TRIASSIC ROOTS OF THE AMPHIASTRAEID SCLERACTINIAN CORALS

EWA RONIEWICZ AND JAROSŁAW STOLARSKI

Instytut Paleobiologii, Polska Akademia Nauk, Twarda 51/55, 00-818 Warszawa, Poland,
<eron@twarda.pan.pl>, <stolacy@twarda.pan.pl>

ABSTRACT—The Early Carnian (Upper Triassic) phaceloid coral originally described by Volz (1896) as *Hexastraea fritschi,* type species of *Quenstedtiphyllia* Melnikova, 1975, reproduced asexually by ''Taschenknospung'' (pocket-budding), a process documented herein for the first time. This type of budding is recognized only in the Amphiastraeidae, a family thus far recorded only from Jurassic-Cretaceous strata. Similar to amphiastraeids, *Quenstedtiphyllia fritschi* (Volz, 1896) has separate septal calcification centers and a mid-septal zone built of serially arranged trabeculae. The most important discriminating characters of the new amphiastraeid subfamily Quenstedtiphylliinae are one-zonalendotheca and radial symmetry of the corallite in the adult stage (in contrast to two-zonal and bilateral symmetry in the adult stage in Amphiastraeinae). *Quenstedtiphyllia fritschi* shares several primitive skeletal characters (plesiomorphies) with representatives of Triassic Zardinophyllidae and, possibly, Paleozoic plerophylline rugosans: e.g., thick epithecal wall and strongly bilateral early blastogenetic stages with the earliest corallite having one axial initial septum. To interpret the phylogenetic status of amphiastraeid corals, we performed two analyses using plerophylline rugosans and the solitary scleractinian *Protoheterastraea,* respectively, as the outgroups. The resulting phylogenetic hypotheses support grouping the Zardinophyllidae with the Amphiastraeidae in the clade Pachythecaliina (synapomorphy: presence of pachytheca). Taschenknospung is considered an autapomorphy for the Amphiastraeidae. This study is the first attempt to analyze the relationships of the Triassic corals cladistically.

INTRODUCTION

SCLERACTINIAN CORALS arose during the Middle/Late Triassic as four major microstructural groups (Roniewicz and Morycowa, 1993; see also Fig. 1): 1) mini-trabecular (e.g., reimaniphylliids); 2) thick-trabecular (e.g., actinastreids, pamiroseriids); 3) fascicular (=non-trabecular, i.e., stylophyllids and gigantostylids); and 4) pachythecal (zardinophyllids). Phylogenetic relationships among these groups are poorly understood, but differences in microstructural characters, especially among pachythecal, stylophyllid, and mini/thick-trabecular groups, suggests a polyphyletic origin (Roniewicz and Morycowa, 1993). A polyphyletic origin of Scleractinia is also suggested by phylogenetic analyses of DNA sequences of shallow-water scleractinians (Romano and Palumbi, 1996; Veron et al., 1996).

Particularly intriguing is the origin and evolution of Triassic corals that have skeletal architecture strikingly similar to that of the late Paleozoic rugosans. One such coral group is the Zardinophyllidae, which resembles plerophylline rugosans by having an identical initial corallite ontogeny, an extremely thick corallite wall (in relation to the calice diameter), rhopaloid septa, and many other aspects of corallum morphology and microstructure (see Cuif, 1975b; Cuif and Stolarski, 1999; Stolarski 1999). Zardinophyllids are represented by four fossil genera: *Pachythecalis* Cuif, 1975 (early Norian), *Pachysolenia* Cuif, 1975 (early Carnian–Norian), *Pachydendron* Cuif, 1975 (early Norian–Rhaetian), and *Zardinophyllum* Montanaro-Gallitelli, 1975 (early Carnian–Rhaetian). Analysis of the skeletal structure and budding of the amphiastraeid *Quenstedtiphyllia fritschi* (Volz, 1896) has yielded new data, which have encouraged us to renew discussion of the origin and evolution of Zardinophyllidae.

MATERIAL AND METHODS

We examined the holotype of *Quenstedtiphyllia fritschi* (Volz, 1896), the only known specimen of this species. The specimen (colony fragment, size 80 × 70 × 40 mm) was collected in the lower Carnian St. Cassian Beds in the Dolomites (Southern Alps), and is housed at the Geiseltal Museum in Halle (Germany). Its original aragonite mineralogy is preserved, thus enabling microstructural and ontogenetic (blastogenetic) observations. We base our observations on thin sections (12 slides), acetate peels taken from transverse and longitudinal sections of the colony, and a series of peels made every 0.1 mm from the budding corallite.

Subsequent stages of the earliest phase of budding were traced at intervals of 2 mm due to a lack of material.

Institutional abbreviations.—MGUWr, Geological Museum, Wrocław University, Wrocław, Poland; ZPAL, Institute of Paleobiology, Warsaw, Poland; GMH, Geiseltal Museum, Halle, Germany; UMIP, University of Montana, Institute of Paleontology, USA.

MORPHOLOGY OF THE SKELETON

Zardinophyllids are solitary, i.e., *Pachythecalis* Cuif, 1975; *Zardinophyllum* Montanaro-Gallitelli, 1975; and phaceloid, i.e., *Pachydendron* Cuif, 1975; *Pachysolenia* Cuif, 1975 (probably the senior subjective synonym of *Lubowastraea* Melnikova, 1986, a form with corallites apposed to each other). A very thick wall is a predominant skeletal character. Septa are non-exsert and usually located deep in the calice. Adult coralla may have quasi-radial symmetry, whereas initial and juvenile stages are often strongly bilaterally symmetrical. In solitary *Pachythecalis* and *Zardinophyllum,* intracalicular space is filled during the ontogeny with compact sclerenchyme (stereome), whereas in phaceloid *Pachysolenia* and *Pachydendron* this space is filled with tabuloid dissepiments.

Protoheterastraeids are restricted herein to solitary *Protoheterastraea* Wells, 1937, represented by the lectotype of the type species *Protoheterastraea leonhardi* (Volz, 1896). *Protoheterastraea* has a relatively thick epithecal wall, tabuloid dissepiments, and radial symmetry. *Cerioheterastrea,* another genus assigned by Cuif (1976) to the ''*Protoheterastraea*-group'', differs significantly from *Protoheterastraea* in septal structure and endotheca, and in our opinion, these two genera should not be grouped together. Ladinian solitary/phaceloid corals with thick epitheca and tabular endotheca that resemble *Protoheterastraea* have been illustrated by Deng and Kong (1984, pl. 3, figs. 7, 9; identified as *Elasmophyllia* and, respectively, *Pinacophyllum*).

Amphiastraeids are solitary (*Cheilosmilia* Koby, 1888), phaceloid (*Amphiaulastrea* Geyer, 1955; *Aulastraea* Ogilvie, 1897; *Mitrodendron* Quenstedt, 1881; *Pleurophyllia* de Fromentel, 1856; *Hexapetalum* Eliašova, 1975; *Pseudopisthophyllum* Geyer, 1955; *Hykeliphyllum* Eliašova, 1975); cerioid (*Pleurostylina* de Fromentel, 1856); or pseudocerioid with separated polygonal corallites (*Amphiastraea* Etallon, 1859). The corallites are usually strongly bilaterally symmetrical. The wall is thick. The endotheca is built of tabuloid dissepiments, which peripherally may pass into a zone of vesicular dissepiments (Melnikova and Roniewicz,
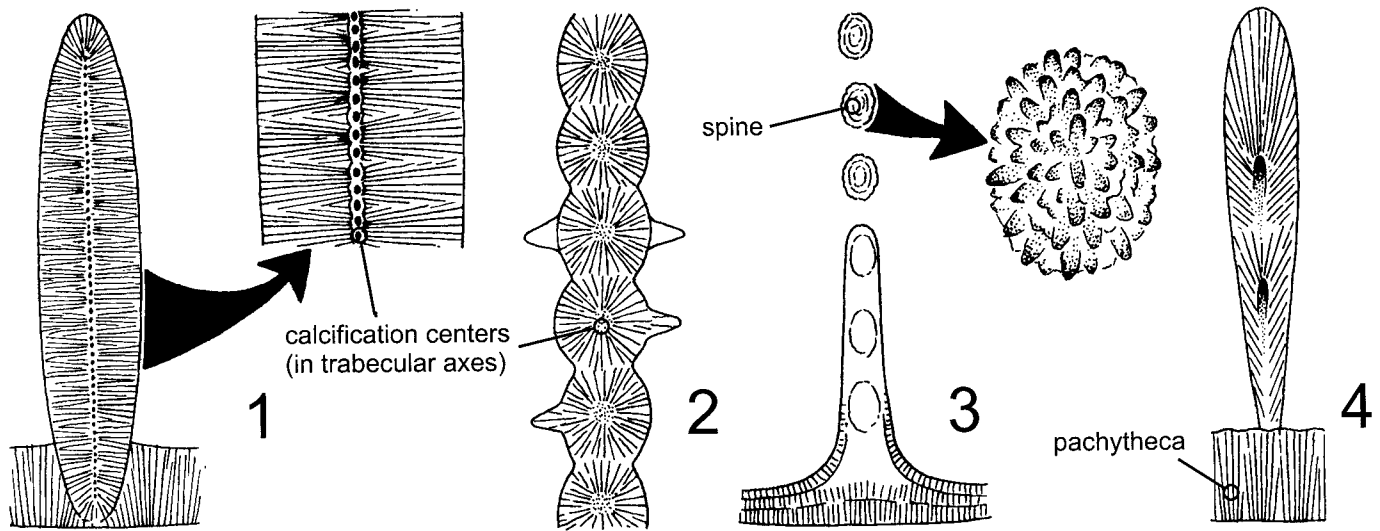
FIGURE *1*—Four basic skeletal microstructures of the Triassic Scleractinia. *1,* Minitrabecular (e.g., *Protoheterastraea*). *2,* thick-trabecular (e.g., *Chondrocoenia*) *3,* fascicular (e.g., *Stylophyllum*). *4,* pachythecal (e.g., *Pachydendron*). After Roniewicz (1996).

