

Evolution of the post-Triassic pachythecaliine corals

Jarosław Stolarski and Antonio Russo

(JS) Instytut Paleobiologii PAN, ul. Twarda 51/55, 00-818 Warszawa, Poland, e-mail: stolacy@twarda.pan.pl; (AR) Dipartimento di Scienze della Terra Università degli Studi di Modena e Reggio Emilia via Università 4, I-41100 Modena, Italy, e-mail: russo@unimo.it

Abstract.—Triassic pachythecaliines i.e., zardinophyllids, and primitive amphiastreids, differ from the coeval scleractinians in having pachythecal wall, septa developed deeply in the calice, smooth septal faces, and two-by-two manners of the protoseptal insertion. Among Jurassic and Cretaceous corals, only amphiastreids have a thick, pachythecal wall (pachythecaliine apomorphy), whereas other supposed post-Triassic pachythecaliines i.e., carolastreaeids, donacosmiliids, intersmiliids, 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*, *Stylohelix*, *Bracthelix*), *Amphimeandra*, *Bodeurina*, and *Palaeohelix*, suggests that their alleged “pachythecaliine” characters are either shared with other scleractinians (trabecular perithecium of agathelliids) or not homologous with those in pachythecaliines (thick wall of *Paleohelix*). *Pseudoastreaopora*, the only Cenozoic (Eocene) coral that originally was classified as pachythecaliid, 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, epithecium wall with characteristic modular structure (= pachytheca, 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., Carolastreaeidae Eliášová, 1976, Donacosmiliidae Krasnov, 1970, Heterocoeniidae

Oppenheim, 1930, and Intersmiliidae Melnikova & Roniewicz, 1976 (herein Pachythecaliina sensu lato).

Pachythecaliines s.s. have early ontogeny and several other aspects of the skeletal architecture closely comparable to that of the late Palaeozoic plerophylline 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-

thecaliines *sensu stricto*: zardinophyllids and amphiastreids). Triassic pachythecaliines s.s. (i.e., zardinophyllids and primitive amphiastreids) 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 pachythecaliines 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) pachythecaliines s.s. and pachythecaliines 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 pachythecaliine taxa make evolutionary studies particularly difficult and open to speculation. It is generally believed that most pachythecaliines 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 pachythecaliines and to review hypotheses about evolutionary pathways of post-Triassic pachythecaliines.

Material and Methods

Reference material used in this study consisted of type species of the Triassic pachythecaliines. 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 *Quenstedtiphyllia fritschi* (Volz, 1896) is housed at GMH. We also examined coralla of various species of intersmiliids, donacosmiliids, carolastreaeids, amphiastreids, and heterocoeniids deposited in collections of MNHN-P, NMNH, UJ, and ZPAL.

We reexamined topotype specimens of the Eocene *Pseudoastraeopora hortensis* (Oppenheim, 1900), a Cenozoic coral that was assigned to pachythecaliines. 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 blù di Cava Cunial, Possagno (Treviso, Italy), and are housed at the Istituto di Paleontologia, Università di Modena.

Comparative materials, including specimens illustrated here of fossil *Etallonasteria minima* (Étallon, 1864) and Recent *Acropora* sp. and *Alveopora allingi*, 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—Muséum 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.

Pachythecaliines *sensu stricto*: Zardinophyllids and amphiastreids

Zardinophyllids, the first Triassic pachythecaliines, 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,

