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 *Hexastraera fritschi*, type species of *Quenstedtophyllia* Melnikova, 1975, reproduced asexually by “Taschennospung” (pocket-budding), a process documented herein for the first time. This type of budding is recognized only in the Amphiastreaidae, a family thus far recorded only from Jurassic-Cretaceous strata. Similar to amphiastreaids, *Quenstedtophyllia fritschi* (Volz, 1896) has separate calcification centers and a mid-septal zone built of serially arranged trabecculae. The most important discriminating characters of the new amphiastreaid subfamily *Quenstedtophyllinidae* are one-zonaledotheca and radial symmetry of the corallite in the adult stage (in contrast to two-zonal and bilateral symmetry in the adult stage in Amphiastreae). *Quenstedtophyllia fritschi* shares several primitive skeletal characters (pleiomorphisms) with representatives of Triassic Zardinophyllidae and, possibly, Paleozoic pleophralline rugosans: e.g., thick epithal wall and strongly bilateral early blastogenetic stages with the earliest corallite having one initial septum. To interpret the phylogenetic status of amphiastreaid corals, we performed two analyses using pleophralline rugosans and the solitary scleractinian *Protoheteractraea*, respectively, as the outgroups. The resulting phylogenetic hypotheses support grouping the Zardinophyllidae with the Amphiastreae in the clad Pachythecalina (synapomorphy: presence of pachytheca). Taschennospung is considered an autapomorphy for the Amphiastreae. 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., reimaniellidids); 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, suggest 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 pleophralline rugosans by having an identical initial corallite ontogeny, an extremely thick corallite wall (in relation to the calice diameter), rhopoidal 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: *Pachysolenia* Cuif, 1975 (probably the *Pachydendron* Cuif, 1975b; Cuif, 1975; Cuif and Stolarski, 1999; Stolarski 1999). Zardinophyllids are represented by four fossil genera: *Pachysolenia* Cuif, 1975 (early Norian), *Pachysolenia* Cuif, 1975 (early Carnian–Norian), *Pachydendron* Cuif, 1975 (early Norian–Rhætian), and *Zardinophyllum* Montanaro-Gallitelli, 1975 (early Carnian–Rhætian). Analysis of the skeletal structure and budding of the amphiastreaid *Quenstedtophyllia 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 *Quenstedtophyllia 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.

MORPHOLOGY OF THE SKELETON

Zardinophyllids are solitary, i.e., *Pachytheclus* Cuif, 1975; *Zardinophyllum* Montanaro-Gallitelli, 1975; and phaceloid, i.e., *Pachyderdon* Cuif, 1975; *Pachysolenia* Cuif, 1975 (probably the senior subjective synonym of *Lubbovastrea* Melnikova, 1986, a form with corallites opposed 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 *Pachytheclus* and *Zardinophyllum*, intracalicular space is filled during the ontogeny with compact sclerenchyme (stereome), whereas in phaceloid *Pachysolenia* and *Pachyderdon* this space is filled with tabuloid dissepiments.

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

Amphiastreaids are solitary (*Cheilosmilia* Koby, 1888), phaceloid (*Amphiulastrea* Geyer, 1955; *Aulastrea* Ogilvie, 1897; *Mitrodendron* Quenstedt, 1881; *Pleurophyllia* de Fromentel, 1856; *Hexapetalum* Eliašova, 1975; *Pseudopithophyllia* Geyer, 1955; *Hykeliphyllum* Eliašova, 1975); cerioid (*Pleurostylina* de Fromentel, 1856); or pseudocerioid with separated polygonal corallites (*Amphiastrea* 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, 1986).
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., *Pachytheclas 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 *Pachytheclas Cuif*, 1975b, fig. 3b, d). To date, longitudinal sections of *Pachysolenia cylindrica* (type species of the genus) have not furnished its 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 axially, 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 denticle 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 *Protoheterastrae*, 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 epithete scleractinians are: 1) corallite division, 2) lateral budding, and, 3) "Taschenknoespung" (=ocket budding). In corallite division (Fig. 5.1), the parental corallite

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**Figure 1**—Four basic skeletal microstructures of the Triassic Scleractinia. 1, Minitrabecular (e.g., *Protoheterastrae*). 2, thick-trabecular (e.g., *Chondrocoenia*), 3, fascicular (e.g., *Stylophylum*), 4, pachythecal (e.g., *Pachydendron*). After Roniewicz (1996).
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 Taschenknos- pung (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 de- scribe a mode of budding in the Jurassic (Tithonian) amphistreids, and by Volz (1896) for the Triassic Hexastraea fritschi. The first comprehensive description of Taschenknospung was based on serial sections of the Late Jurassic amphistreids Pleurophyllia and Mitro dendron (see Roniewicz, 1966; Melnikova and Roniewicz, 1976). Typical Taschenknospung was described only for the Amphistreaeidae. It is also possible that the Hetero- coeniidae budded by Taschenknospung; however, Kolodziej’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 (Pachy dendron 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 centrif- ugal (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 epithelial stereome; ii) appearance of irregularly arranged vertical trabecu lacae 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 Quenstedtphilia mardjunica, 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 Amphistreaeidae: in Mitro dendron (see Roniewicz, 1966; herein Fig. 6), and Pleurophyllia (see Melnikova and Roniewicz, 1976, figs. 1, 2).