1976). For the present purposes, we have not included in this analysis a group of Jurassic scleractinians traditionally classified with amphiastraeids in the suborder Amphiastraeina Alloiteau, 1952: i.e., Donacosmiliidae, Carolastraeidae, Intersmiliidae. They are known only from completely recrystallized specimens, and are generally very poorly characterized, such that many of their characters would be represented in a phylogenetic analysis as missing values, producing unreliable results.

Quenstedtiphyllia fritschi (Volz) has a phaceloid growth form. The corallites are radially symmetrical with penta- and hexameral septal configurations composed of regularly distributed septa in 4 orders. The most striking morphological character is a thick wall (Fig. 2). The calicular lumen is filled by tabuloid (one-zonal) endotheca.

MICROSTRUCTURE OF THE SKELETON

Wall.—Zardinophyllidae and Amphiastraeidae have a unique type of epithecal wall—a pachytheca—with an internal layer (i.e., epithecal, or rather pachythecal stereome) built of radially oriented equal-sized fascicles of fibers ("modules" of Roniewicz and Stolarski, 1999). The calcification centers of these fascicles are at the circumference of the corallite (see Cuif, 1975b, fig. 9b), or form the axes of the fascicles (in this case, "modules" form horizontal trabeculae; see Cuif, 1975b, fig. 5b; herein Fig. 2.4). In transverse sections of various zardinophyllids, fibrous structures of the wall and septa are usually distinctly separated by a suture (indicating a temporal/spatial gap in ontogeny of these structures—e.g., *Pachythecalis, Pachydendron,* and *Pachysolenia*— Cuif, 1975b, figs. 3d, 4, 6b, 9b). Rarely, the fibers of the epithecal stereome continue into radial elements, especially those of higher orders (indicating no temporal/spatial gap in the ontogeny of these structures).

In *Protoheterastraea,* the wall is relatively thick, and built of radially oriented fibers. The fascicles of fibers are arranged into large units which are, however, much larger and less delimited than typical zardinophyllid "modules." Calcification centers are located exclusively on the perimeter of the wall. An identical type of thick epithecal wall (mature epitheca) was recognized in Recent *Gardineria* (Stolarski, 1996a, fig. 5G).

In *Quenstedtiphyllia fritschi,* the organization of fibers of the epithecal stereome shows considerable variation, ranging from fascicles of fibers with various dimensions to well delimited modules without axes (Fig. 2.1, 2.3). Generally, fascicles that form wall modules extend into the septa.

Septa.—In zardinophyllids, calcification centers of the mid-septal zone are, as a rule, not separated. They form a homogeneous zone composed of microcrystalline material in longitudinal and transverse sections of septa (vertical and horizontal sections are required to detect possibly horizontally, or respectively, vertically arranged septal trabeculae). In transverse section, fibers thickening the septum are often oriented strongly oblique to the mid-septal zone, indicating predominant axial accretion of the septum (e.g., *Pachythecalis major, Pachydendron microthallos,* see Cuif, 1975b, figs. 4, 6b respectively). Septal accretion was often rhythmic, and its successive phases can be distinguished in transverse section as superimposed secretional units (e.g., in *Pachythecalis* Cuif, 1975b, fig. 3b, d). To date, longitudinal sections of *Pachysolenia cylindrica* (type species of the genus) have not furnished us with microstructural details of septa. Thus, it is unclear whether this species has non-separated calcification centers of the mid-septal zone. In transverse section, the septa of *P. cylindrica* seem to be composed of several axially directed secretional units that have non-separated calcification centers (Cuif, 1975b, fig. 9b). However, a similar observation can also be made in transverse sections of septa with the trabeculae directed axially; such axialward, serially arranged trabeculae have been actually described in Carnian *Pachysolenia primorica* (see Iljina, 1984, fig. 32.1b).

In the mid-septal zone of *Quenstedtiphyllia fritschi*, calcification centers are separated, and the septa are built of serially arranged trabeculae that are oriented centripetally (Figs. 2.2, 3.1). The trabeculae, ca. 40 μm in diameter, are visible in longitudinal and oblique sections. Their tips form a sharp denticulation on the internal septal edge. Traces of axially directed trabeculae forming a regular denticulation on the axial edge of the septum were also discerned in *Q. mardjanaica* Melnikova, 1975.

In *Protoheterastraea,* calcification centers of the mid-septal zone are well separated (ca. 30–45 μm), and septal trabeculae are arranged in a fan system.

Budding.—The most common modes of asexual increase of solitary and phaceloid epithecate scleractinians are: 1) corallite division, 2) lateral budding, and, 3) "Taschenknospung" (=pocket budding). In corallite division (Fig. 5.1), the parental corallite

splits into more or less equal daughter corallites. In the splitting area, opposite septa of the parental corallite either join and form an incipient wall that separates two daughter corallites, or are not involved in corallite division. In lateral budding (Fig. 5.2), new buds grow centrifugally from the parental corallite almost from the beginning of the corallite division, whereas in Taschenknospung (Fig. 5.3) new buds enlarge at the expense of calicular space in the parental corallite until they ultimately emerge. Long-lasting parallel growth of the parental and daughter corallites results in an increase in the diameter of the latter (Fig. 6).

The term Taschenknospung was used by Ogilvie (1896) to describe a mode of budding in the Jurassic (Tithonian) amphiastreids, and by Volz (1896) for the Triassic *Hexastraea fritschi.* The first comprehensive description of Taschenknospung was based on serial sections of the Late Jurassic amphiastreids *Pleurophyllia* and *Mitrodendron* (see Roniewicz, 1966; Melnikova and Roniewicz, 1976). Typical Taschenknospung was described only for the Amphiastraeidae. It is also possible that the Heterocoeniidae budded by Taschenknospung; however, Kołodziej's (1995) interpretations are not supported by serial sections, and young "buds" may represent rejuvenated corallites.

In phaceloid Zardinophyllidae, new buds are formed by lateral budding with new corallites growing centrifugally (*Pachydendron microthallos* Cuif, 1975, pl. 14, fig. 2; *Pachysolenia cylindrica* Cuif, 1975, fig. 8a).

In *Q. fritschi,* we affirmed typical Taschenknospung budding, with new buds initially growing axialward, at the expense of the space of the parental calice, after which growth becomes centrifugal (Figs. 4.3, 4.4 5.1–5.4). One to three new calices may originate simultaneously in the pachythecal stereome of the parental calice. We distinguished the following stages of Taschenknospung budding in *Q. fritschi* (Fig. 5): i) appearance of a "disturbance" in the radial arrangement of fascicles of fibers of the epithecal stereome; ii) appearance of irregularly arranged vertical trabeculae that form a semilunar palisade of the wall delimiting the future calice; iii) formation of a small, elongated cupule ("pocket") externally to semilunar wall palisade, which is divided into two compartments by a relatively thick, primary "axial" septum; iv) transformation of the primary septum into a free and thin septum; and v) development of one or two septa to the right and left of the primary septum, and the nearly simultaneous appearance of incipient septa on the other side of the cupule.

The septa of the daughter calice are independent from those of the parental one. Observation of several sections testifies that the buds are growing within the limits of the parental calice for some time, and that they emerge at the stage with a highly advanced septal apparatus. Melnikova (1975) reported Taschenknospung in *Quenstedtiphyllia mardjanaica,* and later (Melnikova, 1986, fig. 7:1b) figured a large, daughter corallite with numerous septa that already emerged from the parental corallite.

The same stages of Taschenknospung as described above in *Q. fritschi* were distinguished in Amphiastraeidae: in *Mitrodendron* (see Roniewicz, 1966; herein Fig. 6), and *Pleurophyllia* (see Melnikova and Roniewicz, 1976, figs. 1, 2).

Budding was not observed in *Protoheterastraea leonhardi.* A branching coral assigned by Cuif (1973) to *P. leonhardi* and increasing by subequal septal division (Cuif, 1973, figs. 26, 27), actually represents a different taxon.

BIOMINERALIZATION AND ITS IMPLICATIONS

During early blastogeny of the corallum of *Quenstedtiphyllia fritschi,* two important microstructural changes occur: a) fascicles of fibers that form the inner pachythecal layer differentiate into vertical trabeculae of the primordial wall that separates parental and daughter corallites (Fig. 3.1), b) during the subsequent division of the corallites, the typical trabecular wall transforms again

into pachythecal wall. "Modular" style of biomineralization (with horizontal modules having circumferential calcification centers) is thus changed into trabecular one (with vertical trabeculae having axially arranged calcification centers). The "modular" biomineralization style is restored during the subsequent growth after the separation of daughter and adult corallites (in the blastogeny of corals with a trabecular wall, e.g., *Madrepora,* trabecular style calcification of the wall is uninterrupted; e.g., Stolarski, 1996b, pl. 6.3). In the skeletal ontogeny of extant corals we found the following examples of analogous changes in biomineralizational styles: differentiation of separated septal calcification centers on the basal plate, the primary layer of which consists of non-separated calcification centers (e.g., in *Porites lutea,* see Jell, 1981), or formation of the epithecal wall (non-separated calcification centers) in rejuvenated corallites that otherwise have trabecular walls (e.g., in *Polycyathus muellerae,* see Roniewicz and Stolarski, 1999, fig. 3B). Similarly, in the ontogeny of azooxanthellate *Schizocyathus* and *Pourtalocyathus,* the wall may change from typical smooth epitheca (with non-separated calcification centers) to hispidotheca (with separated calcification centers that are found in spherulite-like bodies; Stolarski, 2000).

Changes in biomineralization styles that occur in skeletal ontogeny provide important clues about possible constraints on microstructural evolution of the scleractinian skeleton. They suggest that borders between microstructural groups may not be so strict as suggested before (Roniewicz and Morycowa, 1993), and that phylogenetic relationships are possible between some of these groups, e.g., pachythecaliines and protoheterastraeids as postulated herein. Nevertheless, the disparity of the Middle Triassic scleractinians is too large for us to assume their monophyletic origin, although it is possible that the number of ancestral groups was smaller than the eight groups suggested by Roniewicz and Morycowa, 1993, or the ten (or more?) groups suggested by Veron, (1995).

