionary relationships between these three new groups within the traditional guyniids, thecal pores are considered to be crucial.

#### *Origin and homology of ‘thecal pores’*

The term ‘thecal pores’ used heretofore in diagnoses of various traditional guyniids has not been precisely defined, resulting in assignation to the Guyniidae of taxa having thecal pores of different origin. Thecal pores and thecal depressions occur in a few groups of Scleractinia.

In Micrabaciidae (Fungiina), e.g., in Recent *Leptopenus* (see Cairns 1995) and in a majority of Dendrophylliina, neighboring costae are interconnected with synaptaculae. Intersynaptic spaces are often not filled with sclerenchymal tissue and the wall remains perforated. Outlines of these pores are smooth and rounded.

In Turbinoliidae (Caryophylliina) pores penetrate the wall of *Trematotrochus* Tenison Woods, 1879; however, in many turbinoliid taxa only circular thecal depressions occur on external (*Alveolocyathus* Filkorn, 1994), internal (*Endocyathopora* Cairns, 1989b), or on both surfaces of the wall (e.g., *Turbinolia* Lamarck, 1816, as well as in the above-mentioned *Sakalaviocyathus collignoni*). Several genera lack thecal depressions and pores: *Notocyathus* Tenison Woods, 1880

and *Tropidocyathus* Milne Edwards & Haime, 1848. Generally, turbinoliid thecal pores and depressions have regular, rounded outlines, and the skeleton in their proximity does not bear traces of etching. The turbinoliids have a synapticulothecal wall (e.g., *Turbinolia* in Alloiteau 1952, fig. 101; or *Truncatocyathus* in Stolarski 1992, fig. 2A) and thecal depressions are located between successive synapticular levels. The costae and external surface of the wall are thickened during growth; however, thecal depressions are apparently not secondarily filled with skeletal material.

Exceptionally, thecal pores occur in some caryophylliids, e.g., in Miocene *Tethocyathus microphyllus* (Reuss, 1871); Stolarski 1991, p. 46, pl. 2:4b. On the inner surface of the wall the pores are not accompanied by thecal depressions.

In Micrabaciidae, Dendrophylliina, and Turbinoliidae thecal depressions and pores are original skeletal structures formed between successive levels of synapticalae. Coralla in all these groups are invested by soft tissue having projections that penetrate thecal depressions and pores from the outer and inner side of the theca. The morphology of these pores and thecal depressions is usually retained during ontogeny suggesting that non-skeletogenous soft tissue projections are retained in these places during growth. Thecal pores in the Miocene caryophylliid *Tethocyathus microphyllus* (Reuss, 1871) are interpreted to be formed as a result of irregular growth. In the majority of specimens, successive thecal rings (polycyclic development) are proximally attached to the substrate and the last theca forms the cylindrical wall of the adult stage. However, in some specimens, especially in those with relatively narrow bases, a sudden increase in corallum diameter (enlargement of the costae) may occur much above the base. As a result, a new wall is formed between enlarged costae, leaving some intercostal parts of the corallum underneath uncovered. These uncovered places are thecal pores, which are not homologous to any of the pores described in this chapter as occurring in other corals.

In Recent, traditional guyniids, thecal pores are formed only in places corresponding to 'white spots'. Outlines of these pores, though rounded, are not as regular as in turbinoliids or micrabaciids, and usually they are slightly frayed on the edges. Location of the 'white spots' corresponds to thecal depressions on the interior part of the wall. Two hypotheses have been proposed to explain the origin of these pores:

1. Thecal pores are structures formed in periods of fast coral growth, whereas in periods of stagnation a non-porous septotheca is produced (Vaughan & Wells 1943, p. 223). According to Wells (1947, 1973), original pores can later be filled with

sclerenchymal tissue and the only traces of their occurrence are 'white spots' on the wall surface.

2. Thecal pores are formed as a result of diagenetic alterations of the skeleton. Hickson (1910) was the first to consider thecal pores as products of the weathering of the corallum. Cairns & Wells (1987, p. 42) suggested that pores in *Pourtalesocyathus* are formed by post-mortem dissolution of the skeleton in places of a 'periodic differential calcification of the theca'.

I here propose a third hypothesis that the origin of thecal pores is a result of biological decalcification of the skeleton restricted only to the 'white spot' areas. The observation that supports this hypothesis is that the skeleton in places with 'white spots' has the same, slightly loose structure as the skeleton exposed to light etching. At the same time, the wall between 'white spots' is composed of typically 'compact' skeleton. Similar differences in skeletal structure are observed in places of biologically induced division of the corallum. It is particularly noticeable on specimens of *Schizocyathus fissilis*, where places of 'pulverized' skeleton occur in places of 'white spots' and as 'white strips' in regions of future skeletal division. Characteristically, 'white spots' occur also in the first phase of transverse division of *Fungia* in the region of the detaching anthocyathus from the anthocaulus, as well as in regions of longitudinal fission in *Diaseris distorta* and *D. fragilis* (see Yamashiro & Yamazato 1987; Yamashiro & Yamazato 1991; Yamashiro & Nishihira 1994). Only in those places is the skeleton partially dissolved. Calicoblastic cells of *Fungia* in the vicinity of skeletal dissolution exhibit increased metabolic activity (Yamashiro & Yamazato 1987). According to Yamashiro (1992), decalcification agents are perhaps enzymes (e.g., carbonic anhydrase) or products of respiration (e.g., succinic acid). These substances have not been identified from the areas of skeletal dissolution but the assumption of their presence is based on observations of etching activity in other invertebrates (sponges, sipunculid worms, gastropods, and bivalves), (see Yamashiro 1992). The only anatomical observation of tissue in sites of decalcification of the skeleton prior to transverse division (in *Fungia fungites*) revealed the presence of fibrous organic matter, which most likely protects a polyp's soft tissue from direct contact with ambient sea-water after dissolution of the skeleton (Yamashiro & Samata 1996).

