Evolution of the post-Triassic pachythecaliine corals

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Abstract.—Triassic pachythecaliine i.e., zardinophyllids, and primitive amphiastreids, differ from the coeval scleractinians in having pachytheal wall, septa developed deeply in the calice, smooth septal faces, and two-by-two manners of the prososeptal insertion. Among Jurassic and Cretaceous corals, only amphiastreids have a thick, pachytheal wall (pachythecaliine apomorphy), whereas other supposed post-Triassic pachythecaliine i.e., carolastraeids, donacosmilids, intersmilids, and heterocoeniids, share either only some morphological characters with pachythecaliines, or their coralla are too badly preserved and no diagnostic microstructural characters are recognizable. Review of various Mesozoic taxa that previously have been linked with pachythecaliines i.e., agathelliids (Agathelia, Stylohelia, Brachthelia), Amphimeandrea, Boeaurina, and Palaeohelia, suggests that their alleged “pachythecaliine” characters are either shared with other scleractinians (trabeular peritheca of agathelliids) or not homologous with those in pachythecaliines (thick wall of Paleo- helia). Pseudoastraepora, the only Cenozoic (Eocene) coral that originally was classified as pachytechaliid, represents, most likely some distinct acroporoid taxon. It is generally assumed that pachythecaliines become extinct at the end of the Mesozoic era, and our review based on presence/absence of apomorphic characters corroborate this hypothesis. However, we still need more arguments to falsify an alternative hypothesis that some, and few apomorphic pachythecaliine characters could have been lost in some lineages that members are thus no longer recognizable as pachythecaliine descendants.

Pachythecaliina Eliášová, 1976 sensu Roniewicz & Stolarski 2001 are unique among post-palaeozoic anthozoans in having a thick, epithecal wall with characteristic modular structure (= pachythea, see Roniewicz & Stolarski 1999). Triassic Zardinophyllidae Montanaro-Galitelli, 1975 (= Pachythecalidae Cuif, 1975) and Triassic, Jurassic-Cretaceous Amphiastreidae Ogilvie, 1897 have established position among pachythecaliines (herein Pachythecaliina sensu stricto), however traditionally, few other post-Triassic groups of Mesozoic have been included to pachythecaliines, i.e., Carolastraeidae Eliášová, 1976, Donacosmilidae Krasnov, 1970, Heterocoeniidae Oppenheim, 1930, and Intersmilidae Melnikova & Roniewicz, 1976 (herein Pachythecaliina sensu lato).

Pachythecaliine s.s. have early ontogeny and several other aspects of the skeletal architecture closely comparable to that of the late Palaeozoic pterophylline rugosans. On the other hand, aragonitic skeletal mineralogy and ?quasi-cyclic septal development in the adult stage clearly suggest their relationships with typical scleractinians (see Roniewicz & Stolarski 2001). These “mixed” rugosan-scleractinian characters of pachythecaliines s.s. are considered by some authors arguments to support their rugosan ancestry (see section entitled Pachy-
thecalines *sensu stricto*: zardinophyllids and amphiasterids). Triassic pachythecalines s.s. (i.e., zardinophyllids and primitive amphiasterids) are strikingly different from the coeval scleractinians, whereas their post-Triassic representatives share several characters (e.g., bilateral symmetry of the corallite, one or two-zonal endotheca and lonsdaleoid septa) with various Late Jurassic and Early Cretaceous corals. Most of the Triassic pachythecalines s.s. are known from excellently preserved fossils, and gross morphology and microstructural observations well corroborate their distinctive status. By contrast, the majority of post-Triassic (especially Jurassic) pachythecalines s.s. and pachythecalines s.l. have poorly preserved coralla and only some general morphological characters can be extracted from fossils. Diagnostic microstructural characters (e.g., presence of the pachytheca) can only be inferred. Numerous stratigraphic gaps in the record of post-Triassic pachythecaline taxa make evolutionary studies particularly difficult and open to speculation. It is generally believed that most pachythecalines s.s. and s.l. went extinct well before the K/T extinction event, however, there exist also suggestions that some Cenozoic taxa may represent their descendants. The aim of this paper is to re-examine supposed Cenozoic pachythecalines and to review hypotheses about evolutionary pathways of post-Triassic pachythecalines.