ADAPTIVE SIGNIFICANCE OF TASCHENKNOSPUNG

Phaceloid corals with an epithecal wall and endotheca form a separate category of "pseudocolonial" corallum organization, lying between solitaries and colonies (see Coates and Jackson, 1985; Rosen, 1986; Roniewicz and Stolarski, 1999). In solitary corals, the coelenteron forms a sort of mesenterially folded sack with one major orifice (monostomatous condition). If solitary corals reproduce asexually by transverse or longitudinal division, then the coelenteral space is shared among parental and daughter coralla for the duration of this process. Just after division, skeleton and soft tissue become, as a rule, permanently separated (e.g., Yamashiro and Yamazato, 1987). In colonial corals, the coelenteron forms a complicated network that connects better or less individualized polyps (polystomatous condition or typical colonies with well delimited polyps and corallites). In colonies, the soft tissue *and* the skeleton continue between corallites. In phaceloid corals, coelenteral space is shared between parental and daugther polyps only early in blastogeny. Formation of the epithecal wall on the entire circumference of the daughter corallite and appearance of the first tabuloid dissepiments suggest that the soft-tissue connection between daughter and parental polyps is cut off *but* the skeleton remains connected. Separation of the young polyp from the parental one was probably relatively fast in phaceloid forms with lateral budding, whereas in those with Taschenknospung, it appears to be prolonged. In *Q. fritschi,* daughter corallites are separated from the parental one by the trabecular wall (Figs. 3, 4). This kind of wall is formed by ectoderm that continues between polyps. Despite the proximity and continuation of certain parts of the soft-tissue, daughter polyps do not inherit the mesenterial system from the parental polyp as suggested by the highly underdeveloped septal system of the daughter coralla. Because development of mesenterial cycles correlates with the formation of the tentacular crown, young polyps most likely had only few tentacles, and were defended primarily by
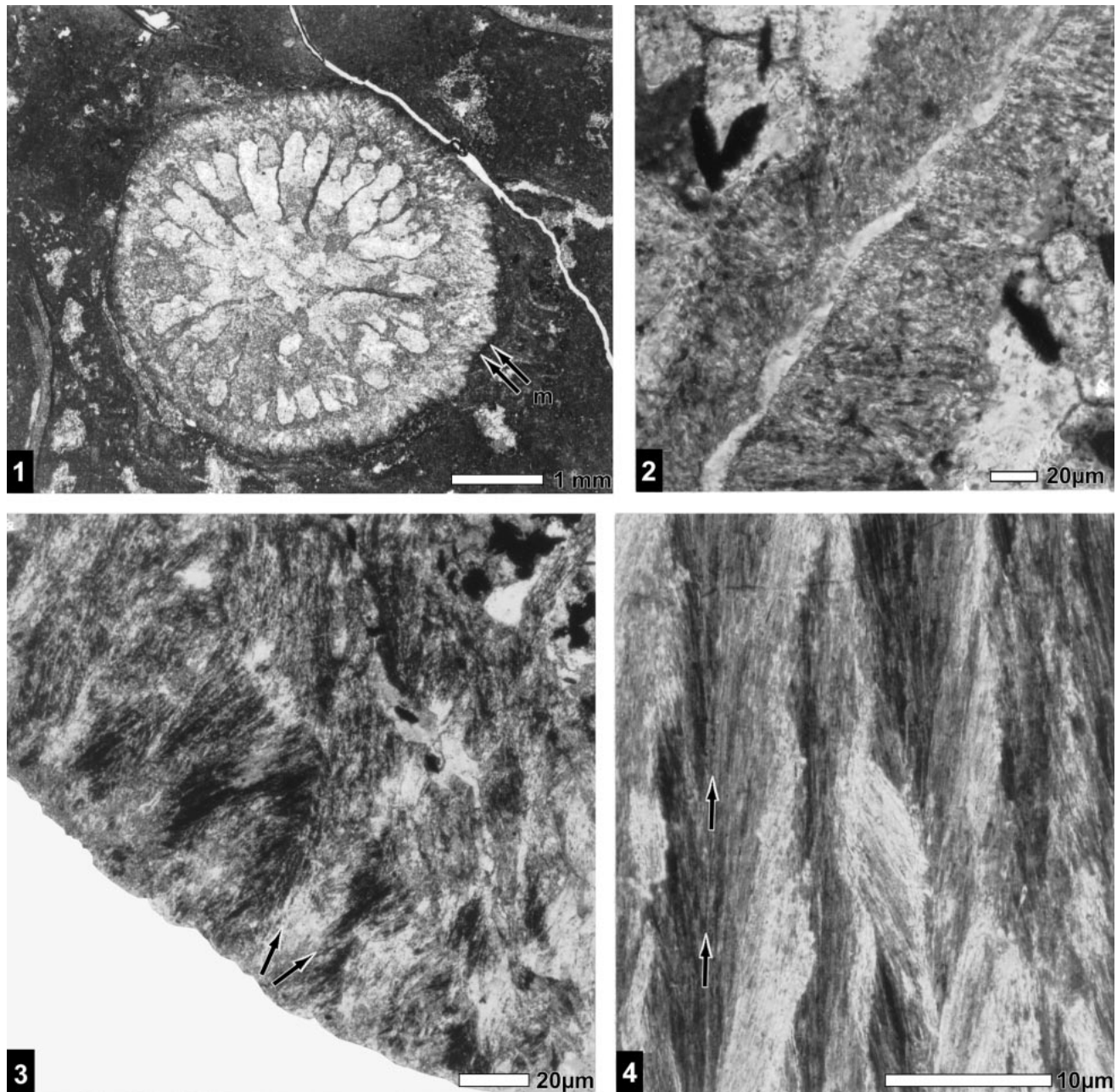
FIGURE 2—1–3, *Quenstedtiphyllia fritschi* (Volz, 1896). Lower Carnian, St. Cassian Formation, Dolomites, Italy. GMH, holotype; *1,* transverse section showing a pachythecal wall with well-delimited modules, and pentameral symmetry of the septal apparatus; *2,* longitudinal section of a septum with obliquely cut trabeculae; *3,* transverse section of the pachythecal wall; the modules have calcification centers situated on the wall circumference (arrows). *4, Pachysolenia cylindrica* (Cuif, 1975). Lower Norian, Alakir Cay, Taurus Mountains, Turkey. UMIP 196100. Transverse section of the pachythecal wall formed by horizontal modules with calcification centers in their axis (i.e., trabecular organization); see arrows.

tentacular crown of their parental polyp. Because tentacles are used in feeding, we suggest also that a young, underdeveloped polyp was dependent for a long time on the parental polyp, not only by the protection afforded by its tentacular crown but also, to some extent, by transfer of nutrients through a shared coelenteron. Ultimate separation from the parental polyp, which is indicated by the circle of epithecal wall, took place at the point of development of very well developed digestion (mesenteria) and defense (tentacular crown) systems. We contrast this budding strategy with typical lateral budding, in which shortly after the division young polyps become independent but also vulnerable to predators. Some analogy to these two types of asexual reproduction are brooding vs. broadcast spawners strategies recognized among generations reproducing sexually (e.g., Rinkevich and Loya, 1979).

PHYLOGENETIC ANALYSIS

Selection of outgroups.—Appearance of only one axial septum in the early blastogenetic stage of *Quenstedtiphyllia* followed by the strongly bilateral (two-by-two) insertion of the next septa, as
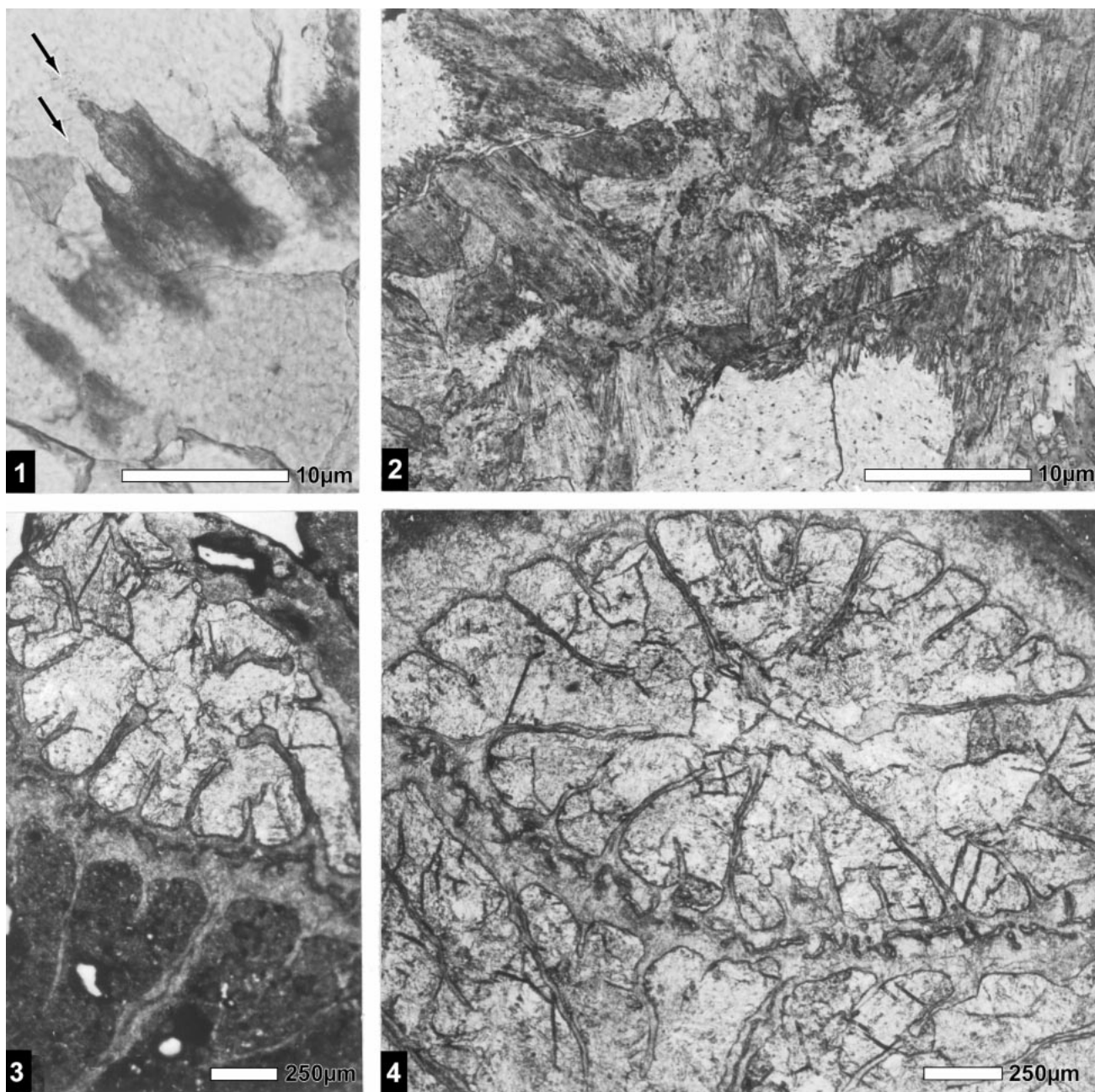
FIGURE 3—*Quenstedtiphyllia fritschi* (Volz, 1896). Lower Carnian, St. Cassian Formation, Dolomites, Italy. GMH, holotype. *1,* Longitudinal thin section of a septum showing tips of trabeculae on its internal border; *2,* transverse thin section of the wall that is developed between the parental and descendant corallite during Taschenknospung. Calcification centers of the zigzag mid-wall zone are slightly diagenetically altered (microcrystalline material is no longer recognized), thus it is not clear whether all centers were well separated (as still recognizable in some parts of this section) or whether well- and non-separated calcification centers coexisted. *3, 4,* peels of budding corallites in transverse section, showing young corallites originating by Taschenknospung. The walls dividing the corallites are formed by thick, vertical trabeculae.