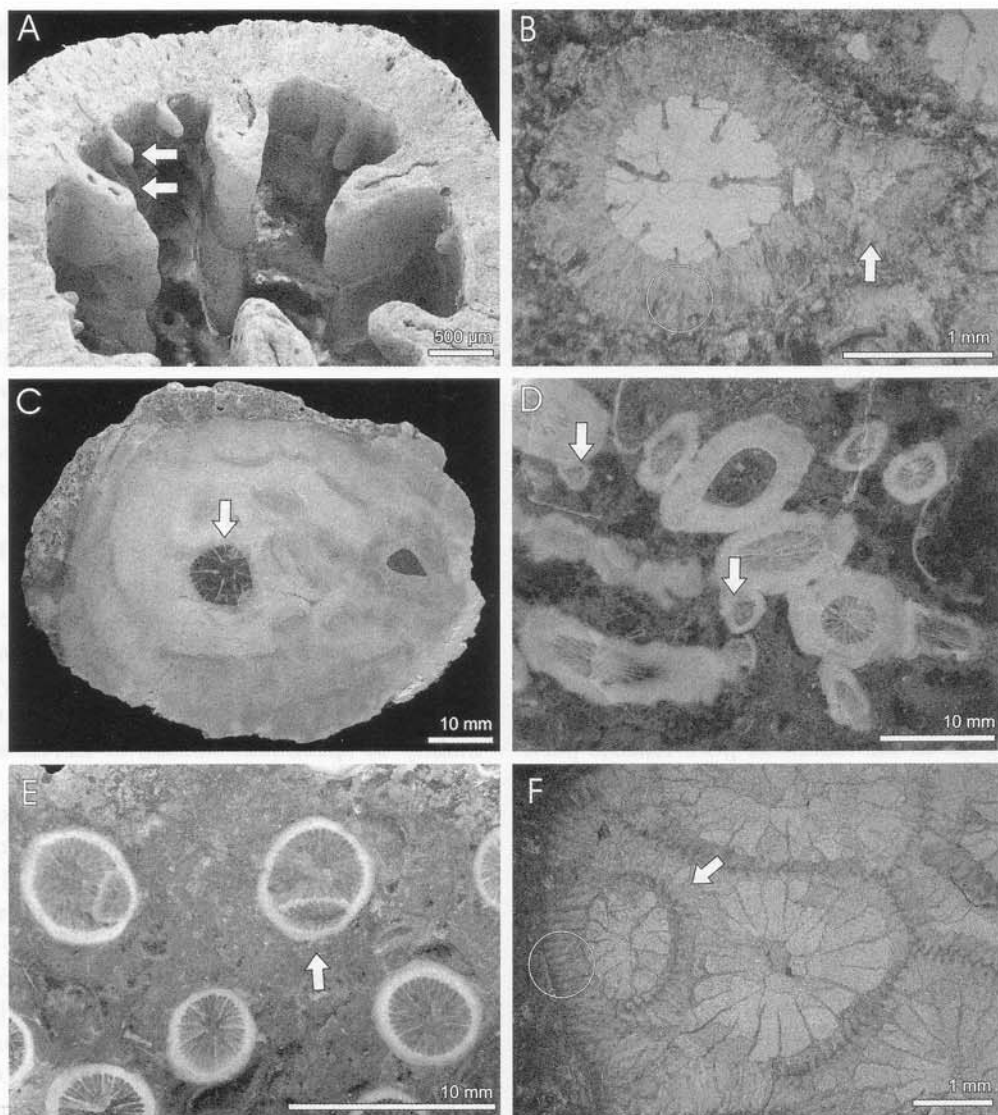


Fig. 1. Corallum morphology and microstructure of the Triassic zardinophyllid (A–D) and amphiastreid (E–F) pachythecaliines. A. *Zardinophyllum zardinii* Montanaro-Gallitelli, 1975, IPUM 7. Note irregular, monacanthid-like septa of higher orders (arrows). B. *Pachydendron microthallos* Cuif, 1975, ZPAL H.XXI/1. Arrow indicates lateral bud. C. *Pachythecalis major* Cuif, 1975, ZPAL H.XXI/3. Note extremely thick wall developed outside the calice with septa (arrow). D. *Pachysolenia cylindrica* Cuif, 1975, ZPAL H.XXI/4. Arrows indicate lateral buds. E. *Quenstedtiphyllia fritschi* (Volz, 1896), GMH, holotype. New buds (arrow) grow axialward, at the expense of the parental calice (Taschenknospung). F. *Sichuanophyllia prima* (Melnikova, 1986), ZPAL H. XXI/5. Arrow indicates new bud formed in Taschenknospung manner. A, E. Triassic (Lower Carnian), San Cassiano Beds, Alpe di Specie (in case E, site locality cannot be precisely determined), Dolomites (Italy). B–D, F. Triassic (Lower Norian), Alakir Çay, Antalya (Turkey).

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 Hexactiniaria (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 plerophyllines. 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 epithelial wall (in relation to the calicular 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 plerophylline 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 & Morycowa 1989). Zardinophyllids are represented by four fossil genera: solitary *Zardinophyllum* Montana-

ro-Gallitelli, 1975 (Fig. 1A), *Pachythecalis* Cuif, 1975 (Fig. 1C), phaceloid *Pachysolenia* Cuif, 1975 (Fig. 1D) and *Pachydendron* Cuif, 1975 (Fig. 1B). They are considered to be the first outgroup to amphistreids (Roniewicz & Stolarski 2001).

Amphistreids 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., pachythecal wall that at least can be observed in some, well-preserved specimens, Fig. 1F; juvenile and often adult coralla 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 pachytheca 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).

Amphistreids are reported as early as the Triassic, i.e., early Carnian phaceloid *Quenstedtiphyllia* Melnikova, 1975 (see Roniewicz & Stolarski 2001); possibly also cerioid *Sichuanophyllia* Deng & Zhang, 1984 (= *Lubowastraea* Melnikova, 1986) represents primitive Triassic amphistreids (Fig. 1F). In post-Triassic strata the following amphistreid genera have been distinguished (see Fig. 6 for the stratigraphic ranges): quasi-cerioid *Amphistrea* Étallon, 1859, *Pleurostylina* de Fromentel, 1856, *Amphipulastraea* Geyer, 1955 (Fig. 2A), phaceloid, *Aulastraea* Ogilvie, 1897, ?*Hexapetalum* Eliášová, 1975, *Hykeliphyllum* Eliášová, 1975, *Mitrodendron* Quenstedt, 1881, *Pleurophyllia* de Fromentel, 1856 (Fig. 2B)—probably synonymous with *Cu-*