Material and Methods

Reference material used in this study consisted of type species of the Triassic pachythecalines. Holotypes of *Pachythecalis major* Cuif, 1975; *Pachydendron microthallos* Cuif, 1975; *Pachysolenia cylindrica* Cuif, 1975 are housed at MNHN-P. Syntypes of *Zardinophyllum zardinii* Montanaro-Gallitelli, 1975 are housed at IPUM. Holotype of *Sichuanophyllia sichuanensis* Deng & Zhang, 1984 is housed at NIPAL. and holotype of *Quenstedtiophyllum fritschi* (Volz, 1896) is housed at GMH. We also examined coralla of various species of intersmillids, donacosmillids, carolastraedids, amphiasterids, and heterocoenids deposited in collections of MNHN-P, NMNH, UJ, and ZPAL.

We reexamined toptotype specimens of the Eocene *Pseudoastraecora hortensis* (Oppenheim, 1900), a Cenozoic coral that was assigned to pachythecalines. Polished and etched sections as well as general morphology and microarchitecture of the skeleton were observed by SEM. Three investigated specimens originate from the Marne blu di Cava Cunial, Possagno (Treviso, Italy), and are housed at the Instituto di Paleontologia, Università di Modena.

Comparative materials, including specimens illustrated here of fossil *Etallonasteria minima* (Étallon, 1864) and Recent *Acropora sp.* and *Alveopora altlingi*, consisted mainly of specimens housed at ZPAL and NMNH.

The following institutional abbreviations are used in the text: CGS—Czech Geological Survey, Praha, Czech Republic; GMH—Geiseltal Museum, Halle, Germany; IPUM—Institute of Paleontology, University of Modena, Italy; NIPAL—Nanjing Institute of Paleontology, China; NMNH—National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; MNHN-P—Museum National d’Histoire Naturelle, Paris, Institut de Paléontologie, France; UJ—Institute of Geological Sciences of the Jagiellonian University, Kraków, Poland; ZPAL—Institute of Paleobiology, Warsaw, Poland.

Pachythecalines *sensu stricto*: Zardinophyllids and amphiasterids

Zardinophyllids, the first Triassic pachythecalines, have a unique skeletal architecture with the corallite wall developed in advance of the septa, forming a long conical or pipe-like calice, whereas relatively few,
smooth septa are later developed, being hidden deeply in the calice. Initial and juvenile coralla show strong bilateral symmetry defined by enlarged primary septum whereas adult coralla often have quasi-radial symmetry. Separated calcification centers have not been observed in septa of *Zardinophyllum* (Fig. 1A) but apparently, they occur in...
septa of *Pachythecalis* and *Pachysolenia* (preliminary observation by the first author; see also Roniewicz & Stolarski 2001: p. 35). Because of the unusual corallum morphology (see Fig. 1A–D), the systematic position of the Triassic zardinophyllids was subject to highly divergent opinions. They were considered: members of an independent anthozoan order Hexactinaria (Montanaro Gallitelli 1975, Eliášová 1978), survivors of Rugosa (Melnikova & Roniewicz 1976, Cuif & Stolarski 1999, Stolarski 1996), or, a peculiar, "aberrant" group of Scleractinia (Oliver 1980). Supporters of the rugosan descent of zardinophyllids argue that their closest outgroup were pterophyllines. The latter are the only terminal Permian rugosans sharing with zardinophyllids initial corallite ontogeny (two-by-two protoseptal insertion, not simultaneous as in Scleractinia), an extremely thick epithecal wall (in relation to the calcareous diameter), smooth and rhopaloid septa (with characteristically bulbous axial edge), lack of extensive dissepimentarium, and many other aspects of corallum morphology and microstructure (Cuif 1975, Stolarski 1999, Cuif & Stolarski 1999).