The pattern of distribution of 'white spots' and corresponding thecal depressions on the inner surface of the wall in traditional guyniids resembles the pattern of distribution of desmocyte attachment scars reported from various groups of Scleractinia (see Wise

1970; Sorauf & Podoff 1977; Roniewicz & Morycowa 1987, pl. 24: 1–2; Chevalier 1987, pp. 530–531), Rugosa and operculate corals (Il'ina 1980; Fedorowski 1985, 1989; Stolarski 1993). Presence of soft tissue projections that are attached to the bases of thecal depressions in *Guynia* and *Stenocyathus* suggests that they are homologous with desmocytes of other corals. Because these projections are the only soft parts that contact the skeleton in these places (the corallum is not covered with tissue from the outside), most likely they release decalcifying agents that cause formation of 'white spots' on the surface of the wall. Secretional activity of desmocytes is plausible since the discovery that they are cellular (Muscatine *et al.* 1997). The consistent pattern of distribution of the deepest thecal depressions in the proximal part of the skeleton reflects successive infilling of the calice with stereome except in places where projections of non-calcifying tissue are anchored to the skeleton.

It seems not to be a coincidence that among traditional Guyniidae forms reproducing by transverse or longitudinal division are particularly frequent (4 out of 10 genera reproduce in this manner). As suggested above, it is likely that the same decalcifying mechanism is employed both in the formation of 'white spots'/thecal pores and in skeleton division. In the proposed scenario of evolutionary development of corallite longitudinal division, the ability to dissolve the skeleton in restricted places (punctual dissolution) was transformed to the ability to dissolve it along entire interseptal spaces (linear dissolution). The first scleractinian that demonstrates longitudinal division is Oxfordian *Microsmilia*. Similarly, development of transverse division required a change from punctual to linear dissolution of the skeleton but only in one, horizontal plane (as in *Temnotrochus* or *Truncatoguynia*). In both cases, skeleton dissolution must be associated with controlled lysis of the soft tissue along the plane of division. Perhaps, similar evolutionary steps were required to develop the ability to control corallite division in Flabellidae (transverse division in *Truncatoflabellum*, *Placotrochus*, *Placotrochides*, *Falcatoflabellum*; and longitudinal division in *Flabellum macandrewi* Gray, 1849). Flabellids, however, do not bear 'white spots' though their desmocyte attachment scars are usually well developed. Also noteworthy is that the presence of distinct thecal depressions in Rugosa and operculate corals (Il'ina 1980; Fedorowski 1985, 1989; Stolarski 1993) does not coincide with the occurrence of forms with thecal pores or their ability to longitudinally divide (however, forms occur that reproduce by transverse division, e.g., *Petronella*; see Birenheide & Soto 1977; Weyer 1982).

The scenario discussed above suggests that the ability of restricted dissolution of the skeleton (pre-

sence of 'white spots') was a prerequisite or a character associated with the controlled division of the corallum. One may wonder, however, whether thecal pores of traditional guyniids may have some functional significance. Filkorn (1994) speculated that turbinoliid pores may serve to reduce the weight of the skeleton, as well as to reduce energetic expenses of producing a skeleton. He suggested also that through these pores the edge-zone is connected with tissues inside the calice. Filkorn (1994, p. 34) suggested that a possible advantage of such connections is increased nutrient exchange or strengthened polypal anchorage to the skeleton. These possible functions (if really served) are not applicable in the case of thecal pores of traditional guyniids, since their skeleton is not covered with soft tissue. The simplest explanation of the purpose of guyniid pores is that they are only a non-functional by-product of skeletal dissolution. Interestingly, among corals with prominent thecal depressions, thecal pores occur only in traditional Guyniidae that predominantly have exceptionally elongated, scolecoïd coralla with a relatively very small calicular diameter. In all extant representatives soft tissue occupies the entire available space inside the corallum and thus one may suggest that pores function as auxiliary regions (to the oral surface) of gas and nutrient exchange, or as a place of metabolite expulsion.

#### *Taxonomic significance of early ontogeny*

The aseptal, early initial stage in ontogeny of *G. annulata* is exceptional among Scleractinia but one may wonder whether this character reflects some peculiar anatomical/physiological properties of the earliest polyp of *Guynia* and thus has some significance for phylogenetic and taxonomic considerations.