well as a thick epithecal wall suggest close phylogenetic relationships among *Quenstedtiphyllia,* amphiastraeids, zardinophyllids, and, possibly, plerophylline rugosans. To test this hypothesis (see also Melnikova and Roniewicz, 1976; Stolarski, 1996a), we have first performed phylogenetic analysis using the discussed taxa and choosing plerophylline rugosans as the presumed outgroup. The concept of using plerophylline rugosans as an outgroup is still considered controversial, because no early Triassic skeletonized anthozoans have been recorded that could show an ideal series of

transitional forms between plerophylline and pachythecaliine corals (see Oliver, 1981; Fedorowski, 1997). However, in the ontogeny of *Zardinophyllum,* phases of septal insertion occur that are strikingly similar to those expected from such an "ideal transitional form" (Stolarski, 1999; see also discussion below concerned characters III to V), and we consider this as a strong argument supporting the hypothesis of the direct plerophylline descent of the pachythecaliine corals. We argue also that disparity between rugosans and scleractinians in skeletal mineralogy may
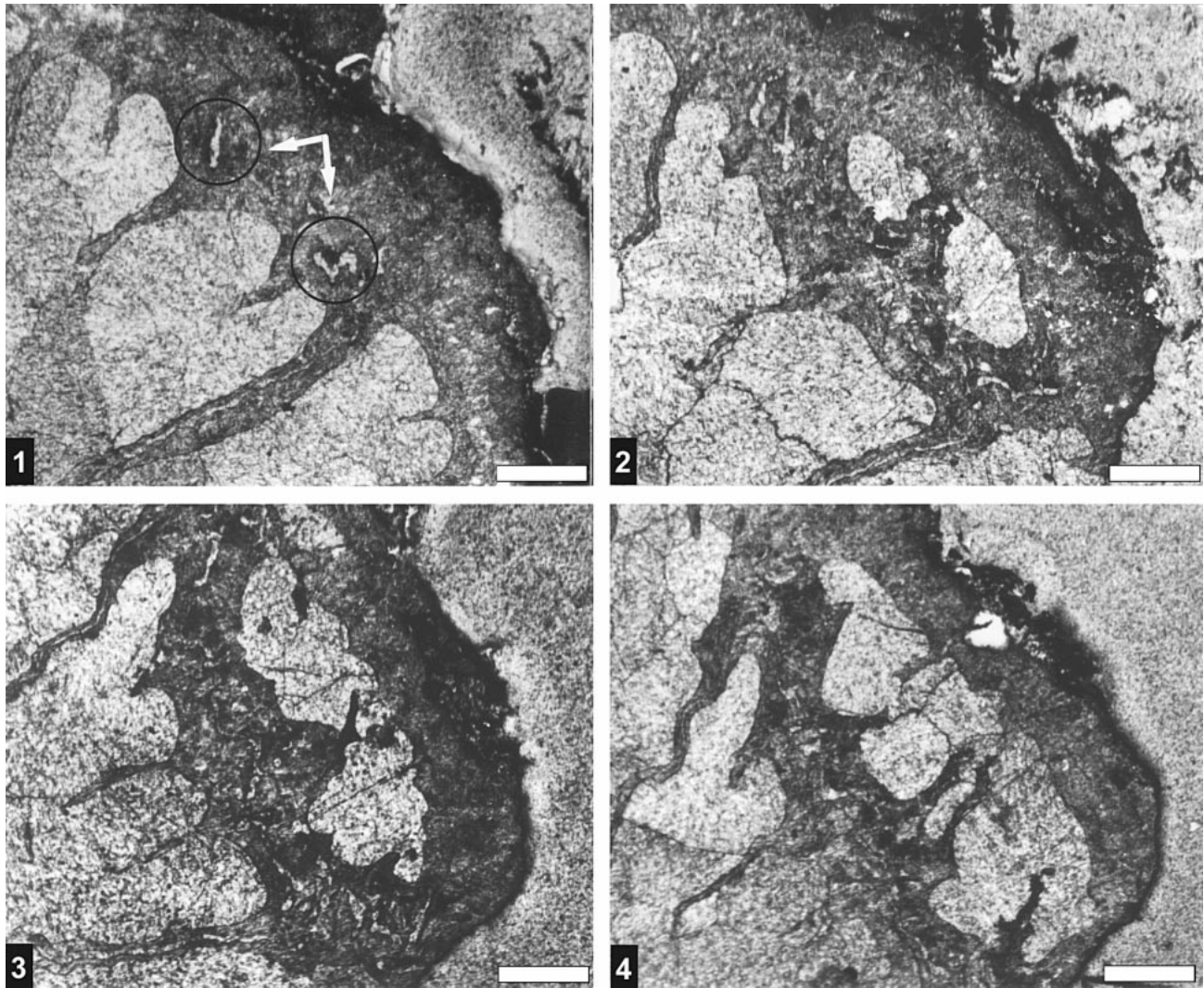
FIGURE 4—*Quenstedtiphyllia fritschi* (Volz, 1896). Lower Carnian, St. Cassian Formation, Dolomites, Italy. GMH, holotype. Early stages of Taschenknospung budding documented by transverse serial sections preserved as peels. The process is herein traced over a distance of 1.1 mm. *1,* Initial stage of formation of the wall between the bud and parental calice. The first vertical trabeculae of the new wall, formed in the widened pachytheca of the adult form, are circled (and marked with arrows); *2,* early stage of calice formation, with thick axial septum dividing the calicular lumen, and with a smooth internal wall surface. *3,* shortening of the axial septum and its transformation into a septal blade. Other septa appear symmetrically on both sides of the axial septum. The internal surface of the wall on the opposite side is covered with low ridges marking the position of appearing septa; *4,* development of the septal apparatus. The axial septum splits into two septa, and some septa appear on the opposite side. The diameter of the bud significantly increases. Measurements (*h*) give vertical height above first peel. All scale bars are 250 μm.

be less important than is traditionally suggested (Oliver, 1981); see discussion on character I.

In the second analysis, we have excluded plerophylline rugosans from the outgroup based on the traditional assumption that pachythecaliines are convergent with them (i.e., Oliver, 1981, p. 399 considered *Zardinophyllum* ''an aberrant scleractinian''). This reasoning is supported by the lack of unquestionable pachythecaliines in the earliest Middle Triassic coral assemblages (the Ladinian *Zardinophyllum* illustrated by Deng and Kong, 1984, pl. 3, fig. 1 represents, most likely, an isolated tube of the lemniscaterine hydrozoan *Cassianastraea* Volz, 1896), although this may well be interpreted as sampling bias (even Carnian–Norian zardinophyllids constitute only a subordinate group in coral assemblages and thus could be overlooked in generally poorly preserved and rare Anisian–Ladinian coral faunas). By excluding plerophyllines, few genera remain that can be reasonably considered

an outgroup of the pachythecaliines. Solitary/phaceloid corals with thick epitheca and tabular endotheca that resemble *Protoheterastraea* (see notes above in the chapter: Morphology of the Skeleton) are rare but distinct components among earliest scleractinian faunas, consisting mostly of colonial corals with relatively well integrated colonies. *Protoheterastraea* is thus used as an outgroup in the second analysis.

By choosing different outgroups, the character polarization is almost completely reversed in two analyses (compare ancestral conditions on Fig. 7).

Characters.—We used the following 10 macro- and microstructural characters (Table 1). The characters of plerophylline rugosans are those used by Hill (1981) for description of Plerophyllina Sokolov, 1960; microstructural and ontogenetic data are extracted mainly from Schindewolf (1942) and Iljina (1984).

