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# SCLERACTINIAN CORALS OF SUBORDERS PACHYTHECALIINA AND RHIPIDOGYRINA: DISCUSSION ON SIMILARITIES AND DESCRIPTION OF SPECIES FROM ŠTRAMBERK-TYPE LIMESTONES, POLISH OUTER CARPATHIANS

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**Abstract:** Similarities between scleractinian corals from extinct suborders Pachythecaliina Eliášová 1976 and Rhipidogyrina Roniewicz 1976 are discussed. Corals of the former suborder are considered by some authors as possible descendants of Palaeozoic Rugosa because of their unusual skeletal characters. Some rhipidogyrinans, especially the family Aulastraeoporidae, despite their different septal microstructure, share more common features with pachythecaliinans than with other scleractinians. The following skeletal features are discussed to show similarities between these two suborders: (1) wall microstructure and its relations to septa, (2) corallite bilateral symmetry, (3) marginarium, (4) lonsdaleoid and apophysal septa, and (5) internal septal margin. These similarities can be explained by convergence, although phylogenetic relationships of both suborders can not be excluded. This hypothesis needs to be verified by more studies, especially on early blastogeny of rhipidogyrinans and wall microstructure of pachythecaliinans. The systematic part gives descriptions of the discussed coral suborders occuring in the Štramberk-type limestones, the Polish Outer Carpathians (Tithonian–?Berriasian, ?Valanginian). Similarly as in the Štramberk Limestone (Moravia), pachythecaliinans are highly diversified (17 species, 12 genera, including *Pachythecophyllia eliasovae* n.gen., n.sp.). Rhipidogyrinans are represented by 4 species of 4 genera, including ?*Ogilvinella morycowae* n.sp.

**Key words:** Corals, Pachythecaliina, Rhipidogyrina, taxonomy, phylogeny, Jurassic, Cretaceous, Outer Carpathians.

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## INTRODUCTION

Corals of the suborder Pachythecaliina Eliášová 1976, because of to their "mixed" scleractinian–rugosan features, occupy a special place among Scleractinia. Skeletal architecture, particularly in the family Zardinophyllidae Montanaro- Galitelli 1975 and the family Amphiastreidae Ogilvie 1897, led some authors to assume their possible evolutionary relationships with Rugosa (e.g., Koby, 1888; Ogilvie, 1897; Cuif, 1975; Montanaro-Gallitelli, 1975; Melnikova & Roniewicz, 1976; Eliášová, 1976b, 1978; Stolarski, 1996; Roniewicz & Stolarski, 2001).

The systematic position of pachythecaliinans was the subject of divergent views. In this paper, following the proposition of Roniewicz and Stolarski (2001), the family Amphiastreidae Ogilvie 1897 is included to the suborder Pachythecaliina. The present author classified here also other families, usually earlier assigned to the suborder Amphiastreina Alloiteau 1952, including Heteroceoniidae Oppenheim 1930 (Kołodziej, 1995).

The suborder Rhipodogyrina Roniewicz 1976 is accepted by most authors working on Jurassic–Cretaceous corals. However, its evolutionary relationships are poorly understood. The family Aulastraeoporidae Alloiteau 1957, recently included to Rhipidogyrina (Morycowa & Kolodziej, 2001), occupies a special place, with its neorhipidacanth microstructure and heterocoeniid-like corallites.

The aim of the first part of this paper is a review of some skeletal features of both suborders, with focus on their similarities, and a discussion on phylogenetic relationships of Rhipidogyrina. The systematic part of the paper gives descriptions of Pachythecaliina and Rhipidogyrina from exotics of the Štramberk-type limestones from the Polish Outer Carpathians.

## MATERIAL

General discussion on Pachythecaliina and Rhipidogyrina is based mostly on literature and on the author's new observations of the following material.

1. *Preverastraea marinosi* Marcopuolu-Diacantoni & Morycowa 2002 (Albian; Agrostylia, Parnassos region, Greece; see Morycowa & Marcopuolu-Diacantoni, 2002; deposited in the Geological Museum of the Institute of Geological Sciences, Jagiellonian University);

2. *Pachycoenia* sp. (Upper Cenomanian, Dresden; coll. Dr. H. Löser; see Löser, 1989; thin sections deposited in the Institute of Geological Sciences, Jagiellonian University);

3. *Carolastraea moravensis* Eliášová 1978 and amphiastreid coral (Štramberk, Tithonian–Early Berriasian; coll. Dr. H. Eliášová, Ústřední Ústav Geologický, Praha).

The systematic part deals with material from the Štramberk-type limestones in the Polish Outer Carpathians. These limestones are believed to be an age and facies equivalent of the Štramberk Limestone from Moravia, which are the best developed of all known Tithonian–Early Berriasian coral reefs (Eliáš & Eliášová, 1984). Numerous, highly diversified corals from a huge quarry in Štramberk (Štramberg) were described already in the 19th century by Ogilvie (1897). Some of the corals (24 species) described by Ogilvie came from exotic blocks occurring in flysch deposits in Bobrek, Inwałd (Inwald), Iskrzyczyn (Iskritschin), Skoczów (Skotschau), Ustroń (Ustron), Wilamowice (Willamowitz) and Wiślica (Wischlitz), now located in Poland (Cieszyn Silesia, except Inwałd near Andrychów).

Limestones of "Štramberk facies" are known in the Polish Flysch Carpathians as pebbles, boulders (exotics) and rarely klippes in uppermost Jurassic–Paleogene flysch sequences. Source areas of the exotic material were continental margins of the Carpathian Basin or intrabasinal ridges called cordilleras (e.g., Książkiewicz, 1965). Lithological analysis of these exotics revealed that the so-called "Štramberk-type limestones" are in fact differentiated and contain deposits of various environments, including reef, lagoon and basin (Hoffmann, 1992). Apart from corals, microbial structures played an important role in the construction of coral patch reefs (Hoffmann, 1992; Hoffmann & Kołodziej, 1997). The studies of the Andrychów Klippes revealed, that apart of shallow-water limestones of Štramberk type, there are also Callovian crinoidal limestones and Oxfordian cherty limestones (Olszewska & Wieczorek, 2001, and references therein).