Most authors correlate development of the septa with the appearance of mesenterial pairs (Duerden 1902, 1904; Hyman 1940; Vaughan & Wells 1943). Mesenteries of the first cycle are supposed to appear initially in the larval stage thus preceding development of the protosepta. Subsequent septa (metasepta) appear either in advance of the next cycle of mesenteries (exosepta), or after its appearance (entosepta). Lack of the protosepta in the earliest part of the initial skeleton of *Guynia* may thus suggest that development of the first cycle of mesenteries is delayed and that the anatomy of planula and earliest polyp is simplified. Other evidence implies a different explanation, however.

Observations on growth of the scleractinian coralla suggest that biocalcification may be facultative, and this particularly concerns development of the septa. Roniewicz (1989, pl. 7: 6) illustrated the appearance

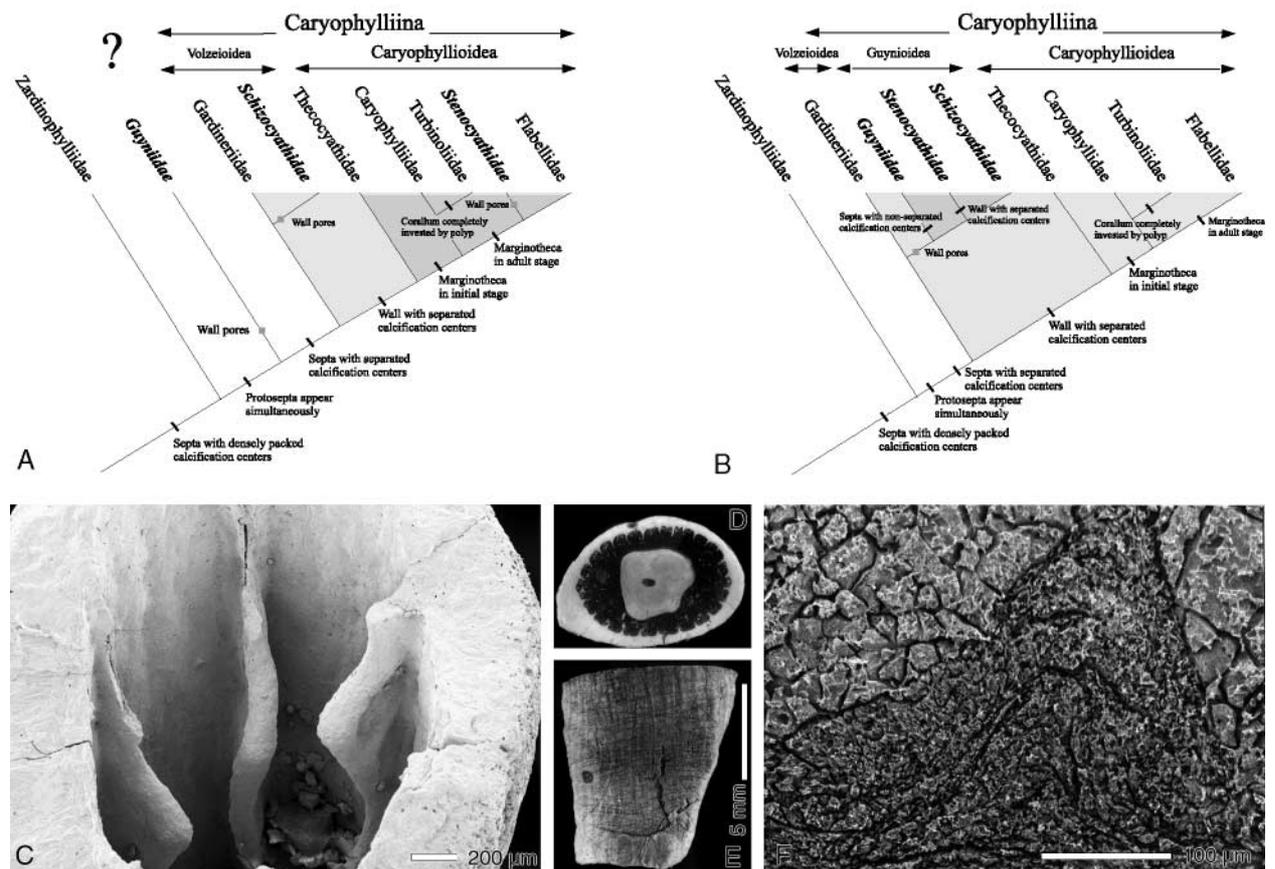


Fig. 8. Phylogenetic relationships within Caryophylliina. □A. Diagram based on characters emphasized in traditional scleractinian taxonomy, i.e., septal microstructure and the wall type. □B. Diagram based on acceptance of overriding taxonomical significance of the thecal 'pores'. □C. Distal view of *Zardinophyllum zardini* Montanaro-Gallitelli, 1975 (ZPAL H.XVIII/1) – note completely smooth septal faces and distal edges, and thick epithelial wall (pachythea). Late Triassic (Carnian), Italy, Dolomites, San Cassiano Beds, Alpe di Specie. □D–F. *Gigantostylis epigonus* Frech, 1890, GBA 1982/12/550 in distal (polished surface – D), and lateral views (E). Note large columella, and numerous but small septa. □F. Etched surface of the septum composed of imposed scale-like units. Late Triassic (Rhaetian), Northern Calcareous Alps, Austria, Fischerwiese.