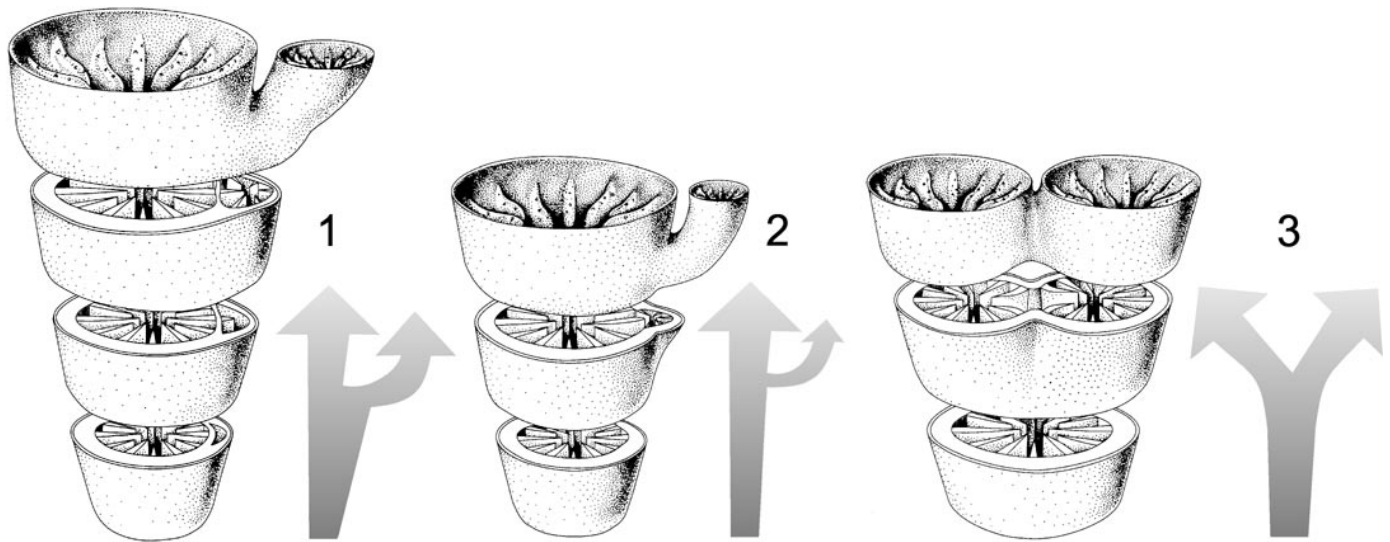*Character I.*—Skeletal mineralogy. Coralla of all scleractinians

FIGURE 5—Common budding strategies in phaceloid epithecate corals (figured models do not represent any particular taxon). *1,* Taschenknospung: new bud enlarges at the expense of calicular space in the parental corallite until ultimately emerges; *2,* lateral budding: new bud grows centrifugally from the parental corallite almost from the beginning of the corallite division; *3,* corallite division: parental corallite splits into equivalent daughter corallites.

thus far analyzed are entirely aragonitic (e.g., Cairns, 1995; Stolarski, 1996a; Cuif and Dauphin, 1998). Traces of calcite recorded from calcification centers (Constantz and Meike, 1990) seems to be of diagenetic origin (see Cuif and Dauphin, 1998; Sorauf and Cuif, 1999). In contrast, skeletons of the majority of rugosans (including Plerophyllina) are calcitic [Note—Wendt (1990) suggested that in addition to *Numidiaphyllum*, redescribed as a Permian scleractinian by Ezaki (1997), the skeleton of the typical rugosan *Ipciphyllum arnouldi* was also originally aragonitic, but this information needs verification]. Global geochemical fluctuations, especially changes in Mg/Ca ratio of seawater, have been suggested as guiding the evolution of skeletal mineralogy in many groups of organisms (e.g., Railsback and Anderson, 1987; Stanley and Hardie, 1998). One may suggest that the radical shift in Mg/Ca ratio of seawater across the P/T boundary, which favored evolution of aragonite secretors in the Triassic, also played an important role in the skeletal mineralogical transformation between the plerophyllines and the pachythecaliines. In our opinion however, geochemical factors themselves were not a main triggering mechanism of the suggested mineralogical change in biocalcification. Rather they could provide a favorable environmental background that coincided with changes in composition of skeletogenous organic matrices (Cuif and Stolarski, 1999). Insights into such biologically driven changes of skeletal mineralogies are provided by the stylasterids (Cnidaria, Hydrozoa), in which calcite vs. aragonite skeletal mineralogies may occur in different species and, interestingly, even in the ontogeny of one species (Cairns and Macintyre, 1992). Calcite-aragonite changes in skeletal mineralogy also occur in the ontogeny of other invertebrates e.g., some bryozoans (see Sandberg, 1975) and ostreid bivalves (Medakovic et al., 1997). At least in mollusks, aragonite vs. calcite polymorphism of shell layers was proven to be controlled by organic macromolecules (Falini et al., 1996; Miyamoto et al., 1996; Choi and Kim, 2000). These data suggest that mineralogical differences between the Rugosa and the Scleractinia may not be as important as thought by some authors as evidence against the hypothesis of the plerophylline → pachythecaliine transition (Oliver, 1981; Fedorowski, 1997). In our analysis, calcitic mineralogy is interpreted to be the plesiomorphic state, as it is found in plerophyllines.

This character is removed from the analysis using *Protoheterastraea* as an outgroup, since aragonitic mineralogy is autapomorphic for Scleractinia.

Character II.—Budding. The solitary state (absence of the budding) is found in many plerophyllines. However, some of them form phaceloid colonies by lateral budding (e.g., *Calophyllum gemmatum* Iljina, 1984, fig. 58). We assumed the polymorphic character state (solitary/lateral budding) to be ancestral.

The solitary character state is found in *Protoheterastraea,* and in the second analysis, the solitary character state is used as ancestral.

Character III.—One/two or axial initial septa. In plerophylline rugosans, the initial ontogeny is fully comparable, including appearance of a one/axial septum as the first radial element of skeletal ontogeny/blastogeny (compare Iljina, 1984; Stolarski, 1999). Presence of one/two or axial initial septa is thus taken as the plesiomorphic state in the first analysis. We assume that the early ontogenetic stages of zardinophyllid and the early blastogenetic stages of amphiastraeids are similar. In the earliest blastogenetic stages in rugose corals (or, hystero-ontogeny using the terminology of rugosan students; see Smith and Ryder, 1926), brephic and sometimes early neanic stages of the protocorallite ontogeny can be skipped (Oliver, 1968; Jull, 1973). However, it is reasonable to assume that in corals with rugose-style early ontogeny, hystero-ontogeny mirrors protocorallite ontogeny because in the hystero-ocorallite no stage of protocorallite ontogeny is skipped (compare early hysterocorallites of *Pachydendron* in Cuif, 1975b, figs. 5a, 7a, and early protocorallite of *Pachythecalis* in Cuif, 1975b, pl. 13:2). In typical scleractinian corals, i.e., with simultaneous insertion of six protosepta, hysterocorallites also mirror this stage of septal development.

In the second analysis with *Protoheterastraea* as an outgroup, absence of one/two or axial septum is used as ancestral state.

Character IV.—Insertion of initial septa. The ancestral condition of this character is considered to be two-by-two protoseptal insertion as found in solitary plerophyllines.

Simultaneous insertion of initial septa is assumed to be ancestral in the second analysis.

Character V.—Metaseptal insertion. Metasepta are inserted serially in plerophylline rugosans and this character state is thus
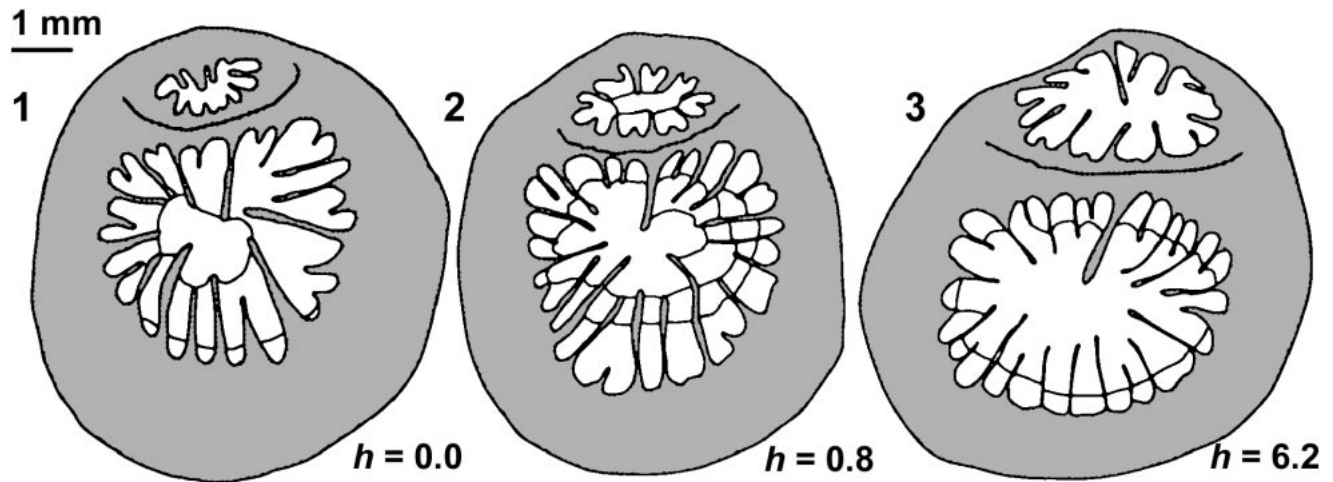
FIGURE 6—*Mitrodendron ogilviae* Geyer, 1955. Lower Kimmeridgian (Upper Jurassic), Swiętokrzyskie Mountains (Holy Cross Mts.), Poland. ZPAL H.III/111. A series of transverse sections showing some stages of formation of a young corallite produced by Taschenknospung. Typical amphiastraeid prominence of an axial septum is shown in the right section. The new bud expands primarily into the cavity of the parental calice. Measurements (*h*) give vertical height above first peel.

considered plesiomorphic in the first analysis. In the adult stage of *Zardinophyllum,* the metasepta appear to be inserted cyclically, but the actual insertion order is irregular and not resolvable into typical cyclic or serial (the problem is discussed in detail by Stolarski 1999).

In the second analysis with *Protoheterastraea* as outgroup cyclic metaseptal insertion is considered ancestral.

Character VI.—Strong bilateral symmetry in the adult stage. In many corals, septa that appear first in ontogeny retain their prime character of being the largest also in the adult growth-stage. In corals with one/two or axial septa in initial ontogeny, some or all these septa (considered directive) are the largest, but also can be disproportionately small or reduced. These septa confer a strong bilateral symmetry on the corallite. The ancestral condition is considered to be the presence of strong bilateral symmetry, as found in plerophyllines.

In the second analysis a quasi-radial symmetry (absence of strong bilateral symmetry) as found in *Protoheterastraea* is considered ancestral.

Character VII.—Morphology of the adult calice. In plerophyllines, septa are formed deeply in the calice, and this character state is assumed to be ancestral.