Zardinophyllids differ from pterophylline rugosans in having an aragonite (vs. calcitic) skeleton and metasepta arranged in scleractinian-like orders. However, as suggested by Stolarski (1999), in Zardinophyllum, metasepta are inserted as spine-like projections in irregular manner (Fig. 1A) and only in late juvenile/adult stages become differentiated and sized as septal orders as in Scleractinia. Hence, they are not comparable to typical scleractinian metasepta inserted cyclically. Interestingly, zardinophyllids do not appear in the fossil record as the first group of skeletonized anthozoans (as one could thought assuming their rugosan ancestry) but they are preceded by various so called mini- and thick-trabecular corals appearing as early as Anisian (see Roniewicz & Morcowa 1989). Zardinophyllids are represented by four fossil genera: solitary *Zardinophyllum* Montana-

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**Cuif, 1975 (Fig. 1C), pachyloid *Pachysolenia* Cuif, 1975 (Fig. 1D) and *Pachydendron* Cuif, 1975 (Fig. 1B). They are considered to be the first outgroup to amphiastreids (Roniewicz & Stolarski 2001).

Amphiastreids were originally considered rugosan (Koby 1888, Ogilvie 1897), and later as zardinophyllid descendants (Melnikova & Roniewicz 1976, Roniewicz & Stolarski 2001). They retain many zardinophyllid characters (e.g., pachyloidal wall that at least can be observed in some, well-preserved specimens, Fig. 1F; juvenile and often adult corallia show strong bilateral symmetry defined by enlarged primary septum) while synapomorphic for them is "Taschenknospung" (Fig. 1E), the peculiar type of asexual increase with new buds initially grow axialward, at the expense of the space of the parental calice, and only later their growth becomes centrifugal (see details about pachyloica and Taschenknospung in Roniewicz & Stolarski 1999, Roniewicz & Stolarski 2001). Septal calcification centers are separated and relatively closely-spaced forming tips of axialward inclined trabeculae ("minitrabeculae" of Kołodziej 1995, Roniewicz & Stolarski 2001).

Amphiastreids are reported as early as the Triassic, i.e., early Carnian pachyloid Quenstedtitiphilla Melnikova, 1975 (see Roniewicz & Stolarski 2001); possibly also ceroid *Sichuanophyllia* Deng & Zhang, 1984 (= *Lubowastrea* Melnikova, 1986) represents primitive Triassic amphiastreids (Fig. 1F). In post-Triassic strata the following amphiastreid genera have been distinguished (see Fig. 6 for the stratigraphic ranges): quasi-ceroid *Amphiastrea* Étalon, 1859, *Pleurostyla* de Fromentel, 1856, *Amphiulastraea* Geyer, 1955 (Fig. 2A), pachyloid, *Aulastraea* Ogilvie, 1897, *Hexapetalum* Eliášová, 1975, *Hykeliphyllum* Eliášová, 1975, *Mitrodendron* Quenstedt, 1881, *Pleurophyllia* de Fromentel, 1856 (Fig. 2B)—probably synonymous with Cu-

Pachythecalines sensu lato Including Mesozoic Corals of Uncertain Affinity

Few other post-Triassic groups of Mesozoic, mostly epitecate corals, have been considered to be related to pachythecalines...
(most likely to amphistreids—Fig. 6): Carolastraeidae Eliášová, 1976, Donacosmilidae Krasnov, 1970, Heterocoeiniidae Oppenheim, 1930, and Intersmilidae Melnikova & Roniewicz, 1976. None of these taxa have typical pachytheal wall (or coralla are too badly preserved to observe this feature) and their affinity with pachytecalines is based on combination of characters.

Corallites of carolastraeids (Carolastraea Eliášová, 1976; Fig. 2C) show bilateral symmetry, defined by one enlarged septum—the character shared also by coeval amphistreids (and heterocoeiniids). However, unlike Amphistreids, carolastraeids have one-zonal endotheca (vs. two-zonal) and asexually increase via lateral budding (vs. Taschenknospung). Carolastraeids share most features with intersmilids (monotypic Intersmilia Eliášová, 1974; Fig. 2D), the only significant difference between them being corallite symmetry (bilateral vs. radial, respectively). Intersmilids and carolastraeids have smooth septal faces that is a rare feature among coeval scleractinians except for pachytecalines. Unfortunately, all listed characters are too general to settle the problem of the possible relationships between carolastraeids and intersmilids and between these two taxa and pachytecalines (this suggestion is presented in Fig. 6).