Budding was not observed in Prototetadera 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 Quenstedtphilia 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-sepa- rated calcification centers (e.g., in Porites lutea, see Jell, 1981), or formation of the epithelial wall (non-separated calcification centers) in rejuvenated corallites that otherwise have trabecular walls (e.g., in Polycyathus muelleriae, see Roniewicz and Stolar- ski, 1999, fig. 3B). Similarly, in the ontogeny of azooxanthellate Schizocyathus and Pourtalocyathus, the wall may change from typical smooth epithea (with non-separated calcification centers) to hispidothea (with separated calcification centers that are found in sphurerite-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 Morzyowa, 1993), and that phylogenetic re- lationships are possible between some of these groups, e.g., pachy- thecalines and protoheterotereids 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 sug- gested by Roniewicz and Morzyowa, 1993, or the ten (or more?) groups suggested by Veron, (1995).

ADAPTIVE SIGNIFICANCE OF TASCHENKNOSPUNG

Phaceloid corals with an epithelial wall and endotheca form a separate category of “pseudocolonial” corallum organization, lying between solitary and colonies (see Coates and Jackson, 1985; Ro- sen, 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 asex- ually by transverse or longitudinal division, then the coelenteral space is shared among parental and daughter polypa for the duration of this process. Just after division, skeleton and soft tissue become, as a rule, permanently separated (e.g., Yamasuhiro and Yamazato, 1987). In colonial corals, the coelenteron forms a complicated network that connects better or less individualized polyps (polystomatous condi- tion 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 daughter polyps only early in blastogeny. Formation of the epithelial 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, daugh- ter polyps do not inherit the mesenterial system from the parental polyp as suggested by the highly underdeveloped septal system of the daughter corall. Because development of mesenterial cycles cor- relates with the formation of the tentacular crown, young polyps most likely had only few tentacles, and were defended primarily by...
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 epithelial 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., Rink-evich 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*, amphiastreaids, 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 pachyteleline 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 pachyteleline corals. We argue also that disparity between rugosans and scleractinians in skeletal mineralogy may
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 pachythecalines are convergent with them (i.e., Oliver, 1981, p. 399 considered Zardinophyllum “an aberrant scleractinian”). This reasoning is supported by the lack of unquestionable pachythecalines 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 lemniscate-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 pachythecalines. Solitary/phaceloid corals with thick epitheca and tabular endotheca that resemble 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
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 bud) 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/blastostratification (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 amphiastreaids 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 hysterocorallite no stage of protocorallite ontogeny can be skipped (Oliver, 1968; Jull, 1973).

**Character IV**—Simultaneous insertion of initial septa is assumed to be ancestral. In the second analysis with *Protoheterastraea* as an outgroup, absence of one/two or axial septum is used as ancestral state.

**Character V**—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 VI**—Metaseptal insertion. Metasepta are inserted serially in plerophylline rugosans and this character state is thus
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 *Protoheterastraeida* as outgroup cyclical 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 in the second analysis.

In the second analysis a quasi-radial symmetry (absence of strong bilateral symmetry) as found in *Protoheterastrea* 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 *Protoheterastrea* (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 *Protoheterastrea*, 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 *Protoheterastrea* (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 *Protoheterastrea* 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 Amphiasterinae (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 (*Protoheterastrea* 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 Amphiasterinae (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 (Amphiasterinae 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 amphiasterinae, quenstedtiphylline and zardinophyllid genera, is supported by the synapomorphy: presence of the pachytheccal 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 protoheterastraeids will be published separately. There are several questions concerning usefulness of cladistic methodology for coral studies in general.
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: Cui f, 1975b; Melnikova, 1986; Montanaro-Gallitelli, 1975; Morycowa, 1971; Morycowa and Marcopoulou-Diacantoni, 1994; Roniewicz and Michalik, 1991; Turnšek and Ramovš, 1987.
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 PACHYTHECALINA Eliašova, 1976 emended herein

Emended diagnosis.—Coralines with pachytheca.

Family AMPHIASTRAEDIAE Ogilvie, 1897 emended herein

Emended diagnosis.—Pachythecinae with the Taschenknos-
CONCLUSIONS

1) The Early Carnian (Upper Triassic) placeloid Quenstedtiphyllia fritschi (Volz, 1896) reproduced asexually by Taschenkospung (pocket-budding), a character considered an autapomorphy for Amphistaeriae.

2) New polyps created by Taschenkospung 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 protoheterasta) which have thus far been considered unreleated.

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 Amphistaeriae) is a distinguishing character of the new amphistaeid subfamily Quenstedtiaphylliinae. Phylogenetic analysis of zardinophyllids and amphistaeads supports the grouping of Zardinophyllidae with Amphistaeriae in the clade Pachythechalina (synapomorphy: presence of pachytheca).

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