Traditionally, the Štramberk Limestone is assigned to Tithonian. This age is also given in Eliášová's papers on corals from the Štramberk Limestone. However, apart of Tithonian, Early Berriasian calpionellids and ammonites have been determined in both: the Štramberk Limestone in Moravia and in the Štramberk-type limestones in the the Polish Carpathians (e.g., Morycowa, 1964a, 1968; Houša, 1990; Eliáš & Vašíček, 1995; Ciborowski & Kołodziej, 2001). Detailed examination of about 100 coral-bearing exotics from the Polish Outer Carpathians revealed that calpionellids occur in 15 percent of them. Most of them contain calpionellids of Late Tithonian age (Crassicolaria Zone) and Late Tithonian–Early Berriasian; few contain only Early Berriasian (Calpionella Zone; Ciborowski & Kołodziej, 2001).

In the present paper, a Late Tithonian–?Early Berriasian age is assumed for most of the studied corals. However, it can not be excluded that some of these exotics are older than Tithonian or younger than Early Berriasian. The upper

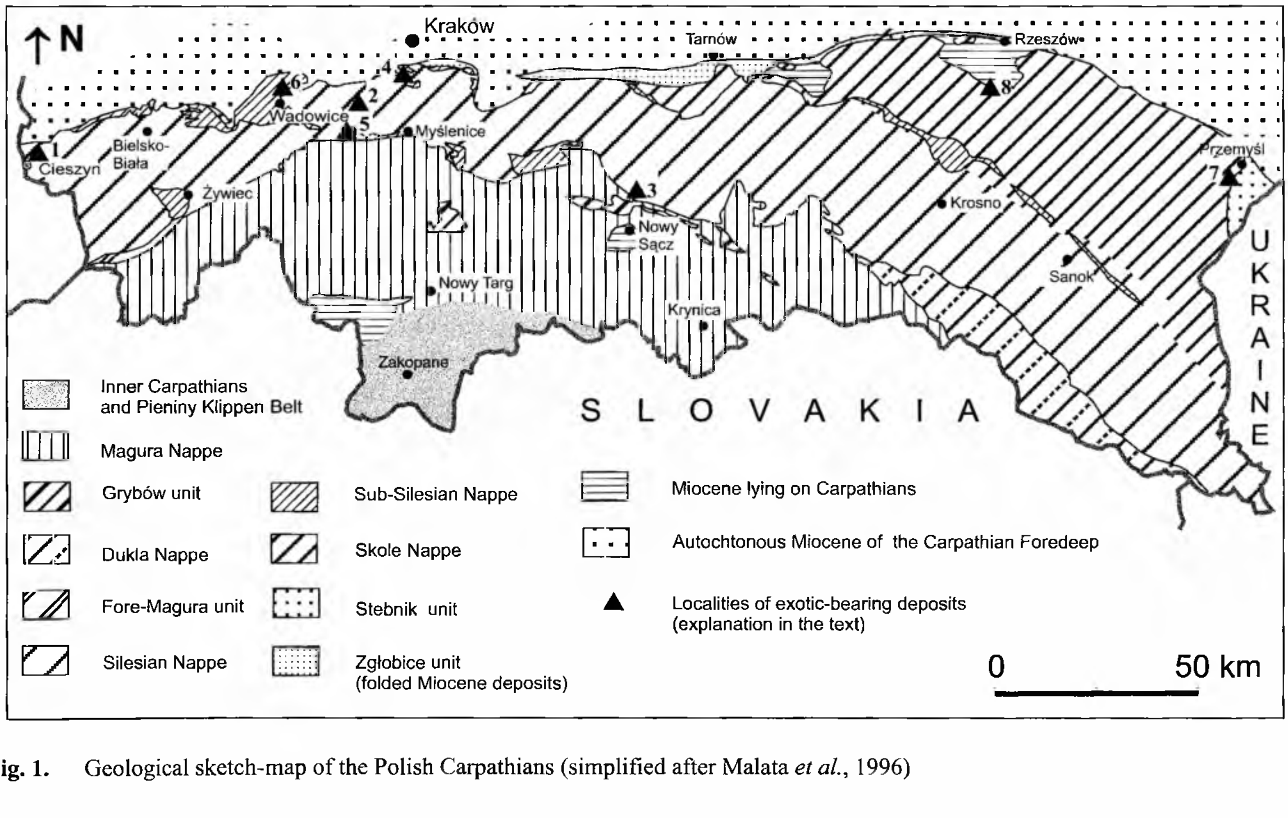

**Fig. 1.** Geological sketch-map of the Polish Carpathians (simplified after Malata *et al.*, 1996)

age limit of a coral from an exotic pebble from Zamarski is limited by the age of the Lower Cieszyn Beds (Kimmeridgian–middle Upper Tithonian). Recent studies by Ivanova (Ivanova & Kołodziej, in press) revealed foraminiferal species *Montsalevia salevensis* (Charollais, Broennimann & Zaninetti), *Meandrospira favrei* (Charollais, Broennimann & Zaninetti), *Patellina turriculata* Dieni & Massari and *Neotrocholina valdensis*, suggesting Valanginian age for three coral-bearing exotic pebbles (corals from exotics UJ 140/31 and 39 are presented in this paper), including the one with *Pachythecophyllia eliasovae* n.gen., n.sp. described in this paper. Where information about age was not available, Tithonian-?Early Berriasian age was assumed for the studied corals.

Figure 1 shows general geographical and geological position of seven localities from which the studied corals come. The localities and stratigraphic position of the exotic-bearing deposits with relation to the Outer Carpathian nappes are given below.