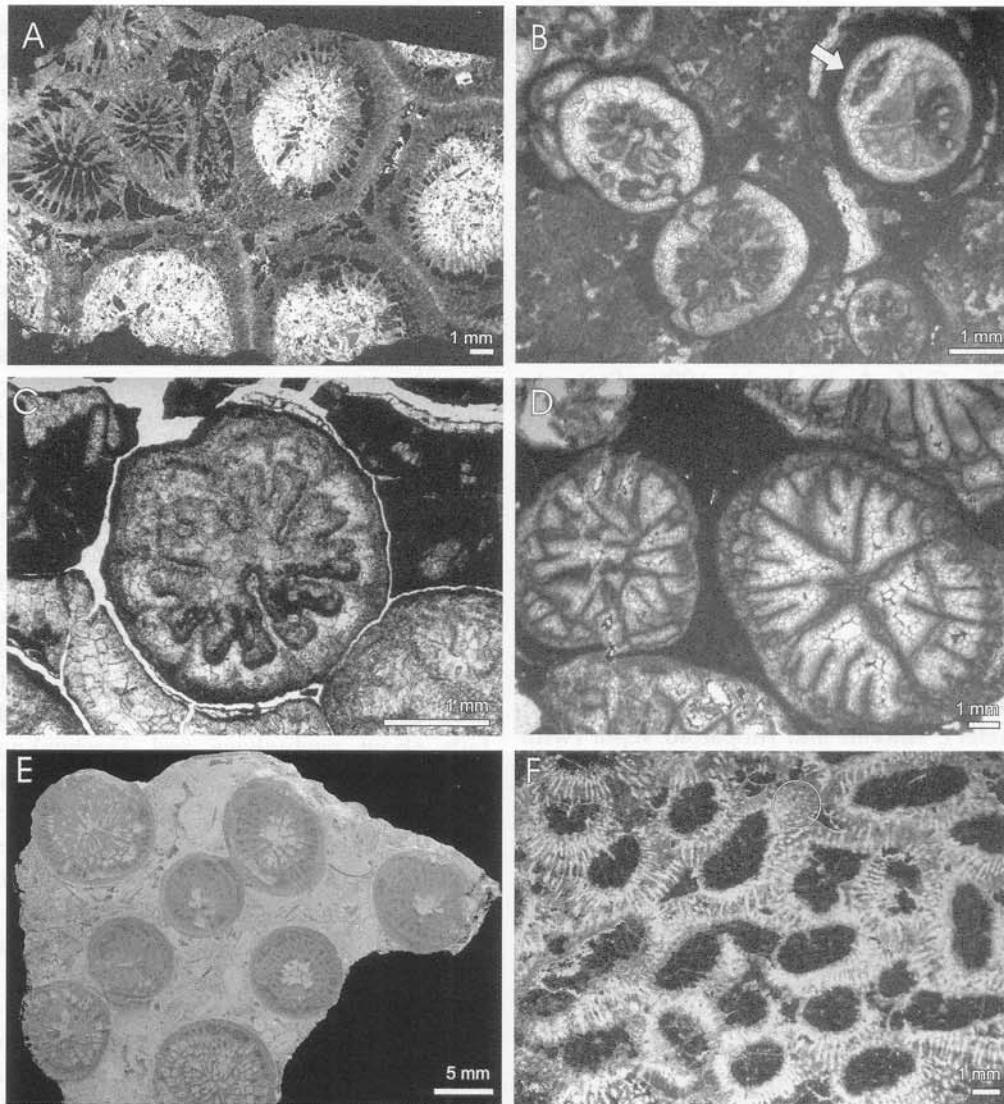


Fig. 2. Corallum morphology and microstructure of the post-Triassic pachythecales s.l. i.e., amphiastreids (A, *Amphiaulastraea rarauensis* (Morycowa, 1971), Cretaceous (Lower Aptian), Valea Izvorul Alb, Romania, UJ 120); B, *Pleurophyllia minuscula* Roniewicz, 1976, Jurassic (Kimmeridgian), Topalu, Romania, ZPAL z.p. H/352), carolastraes (C, *Carolastraea fraji* Eliášová, 1976, Jurassic (Tithonian), Štramberk, Czech Republik, Holotype CGS—HF 356), intersmiliids (D, *Intersmilia irregularis* Roniewicz, 1976, ZPAL z.p. H/334, Jurassic (Kimmeridgian), Topalu, Romania), donacosmiliids (E, *Donacosmilia coralline* de Fromentel, 1861, MNHN-P/MO3913, Jurassic (Oxfordian), La Monille, France), and heterocoeniids (F, *Latusastraea exiguis* de Fromentel, Valea Izvorul Alb, Romania UJ 70).

neiphyllia Eliášová, 1978, ?*Selenegyra* Ogilvie, 1897, ?*Simplexstraea* Eliášová, 1976, and solitary *Cheilosmilia* Koby, 1888 (possible synonyms are *Lingulosmilia* Koby, 1888, *Sclerosmilia* Koby, 1888, and *Opisthophyllum* Ogilvie, 1897).

Pachythecales sensu lato Including Mesozoic Corals of Uncertain Affinity

Few other post-Triassic groups of Mesozoic, mostly epithecate corals, have been considered to be related to pachythecales.

(most likely to amphistreids—Fig. 6): *Carolastraeidae* Eliášová, 1976, *Donacosmiliidae* Krasnov, 1970, *Heterocoeniidae* Oppenheim, 1930, and *Intersmiliidae* Melnikova & Roniewicz, 1976. None of these taxa have typical pachythecal wall (or coralla are too badly preserved to observe this feature) and their affinity with pachythecaliines 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 heterocoeniids). However, unlike Amphistreids, carolastraeids have one-zonal endotheca (vs. two-zonal) and asexually increase via lateral budding (vs. Taschenknospung). Carolastraeids share most features with intersmiliids (monotypic *Intersmilia* Eliášová, 1974; Fig. 2D), the only significant difference between them being corallite symmetry (bilateral vs. radial, respectively). Intersmiliids and carolastraeids have smooth septal faces that is a rare feature among coeval scleractinians except for pachythecaliines. Unfortunately, all listed characters are too general to settle the problem of the possible relationships between carolastraeids and intersmiliids and between these two taxa and pachythecaliines (this suggestion is presented in Fig. 6). On the other hand, carolastraeids and intersmiliids are so different from other Jurassic scleractinians (e.g., actinastraeids, dermosmiliids, haplaraeids, montlivaltiids, stylophyllids, stylinids) that *in absentia* of other similar to them but different from pachythecaliines groups they are naturally clustered with the latter. Similar arguments have been used to demonstrate possible donacosmiliid-amphistreid phylogenetic relationships.