and then disappearance of  $S_4$  during growth of Triassic remaniphylliid *Retiophyllia frechi* Roniewicz, which appears to be connected with minute changes in corallum diameter. Similar observations concern corals undergoing rejuvenescence or sudden reduction of the corallum diameter. Calices of such corals become narrow and the number of septa is often radically reduced or even disappear altogether (Fig. 4B, F) (similar observations also concern rejuvenescence in Rugosa, e.g., Fedorowski 1987, pl. 20: 17b presented a specimen of *Lophotichium dugoutense* with 'four subsequent rejuvenescens innermost one aseptal'). Relationships between skeleton and polyp anatomy of rejuvenating corals have not been investigated so far, but at least part of the observed growth disturbances can be explained by referring to physiological, not anatomical (e.g., disappearance of mesenteries), changes occurring in the polyp. Experiments suggest that calcification rate may significantly decrease as a result of decreases in the saturation level

of aragonite (e.g., Gattuso *et al.* 1998). In addition, in stressful environments the skeleton of young, rejuvenating polyps may consist initially only of theca, despite the internal anatomy of the polyp appearing to be intact (Richmond 1985, fig. 3). Is environmental stress also responsible for the development of the aseptal part of the initial *Guynia*?

Skeletons of *Guynia* with aseptal stages have been collected from Mediterranean submarine caves. It is possible that these environments differ in their geochemical characteristics from deep-water environments in the open sea. However, only the initial stages of *G. annulata* are aseptal, and other corals from the same submarine cave environments (e.g., *Polycyathus muelleriae*, '*Ceratotrochus magnaghii*', or *Caryophyllia inornata*) always have septate initial coralla. This suggests that the ability to form an aseptal phase is unique to *Guynia*. It cannot be excluded that a delay in formation of the protosepta is triggered by some environmental factor (perhaps of a geochemical

Table 2. Two hypotheses for the origin of traditional Guyniidae – arguments for and against their polyphyly (hypothesis A) and monophyly (hypothesis B).

Hypothesis A (polyphyly)	Hypothesis B (monophyly)
1. Fundamental differences exist among Guyniidae, Schizocyathidae, and Stenocyathidae in septal (calcification centers separated or non-separated) and wall microstructure (epitheca, marginotheca, trabeculotheca).	1'. Microstructure of septa and wall may be subject to variation and the difference between separated (but still crowded) vs. non-separated calcification centers is acceptable even within intra-specific variability.
2. Supposed relationship between development of thecal 'pores' and ability to control division of the corallum (transverse, and longitudinal division). Almost certainly, various types of asexual reproduction develop independently in different scleractinian evolutionary lineages.	2'. Formation of thecal 'pores' by limited dissolution of the skeleton may be a unique character. Many corals with ability to divide transversely or longitudinally do not have thecal depressions and, in turn, taxa with thecal depressions are not capable of corallum division.
3. Presence of corals from various geological periods with general morphologies similar to that of various guyniids except having no thecal 'pores' (e.g., pair <i>Onchotrochus serpentinus</i> -> <i>Stenocyathus vermiformis</i> ). This may suggest an ancestral position of these taxa in evolution of various 'guyniid' lineages.	3'. Corals with general morphology similar to that of various guyniids but having no thecal 'pores' may exemplify a frequency of convergences in Scleractinia.
4. Time gap between appearance of first coral with thecal 'pores' (Oxfordian <i>Microsmilia</i> ) and appearance of next representatives of these corals (Eocene <i>Stenocyathus</i> , Miocene <i>Guynia</i> ).	4'. Time gaps are common in scleractinian fossil record (including their origin). This is especially true for poorly sampled deep-water faunas.

nature), but, if so, this factor affects only the initial development of *Guynia*. A similar explanation may apply also to the presence of aseptal initial stages in *Gardinieria minor* Wells, 1983. In this case, however, only a part of the initial 'spat' is aseptate, whereas other initial specimens have more or less developed septa (Fig. 4A, E). This suggests that either the factor postponing septal calcification is dispersed in a mosaic manner and specimens show phenotypic plasticity or this biocalcificational phenomenon is entirely genetically controlled.

Clearly, data on the physiology of scleractinians in a stressful environment, as well as on micro-scale environmental factors that may affect corallum growth, are very limited – thus it is premature to suggest a special taxonomic significance of the ability of *G. annulata* or *G. minor* to form aseptate initial stages. It is noteworthy that this phenomenon has been described so far only in corals having epithecate walls (though, not all epithecate corals have aseptate initial stages, e.g., Recent *G. paradoxa*, see Stolarski 1996). Aseptal initial stages have consistently been recorded also in some entirely extinct groups of corals – in epithecate rugosans, e.g., Devonian *Protomacgeea* (see Rózkowska 1956), Carboniferous *Ankhelasma* (see Sando 1961), or in Devonian epithecate operculate cothoniid *Calceola sandalina* (see Stolarski 1993) – see also Fedorowski 1985, 1991, 1997.