***Silesian Nappe***

1 – Zamarski – 6 km north of Cieszyn; Lower Cieszyn Beds (Kimmeridgian–middle Upper Tithonian); one exotic.

2 – stream in the Leńcze village, 5 km north of Kalwaria Zebrzydowska; Lower Istebna Beds (Late Senonian); two exotics.

3 – Gródek on the Dunajec (Rożnów Lake), 15 km north of Nowy Sącz; Ciężkowice Beds (Eocene); two exotics.

***Sub-Silesian Nappe***

4 – Krzywa stream in the Krzywica village, 7 km west of Skawina; Verovice Beds (Barremian); five exotics.

5 – Jastrzębia stream in the Jastrzębia village, 1.5 km east of Lanckorona; Grodziszcze Beds (Early Aptian); two exotics.

6 – Rędzina stream in the Woźniki village, 6 km north of Wadowice; black shales within Gaize Beds (Late Aptian–Albian); five exotics.

***Skole Nappe***

7 – Lipnik Hill (Wapielnica) near Przemyśl, 5 km south-east of Przemyśl; Ropianka Formation (Maastrichtian–Palaeocene). The locality is in the vicinity of the Kruhel Klippe; five exotics.

Exotics and thin sections are deposited in the Geological Museum of the Institute of Geological Sciences, Jagiellonian University, Kraków (collection UJ 140P – specimens; UJ 30 – thin sections).

## SIMILARITIES BETWEEN PACHYTHECALIINA AND RHIPIDOGYRINA

Skeletal architecture and microstructure of zardinophyllids were discussed by Montanaro-Gallitelli (1975), Cuif (1975), Stolarski (1996), Roniewicz & Stolarski (2001), and Stolarski & Russo (2001). Amphiastreids, heterocoeniids and related families were discussed among others by Alloiteau (1957), Morycowa (1964b, 1971), L. Beauvais (1976), Melnikova & Roniewicz (1976), M. Beauvais (1977), Eliášová (1975, 1976a, b, 1978), Kołodziej (1995), Roniewicz & Stolarski (2001), Stolarski & Roniewicz (2001) and Stolarski & Russo (2001).

The suborder Rhipidogyrina has not been a subject of a detailed analysis of high rank taxonomy or phylogeny. General discussion on these corals can be found in Alloiteau (1957), Eliášová (1973, 1990), L. Beauvais (1976), Roniewicz (1976), Morycowa (1997), Roniewicz & Stolarski (1999), Morycowa & Kolodziej (2001), Stolarski & Roniewicz (2001) and Morycowa & Marcopoulou-Diacantoni (2002).

## MICROSTRUCTURE AND WALL–SEPTA RELATIONS

Pachytheca – the diagnostic feature of Pachythecaliina – is a type of epithecal wall with internal layer built of radially orientated equal-sized fascicles of fibres (modules). Calcification centres of these modules occur at the circumference of the corallite or form the axes of the fascicles giving in result horizontal trabeculae. Fibrous structures of the wall and septa are separated by suture or, rarely, wall fibres continue to septa. Pachytheca is a wall, developed in advence of septa, forming a conical or pipe-like calice (Cuif, 1975; Roniewicz & Stolarski, 1999, 2001).

The wall modules called *septaldornen* by Ogilvie (1897) or *septes abortifs* by Alloiteau (1957) were interpreted by Kołodziej (1995) as horizontal trabeculae and recognized in both: amphiastreids (*Amphiastrea basaltiformis* Étallon 1859; = *Amphiastrea* sp. 1 in this paper) and heterocoeniids (*Latusastrea exiguis* de Fromentel 1862). The skeletal microstructure of both families is similar; septa are composed of minitrabeculae and wall is composed of horizontally arranged thick, compound polyaxial trabeculae (Kołodziej, 1995; figs. 3, 4, 6).

Although wall microstructure of carolastreids, donacosmiliids and intersmiliids is poorly preserved, it is considered here to be in structural continuation with septa. Taking into consideration other features shared by them with Pachythecaliina one can infer the pachythecal character of the wall (although type of wall in donacosmiliids seems to be problematic). Also in case of some amphiastreids, the pachythecal character of the wall is only assumed, based on microstructural vestiges.

Calcification centres in septa are not, as a rule, separated in zardinophyllids or, as in amphiastreids, occur in minitrabeculae measuring up to ca. 50 μm in diameter (e.g., Roniewicz & Stolarski, 2001). Heterocoeniids also show minitrabecular septal microstructure (Kołodziej, 1995). Minitrabeculae in septa and thick, compound polyaxial trabeculae in the wall have been recognized by the author in another heterocoeniid coral *Pachycoenia* sp. (Fig. 2A-C), in the Cenomanian specimen from collection of Dr. H. Löser (see Löser, 1989). It should be stressed that Eliášová (1996) placed with reservation *Pachycoenia* sp., described by Löser (1989) in the synonymy list of *Canleria clemens*, a new genus and species from the family Heterocoeniidae.