Donacosmiliids (*Cylismilia* Roniewicz, 1988; *Donacosmilia* de Fromentel, 1861, fig. 2E; *Prodonacosmilia* 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).

Heterocoeniidae are herein restricted to the following genera: *Heterocoenia* Milne-Edwards & Haime, 1849, *Latusastraea* d'Orbigny, 1850, Fig. 2E, *Latusastraeopsis* Morycowa & Marcopoulo-Diacantoni, 1997, *Pachycoenia* Alloiteau, 1952, *Thecidiosmilia* Koby, 1888, fig. 2F, and *Confusaforma* Löser, 1987 (Morycowa & Kołodziej 2001 detected neorhipidicant septal microstructure in *Aulastraeopora* aff. *deangelisi* Prever, 1909 and *Preverastraea diplothecata* (Hackemesser, 1936) thus suggesting placement of these traditional heterocoeniid taxa among Rhipidogyrina). Heterocoeniid colonies are perithecate (i.e., with coenosteum) or cerioid. 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, heterocoeniid septa were considered “thick-trabeculate”, i.e., having widely-spaced septal calcification centers vs. mini-trabeculate of amphistreids (see *Heterocoenia*, *Latusastraea* in Morycowa 1971, fig. 21). Kołodziej (1995) provided a new insight concerning heterocoeniid 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 “minitrabecular” microstructure (i.e., calcification centers are separated but closely spaced; see Kołodziej 1995: fig. 3I). Another observation by Kołodziej (1995) that may bridge the gap between amphistreids and heterocoeniids concerns calicular structures similar to Taschenknospung in *Thecidiosmilia morycowae* Kołodziej, 1995. This important suggestion still needs to be proven by means of serial sections.

Other Mesozoic taxa have been considered related to pachythecaliines:

Beauvais & Beauvais (1975) proposed that agatheliids (a family to include Cretaceous *Agathelia* Reuss, 1854, Middle-Late Jurassic *Stylohelix* de Fromentel, 1861, and Middle Jurassic *Brachelia* Beauvais & Beauvais, 1975) are intermediate between typical stylinids (in having trabecular structure of the septa) and heterocoenids and amphiastreids (in having perithea composed of successive lamellae with trabeculae perpendicular to lamellar growth). Amphiastreids cannot be compared directly with agatheliids as they do not form perithea, nevertheless, perithea in *Brachelia* and *Agathelia* is similar to that known in heterocoenid *Pachycoenia* (see Beauvais 1982: pl. LII:3). However, some caryophylliids 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 rhipidogyriid *Bodeurina languedociensis* Beauvais, 1980 is related to amphiastreids, heterocoeniids, and to stylophyllids, because of dense and extensive endotheca, presence of perithea and structural continuity between septa and dissepiments, respectively. Rhipidogyrids differ from pachythecaliines 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 stylinids, not with pachythecaliines (Roniewicz & Morycowa 1993). Yet another suggestion that rhipidogyrids share some features with pachythecaliines was given by Lebedev (1991: 37, fig. 7), who illustrated a section of juvenile blastogenetic stage of the Tithonian rhipidogyrid *Aplosmilium coalescens* Eliášová, 1973, with one primary septum enlarged after amphiastreid fashion. For the lack of precisely oriented serial sections,

the presence of a "cardinal septum" in *A. coalescens*, as expressed by Lebedev (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 albiensis* Beauvais, 1982 is related to Triassic volzeiids (*Pachythecaliina* 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 caryophylliids and oculinids, whereas in pachythecaliines it grows thicker centripetally (Stolarski 1995, Roniewicz & Stolarski 1999). A different mode of wall thickening in *Palaeohelia* and pachythecaliines reflect essentially different anatomic designs of polyps: in *Palaeohelia* tissue controlling wall thickening was laid outside the corallum, whereas in pachythecaliines it was entirely intracalicular. Hence, buds of *Palaeohelia* are not "intracalicular and marginal as in amphiastreids" 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*, *Sclerhelix hirtella*) show that all these taxa have well-differentiated septal calcification centers (occasionally, in *Sclerhelix*, septal calcification centers are closely spaced). Septal calcification centers are susceptible to diagenetic 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 Pachythealina" of *Palaeohelia* are not confirmed herein.

Beauvais & Mori (1988) considered meandroid *Amphimeandra* Beauvais & Mori, 1988 (Jurassic of Japan) representative of amphiastreids, and later (Kołodziej 1995) suggested its heterocoenid affinity. In fact, monotypic *A. eguchii* (Mori, 1963) shows large peripheral lonsdaleoid dissepiments arranged along the wall separating series of corallites, which greatly resembles that of some amphiastreids (e.g., *Mitrodendron*). However, the species has no unambiguous amphiastroid characters (pachytheal wall, Taschenknospung budding, presence of principal septum). Most likely *Amphimeandra* represents lineage of faviid corals that in Cretaceous were represented by *Eugyra* (see Morycowa & Masse 1998: fig. 18).

Cenozoic Corals of Possible Pachythealiine 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 pachythealiines sensu lato (including zardinophyllids, amphiastreids 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) pachythealiines (sensu stricto) are not represented as a monophyletic unit and do not reach even the Cretaceous (see Veron 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 pachythealiine 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 amphiastreids at the end of Mesozoic (*Amphiastreidae* sensu Wells 1956

included some representatives of aphiastraeids, heterocoeniids, donacosmiliids as understood herein). This suggestion was elaborated by Roniewicz & Stolarski (1999), who suggested that shallow-water epithecate (or pachytheate) corals were decimated and finally become extinct as a result of combined geological (demise of carbonate platforms) and biological (increased role of bioerosion by the end of Mesozoic) factors.