Another unusual phenomenon observed in some specimens of *G. annulata* is that septa in the proximal part can grow toward the aseptal base. Septa growing in two opposing directions (bipolar growth) were also observed in accidentally broken specimens of *Stenocyathus vermiformis* (see Pourtalès 1871, p. 10, pl. 3: 11; Zibrowius 1980, p. 165, pl. 84: N–O); however, in *Guynia* they grow inside non-damaged coralla. If the

growth of the initial skeleton of *Guynia* is actually facultative, as suggested above, then downward growth of the protosepta can be considered as a peculiar regeneration of the initial corallite.

#### Evolutionary relationships among traditional guyniids

*Hypothesis A* (Fig. 8A). In this hypothesis, relationships between newly established families of traditional guyniids (i.e., Guyniidae, Schizocyathidae, and Stenocyathidae – see Taxonomy) are proposed based on characters traditionally recognized as important in high-level scleractinian classification, i.e., on septal and wall microstructure. According to this hypothesis these three families do not form a clade.

Non-separated calcification centers in septa, completely smooth septa and the presence of an unusual aseptate initial stage (however, as mentioned in the section above, the real taxonomic significance of this character requires separate investigation) provide arguments to set *Guynia* apart from other caryophyllines. In this hypothesis, *Guynia* forms a separate clade (Guyniidae sensu stricto) and Zardinophyllidae (Middle-Upper Triassic) are proposed as the first outgroup. Zardinophyllidae, with calices of a few- to up to several millimeters in diameter, have as in *Guynia*, completely smooth, non-ornamented septa (Fig. 8C), with fused calcification centers in the mid-septal line (Montanaro-Gallitelli 1973, 1975; Cuif 1975; Sorauf 1996). Zardinophyllidae and *Guynia* have an epithecate wall, which in zardinophyllids, has a penicellate organization of fibers in its internal layer (Roniewicz & Stolarski 1999). *Guynia* differs from zardinophyllids also in the pattern of proto-septal insertion, and in the presence of 'thecal pores'

and axial structure. In Zardinophylliidae, protosepta arise two-by-two, as in some Rugosa. Montanaro-Gallitelli (1975) considered this character to be diagnostic of a new anthozoan order – Hexanthiniaria – intermediate between Rugosa and Scleractinia (see also Cuif 1975, Stolarski 1999). Among Triassic Scleractinia *Gigantostylis* (Stylophylliina: Gigantostylidae) also has non-ornamented septa, an epithecal wall, and a large, mace-like columella (Fig. 8D, E). The septa and other parts of the skeleton of *Gigantostylis*, however, are built of scale-like units in contrast to the more or less continuous skeletal layers of *Guynia* and other non-stylophylline Scleractinia (Fig. 8F and Roniewicz 1989; see also Cuif 1965). Coralla of *Gigantostylis* are also of about a magnitude larger than those of *Guynia*. Most likely, stylophyllines (including *Gigantostylis*) represent a lineage separate from *Guynia* and other scleractinians. The fundamental obstacle to suggesting zardinophyllid-like or gigantostylid-like ancestors for *Guynia* is the ca. 180 Ma stratigraphic gap between their disappearance from the fossil record (Late Triassic) and the appearance of the first unquestionable representatives of *Guynia* (Miocene). The only defense of this reasoning is that the Mesozoic representatives of this evolutionary lineage had miniature and fragile coralla as in *Guynia*, and that the stratigraphic gap in their record may reflect only a sampling/taphonomic bias (see also Table 2).

Evolutionary affinities of other traditional guyniids appear to be rooted within the caryophylline stem – they generally have separated but closely spaced septal calcification centers.

Schizocyathidae date back as early as the Late Jurassic (Oxfordian *Microsmilia*) and may have ancestors related to the Volzeioidea which encompass

caryophyllines having an entirely epithecal wall. Direct ancestors of *Microsmilia* could be some volzeioides with elongated coralla, paliform lobes and a papillar columella that developed strong desmocyte attachments (e.g., similar to elongated morphotypes of Toarcian *Thecocyathus tintinnabulum* [Goldfuss, 1826], but yet without trabecular theca).

Stenocyathidae are similar to the Caryophyllioidea in regard to presence of the wall with separated calcification centers. Corals similar to the Cretaceous *Onchotrochus* or Paleocene '*Stenocyathus*' *alabamensis* Wells, 1947, which by gross morphology and perhaps microstructure of the skeleton (at least '*S.*' *alabamensis* has typical marginothecal wall), resemble *S. vermiformis* (Fig. 7C), could be ancestral to the stenocyathid evolutionary lineage. Occurrence of the marginotheca throughout ontogeny suggests phylogenetic relationships with flabellid lineage. Supposedly, 'thecal pores' appeared in this lineage in the Late Cretaceous–Eocene period (the first unquestionable record of *Stenocyathus* (*S. hoffmeisteri* Wells, 1977) is from the Eocene of Tonga (Fig. 7D).

The probability of the appearance of the 'thecal pores' in independent evolutionary lineages can be compared to the acquisition of transverse or longitudinal division in three independent lineages – Fungiina, Caryophylliina, and Dendrophylliina. This hypothesis assumes stability of the basic microstructural architecture of the skeleton in those evolutionary lineages that gave rise to the three groups of traditional guyniids. Other arguments supporting this hypothesis are presented in Table 2.