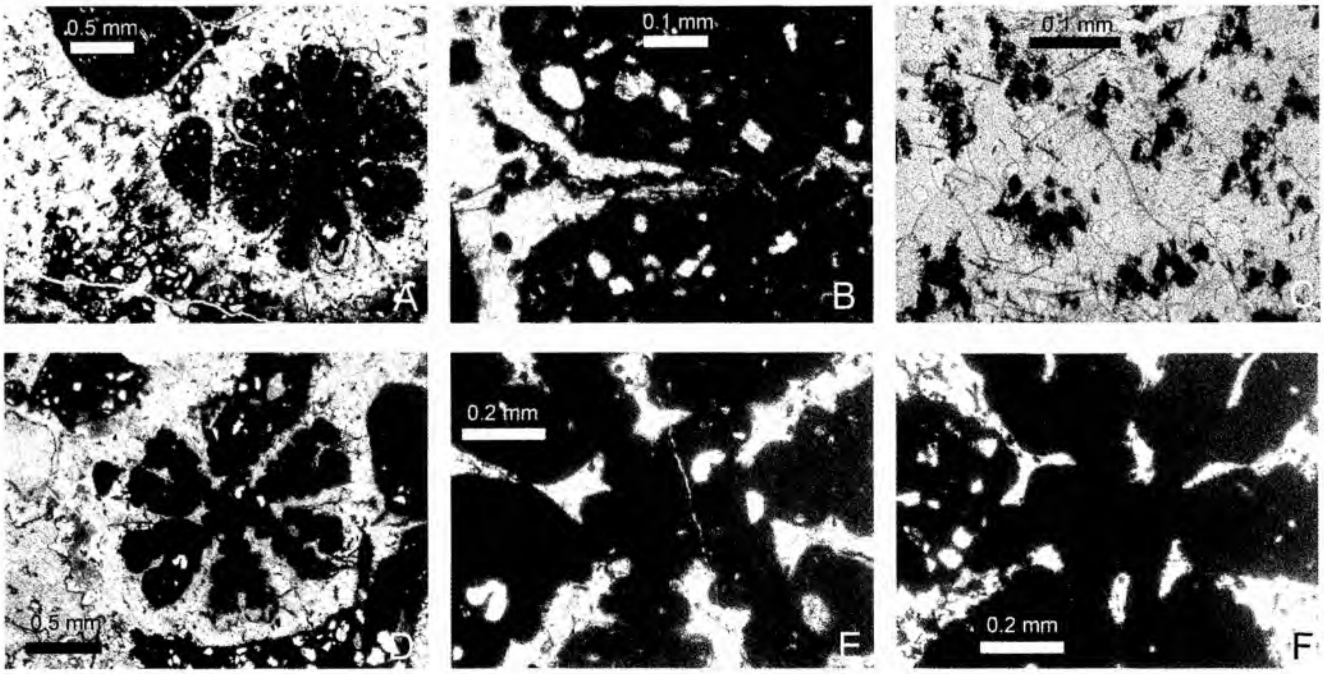

**Fig. 2.** *Pachycoenia* sp.; transverse sections; **A** – section across of corallite and *lames perithecales*; **B** – minitrabeculae in septum; **C** – thick trabeculae in *lames perithecales*; **D–F** – internal edges of septa bearing auriculae-like structures; Upper Cenomanian, Dresden (coll. H. Löser)

Septa and wall (when in structural continuity with septa) in Rhipidogyrina are formed by the neorhipidacanth trabeculae, namely compound trabeculae, characterized by the presence of monoaxial main trabeculae sending off secondary trabeculae (Roniewicz, 1976; Morycowa & Roniewicz, 1995). Rhipidogyrinan microstructure basically differs from that of Pachythecaliina in having numerous secondary trabeculae in the septa. In the Amphiastreidae, such lateral expansions are absent, and in the Heterocoeniidae are poorly developed. Wall and perithecal trabeculae in heterocoeniids wall (*Latusastrea exiguis*, *Pachycoenia* sp.) are compound as well, but probably secondary lateral trabeculae go off from polyaxial, and not monoaxial primary trabecula (Kołodziej, 1995). As noted by Morycowa (Morycowa & Marcopoulou-Diacantoni, 2002), horizontally distributed trabeculae in the wall (rhipidotheca) of some rhipidogyrinans resemble the trabeculae pattern of the wall in amphiastreids. Indeed, when we compare trabeculae pattern in longitudinal sections of the wall or septa of some Rhipidogyrina (*Ironella rutimeyeri* (Koby 1889) – Roniewicz, 1976, pl. 21, fig. 2b; *Pseudoironella regularis* – Sikhuralidze, 1979, pl. 16, fig. 16; *Diplocoeniella gerochi* – Morycowa, 1997, fig. 4d), it resembles trabeculae distribution in the wall of *Latusastrea exiguis* and *Amphiastrea basaltiformis* (=*Amphiastrea* sp.1 in this paper; Kołodziej, 1995). However, these trabeculae have not the "brush-like" appearance, shown by rhipidogyrinan trabeculae.

Most authors described the wall in Rhipidogyrina, even in cerioid taxa, as septothecal or parathecal. According to Eliášová (1973), the wall of the cerioid rhipidogyrids (*Acanthogyra* Ogilvie 1897, *Pruvostastraea* Alloiteau 1957) resulted from fusing of peripheral, curving edges of septa. In L. Beauvais' (1974, 1976) interpretation, corals from the family Pruvostrastraeidae have septa originated by invagination of the wall, though she described the wall in the Pruvostastraeidae as septotheca. In this family and in the Aulastraeoporidae, the wall is not septo- or parathecal (as in Rhipidogyridae Koby 1905), but is in structural continuity with septa (Kołodziej, 1997). Morycowa (Morycowa & Marcopoulou-Diacantoni, 2002), basing on study of the Aulastraeoporidae proposed a new type of wall – a rhipidotheca – wall formed by neorhipidacanth trabeculae. This wall, similarly as marginotheca and pachytheca, is in structural continuity with septa. In my opinion, this type of wall occurs also in the family Pruvostastraeidae.

Dr H. Eliášová provided a photograph of a coral from the Štramberk Limestone determined as ?*Mitrodendron* sp. (Fig. 3). Skeletal features (bilateral symmetry, smooth septa) suggest that this coral, although possibly not *Mitrodendron*, represents amphiastreids. However, in my opinion the wall microstructure resembles the one occurring in Rhipidogyrina (*cf.*, Roniewicz & Stolarski, 1999; fig. 14). Lateral branches (although the "brush-like" appearance is not as strongly developed as in rhipidogyrinans) seem to occur even in the part of some septa near the wall. Microstructure of the wall in *Carolastraea moravensis* (family Carolastraeidae) has been recognized by Eliášová (1978) as two-zonal, fibrous–fibrous-lamellaire. My observations show that wall trabeculae in this species (Dr. H. Eliášová's collection) bear poorly developed lateral trabeculae (Fig. 4).