The first suggestion that some pachythealiine 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 character), completely smooth septal faces, pipe-like epithecal calice with deeply recessed septa in respect to the calicular rim in the adult coralla; an aseptal part of the initial ontogenetic stage (the state assumed to occur in some rugosans and pachythealiines—see Fedorowski 1997, Stolarski 1999). However, diagnostic pachythealiine 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. pachytheal) 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-*

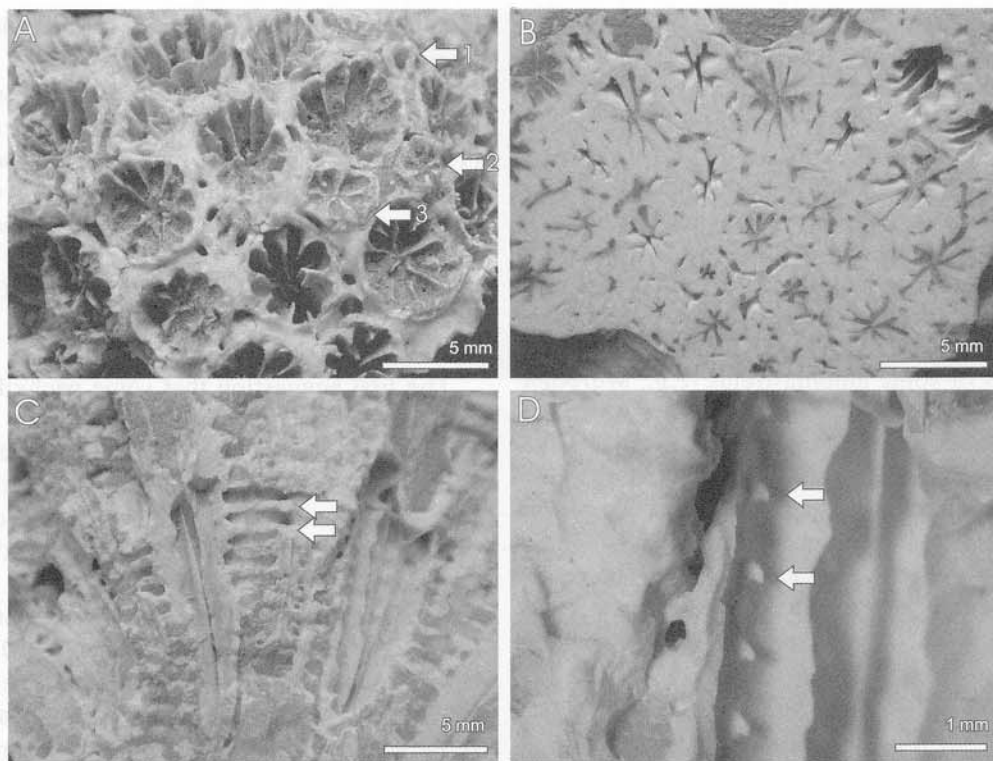


Fig. 3. *Pseudoastraeopora hortensis* (Oppenheim, 1901), corallum morphology, IPUM n. 19174. A. Upper colony surface. Corallites at different blastogenetic stages (1–3 arrows, respectively). B. Polished, lower colony surface in transverse and slightly oblique section. Note smooth septal faces (upper right corner) and holotheca (lower left corner). C. Corallum fractured longitudinally with regularly distributed perithecal processes (arrows). D. S_2 developed as septal spines (arrows). Paleocene (Eocene), Marne blu di Cava Cunial, Possagno, Treviso, Italy.

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 pachythealiines (order Hexanthiniaria). Russo (1979) argued that *Pseudoastraeopora* has, similarly to pachythealiines, 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 archi-

tecture justify distinctive status among coeval scleractinians.

Morphology.—Colony plocoid, holotheca (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. S_1 straight, entire, S_2 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