On the other hand, carolastraeids and intersmilids are so different from other Jurassic scleractinians (e.g., actinastreids, dermosmilids, haplarooids, montlivaltids, stylophyllids, stylids) that in absenitia of other similar to them but different from pachytecalines groups they are naturally clustered with the latter. Similar arguments have been used to demonstrate possible donacosmilid-amphistreid phylogenetic relationships.

Donacosmilids (Cylismilia Roniewicz, 1988; Donacosmia de Fromentel, 1861, fig. 2E; Prodonacosmia Melnikova, 1976; Parepismilia Beauvais, 1964) have, similar to amphistreids, two-zonal endotheca and lonsdaleoid septa but differ from them in their quasi-radial symmetry of corallites and asexual increase via lateral budding (see Roniewicz 1976).

Heterocoeiniidae are herein restricted to the following genera: Heterocoeenia Milne-Edwards & Haime, 1849, Latusastraea d’Orbigny, 1850, Fig. 2E, Latusastraeopsis Morycop & Marcopoulou-Diacantoni, 1997, Pachycoenia Alloiteau, 1952, Thecidosmilia Koby, 1888, fig. 2E, and Confusafnforma Löser, 1987 (Morycowa & Kołodziej 2001 detected neorhizopidanth septal microstructure in Aulastraeporaf aff. deangelisi Prever, 1909 and Preverastraep diaiptothecata (Hackemesser, 1936) thus suggesting placement of these traditional heterocoeiniid taxa among Rhipidogyrrina). Heterocoeiniid colonies are perithetate (i.e., with coenosteum) or ceroiid. Their corallites (except for Pachycoenia) exhibit strong bilateral symmetry (a feature common with amphistreids) but have septal faces covered with spiniform ornamentation (unlike amphistreids that usually have non-ornamented, nearly smooth septa). Traditionally, heterocoeiniid septa were considered “thick-trabeulate”, i.e., having widely-spaced septal calcification centers vs. mini-trabeulate of amphistreids (see Heterocoeenia, Latusastraea in Morycowa 1971, fig. 21).

Kołodziej (1995) provided a new insight concerning heterocoeiniid microstructures and showed that in Latusastraea exiguis de Fromentel, 1862 rudimentary septa of higher cycles are indeed formed by “thick trabeculae” deriving from the wall whereas larger septa show typical “minitrabeicular” microstructure (i.e., calcification centers are separated but closely spaced; see Kołodziej 1995: fig. 31). Another observation by Kołodziej (1995) that may bridge the gap between amphistreids and heterocoeiniids concerns calcular structures similar to Taschenknoespung in Thecidosmilia morycopwae Kołodziej, 1995. This important suggestion still needs to be proven by means of serial sections.

Other Mesozoic taxa have been considered related to pachytecalines:
Beauvais & Beauvais (1975) proposed that agatheiliids (a family to include Cretaceous Agathelia Reuss, 1854, Middle-Late Jurassic Stylohelia de Fromontel, 1861, and Middle Jurassic Brachelia Beauvais & Beauvais, 1975) are intermediate between typical stylolids (in having trabecular structure of the septa) and heterocoeoids and amphistaereids (in having peritheca composed of successive lamellae with trabeculae perpendicular to lamellar growth). Amphistaereids cannot be compared directly with agatheiliids as they do not form peritheca, nevertheless, peritheca in Brachelia and Agathelia is similar to that known in heterocoeoid Pachycoenia (see Beauvais 1982: pl. II:3). However, some caryophyllids have similar organization of extracalicular, trabecular sclerenchyme (Stolarski 1995, fig. 8A, B) and thus, microstructural criteria used by Beauvais & Beauvais (1975) are too general to allow presentation of a credible evolutionary scheme. Similar criticism concerning chosen criteria deals with Beauvais’ (1980) suggestion that late Jurassic rhipidogyrinid Bodeurina languedociensis Beauvais, 1980 is related to amphistaereids, heterocoeoids, and to stylolids, because of dense and extensive endotheca, presence of peritheca and structural continuity between septa and dissepiments, respectively. Rhipidogyrins differ from pachyhelicalines in having distinct “neorhipidicanth” septal microstructure (Roniewicz 1976) and in having an external corallite surface covered with successive tectural layers (Roniewicz & Stolarski 1999). In modern studies, they are considered related with stylolids, not with pachyhelicalines (Roniewicz & Morycowa 1993). Yet another suggestion that rhipidogyrins share some features with pachyhelicalines was given by Lebanidze (1991: 37, fig. 7), who illustrated a section of juvenile blastogenetic stage of the Tithonian rhipidogyrin Aplosmilia coalescens Ellášóvá, 1973, with one primary septum enlarged after amphistaereid fashion. For the lack of precisely oriented serial sections, the presence of a “cardinal septum” in A. coalescens, as expressed by Lebanidze (1991), should be taken cautiously (sections should exclude possibility that columella and primary septum fused—a common situation in coralla with a lamellar columella).