## SYMMETRY OF SEPTAL APPARATUS

Bilateral symmetry defined by the enlarged primary ("cardinal") septum or main ("cardinal") sector is a distinctive feature of the most pachythecaliinans, but is very rare in other scleractinians.

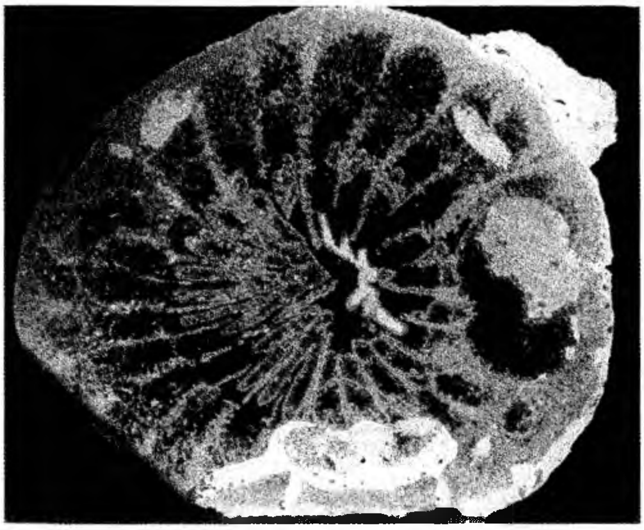

**Fig. 3.** Amphiastreid coral; transverse section (negative, scale not known); Tithonian–Early Berriasian, Štramberk (coll. H. Eliášová)

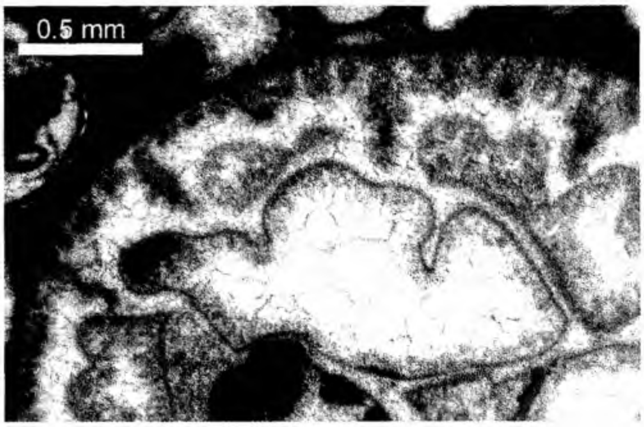

**Fig. 4.** *Carolastraea moravensis* Eliášová 1978; transverse section; lonsdaleoid septa and microstructure of wall; Tithonian–Early Berriasian, Štramberk (thin section No. 859, Ústřední ústav geologický, Praha)

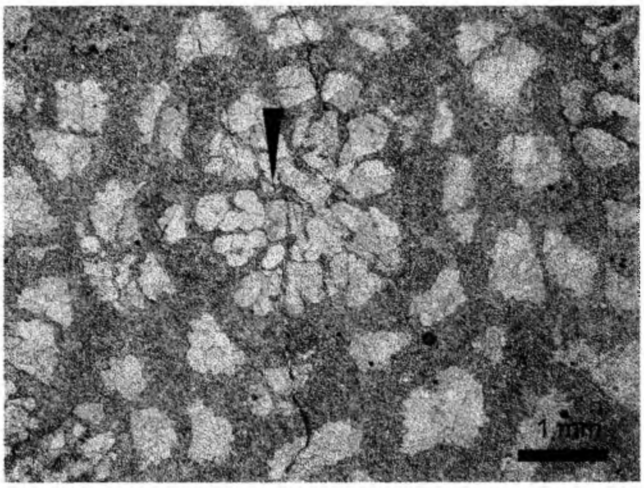

**Fig. 5.** *Preverastraea marinosi* Marcopoulou-Diacantoni & Morycowa, 2002; transverse section; Albian, Agrostylia (UJ 158P 16). Arrow show enlarged main septum

Although not as strong as in amphiastreids, bilateral symmetry defined by enlarged primary septum is present in the Aulastraeoporidae (e.g., *Preverastraea marinosi* – Morycowa & Marcopoulou-Diacantoni, 2002, fig. 16a; and herein Fig. 5), assigned recently to Rhipidogyrina (Morycowa & Kolodziej, 2001). Other pachythecaliinan-like features of this family are discussed in other parts of this chapter.

The presence of lamellar columella produces bilateral symmetry in some rhipidogyrinan corals. Eliášová (1973) noted that in *Acanthogyra*, *Ogilvinella* (previous name *Ogilviella* – see Eliášová, 1976c), *Placogyra* Koby 1904 and *Aplosmilia* d'Orbigny 1849 the symmetry of septal apparatus is radial and bilateral at the same time. In the opinion of Eliášová (1973), bilateral symmetry is better marked in the juvenile stage of these genera. Interestingly, Lebanidze (1991; p. 37, fig. 7, pl. 15, fig. 2a) reported that in the juvenile stage of ontogeny of *Aplosmilia coalescens* Eliášová 1973, the primary septum is present, but the columella is absent. Detailed studies of colony blastogeny in rhipidogyrinans are necessary to reveal possible changes in symmetry and development of columella in the ontogeny of individual polyps.

It is worth to note that bilateral symmetry is better developed in juvenile stages of pachythecaliinans. Quasi-radial symmetry of adult corallites has been recently recognized by Morycowa (Morycowa & Marcopoulou-Diacantoni, 2002) in a newly established amphiastraeid, *Mitrodendron parnassus*.