Exsert septa are typical of *Protoheterastraea* (and the majority of scleractinians) and this character state is considered ancestral in the second analysis.

Character VIII.—Septal microstructure. The mid-septal zone of the plerophylline skeleton may consist of non-separated or separated calcification centers, and we assume this polymorphic character state is ancestral in the first analysis. Septa grow in an axial direction.

In *Protoheterastraea,* calcification centers of the mid-septal zone are well separated, and we assume that this is the ancestral condition in the second analysis.

Character IX.—Wall. Presence of thick epitheca is the assumed ancestral state as found in plerophyllines (first analysis) and *Protoheterastraea* (second analysis).

Character X.—Endotheca. Plerophyllines have endothecate and non-endothecate coralla, and this polymorphic state is a plesiomorphic character in the first analysis. Because *Protoheterastraea* has endotheca, this character state is assumed ancestral in the second analysis.

Methods and results.—Phylogenetic trees were generated using PAUP 4.0b (Swofford, 1998). Characters were coded as binary variables (0,1) or as multistate characters (0, 1, 2), the 0 state reflecting the presumed ancestral condition. Polymorphic states were coded as (0/1) and missing values were indicated by "?". All multistate characters were treated unordered.

The first analysis (plerophylline rugosans as an outgroup) resulted in 20 equally parsimonious trees generated in the exhaustive search algorithm, each having 16 steps and a consistency index (CI) of 0.8125. Successive weighting by maximum value of rescaled consistency indices—a procedure for weighting characters a posteriori according to their cladistic consistency (see Kitching et al., 1998)—reduces the number of trees to five, with a consistency index CI = 0.9732. In all five trees the Quenstedtiphylliinae (a new subfamily to enclose *Quenstedtiphyllia*—see systematic paleontology section) is grouped with Amphiastraeinae (the synapomorphy is Taschenknospung). The 50 percent majority rule consensus tree of all five trees (consensus tree formed from those components that occur in at least 50 percent of five trees) is illustrated as Figure 7.1. This tree is identical to one of five equally parsimonious trees and apomorphies from this tree are added to this cladogram.

The second analysis (*Protoheterastraea* as an outgroup; plerophyllines removed) resulted in 5 equally parsimonious trees generated in the exhaustive search algorithm, each having 13 steps and a consistency index (CI) of 0.8462. In all five trees the Quenstedtiphylliinae is grouped with Amphiastraeinae (the synapomorphy is Taschenknospung). The 50 percent majority rule consensus of all five trees is illustrated as Figure 7.2.

In both analyses, the clade (Amphiastraeinae and Quenstedtiphylliinae) is supported by the same synapomorphy: Taschenknospung type of asexual increase. Pachythecaliina (or, Hexanthiniaria Montanaro-Gallitelli, 1975 considered as separate from the anthozoan order Scleractinia), the larger clade that includes amphiastraeinae, quenstedtiphylliine and zardinophyllid genera, is supported by the synapomorphy: presence of the pachythecal wall.

Rationale for using microstructural characters in coral phylogenetic analysis.—This is a first and preliminary study of phylogenetic relationships of pachythecaliine corals; comprehensive analysis of all groups of Mesozoic corals considered to be related to pachythecaliines and protoheterastreids will be published separately. There are several questions concerning usefulness of cladistic methodology for coral studies in general. Some workers
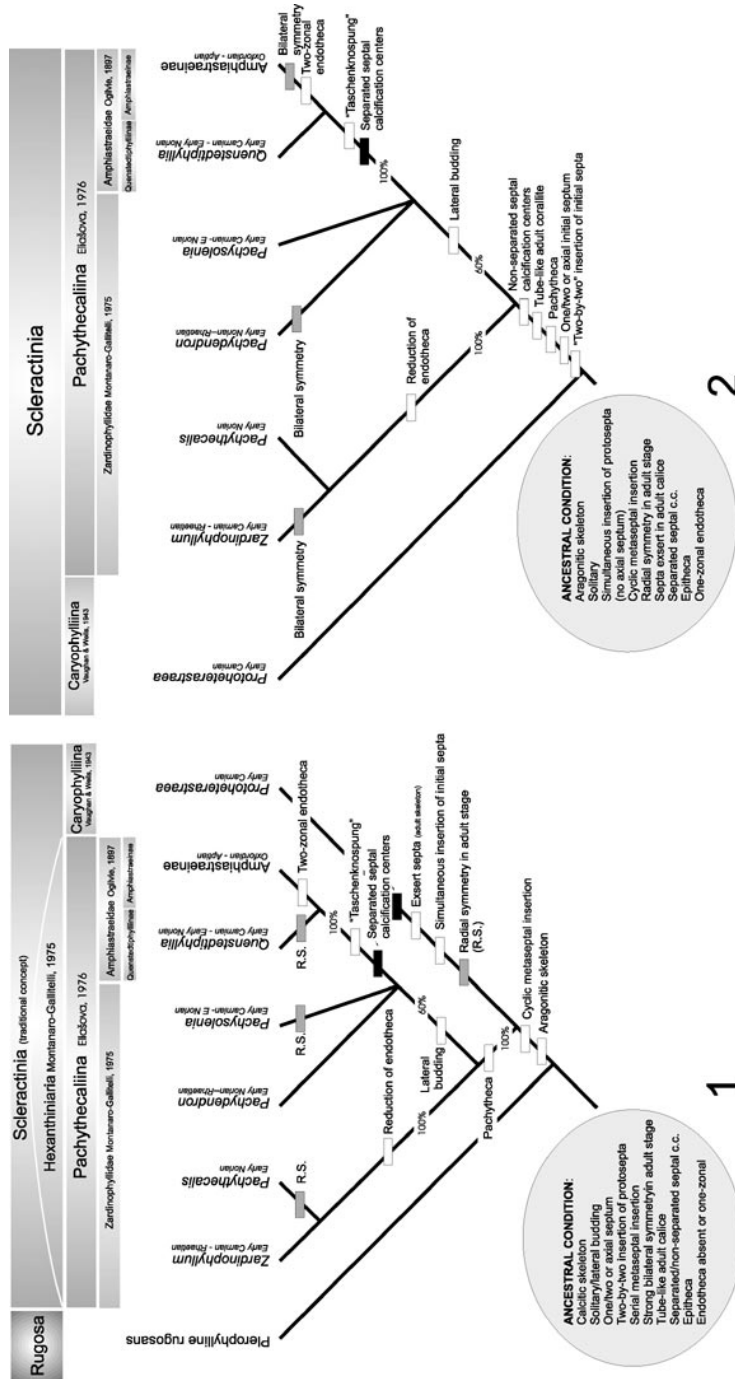
FIGURE 7—1, Fifty-percent majority-rule consensus tree of five trees obtained in analysis (characters reweighted by maximum value of rescaled consistency indices) using plerophylline rugosans as an outgroup. Numbers on internode branches indicate the percent of trees that supports each node, R.S. is abbreviation of the character state: radial symmetry in adult stage). This tree is identical to one of five equally parsimonious trees and apomorphies from this tree are added to this cladogram. 2, Fifty-percent majority-rule consensus of five trees obtained in analysis with *Protoheterastraea* as an outgroup (all characters have equal weight). This tree is identical to one of five equally parsimonious trees and apomorphies from this tree are added to this cladogram. Numbers on internode branches indicate the percent of trees that supports each node. Stratigraphic ranges of taxa after: Cuif, 1975b; Melnikova, 1986; Montanaro-Gallitelli, 1975; Morycowa, 1971; Morycowa and Marcopoulou-Diacantoni, 1994; Roniewicz and Michalik, 1991; Turnšek and Ramovš, 1987.

TABLE *1*—Characters and character states (1) and character matrix (2) used in the phylogenetic analyses of pachythecaliine families. The full set of characters was used in the first analysis, which uses plerophylline rugosans as the outgroup. Bold characters and taxa are those that were removed from the second analysis, which uses *Protoheterastraea* as the outgroup.

1.

Character	Character states
I. Skeletal minerology	**0. Calcitic; 1. Aragonitic**
II. Budding	0. Absent (solitary); 1. Parietal-lateral; 2. Parietal-Taschenknospung
III. One/two or axial initial septum	0. Present; 1. Absent
IV. Insertion of initial septa	0. Two-by-two; 1. Simulataneous
V. Metaseptal insertion	**0. Serial; 1. Cyclic**
VI. Strong bilateral symmetry in the adult corallite	0. Present; 1. Absent (radial symmetry)
VII. Morphology of the adult calice	0. Tube-like; 1. Septa exsert
VIII. Septal microstructure	0. Non-separated c.c. (axialward growth); 1. Separated c.c. (axialward growth); 2. Separated c.c. (fan-like growth)
IX. Wall	0. Epitheca; 1. Pachytheca
X. Endotheca	0. Absent; 1. One-zonal (tabular); 2. Two-zonal (tabular and vesicular)

2.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
Plerophyllina	*0*	*0/1*	*0*	*0*	*0*	*0*	*0*	*0/1*	*0*	*0/1*
Zardinophyllum	0	0	0	0	**0**	0	0	0	1	0
Pachythecalis	1	0	0	0	**1**	1	0	0	1	0
Pachydendron	1	1	0	0	**1**	0	0	0	1	1
Pachysolenia	1	1	?	?	**1**	1	0	?	1	1
Quenstedtiphyllia	1	2	0	0	**1**	1	0	1	1	1
Amphiastraeinae	1	2	0	0	**1**	0	0	1	1	2
Protoheterastraea	**1**	0	1 (?)	1	**1**	1	1	2	0	1

argue that cladistics may not be successful, firstly, because homoplasy is very abundant and recurrent evolutionary trends were recognized in many coral lineages (Webb, 1993, 1996), and secondly because coral evolution shows a reticulate pattern (Veron, 1995). Webb's (1993) arguments that convergent characters used in most coral studies are not compensated in phylogenetic analysis by non-convergent characters, clearly hold for many morphologic characters (e.g., colony type and shape) which, almost exclusively, have been used in phylogenetic analyses of corals. However, many microstructural characters (e.g., pattern of distribution of calcification centers) and those concerning skeletal ontogeny (e.g., early phases of skeleton formation) appear more stable during coral evolution (but see discussion in "Biomineralization and its implication" chapter and Stolarski, 2000), and we believe that their use may help to refine application of the cladistic approach to corals. Veron's (1995) concept of reticulate evolution, though of potentially great impact on coral evolutionary studies, still needs to be confirmed by empirical studies like those by Kenyon (1997) on *Acropora*.