Beauvais (1982) suggested that Albian Palaeohelia albienensis Beauvais, 1982 is related to Triassic volzeiids (Pachyhelicalina sensu Beauvais 1980) based on very thick corallite wall and septa with non-trabecular microstructure. However, in Palaeohelia the wall is thickened centrifugally (Beauvais 1982, pl. 3: 1) as in many caryophyllids and oculinids, whereas in pachyhelicalines it grows thicker centripetally (Stolarski 1995, Roniewicz & Stolarski 1999). A different mode of wall thickening in Palaeohelia and pachyhelicalines reflect essentially different anatomic designs of polyps: in Palaeohelia tissue controlling wall thickening was lain outside the corallum, whereas in pachyhelicalines it was entirely intracalicular. Hence, buds of Palaeohelia are not “intracalicular and marginal as in amphistaereids” as interpreted by Beauvais (1982: 673) but extracalicular, enclosed during the ontogeny by the thick corallite wall. In these respects Palaeohelia fits well among traditional oculinids. Observation of septal microstructure of various Recent oculinids by the first author (Bathelia candida, Cyathelia sp., Oculina patagonica, Neohelia sp., Schizoculina africana, Sclerhelia hirtella) show that all these taxa have well-differentiated septal calcification centers (occasionally, in Sclerhelia, septal calcification centers are closely spaced). Septal calcification centers are susceptible to diagentic alteration and in corals with originally closely spaced calcification centers (like Caryophyllia—see Stolarski 1996: fig. 3C), their position is often preserved as homogenous line (compare Stolarski 1995: figs. 6A, B, 7D). Thus the homology or interpretation of characters crucial in Beauvais’ proposal and claims about “very important place in the phylogeny of the sub-
order Pachythecaleina” of *Palaeohelia* are not confirmed herein.

Beauvais & Mori (1988) considered meandroid *Amphimeandra* Beauvais & Mori, 1988 (Jurassic of Japan) representative of amphistreids, and later (Kolodziej 1995) suggested its heteroconid affinity. In fact, monotypic *A. eguchi* (Mori, 1963) shows large peripheral lonsdaleoid dissepiments arranged along the wall separating series of corallites, which greatly resembles that of some amphistreids (e.g., *Mitroden- dron*). However, the species has no unambiguous amphistreid characters (pachythe- cal wall, Taschenknoespung budding, presence of principal septum). Most likely *Amphi meandra* represents lineage of favid corals that in Cretaceous were represented by *Eugyrza* (see Morycowa & Masse 1998: fig. 18).

**Cenozoic Corals of Possible Pachythecaleine Ancestry**

As we have already mentioned in the introductory section, most authors presenting family trees that included critically revised fossil data (bottom-up approach) suggested that pachythecaleines sensu lato (including zardinophyllids, amphistreids and other possibly related coral groups) become extinct by the end of the Mesozoic (Wells 1956, Roniewicz & Morycowa 1993). In phylogenetic schemes that are based mostly on data of extant corals (top-down approach) pachythecaleines (sensu stricto) are not represented as a monophyletic unit and do not reach even the Cretaceous (see Ver- ron et al. 1996). Ignoring the problem of the data reliability used by authors from these two camps, it seems that there is a common agreement that corals of the pachythecaleine ancestry do not occur in the modern seas.