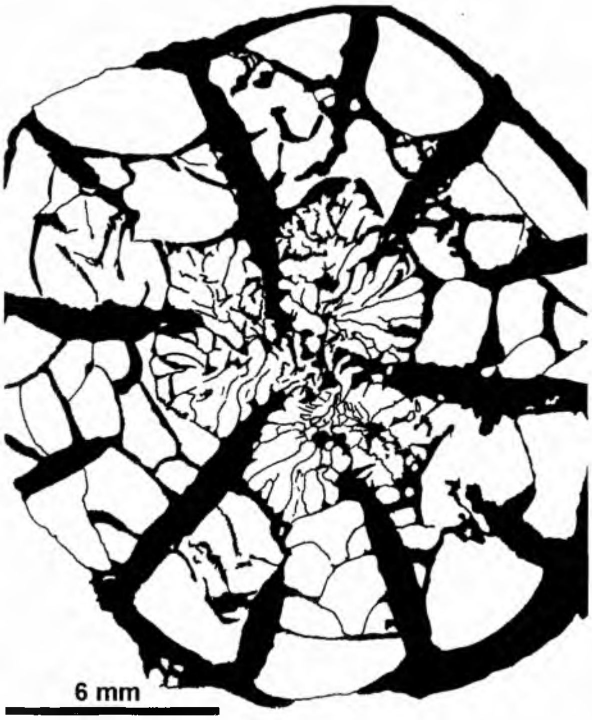

**Fig. 6.** ?*Aulastraeopora deangelisi* Prever 1909; transverse section; Lower Aptian, Arachowa; based on photograph from Baron-Szabo & Steuber (1996: pl. 9, fig. 1)

## MARGINARIUM

Well developed marginarium, a very rare structure in Scleractinia, is characterestic for some pachythecaliinans, particularly amphiastreids (cf., Fig. 14). "Internal calice" developed in aulastraeoporids gives them amphiastreid-like appearance (Figs 5, 6; cf., Prever; 1909; M. Beauvais, 1977; Baron-Szabo & Steuber, 1996; Löser, 1998a; Morycowa & Marcopoulou-Diacantoni, 2002). Because septa run from corallite wall to "internal calice", typical marginarium is not developed. However, similar relation between septa and "internal calice" is present in some corallites of amphiastraeid *Amphiaulastrea rarauensis* (Morycowa) (Morycowa, 1971; pl. 26, fig. 1b).

## LONSDALEOID SEPTA

Lonsdaleoid septa occur in some taxa of both discussed suborders. These septa, characteristic of Rugosa, have not been described in other scleractinians. In Rhipidogyrina, except of the family Aulastraeoporidae, lonsdaleoid septa are usually poorly developed. They are also well developed in *Acanthogyra aptiana* Turnšek 1981 (Turnšek & Mihajlović,1981) (family Pruvostastraeidae). According to Morycowa and Marcopoulou-Diacantoni (1997), it belongs to *Paraacanthogyra* Morycowa or represents another new rhipidogyrinan genus.

## APOPHYSAL SEPTA

Apophysal septa are high-order septa which in their basal parts are not parallel to the septa from which they are growing out (Eliášová, 1973). They are a characteristic feature of the suborder Rhipidogyrina, including the family Aulastraeoporidae (e.g., *Preverastraea iselli* (Prever 1909) – see M. Beauvais, 1977; pl. 2, fig. 2; pl. 3, fig. 1). According to Baron-Szabo (Baron-Szabo & Steuber, 1996), apophysal septa are a diagnostic feature of the family Aulastraeoporidae (classified by these authors as Heterocoeniina). They recognized these structures in *Aulastraeopora* sp. and *Preverastraea aptiana* (Turnšek 1981). Also offsets visible on lateral parts of septa S1 *Aulastraeopora deangelisi* Prever 1909, illustrated by Baron-Szabo and Steuber (1996; pl. 9, fig. 1; and Fig. 6 herein); resemble apophysal septa. Because the specimen described by Baron-Szabo and Steuber differs from type-material, following Löser (1998a), I classify this species as ?*Aulastraeopora deangelisi*. Skeletal structures resembling apophysal septa occur in some heterocoeniids, especially when the basal part of septum is very wide, e.g., *Pachycoenia fuchsi* (Félix 1903; M. Beauvais, 1977; pl. 2, fig. 2), *Selenegyra* sp. (herein Fig. 22A, B) and in specimens described by Schöllhorn (1998) as cf. *Comalia* sp. (text.-fig. 38, pl. 21, figs 7, 8) and by Kołodziej (1995; figs 7g, h) as *Preverastraea tenuiseptata* Kołodziej 1995. The latter species does not belong to *Preverastraea*, but possibly to a new genus (Löser, 1998a).

## INTERNAL MARGIN OF SEPTA

Septal internal margins of rhipidogyrinans (including aulastraeoporids) display auricular ornamentation (spoon-like outgrowths; Roniewicz & Morycowa, 1993; Morycowa & Roniewicz, 1995; Morycowa & Kolodziej, 2001), known also in the stylinids. It appears however, that auriculae can occur also in some heterocoeniids. M. Beauvais (1977) noticed that internal margins of *Pachycoenia* Alloiteau 1952 display expansions (*ramifiés*). My observations of the internal margin of cross sections of *Pachycoenia* sp. (Fig. 2D–F) revealed the presence of structures resembling auriculae (*cf.*, Gill, 1977). They are also present in *Preverastraea iselli* (Prever 1909) (M. Beauvais, 1977; pl. 3, fig. 1). This supposition should be confirmed by longitudinal sections.