The results of molecular studies based on 16S mitochondrial rRNA sequences (Romano & Cairns, submitted) suggest that *Guynia annulata* groups with 'complex' corals of Romano & Palumbi (1996). These

#### TAXONOMY

Hypothesis A	Hypothesis B
Suborder Incertae sedis	Suborder Caryophylliina Vaughan & Wells, 1943
Family: Guyniidae Hickson, 1910	Superfamily Volzeioidea Melnikova, 1974
Suborder Caryophylliina Vaughan & Wells, 1943	Family: Protoheterastraeidae Cuif, 1977
Superfamily Volzeioidea Melnikova, 1974	Family: Gardineriidae Stolarski, 1996
Family: Protoheterastraeidae Cuif, 1977	Family: Volzeiidae Melnikova, 1974
Family: Gardineriidae Stolarski, 1996	Family: Cycliphylliidae Roniewicz, 1991
Family: <b>Schizocyathidae</b> fam. n.	Family: Reimaniphylliidae Melnikova, 1974
Family: Volzeiidae Melnikova, 1974	Family: Margarophyllidae Cuif, 1977
Family: Cycliphylliidae Roniewicz, 1991	Superfamily Guynioidea Hickson, 1910
Family: Reimaniphylliidae Melnikova, 1974	Family: <b>Guyniidae</b> Hickson, 1910
Family: Margarophyllidae Cuif, 1977	Family: <b>Schizocyathidae</b> fam. n.
Superfamily Caryophyllioidea	Family: <b>Stenocyathidae</b> fam. n.
Family: Thecocyathidae Vaughan & Wells, 1943	Superfamily Caryophyllioidea
Family: Caryophylliidae Dana, 1846	Family: Thecocyathidae Vaughan & Wells, 1943
Family: Flabellidae Bourne, 1905	Family: Caryophylliidae Dana, 1846
Family: <b>Stenocyathidae</b> fam. n.	Family: Flabellidae Bourne, 1905
Family: Turbinoliidae Milne Edwards & Haime, 1857	Family: Turbinoliidae Milne Edwards & Haime, 1857

results may suggest that there is no large genetic discrepancy between *Guynia* and other extant scleractinians, which would be expected if this Recent taxon has Triassic zardinophylliid or gigantostyliid ancestors.

*Hypothesis B* (Fig. 8B). This hypothesis accepts the overriding taxonomic importance of thecal 'pores' and limits the usefulness of septal and wall microstructures in phylogenetic reconstructions above the family level. The monophyly of traditional Guyniidae (here Guynioidea) is maintained.

As in hypothesis A, in this evolutionary scenario solitary Volzeioidea are also considered ancestral to schizocyathids that separated from the ancestral lineage by development of 'thecal pores'. Perhaps, very early in the evolution of schizocyathids, weakness of the skeleton in places of 'white spots' was co-opted for a new use in asexual reproduction. This mechanism of effective longitudinal corallum division was perfected and, as in *Microsmilia*, potentially regenerable fragments consist of an inconsistent number of septa. In *Schizocyathus* they invariably involve regular, 3-septal modules, and planes of division are performed early in ontogeny (reduced  $S_2$  and 'white strips' of pulverized skeleton). Most likely in the Early Tertiary, from *Microsmilia*-like ancestors arose taxa without the ability to longitudinal fission (but some capable of transverse division) with developed pali and columella – *Pourtalocyathus* (Miocene–Recent), *Temnotrochus* (Recent).

Perhaps in the Early Cenozoic, *Guynia* became separated from the schizocyathid evolutionary lineage by formation of septa with non-separated calcification centers, and by retardation of septal development in the initial stage. Assumed ancestors of the *Guynia* evolutionary lineage had larger coralla and did not reproduce asexually by corallum division.

In the Late Cretaceous or Early Tertiary, Stenocyathidae became differentiated from the schizocyathid stem by development of a marginotheca. Two possible ways for the development of a marginotheca are assumed: (1) directly from the epitheca by differentiation of separate calcification centers within the outer layer of the epitheca (see terminology Roniewicz & Stolarski 1999), or (2) by reduction and ultimately elimination of the epitheca and formation, between the septa, of a new wall with separated calcification centers. So far there are no unambiguous arguments to support any of these options; however, observations that the epitheca in some morphotypes of *Schizocyathus* and *Pourtalocyathus* can be transformed into hispidotheca (with separated spherulite-like bodies with their own calcification centers) incline me to favor the first possibility. Schizocyathids are considered ancestral to

the stenocyathid branch that did not reproduce asexually but that had pali (e.g., *Pourtalocyathus*-like forms).

At the current stage of morphological and molecular knowledge of the Scleractinia there are no clear-cut arguments favoring either hypothesis A or B. In particular, there are no molecular or in-depth anatomical studies of representatives of all families distinguished here. Acceptance of either hypothesis will have significant consequences for the traditional classification of Guyniidae: either taxonomic importance of general microstructural organization should be favored (hypothesis A), causing significant revision within the family Guyniidae, or the presence of specialized morphological structures (i.e., 'thecal pores') should be favored over the general microstructural organization (hypothesis B).