SYSTEMATIC PALEONTOLOGY

Suborder PACHYTHECALIINA Eliašova, 1976 emended herein

Emended diagnosis.—Corals with pachytheca.

Family AMPHIASTRAEIDAE Ogilvie, 1897 emended herein

Emended diagnosis.—Pachythecaliines with the Taschenknospung type of asexual increase. Separated septal calcification centers.

Discussion.—More details about amphiastraeids can be found in Beauvais (1974, 1976), Eliasova (1975, 1976, 1978), and Kołodziej (1995). Among the amphiastraeids we distinguish two subfamilies: Amphiastraeinae Ogilvie, 1897 and Quenstedtiphylliinae subfam n.

Subfamily AMPHIASTRAEINAE Ogilvie, 1897

Diagnosis.—Amphiastraeids with two-zonal endotheca. Corallites with bilateral symmetry in the adult stage.

Genera included.—*Amphiastraea* Étallon, 1859 (?Callovian, Kimmeridgian–Aptian), *Pleurostylina* de Fromentel, 1856 (Argovien–Tithonian), *Amphiaulastraea* Geyer, 1955 (Tithonian–Albian), *Aulastraea* Ogilvie, 1897 (Tithonian), *Mitrodendron* Quenstedt, 1881 (Oxfordian–Aptian), *Pleurophyllia* de Fromentel, 1856 (Oxfordian–Tithonian), *Hexapetalum* Eliašova, 1975 (Tithonian), *Hykeliphyllum* Eliašova, 1975 (Tithonian), *Cheilosmilia* Koby, 1888 (Kimmeridgian–Tithonian).

Occurrence.—Jurassic (Oxfordian)–Cretaceous (Aptian); Europe, Africa,? North America.

Subfamily QUENSTEDTIPHYLLIINAE new subfamily

Diagnosis.—Amphiastraeids with one-zonal (tabular) endotheca. Corallites with quasi-radial symmetry in the adult stage.

Genera included.—*Quenstedtiphyllia* Melnikova, 1975
Occurrence.—Lower Carnian (Upper Triassic); Eurasia.

Genus QUENSTEDTIPHYLLIA Melnikova, 1975, emended herein

Type species.—*Hexastraea fritschi* Volz, 1896; figured in Volz, 1896, pl. 11, figs. 14–20, and herein, Figures. 1.1–1.3, 2, 3 (non *Volzeia* (*Hexastraea*) *fritschi* (Volz) *in* Cuif, 1975a, figs. 25, 26).

Species included.—*Quenstedtiphyllia fritschi* (Volz, 1896); *Quenstedtiphyllia mardjanaica* Melnikova, 1975.

Emended diagnosis.—Phaceloid with quasi-radial symmetry in the adult stage.

Occurrence.—Lower Carnian (Upper Triassic); Eurasia.

Discussion.—The generic name *Hexastraea* proposed by Volz (1896) to contain two species, *H. leonhardi* and *H. fritschi,* was rejected by Wells (1937) as preoccupied, and was replaced by a new name, *Protoheterastraea.* The lectotype specimen of *Protoheterastraea leonhardi* (indicated by Roniewicz and Morycowa, 1993), figured many times (Volz, 1896, pl. 11, figs. 22, 23; Roniewicz and Morycowa, 1993, fig. 2.1–2.3; Stolarski, 1996a, fig. 9a–c; Roniewicz and Stolarski, 1999, fig. 7a, b; non *Hexastraea leonhardi* Volz *in* Cuif, 1973, figs. 23–26), is well preserved. *P. leonhardi* is the monotypic species of the family Protoheterasteidaeae Cuif, 1977. The other species, *Hexastraea fritschi,* with a new generic name *Quenstedtiphyllia,* was included by Melnikova (1975) in the family Amphiastraeidae Ogilvie, 1897. This species was illustrated only once, in the original description by Volz (1896, pl. 11, figs. 14–20).

Among the pachythecaliines, *Quenstedtiphyllia* resembles *Pachysolenia* Cuif, 1975. Features in common with *Pachysolenia* are: phaceloid growth form, radial symmetry, and tabular endotheca. Differences between them lie in: (1) the microstructure of the pachytheca, which in *Quenstedtiphyllia* is built of modules that are centered on the wall (Fig. 2.3), not along subhorizontal axes (Fig. 2.4), as in *Pachysolenia* (and zardinophyllids), (2) the mode of budding, which in *Quenstedtiphyllia* is a typical Taschenknospung and different from the lateral budding observed in *Pachysolenia,* and possibly (3) in the microstructure of the septa: the non-separated calcification centers of the mid-septal zone in *Pachysolenia* (see remarks on septal microstructure, above in the text) are different from the separated calcification centers in amphiastraeids.

CONCLUSIONS

1) The Early Carnian (Upper Triassic) phaceloid *Quenstedtiphyllia fritschi* (Volz, 1896) reproduced asexually by Taschenknospung (pocket-budding), a character considered an autapomorphy for Amphiastraeidae.

2) New polyps created by Taschenknospung became separated from the parental polyp after digestive (mesenteria) and defense (tentacular crown) systems were well developed. They thus were possibly better adapted to feeding and less vulnerable to predators than polyps created by lateral budding.

3) Changes in biomineralization styles that occur in blastogeny of *Q. fritschi* (modular vs. trabecular style of biocalcification) provide important clues about possible constraints on the microstructural evolution of the scleractinian skeleton. This casts light on possible phylogenetic relationships between corals with different types of skeletal microstructures (e.g., zardinophyllids and protoheterastraeids), which have thus far been considered unrelated.

4) *Quenstedtiphyllia fritschi* shares several plesiomorphies with Triassic Zardinophyllidae: e.g., very thick, modular epithecal wall (pachytheca) and strongly bilateral early blastogenetic stages with the earliest corallite having one axial initial septum. One-zonal-endotheca (vs. two-zonal in Amphiastraeinae) is a distinguishing character of the new amphiastraeid subfamily Quenstedtiphylliinae. Phylogenetic analysis of zardinophyllids and amphiastraeids supports the grouping of Zardinophyllidae with Amphiastraeidae in the clade Pachythecaliina (synapomorphy: presence of pachytheca).

REFERENCES

BEAUVAIS, L. 1974. Studies upon the characters of the suborder Amphiastraeida Alloiteau, p. 238–248. *In* B. S. Sokolov (ed.), Ancient Cnidaria 1. Nauka, Novosibirsk.

BEAUVAIS, L. 1976. Etude morphologique, taxonomique et phylogénétique du sous-ordre Amphiastraeida Alloiteau. Mémoires de la Société Géologique de France, nouvelle sér., 50 (126):5–42.

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

CAIRNS, S. D. AND I. G. MACINTYRE. 1992. Phylogenetic implications of calcium carbonate mineralogy in the Stylasteridae (Cnidaria: Hydrozoa). Palaios, 7:96–107.

CHOI, C. S., AND Y. W. KIM. 2000. A study of the correlation between organic matrices and nanocomposite materials in oyster shell formation. Biomaterials, 21:213–222.

COATES, A. G., AND J. B. C. JACKSON. 1985. Morphological themes in the evolution of clonal and aclonal marine invertebrates, p. 67–106. *In* J. B. C. Jackson, L. W. Buss, and R. E. Cook (eds.), Biology and Evolution of Clonal Organisms. Yale University Press, New Haven.

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

CUIF, J. P. 1973. Recherches sur les Madréporaires du Trias. I. Famille

Stylophyllidae. Bulletin du Muséum National d'Histoire Naturelle, Sciences de la Terre, 17 (for 1972):211–291.

CUIF, J. P. 1975a. Recherches sur les Madréporaires du Trias. II. Astraeoida. Révision des genres *Montlivaltia* et *Thecosmilia*. Etude de quelques types structuraux du Trias de Turquie. Bulletin du Muséum National d'Histoire Naturelle, Sciences de la Terre, 40 (for 1974):293–400.

CUIF, J. P. 1975b. Caractères morphologiques, microstructuraux et systématiques des Pachythecalidae nouvelle famille de Madréporaires triasiques. Géobios, 8:157–180.

CUIF, J. P. 1976. Recherches sur les Madréporaires du Trias. Formes cério-méandroides et thamnastérioides du Trias des Alpes et du Taurus sud-anatolien. Bulletin du Muséum National d'Histoire Naturelle, Sciences de la Terre, 53:65–195.

CUIF, J. P. 1977. Arguments pour une relation phylétique entre les Madréporaires paléozoïques et ceux du Trias. Implications systématiques de l'analyse microstructurale des Madréporaires triasiques. Mémoires de la Société Géologique de France, n.s., 56 (129):1–54.

CUIF, J. P., AND Y. DAUPHIN. 1998. Microstructural and physico-chemical characterization of 'centers of calcification' in septa of some Recent scleractinian corals. Paläontologische Zeitschrift, 72:257–270.

CUIF, J. P., AND J. STOLARSKI. 1999. Origin and paleobiology of wall-based corals. Abstracts of the 8th International Symposium on Fossil Cnidaria and Porifera, Sendai, 95.

DENG ZHANQIU, AND KONG LEI. 1984. Middle Triassic corals and sponges from Southern Guizhou and Eastern Yunnan. Acta Palaeontologica Sinica, 23:489–504. (In Chinese, with English summary)

ELIAŠOVA, H. 1975. Sous-ordre Amphiastraeina Alloiteau, 1952 (Hexacorallia) des calcaires de Štramberk (Tithonien, Tchécoslovaquie). Časopis pro mineralogii a geologii, 20:1–23.

ELIAŠOVA, H. 1976. Les coraux de l'ordre Hexanthiniaria Montanaro-Gallitelli, 1975, Zoantharia de Blainville, 1830 dans les calcaires de Štramberk (Tithonien, Tchécoslovaquie). Věstnik Ústředniho ústavu geologického, 51:357–366.