## BUDDING

Taschenknospung (pocket-budding), a diagnostic feature of Amphiastreidae, is discussed in detail by Roniewicz (1966) and Roniewicz & Stolarski (2001). The oldest record of this unique type of reproduction was found by these authors in the Late Triassic amphiastraeid coral *Quenstedtiphyllia fritschi* (Voltz 1896). Apart of amphiastreids, Taschenknospung was recognized by Kołodziej (1995) in the Aptian heterocoeniid coral *Thecidiosmilia morycowae* Kołodziej 1995. The presence of Taschenknospung in this species (an autapomorphy of the Amphiastreidae according to Roniewicz & Stolarski, 2001), supports phylogenetic relations between heterocoeniids and amphiastreids.

Taschenknospung has not been found in other pachythecaliinans. However, budding occurring in *Carolastraea* (family Carolastraeidae) seems to be similar to this kind of budding. Eliášová (1976a) determined budding in *Carolastraea* as extracalicinal marginal, but later Eliášová (1978) called this budding as intramural. Following Eliášová (1978), I agree that Taschenknospung is a kind of mural budding, i.e. buds are established in the wall of the parental individual. In Taschenknospung, new buds enlarge at the expense of the space of the parental calice, and later their growth becomes centrifugal. In *Carolastraea*, in contrast to lateral budding, new buds do not rapidly lose connection with the parent individual. Eliášová (1976b) interpreted budding occuring in *Hexapetalum* Eliášová 1975, *Simplexastraea* Eliášová 1975 and *Selenegyra* Ogilvie 1897 as intramural extracalicinal. However, interpretation of this budding as Taschenkospung can not be excluded. Therefore, classification of these genera within the family Amphiastreidae by L. Beauvais (1981) and, with question mark, also by Stolarski and Russo (2001) would be justified (see discussion of these genera in the systematic part).

Mural budding is not known in Rhipidogyrina. Only Morycowa and Marcopoulou-Diacantoni (1997) suggested the presence of mural budding in *Preverastraea diplothecata* (Hackemesser 1936). A question arises: did the buds originated in the marginarium of the parental calice or, like in Taschenknospung, they were initiated in the wall? The difficulties with identification of the place of origin of the buds led some authors to consider Taschenknospung as a synonymy of intracalicular, marginal budding (e.g., L. Beauvais, 1974, 1976, 1981).

# STRATIGRAPHIC DISTRIBUTION OF PACHYTHECALIINA AND RHIPIDOGYRINA

The suborder Pachythecaliina is known from the Late Triassic to Maastrichtian and the suborder Rhipidogyrina – from the Middle Jurassic to Maastrichtian strata (Roniewicz & Morycowa, 1993; Löser, 1998b; Stolarski & Russo, 2001). Zardinophyllidae, the first pachythecaliinans, occurred only in the Late Triassic. Taxonomical diversification of other pachythecaliinans (particularly amphiastreids) and rhipidogyrinans took place in similar geological time. After strong radiation in the Late Jurassic, first of all in the Tithonian, these corals were drastically reduced in diversity in the Early Cretaceous.

Pachythecaliinans from Moravia and from the Polish Carpathians represent a period of highest radiation in a history of this coral group. Seventeenth genera and 35 species of pachythecaliinans, and 8 genera and 22 species of rhipidogyrinans have been described from Moravia (Ogilvie, 1897; Geyer, 1955, Eliášová, 1973, 1974, 1975, 1976a, b, c, d, 1978). In the Štramberk-type limestones from Poland, there occur 14 genera and 22 species of pachythecaliinans and 4 genera and 4 species of rhipidogyrinans (Ogilvie, 1897; Geyer, 1955; Morycowa; 1964a, 1974; Kołodziej, 1995, and this paper). In the studied material, rhipidogyrinans are less differentiated in comparison to the material from Moravia (specimens mainly form a huge quarry in Štramberk), what can be attributed to the low number of samples.

The second high radiation, mainly within heterocoeniids and rhipidogyrinans, took place in some regions (although less intensively) during Aptian–Cenomanian (e.g., Prever, 1909; Sikhuralidze, 1979; Eliášová, 1991; Baron-Szabo & Steuber, 1996; Löser, 1998a; Morycowa & Marcopoulou-Diacantoni, 1997, 2002).

# CLASSIFICATION OF PACHYTHECALIINA AND RHIPIDOGYRINA

## PACHYTHECALIINA

Eliášová (1976b) included two families in a new suborder Pachythecaliina: Pachythecaliidae Cuif 1975, and a newly established family Hexapetalidae. Most pachythecaliinan corals discussed in the present paper have been placed usually in the suborder Amphiastreina (see review in Kołodziej, 1995). Following Melnikova and Roniewicz (1976), most coral researchers included four families into Amphiastreina: Amphiastreidae Ogilvie 1897, Carolastraeidae Eliášová 1976, Donacosmillidae Krasnov 1970, and Intersmiliidae Melnikova & Roniewicz 1976. In Chevalier and L. Beauvais' (1987) classification, heteoroceniids are included to the Volzeidae L. Beauvais 1981, and together with the Pachythecaliidae (but without *Zardinophyllum*) included to Pachythecaliina. Kołodziej (1995) transferred to Amphiastreina the corals assigned earlier to the suborder Heterocoeniina Morycowa 1964. It should be stressed that M. Beauvais (1977) is believed to be the creator of this suborder, although Morycowa (1964) was the first who rised the family Heterocoeniidae to the level of suborder, giving Alloiteau as the creator. Roniewicz and Stolarski (2001) included the Amphiastreidae together with the Zardinophyllidae (= Pachythecaliidae) to Pachythecaliina. According to Stolarski and Russo (2001), carolastraeids, donacosmillids, intersmiliids, and heterocoeniids are other supposed post-Triassic pachythecallinans (pachythecaliinans *sensu lato*), although these authors did not classify these corals as Pachythecaliina. Morycowa (Morycowa & Marcopoulou-Diacantoni, 2002), following proposition of Roniewicz and Stolarski (2001), assigned amphiastreids to Pachythecaliina. In the present paper, all the above mentioned pachythecaliinans *s.l.* have been included to the discussed suborder. Despite some differences, these corals have more in common with Pachythecaliina than with other scleractinian suborders.