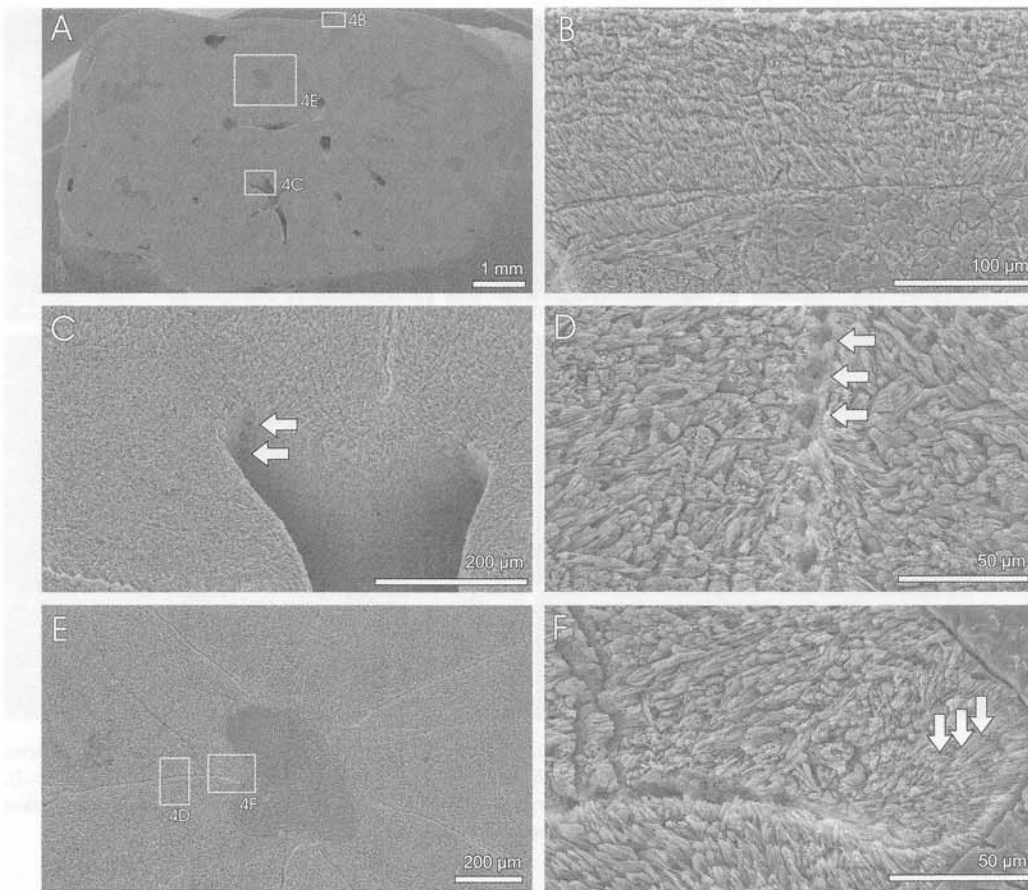


Fig. 4. *Pseudoastreaopora hortensis* (Oppenheim, 1901), skeletal microstructure in transverse sections. A. Proximal part of the colony IPUM n. 19174. Frames show position of enlargements in B, C, E. B. Holotheca (wall of the colony) with typical epithelial microstructure (non-separated calcification centers, centripetal organization of aragonitic fibers). C. Calicular lumen partially filled with the stereome. Small depressions in corners (arrows) most likely represent desmocyte 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 ster-

eomal 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

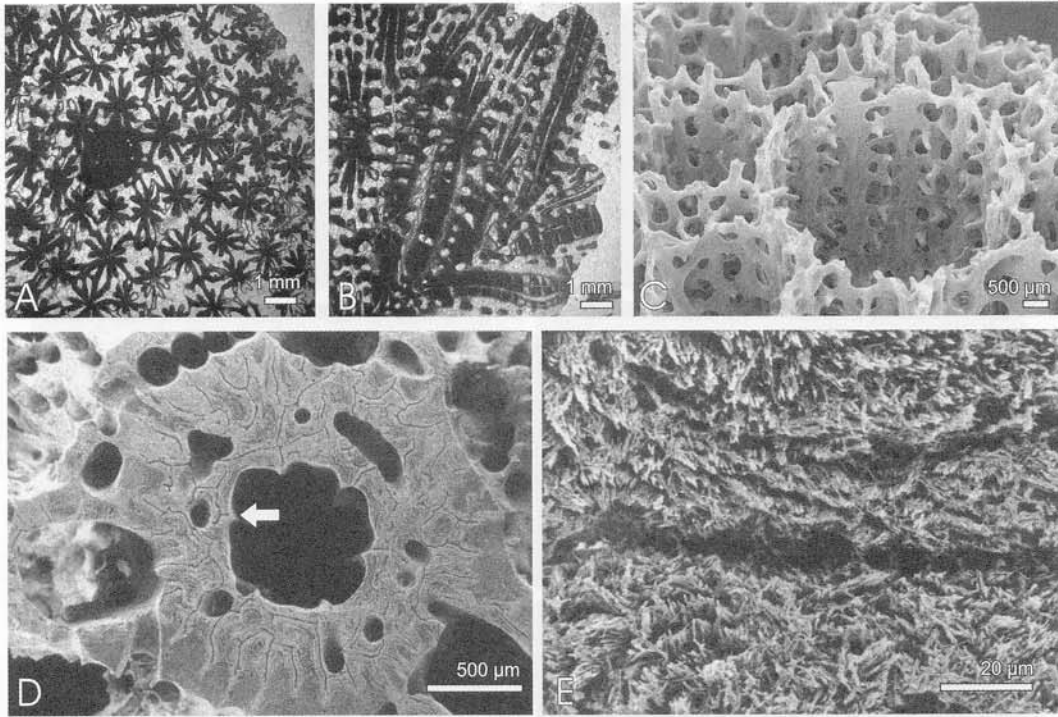


Fig. 5. A–B. *Etallonasteria minima* (Étallon, 1864), ZPAL n.372 in transverse (A) and longitudinal sections (B). Jurassic (Kimmeridgian), Topalu, Romania). C. *Alveopora allingi* Hoffmeister, 1925. NMNH 82738. D–E. *Acropora* sp. Recent. Polished and etched transverse section of the axial corallite. Densely packed calcification centers (E—enlargement) form zones that may continue between septa and wall (arrow on D).

the mid-septal zone. Holothecal wall consists of centripetally organized fibres (Fig. 4B) not organized in modules (as in pachytheca).

Discussion.—No diagnostic pachythecaliine characters have not been found in the skeleton of *Pseudoastreaopora hortensis*: corallite wall is marginothecal and colony wall is epithecate (vs. pachythecate corallite/colony wall in pachythecaliines); corallites have quasi-radial symmetry in blastogeny and during later growth (vs. strong bilateral at least at initial ontogenetic/blastogenetic stages in pachythecaliines); few septal projections into stereome-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 pach-

ythecaliines). 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 scleractinian suborders, (Fig. 5C shows this in *Alveopora allingi*; similar to *Pseudoastreaopora* 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 *Pseudoastreaopora* 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; Glatfelter 1982: fig. 3A).