ELIAŠOVA, H. 1978. La redéfinition de l'ordre Hexantiniaria Montanaro-Gallitelli, 1975 (Zoantharia). Věstnik Ústředniho ústavu geologického, 53:89–101.

ÉTALLON, A. 1859. Études paléontologiques sur le Haut-Jura. Rayonnées du Corallien. Mémoires de la Société d'Émulation du Departement du Doubs, sér. 3, 3:401–550.

EZAKI, Y. 1997. The Permian coral *Numidiaphyllum*: new insights into anthozoan phylogeny and Triassic scleractinian origins. Palaeontology, 40:1–14.

FEDOROWSKI, J. 1997. Rugosa and Scleractinia—a commentary on some methods of phylogenetic reconstructions. Acta Palaeontologica Polonica, 42:446–456.

FROMENTEL, E. DE 1856. Note sur les polypiers fossiles de l'étage portlandien de la Haute-Saône. Bulletin de la Société géologique de France, sér. 2, 13:851–864.

GEYER, O. 1955. Beträge zur Korallenfauna des Stramberger Titon. Paläontologische Zeitschrift, 29:177–216.

HILL, D. 1981. Rugosa and Tabulata, p. F5-F743. *In* C. Teichert (ed.), Treatise on Invertebrate Paleontology, Pt. F (Coelenterata), Supplement I. Geological Society of America and University of Kansas Press, Lawrence.

ILINA, T. G. 1984. Historical development of Anthozoa. Suborder Polycoeliina. Trudy Paleontologiceskogo Instituta, 198:1–183. (In Russian)

JELL, J. S. 1981. Skeletogenesis of newly settled planulae of the hermatypic coral *Porites lutea*. Acta Palaeontologica Polonica, 25 (for 1980): 311–320.

JULL, R. K. 1973. Ontogeny and hystero-ontogeny in the Middle Devonian rugose coral *Hexagonaria anna* (Whitfield), p. 59–68. *In* R. S. Boardman, A. H. Cheetham and W. A. Oliver, Jr. (eds.), Animal Colonies. Dowden, Hutchinson and Ross, Stroudsburg.

KENYON, J. C. 1997. Models of reticulate evolution in the coral genus *Acropora* based on chromosome numbers: parallels with plants. Evolution, 51:756–767.

KITCHING, I. J., P. L. FOREY, C. J. HUMPHRIES, AND D. M. WILLIAMS. 1998. Cladistics: The Theory and Practice of Parsimony Analysis (second edition). Oxford University Press, Oxford, 223 p.

KOBY, F. 1888. Monographie des polypiers jurassiques de la Suisse. Mémoires de la Société Paléontologique Suisse, 25:401–456.

KOŁODZIEJ, B. 1995. Microstructure and taxonomy of Amphiastraeina (Scleractinia). Annales Societatis Geologorum Poloniae, 65:1–17.

MEDAKOVIC, D., S. POPOVIC, B. GRZETA, M. PLAZONIC, AND M. HRS-BRENKO. 1997. X-ray diffraction study of calcification processes in embryos and larvae of the brooding oyster *Ostrea edulis.* Marine Biology, 129(4):615–623.

MELNIKOVA, G. K. 1975. Late Triassic Scleractinians of the South-Western Pamirs. p. 1–234, Donish, Dushanbe. (In Russian)

MELNIKOVA, G. K. 1986. New data on systematics and phylogeny of the pachythecaliids (Scleractinia). *In* B. S. Sokolov (ed.), Fanerozoiskie rify i korally SSSR. Nauka, Moskva. (In Russian)

MELNIKOVA, G. K., AND E. RONIEWICZ. 1976. Contribution to the systematics and phylogeny of Amphiastraeina (Scleractinia). Acta Palaeontologica Polonica, 21:97–114.

MIYAMOTO, H., T. MIYASHITA, M. OKUSHIMA, S. NAKANO, T. MORITA, AND A. MATSUSHIRO. 1996. A carbonic anhydrase from the nacreous layer in oyster pearls. Proceedings of the National Academy of Sciences of the United States of America, 93:9657–9660.

MONTANARO-GALLITELLI, E. 1975. Hexanthiniaria a new ordo of Zoantharia (Anthozoa, Coelenterata). Bollettino della Società Paleontologica Italiana, 14(1, preprint):21–25.

MORYCOWA, E. 1971. Hexacorallia et Octocorallia du Crétacé inférieur de Rarău (Carpathes orientales roumaines). Acta Palaeontologica Polonica, 16:1–149.

MORYCOWA, E., AND A. MARCOPOULOU-DIACANTONI. 1994. Cretaceous scleractinian corals from the Parnassos area (Central Greece) (preliminary note). Bulletin of the Geological Society of Greece, 30:249–273.

OGILVIE, M. 1896. Microscopic and systematic study of madreporarian types of corals. Philosophical Transactions of the Royal Society, B 187:83–345.

OGILVIE, M. 1897. Die Korallen der Stramberger Schichten. Palaeontographica (Suppl. 2), 7:76–284.

OLIVER, W. A., JR. 1968. Some aspects of colony development in corals. Journal of Paleontology, 42:16–34.

OLIVER, W. A., JR. 1981. On the relationship between Rugosa and Scleractinia (Summary). Acta Palaeontologica Polonica, 25(for 1980):339–367.

QUENSTEDT, F. A. 1881. Petrefactenkunde Deutschlands, 6: Korallen. Fues Verlag, Lepzig, 1093 p.

RAILSBACK, L. B., AND T. F. ADERSON. 1987. Control of Triassic seawater chemistry and temperature on the evolution of post-Paleozoic aragonite-secreting faunas. Geology, 15:1002–1005.

RINKEVICH, B., AND Y. LOYA. 1979. The reproduction of the Red Sea coral *Stylophora pistillata.* I. Gonads and planulae. Marine Ecology Progress Series, 1:133–144.

RONIEWICZ, E. 1966. Les Madréporaires du Jurassique supérieur de la bordure des Monts de Sainte-Croix, Pologne. Acta Palaeontologica Polonica, 11:157–264.

RONIEWICZ, E. 1996. The key role of skeletal microstructure in recognizing high-rank scleractinian taxa in the stratigraphical record. Paleontological Society Papers, 1:187–206.

RONIEWICZ, E., AND J. MICHALIK. 1991. *Zardinophyllum* (Scleractinia) from the Upper Triassic of the Central Western Carpathians (Czecho-Slovakia). Geologica Carpathica, 42:361–363.

RONIEWICZ, E., AND E. MORYCOWA. 1993. Evolution of the Scleractinia in the light of microstructural data. Courier Forschungsinstitut Senckenberg, 164:233–240.

RONIEWICZ, E., AND J. STOLARSKI. 1999. Evolutionary trends in the epithecate scleractinian corals. Acta Palaeontologica Polonica, 44:131–166.

ROSEN, B. R. 1986. Modular growth and form of corals: a matter of metamers?. Philosophical Transactions of the Royal Society of London, B 313:115–142.

SANDBERG, P. A. 1975. Bryozoan diagenesis: bearing on the nature of the original skeleton of rugose corals. Journal of Paleontology, 49:587–606.

SCHINDEWOLF, O. 1942. Zur Kenntnis der Polycoelien und Plerophyllen. Eine Studie über den Bau der ''Tetrakorallen'' und ihre Beziehungen zu den Madreporarien. Abhandlungen des Reichsamts für Bodenforschung, Neue Folge, 204:1–324.

SMITH, S., AND T. A. RYDER. 1926. The genus *Corwenia,* gen. nov. Annals and Magazine of Natural History, (9) 17:149–159.

SORAUF, J., AND CUIF, J. P. 1999. Diagenesis in Scleractinia. Abstracts of the 8th International Symposium on Fossil Cnidaria and Porifera, Sendai, 45.

STANLEY, S. M., AND L. A. HARDIE. 1998. Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in seawater chemistry. Palaeogeography, Palaeoclimatology, Palaeoecology, 144:3–19.

STOLARSKI, J. 1996a. *Gardineria*—scleractinian ''living fossil''. Acta Palaeontologica Polonica, 41:339–367.

STOLARSKI, J. 1996b. Paleogene corals from Seymour Island, Antarctic Peninsula. *In* A. Gaździcki (ed.), Palaeontological Results of the Polish Antarctic Expeditions. Pt. II. Palaeontologia Polonica, 55:51–63.

STOLARSKI, J. 1999. Early ontogeny of the skeleton of Recent and fossil Scleractinia and its phylogenetic significance. Abstracts of the 8th International Symposium on Fossil Cnidaria and Porifera, Sendai, 37.

STOLARSKI, J. 2000. Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data. Lethaia, 33:13–38.

SWOFFORD, D. L. 1998. PAUP, Phylogenetic Analysis Using Parsimony, version 4. 0b2 for Macintosh. Sinauer Associates, Inc.

TURNŠEK, D., AND RAMOVŠ, A. 1987. Upper Triassic (Norian-Rhaetian) reef buildups in the northern Julian Alps (NW Yugoslavia). Rozprave Slovenska Akademija Znanosti in Umetnosti 28(2):27–67.

VERON, J. E. N. 1995. Corals in Space and Time: Biogeography and Evolution of the Scleractinia. Cornell University Press, Ithaca, N.Y., 321 p.

VOLZ, W. 1896. Die Korallenfauna der Trias. II. Die Korallen der Schichten von St. Cassian in Süd Tirol. Palaeontographica, 443:1–124.

WEBB, G. E. 1993. Phylogeny reconstruction: problems posed by Paleozoic corals. Courier Forschungsinstitut Senckenberg, 164:71–74.

WEBB, G. E. 1996. Morphological variation and homoplasy: the challenge of Paleozoic coral systematics. Paleontological Society Papers, 1:135–157.

WELLS, J. W. 1937. New genera of Mesozoic and Cenozoic corals. Journal of Paleontology, 11:73–77.

WENDT, J. 1990. The first aragonitic rugose coral. Journal of Paleontology, 64:335–340.

YAMASHIRO, H., AND K. YAMAZATO. 1987. Studies on the detachment of the disc of the mushroom coral *Fungia fungites* with special reference to hard structural changes. Galaxea, 6:163–175.