Wells (1956: F367) speculated that the lack of ability to form the edge zone was an important factor leading to the disappearance of amphistreids at the end of Me- sozoic (Amphistreidae sensu Wells 1956 included some representatives of aphi- straids, heteroconids, donacosmilids as understood herein). This suggestion was elaborated by Roniewicz & Stolarski (1999), who suggested that shallow-water epizooic (or pachythecal) corals were decimated and finally become extinct as a result of combined geological (demise of carbonate platforms) and biological (increased role of bioturbation by the end of Mesozoic) factors.

The first suggestion that some pachythe- caline descendants could transcend the K/ T boundary was given by the second author (Russo 1979). Nearly 20 years after this publication and having access to new observations, we would like to endorse this hypothesis.

Also recently, the first author suggested that *Guynia annulata* Duncan, 1872 (Miocene-Recent) differs in several skeletal characters from the typical scleractinian and show some resemblance to solitary zardinophyllids (Stolarski 2000). The common features of *Guynia* and *Zardinophyllum* skeleton comprise: undifferentiated septal calcification centers (possibly not all zardinophyllids share this characteristic), completely smooth septal faces, pipe-like epithecal calice with deeply recessed septa in respect to the calicular rim in the adult cor- alla; an aseptal part of the initial ontoge- netic stage (the state assumed to occur in some rugosans and pachythecaleines—see Fedorowski 1997, Stolarski 1999). However, diagnostic pachythecaleine characters have not been traced in *Guynia*: protosepta are inserted simultaneously (vs. two-by-two in zardinophyllids), corallites show radial symmetry (vs. bilateral), and the wall is typical epithecal (vs. pachytheateral) bearing specialized thecal pores. The lack of diagnostic characters is the main obstacle to suggesting zardinophyllid-like ancestors for *Guynia* but equally important is the lack of a continuous record of *Guynia*-like forms. Leaving open the problem of the puzzling “ancient look” of *Guynia* (as well as Gar-
**dineria**—see Stolarski 1996) we will concentrate on the first case.

**Pseudoastraeopora hortensis**

The Eocene *Pseudoastraeopora* Russo, 1979 is the only Cenozoic coral that formally was assigned to pachytheocalines (order Hexanthiniaria). Russo (1979) argued that *Pseudoastraeopora* has, similarly to pachytheocalines, a fibrolamellar wall consisting of series of concentric layers ("onion skin") and simplified septal apparatus in early growth stages consisting only of 2 or 3 protosepta (see Russo 1979: pl. 1:2c). Our new SEM observations of this coral suggest a different taxonomic assessment of this coral than suggested by Russo (1979), albeit, microstructure and corallum architecture justify distinctive status among coeval scleractinians.

**Morphology.**—Colony plocloid, holothecate (epithecal wall common to peripheral corallites developed in the lower part of the colony; Figs. 3B, 4A). Coenosteum consists of regularly produced calcareous sheets or processes (Fig. 3C, see also connections between corallites visible in Fig. 3A, B). Corallites semicircular, adult ca. 4–5 mm in diameter (Fig. 3A). Nonexsert septa usually in two cycles. S1 straight, entire, S2 often rudimentary, represented by a series of spines (Fig. 3D). Septal faces completely smooth. Budding extramural. First blastogenetic stage (ca. 1 mm in diameter) apparently aseptal (Fig. 3A, arrow 1); six, equally-sized septa occur in ca. 2 mm (and
Fig. 4. *Pseudoastraeopora hortensis* (Oppenheim, 1901), skeletal microstructure in transverse sections. A. Proximal part of the colony IPUM n. 19174. Frames show position of enlargements in B, C, E. B. Holotheca (wall of the colony) with typical epithelial microstructure (non-separated calcification centers, centripetal organization of aragonitic fibers). C. Calicular lumen partially filled with the stereome. Small depressions in corners (arrows) most likely represent desmoïde attachment scars. D. Closely spaced and separated septal calcification centers (3 of them indicate arrows). E. Corallite lumen largely filled with the stereome with one septum projecting toward the corallite center. Note on picture A or Fig. 3B that shapes of stereome-filled calicular lumens vary considerably. Frames show position of enlargements in D and F. F. Axial part of septum with transverse zonation of fibers resulting from incremental growth during the successive elementary cycles of biomineralization (arrows).