The morphological distinctness of *Guynia* from other Recent scleractinians at almost each grade of skeletal organization, and the conventional scleractinian character of other traditional guyniids naturally incline me to favor hypothesis A, as proposed here, but the possible relationships of *Guynia* with zardinophyllid- or gigantostyliid-derived ancestors are weakly substantiated. Although hypothesis B seems to solve this particular problem, implying that major skeletal modification appeared much later, within the evolutionary lineage of *Microsmilia*-like ancestors, it requires acceptance of the possibility that microstructural features of the skeleton may be more variable than previously thought. An additional argument that inclines me to favor hypothesis A is the assumed affinity of formation of 'thecal pores' with formation of 'white strips' preceding longitudinal division of the corallum (best exemplified in *Schizocyathus fissilis*). Since various modes of asexual reproduction involving skeletal dissolution developed independently in several scleractinian lineages, it is likely that 'thecal pores' could also develop repeatedly and independently in scleractinian history.

## Taxonomy

Family: Guyniidae Hickson, 1910.

*Diagnosis.* – Septal calcification centers not separated; septal faces smooth. Epithecal wall with regularly distributed thecal depressions on inner side and corresponding pulverization spots on outer side.

*Genera included:* *Guynia* Hickson, 1910.

## Family: Schizocyathidae fam. n.

*Diagnosis.* – Septal calcification centers closely spaced but usually well separated. Septal faces ornamented. Wall epithecate but occasionally with strong hispid ornamentation (hispidotheca); thecal depressions on inner side and corresponding pulverization spots on outer side of the theca.

*Genera included:* *Microsmilia* Koby, 1888; *Schizocyathus* Pourtalès, 1874; *Pourtalocyathus* Cairns, 1979, *Temnotrochus* Cairns, 1994

## Family: Stenocyathidae fam. n.

*Diagnosis.* – Septal calcification centers closely spaced but well separated. Septal faces ornamented. Wall marginothecate with thecal depressions on inner side and corresponding pulverization spots on outer side.

*Genera included:* *Truncatoguynia* Cairns, 1989b; *Stenocyathus* Pourtalès, 1874.

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## APPENDIX. Stratigraphic and geographic ranges of traditional guyniids. Type materials examined

### *Gillicyathus* Russo, 1979 (monotypic)

*Type species.* – *Lophosmilia alpina* d'Achiardi, 1868 by subsequent designation (Russo 1979).

*Type locality.* – Tertiary (Eocene: Priabonian), Italy, Possagno.

*Stratigraphic and geographic range.* – Tertiary (Eocene; Priabonian) of Italy.

*Type material examined.* – Lectotype (Museo di Geologia e Paleontologia, Università di Pisa, No. 610). Other types: Five syntypes (Museo di Geologia e Paleontologia, Università di Pisa, No. 610)

### *Guynia* Duncan, 1872 (monotypic)

*Type species.* – *Guynia annulata* Duncan, 1872, by monotypy.

*Type locality.* – Recent, Mediterranean (Adventure Bank), 168 m.

*Stratigraphic, geographic, and bathymetric range:* Tertiary. – Miocene of Haiti (Cairns & Wells 1987),

Pliocene-Recent of Costa Rica, and Panama (Cairns in press). *Recent* – nearly global distribution (not yet known subantarctic and Antarctic seas): Mediterranean (Duncan 1872, Zibrowius 1980); Eastern Atlantic (Zibrowius 1980), Western Atlantic: Bermuda (Wells 1972), Caribbean (Wells 1973, Cairns 1979); Persian Gulf (Hickson 1910, Harrison 1911); Indian Ocean: off South Australia (Cairns & Parker 1992), off South Africa, Madagascar (Cairns & Keller 1993); Pacific Ocean, Hawaiian Islands (Cairns 1984), Indonesia, Philippines, New Caledonia (Cairns 1989, Cairns & Zibrowius 1997), Wallis, Futuna and Vanuatu region (Cairns 1999): 28–653 m (700–750 m: Zibrowius, unpublished station data ‘Seamount 2’ DW 192).

*Type material examined.* – 18 syntypes of *Guynia annulata* Duncan, 1872 deposited at the Natural History Museum, London (NHM 1883.12.10.110–120) – Adventure Bank, Mediterranean (168m).

*Microsmilia* Koby, 1888 (monotypic, see comments in the chapter: Mesozoic Guyniidae)

*Type species.* – *Anthophyllum erguelense* Thurmann, 1851, by subsequent designation (Koby 1888).

*Type locality.* – Jurassic (Oxfordian), Switzerland, Jura Mountains (Combe-Chavatte, Montvoie, Soyhieres).

*Stratigraphic and geographic range.* – Jurassic (Oxfordian), Switzerland.

*Type material examined.* – Hypotypes NHMB D4864–4880.

#### *Onchotrochus* Duncan, 1870

*Type species.* – *Onchotrochus serpentinus* Duncan, 1870, by monotypy.

*Type locality.* – Late Cretaceous (Senonian), England, Charlton (Kent).

*Stratigraphic and geographic range.* – England: *O. serpentinus* (Senonian; Grey Chalk, Lower White Chalk; Duncan 1870). Germany (Helgoland): *O. cf. serpentinus* (middle-late Turonian; Hillmer & Scholz 1991), Senonian of Poland (herein).