Taxonomic comparisons of *Pseudoastreaopora* with acroporids seem justifiable since, as shown above, it shares with them many gross morphology and microstructural characters. The only distinctive *Pseudoastreaopora* 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 calcular 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 caryophylliines, marginotheca can be replaced by other wall types as growth dynamics of septa and wall changes, and its retainment in adult corallites of *Pseudoastreaopora* can be considered generic or (?sub)familial distinctive character of that otherwise typical acroporoid taxon.

Conclusions and Questions

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

Pachythecaliina 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 pachythechal wall is diagnostic for all pachythecaliines s.s. The last member of this lineage was probably *Aphiaulastraea*, which reached the Ceno-

manian—compare Morycowa & Marcopoulou-Diacantoni 1997. The Early Jurassic gap in pachythecaliine 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 pachythecaliines s.s. heterocoeniids (with corallite bilateral symmetry defined by one enlarged septum after pachythecaliines s.s. fashion) and, possibly, donacosmiliids, intersmiliids, and carolastraeids are, indeed, much easier clustered with pachythecaliines than with other coeval scleractinians.

Acceptance of the hypothesis, that pachythecaliines s.s. and heterocoeniids, donacosmiliids, intersmiliids, carolastraeids form a clade (pachythecaliines s.l.) would mean that characters typical of pachythecaliine 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 pachythecaliines and other Triassic scleractinians was, in subsequent periods, obscured to such extent that pachythecaliine ancestry of various late Mesozoic corals became no longer recognizable in their skeletal characters. Would it mean that some pachythecaliine descendants may still be alive and could be recognized as a “foreign” element only in molecular studies? Or, conversely, did all these pachythecaliine-like characters appear independently in parallel/convergent evolution of various groups of Scleractinia, and pachythecaliines s.s. are actually extinct?

Ockham's razor is the best tool to stop these speculations at this point: no pachythecaliine apomorphies have been recog-

nized in heterocoeniid, donacomiliid, intersmiliid or carolastreaid coralla nor evidences have been presented to prove character transition/replacement between pachythealiines s.s. and these corals. Similar straight-forward arguments were applied above to disprove pachythealiine affiliation for agatheliids, *Palaeohelia*, or *Pseudoastraeopora*.

Acknowledgments

We would like to dedicate this work to Dr. Frederick M. Bayer who, although did not publish on fossil corals, did contribute greatly to our knowledge of living cnidarians. We are very grateful to Dr. Elżbieta Morycowa (Kraków) for thorough review and to Dr. Bogusław Kołodziej (Kraków) for reading of the manuscript and providing comments. Dr. Hannes Löser (Dresden) helped to check dating of some taxa (however, comprehensive review of dating and taxonomic revision of all pachythealiine species is pending). The work has been accomplished with the support of the Committee for Scientific Research (KBN) grant 6 P04D 037 14 to J. Stolarski, and grant Cofin 2000 of Italian Murst to A. Russo.

Literature Cited

- Baron-Szabo, R. C., & P. A. Fernandez-Mendiola. 1997. Cretaceous scleractinian corals from the Albian of Cabo de Ajo (Cantabria Province, N-Spain).—*Palaeontologische Zeitschrift* 71:35–50.
- , & C. M. Gonzalez-Leon. 1999. Lower Cretaceous corals and stratigraphy of the Bisbee Group (Cerro de Oro and Lampazos areas), Sonora, Mexico.—*Cretaceous Research* 20:465–497.
- , & T. Steuber. 1996. Korallen und Rudisten aus dem Apt im tertiären Flysch des Parnass-Gebirges bei Delphi-Arachowa.—*Berliner Geowissenschaftliche Abhandlungen E* 18:3–75.
- Beauvais, L. 1980. *Bodeurina*: un nouveau genre de Madréporaire de la famille des Rhipidogyriidae, dans le Jurassique supérieur du Languedoc.—*Compte Rendu Sommaire Des Séances De La Société Géologique De France* 6:228–231.
- . 1982. Révision de genre *Palaeohelia* Alloiteau (Scleractiniaire méso-crétacé).—*Eclogae Geologicae Helvetiae* 75:669–687.
- , & M. Beauvais. 1975. Une nouvelle famille dans le sous-ordre des Stylinida All.: les Agatheliidae nov. fam. (Madréporaires mésozoïques).—*Bulletin De La Société Géologique De France* 17:576–581.
- , & K. Mori. 1988. *Amphimeandra*, a new genus in the family Amphiastreida (Mesozoic Scleractinia).—*Geobios* 21:103–108.
- Beauvais, M. 1982. Révision systématique des Madréporaires des Couches de Gosau (Crétacé supérieur, Autriche).—*Trauvau De Laboratoire De Paléontologie Des Invertébrés Université Pierre Et Marie Curie*.
- Cuif, J. P. 1975. Caractères morphologiques, microstructuraux et systématiques des Pachythealiidae nouvelle famille de Madréporaires Triasiques.—*Géobios* 8:157–180.
- , & J. Stolarski. 1999. Origin and paleobiology of wall-based corals.—Abstracts of the 8th International Symposium on fossil Cnidaria and Porifera, Sendai 95.
- Eliášová, H. 1974. Genre nouveau *Intersmilia* (Hexacorallia) du Tithonien des calcaires de Štramberg (Tchécoslovaquie).—*Časopis Pro Mineralogii a Geologii* 19:415–417.
- . 1975. Sous-ordre Amphiastreina Alloiteau, 1952 (Hexacorallia) des calcaires de de Štramberg (Tithonien, Tchécoslovaquie).—*Časopis Pro Mineralogii a Geologii* 20:1–23.
- . 1976. Nouvelle famille du sous-ordre Amphiastreina Alloiteau, 1952 (Hexacorallia), Tithonien de Tchécoslovaquie.—*Věstník Ústředního Ústavu Geologického* 51:177–178.
- . 1978. La redéfinition de l'ordre Hexanthinaria Montanaro Gallitelli, 1975 (Zoantharia).—*Věstník Ústředního Ústavu Geologického* 53: 89–102.
- Fedorowski, J. 1997. Remarks on the palaeobiology of Rugosa.—*Geologos* 2:5–58.
- Gladfelter, E. H. 1982. Skeletal development in *Acropora cervicornis*: I. Patterns of calcium carbonate accretion in the axial corallite.—*Coral Reefs* 1:45–51.
- Koby, F. 1888. Monographie des polypiers jurassique de la Suisse.—*Mémoires De La Société Paléontologique Suisse* 25:401–456.
- Kołodziej, B. 1995. Microstructure and taxonomy of Amphiastreina (Scleractinia).—*Annales Societatis Geologorum Poloniae* 65:1–17.
- Lebanidze, Z. M. 1991. Pozdneurskie korally zapadnoj Gruzii (Abhazii).—*Trudy, Geologičeskij Institut, Akademiâ Nauk Gruzii, nowaâ seriâ* 105:1–64.
- Löser, H. 1987. Zwei neue Gattungen der Korallen aus der Sächsischen Oberkreide.—*Věstník UUG* 62:233–237.