larger) corallites (Fig. 3A, arrows 2–3). Endothecal dissepiments rare. Septa down the calice covered with the stereome, and in their proximal part interseptal spaces often completely filled up (Figs. 3B, 4A, C, E).

**Microstructure.**—Transverse sections reveal that the mid-septal zone consists of closely spaced and distinctly separated calcification centers (distance between centers ca. 10 μm; Fig. 4C–E). The zone is surrounded by fine scale layers of fibrous stereomal tissue (Fig. 4C–F). Thickness of the stereome progressively increase down the calice (compare Fig. 3A, B). Some calices, extensively filled with the stereome show only few septa in their lumen though, normally developed septa are visible in section (Fig. 4E). Corallite wall marginothecal, i.e., wall consists of closely spaced and distinctly separated calcification centers (distance between centers the same as in septa—ca. 10 μm) which are continuous with those of
the mid-septal zone. Holothecal wall consists of centripetally organized fibres (Fig. 4B) not organized in modules (as in pachytycheal).

Discussion.—No diagnostic pachytycheal characters have not been found in the skeleton of *Pseudoastraeopora hortensis*: corallite wall is marginothecal and colony wall is epithetic (vs. pachytycheal corallite/colony wall in pachytychealines); corallites have quasi-radial symmetry in blastogenesis and during later growth (vs. strong bilateral at least at initial ontogenetic/blastogenetic stages in pachytychealines); few septal projections into stereotype-filled lumen do not reflect actual septal number at this growth stage as revealed in etched sections (Fig. 4E), and earliest blastogenetic stages invariably have 6 septa inserted simultaneously (vs. two-by-two septal insertion in early ontogeny/blastogeny of pachytychealines). Other characters, such as like spine-like septa of higher cycles, coenosteal regular connections, or completely smooth septal faces, are dispersed among various groups of extant Scleractinia. (spiny septa are shared with representatives of most scleractinan suborders, (Fig. 5C shows this in *Alveopora allingi*; similar to *Pseudoastraeopora* coenosteal connections have Jurassic acroporid *Etallonasterina*—Fig. 5A, B, and Cretaceous *Paretallonia*—see Sikharulidze 1972: figs. 1, 2). Smooth septal faces are much less common but occur in *Guynia* (Stolarski 2000: fig. 2, or in *Acropora* Gladfelter 1982: fig. 1A). Regularly and closely-spaced septal calcification centers like those in *Pseudoastraeopora* have been described in few coral groups in flabellids (see Stolarski 1996: fig. 3G–I), stenocyathids (Stolarski 2000: fig. 5H, I), some traditional caryophylliids, reimaniphylliids
(Roniewicz 1984: pl. 1:4, text-figs. 1–2), and acroporids (Fig. 5D, E; Glaßfelder 1982: fig. 3A).

Taxonomic comparisons of *Pseudoastraeopora* with acroporids seem justifiable since, as shown above, it shares with them many gross morphology and microstructural characters. The only distinctive *Pseudoastraeopora* character is corallite marginothecal wall. Among Recent Scleractinia, only Flabellidae and Stenocyathidae have adult solitary coralla with marginotheca but this feature is widespread in juvenile stages of many solitary and colonial corals (wall patterns C, D of Roniewicz & Stolarski 1999). Presence of marginotheca reflects the state where septa and wall having closely spaced calcification centers grow at calicular rim at similar rate. In *Acropora*, septal and wall calcification centers form, in places, a continuous zone that, however, does not encircle the entire corallite (Fig. 5D). By analogy with ontogeny of many Caryophyllines, marginotheca can be replaced by other wall types as growth dynamics of septa and wall changes, and its retention in adult corallites of *Pseudoastraeopora* can be considered generic or (?sub)familial distinctive character of that otherwise typical acroporid taxon.