*Other species attributed.* – *O. cartei* – England (Early Cretaceous, Albian (Upper Greensand) – Duncan 1870), Crimea (Late Cretaceous, Cenomanian – Kuz'mičeva 1987).

#### *Pedicellocyathus* Cairns, 1995 (monotypic)

*Type species.* – *Pedicellocyathus keyesi* Cairns, 1995, by original designation.

*Type locality.* – Recent Pacific Ocean, off North-Eastern New Zealand, 37°38.5'S/178°56.4'E, 143–153 m.

*Stratigraphic, geographic, and bathymetric range.* – Recent, endemic to NE coast of New Zealand, 70–194 m (Cairns 1995).

*Type material examined.* – Holotype: MoNZ CO285. Paratypes: USNM 94268 (1), USNM 94269 (1), USNM 94270 (1).

#### *Pourtalocyathus* Cairns, 1979 (monotypic)

*Type species.* – *Ceratotrochus hispidus* Pourtalès, 1878, by original designation.

*Type locality.* – Recent, Atlantic Ocean, Straits of Florida, 23°02'N/83°10'W, 567 m.

*Stratigraphic, geographic, and bathymetric range.* – Tertiary (Late Miocene–Middle Pliocene: Greater Antilles – Haiti (Cairns & Wells 1987). Recent: Caribbean Sea (Greater Antilles), Straits of Florida (Cairns 1979); 349–1200 m.

*Type material examined.* – Holotype: MCZ 5583.

#### *Sakalavicyathus* Alloiteau, 1958 (monotypic)

*Type species.* – *Sakalavicyathus collignoni* Alloiteau, 1958.

*Type locality.* – Cretaceous (Maastrichtian), Mitsinjo, Madagascar.

*Stratigraphic, geographic range.* – Cretaceous (Maastrichtian), Mitsinjo, Madagascar.

*Type material examined.* – Holotype (Alloiteau 1958, pl. 27: 18, 16–17 – with erroneous caption as *Aplopsammia collignoni* nov. gen. nov. sp., and erroneous stratigraphic and locality data – not Albian of Ambarananga but Maastrichtian of Mitsinjo), and paratypes (Alloiteau 1958, pl. 27: 10–15 – only even numbers were actually given). MNHN, Paris (coll. M. Collignon).

#### *Schizocyathus* Pourtalès, 1874 (monotypic)

*Type species.* – *Schizocyathus fissilis* Pourtalès, 1874, by monotypy.

*Type locality.* – Recent; Atlantic Ocean, Barbados (Josephine Bank), 183 m.

*Stratigraphic, geographic, and bathymetric range.* – Recent: Atlantic Ocean (e.g., West Atlantic – Pourtalès 1874, Linström 1877, Cairns 1979; East Atlantic – Gravier 1920, Zibrowius 1980); 88–1450 m.

*Type material examined.* – 41 syntypes (3 lots): MCZ, Harvard (5470, 2791).

*Stenocyathus* Pourtalès, 1874

*Type species.* – *Coenocyathus vermiformis* Pourtalès, 1868, by monotypy.

*Type locality.* – Recent; Atlantic Ocean, Florida; 274–329 m.

*Stratigraphic, geographic, and bathymetric range.* – *Pliocene* (Sicilia – Helmut Zibrowius, unpublished data). *Recent* (nearly global distribution – unknown only from eastern Pacific): Atlantic Ocean (Portalès 1868, 1874; Cairns 1979; Zibrowius 1980), Mediterranean (Zibrowius 1980), Indian Ocean (Marenzeller 1904, Zibrowius 1974, Cairns & Keller 1993), West Pacific Ocean (Cairns 1994, 1995), circum-Antarctic seas (Cairns 1982); 80–1229 m.

*Type material examined.* – 38 syntypes (4 lots): MCZ, Harvard 2790, 5587, 5605, and one unnumbered).

*Other species attributed.* – Eocene: Tonga (Eua Island): *Stenocyathus hoffmeisteri* Wells, 1977. Wells (1977, p. G11) mentioned also one undescribed Late Oligocene species of *Stenocyathus* from Australia (Spring Creek).

*Temnotrochus* Cairns, 1995 (monotypic)

*Type species.* – *Temnotrochus kermadecensis* Cairns, 1995, by original designation.

*Type locality.* – Recent; Pacific Ocean, 3.7 km off Kermadec, 366–402 m.

*Stratigraphic, geographic, and bathymetric range.* – Recent: Pacific Ocean: Kermadec Ridge, Vanuatu region, 321–402 m.

*Type material examined.* – MoNZ BS441 (holotype), USNM 94287 (paratype).

*Truncatoguynia* Cairns, 1989 (monotypic)

*Type species.* – *Truncatoguynia irregularis* Cairns, 1989, by original designation.

*Type locality.* – Recent, South China Sea, 'Albatross' Sta. 5311: 21°33'N, 116°15'E, 161 m.

*Stratigraphic, geographic, and bathymetric range.* – Recent: Pacific Ocean: Riuku Islands, South China Sea, New Zealand and Vanuatu region (Cairns 1995, 1999); 80–350 m.

*Type material examined.* – Holotype (USNM 81890), Paratypes USNM 81891 (8 specimens).