- . 1998. Remarks on the Aulastraeoporidae and the genus Aulastraeopora (Scleractinia: Cretaceous) with the description of a new species.—*Abhandlungen Und Berichte Für Naturkunde* 20:59–75.
- , & M. Raeder. 1995. Coral assemblages from the Aptian/Albian in the Helicon Mountains (Boeotia, Greece): palaeontological, palaeoecological and palaeogeographical aspects.—*Coral Research Bulletin* 4:37–63.
- Melnikova, G. H. & Roniewicz E. 1976. Contribution to the systematics and phylogeny of Amphiasireina (Scleractinia).—*Acta Palaeontologica Polonica* 21:97–114.
- Montanaro Gallitelli, E. 1975. Hexanthiniaria a new ordo of Zoantharia (Anthozoa, Coelenterata).—*Bolletino Della Societa Paleontologica Italiana* 14:21–25.
- Morycowa, E. Decrouez D., & Schenk K. 1995. Présence de *Latusaeraea exiguis* (Scléractiniaire) dans le Schratenkalk du Rawil (Helvétique, Suisse) et quelques remarques sur les espèces crétaées du genre *Latusaeraea* d'Orbigny, 1949.—*Annales Societatis Geologorum Poloniae* 64:15–22.
- , & A. Marcopoulou-Diacantoni. 1997. Cretaceous scleractinian corals from the Parnassos area (central Greece) (Preliminary note).—*Bulletin of the Geological Society of Greece* 30: 249–273.
- , & J. P. Masse. 1998. Les Scléractiniaires du Barrémien-Aptien inférieur de Provence (SE de la France).—*Geobios* 31:725–766.
- Ogilvie, M. M. 1897. Korallen der Stramberger Schichten.—*Palaeontographica*, Supplement 2:73–282.
- Oliver, W. A. Jr. 1980. The relationship of the scleractinian corals to the rugose corals.—*Paleobiology* 6:146–160.
- Roniewicz, E. 1976. Les Scléractiniaires du Jurassique supérieur de la Dobrogea Centrale, Roumanie.—*Palaeontologia Polonica* 34:17–118.
- . 1984. Microstructural evidence of the distichophylliid affinity of the Caryophylliina (Scleractinia).—*Palaeontographica Americana* 54:515–518.
- , & E. Morycowa. 1989. Triassic Scleractinia and the Triassic/Liassic boundary.—*Memoirs of the Association of AustralAsian Palaeontologists* 8:347–354.
- , & ———. 1993. Evolution of the Scleractinia in the light of microstructural data.—*Courier Forschungsinstitut Senckenberg* 164:233–240.
- , & J. Stolarski. 1999. Evolutionary trends in the epithecate scleractinian corals.—*Acta Palaeontologica Polonica* 44:131–166.
- , & ———. 2001. Triassic roots of the amphistroid scleractinian corals.—*Journal of Paleontology* 75:34–35.
- Russo, A. 1979. Studio monografico sui Coralli dell'Eocene di Possagno (Treviso, Italia).—*Atti e Memorie Della Accademia Nazionale Di Scienze, Lettere e Arti Di Modena* 21:1–87.
- Sikharulidze, G. J. 1972. A new genus *Paretallonia* (Hexacoralla) from the Lower Cretaceous deposits of Western Georgia.—*Bulletin of the Academy of Sciences of the Georgian SSR* 68: 641–644.
- Stolarski, J. 1995. Ontogenetic development of the thecal structures in caryophylliine scleractinian corals.—*Acta Palaeontologica Polonica* 40:19–44.
- . 1996. *Gardineria*—a scleractinian living fossil.—*Acta Palaeontologica Polonica* 41:339–367.
- . 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.
- . 2000. Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data.—*Lethaia* 33:13–38.
- Turnsek, D. 1997. Mesozoic Corals of Slovenia. Znanstvenoraziskovalni center SAZU, Zalo ba ZRC, Ljubljana.
- Veron, J. E. N. Odorico D. M. Chen C. A. & Miller D. J. 1996. Reassessing evolutionary relationships of scleractinian corals.—*Coral Reefs* 15: 1–9.
- Wells, J. W. 1956. Scleractinia. In R. C. Moore, ed., *Treatise on invertebrate paleontology*, part F (Coelenterata). The University of Kansas Press, Lawrence, Kansas, pp. F328–F444.