Conclusions and Questions

The above survey of various hypotheses about phylogenetic relationships of the Triassic and post-Triassic pachythecalellines can be summarized in two following points.

Pachythecalellina s.s., since their appearance in the Middle Triassic, are diversified morphologically and are represented by taxa having solitary, phaceloid, and pseudoceroid coralla with strong bilateral or quasi-radial corallite symmetry. Many of them have one-zonal or two-zonal endotheca, and in some there is no endotheca. Despite this variability, the pachythecal wall is diagnostic for all pachythecalines s.s. The last member of this lineage was probably *Aphialulastraesia*, which reached the Cenomanian—compare Morycowa & Marco-poulou-Diacantoni 1997. The Early Jurassic gap in pachythecalelline record (Fig. 6) results, most likely, from the sampling bias (recently there have been recovered thick-walled, *Pachysolenia*-like corals from the Early Jurassic of SE Pamir (south-central Asia), Galina Melnikova, pers. comm. 2001).

Few other groups of post-Triassic corals share morphological characters with pachythecalellines s.s. heteroconiids (with corallite bilateral symmetry defined by one enlarged septum after pachythecalellines s.s. fashion) and, possibly, donacosmilids, intersmilids, and carolastraeids are, indeed, much easier clustered with pachythecalellines than with other coeval scleractinians.

Acceptance of the hypothesis, that pachythecalellines s.s. and heteroconiids, donacosmilids, intersmilids, carolastraeids form a clade (pachythecalellines s.l.) would mean that characters typical of pachythecalelline s.s. became supplemented/replaced in related corals by characters typical of the majority of scleractinians, i.e., quasi-radial corallite symmetry (possibly with simultaneous protoseptal insertion), epithecal/trabecular or septothecal corallite wall, and septal faces bearing various ornamentations. An extreme view that may result from this hypothesis is that sharp division between pachythecalellines and other Triassic scleractinians was, in subsequent periods, obscured to such extent that pachythecalelline ancestry of various late Mesozoic corals became no longer recognizable in their skeletal characters. Would it mean that some pachythecalelline descendants may still be alive and could be recognized as a “foreign” element only in molecular studies? Or, conversely, did all these pachythecalelline-like characters appear independently in parallel/convergent evolution of various groups of Scleractinia, and pachythecalellines s.s. are actually extinct?

Ockham’s razor is the best tool to stop these speculations at this point: no pachythecalelline apomorphies have been recog-
Fig. 6. Presumed phylogenetic relationships and preliminary stratigraphic distribution of zardinophyllids and amphiastrids (pachythecalella s.s.) and other possibly related taxa (pachythecalella s.l.). White bars show preliminary stratigraphic range of the taxa (approximation: each bar ends at the beginning and the end of certain geological epoch); black circles indicate actual records (approximation: each circle is placed in the middle of certain geological epoch). Black-outlined triangles suggest the main apomorphies. Possible plesiomorphies are listed at the base of the tree. Pachytheca, depending on the hypothesis of the origin of pachythecalellas, can be their apomorphy (origin from the scleractinian stock) or plesiomorphy (rugosan-descend origin); compare Roniewicz & Stolarski 2001; fig. 7. Stratigraphic data after: Baron-Szabo & Fernandez-Mendiola 1997; Baron-Szabo & Steuber 1996; Baron-Szabo & Gonzalez-Leon 1999; Lüser 1998; Lüser & Rücker 1995; Eliášová 1974, 1976, 1978; Melnikova & Roniewicz 1976; Morycowa & Marcopoulou-Diacantoni 1997; Morycowa, Decouez & Schenk 1995; Morycowa & Masse 1998; Roniewicz & Stolarski 2001; Turnsek 1997.
nized in heterocoeniid, donacomilid, intersmilid or carolastraeid coralla nor evidences have been presented to prove character transition/replacement between pachythecallines s.s. and these corals. Similar straight-forward arguments were applied above to disprove pachythecline affiliation for agathelids, *Palaeohelia*, or *Pseudoaustraeopora*.

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