The necessity of recognizing the family Carolastraeidae is in my opinion problematic. According to Eliášová (1976a), these corals differ from the Amphiastreidae by the presence of lateral budding, one-zonal endotheca and lack of lonsdaleoid septa. However, my examination of a thin section of *Carolastraea moravensis* (collection of Dr. H. Eliášová) shows that lonsdaleoid septa, although rare, are present in this species (Fig. 4). Moreover, the budding occurring in this genus seems to be similar to Taschenknospung (see the section on budding). Eliášová (1976a, 1978) determined (but did not illustrate) endotheca as one-zonal, whereas Baron-Szabo (Baron-Szabo & Steuber, 1996) observed both tabular and vesicular dissepiments in the new species *C. gracea*. If those features were taken into consideration, *Carolastraea* Eliášová 1978 and *Pleurophyllia* de Fromentel 1856 would be very close. The systematic position of *Carolastraea* needs to be clarified through additional study of the type specimen of *C. fraji* Eliášová 1976. Even if distinguishing of the family Carolastraeidae is justified, these corals share with amphiastreids many features supporting their systematic position within Pachythecaliina.

## RHIPIDOGYRINA

Roniewicz (1976) distinguished the suborder Rhipidogyrina basing on neorhipidacanth microstructure. Different rhipidogyrinan genera have been previously assigned to the suborders Caryophylliina (e.g., Vaughan & Wells, 1943; Wells, 1956; Geyer, 1955), Amphiastreina (e.g., L. Beauvais, 1964, 1970, 1974, 1976), but most commonly to Meandriniina (e.g., Alloiteau, 1952, 1957; Roniewicz, 1966; Eliášová, 1973; L. Beauvais 1970, 1976). Some genera have been included by L. Beauvais (1970, 1974, 1976) to Amphiastreina (family Pruvostastraeidae) and others to Meandrinina (family Rhipidogyridae). At present, most workers accept the suborder Rhipidogyrina; the neorhipidacanth microstructure is a distinctive characteristic of this coral group. However, this suborder has been not distinguished in the classification scheme of Scleractinia outlined by L. Beauvais (1981), who included some of rhipidogyrinans to the subfamily Pruvostastraeinae (family Amphiastreidae, suborder Distichophylliina), and other to the family Rhipidogyridae (suborder Meandriniina).

Recently, the family Aulastraeoporidae, usually considered as Heterocoeniina (or as Amphiastreina, family Heterocoeniidae – Kołodziej, 1995) on the basis of microstructural criteria and of the presence of auriculae, have been assigned by Morycowa and Kolodziej (2001) to Rhipidogyrina. This family occupies a special place in Rhipidogyrina, because of its heterocoeniid/amphiastreid-like appearance, discussed above.

## PHYLOGENY OF PACHYTHECALIINA AND RHIPIDOGYRINA

### PACHYTHECALIINA

Peculiar morphological features led various authors to consider zardinophyllids, amphiastreids and related families as descendants of Rugosa. Koby (1888) placed amphiasterids directly among Rugosa. Zardinophyllidae were considered as members of a new independent anthozoan order Haxanthinaria, which according to Montanaro-Gallitelli (1975) occupies a systematic position between Rugosa and Scleractinia. Archaic morphology, microstructure and ontogeny observed in the Pachythecaliidae (now Zardinophyllidae) were considered by Cuif (1975, 1981) as evidence of their relationships with Permian corals. Eliášová (1978) included Amphiastreina, Heterocoeniina and her two new suborders, Pachythecaliina and Carolastraeina (Eliášová, 1976b), to the order Haxanthinaria. Melnikova and Roniewicz (1976) considered Pachythecaliidae as a transitional link between Amphiastreina and their presumed ancestors, Permian Polycoeliidae, suborder Pleurophyllina Sokolov 1960 (see also Stolarski, 1996). The presumed scenario of transition between Permian Pleurophyllina and Triassic Zardinophyllidae was preliminarily presented by Cuif and Stolarski (1999). According to Stolarski (1999), amphiastreids and heterocoeniids supposedly share with zardinophyllids a similar ontogenetic pattern that suggests a relationship with pleurophylline rugosans. Stolarski and Russo (2001) included the Zardinophyllidae and the Amphiastreidae to Pachythecaliina, whereas the families Carolastraeidae, Donacosmiliidae, Intersmiliidae, and Heterocoeniidae have been considered as supposed post-Triassic pachythecaliinans.

Roniewicz and Stolarski (2001) have performed two cladistic analyses in order to interpret the phylogeny of amphiastraeid corals. In the first analysis, pleurophylline rugosans were used as outgroup. According to these authors, such features as (i) one axial septum in early blastogeny of Triassic amphiastreid *Quenstedtiphyliia* Melnikova 1975, (ii) bilateral insertion of the next septa, and (iii) thick epithecal wall, suggest phylogenetic relationships among amphiastreids, zardinophyllids, and possibly pleurophyllines. In the second analysis, the authors based on traditional assumption that pachythecaliinans are convergent with pleurophyliinans. The solitary scleractinian coral *Protoheterastraea* Wells 1937 (suborder Caryophylliina Vaughan & Wells 1943) was considered as an outgroup of the pachythecaliinans. The authors considered the presence of pachytheca as the synapomorphy that supports grouping zardionophyllids and amphiastreids in the clade Pachythecaliina. Taschenknospung budding is considered an autapomorphy of the Amphiastreidae.

### RHIPIDOGYRINA

This suborder has not been a subject of a detailed phylogenetical analysis. The review of classification of Rhipidogyrina presented above shows that corals of this suborder have been classified in different suborders, although the suborder Rhipidogyrina is now commonly accepted by coral workers. Roniewicz and Morycowa (1993; see also Morycowa & Roniewicz, 1995) considered these corals as descendants of stylinid stem, because internal margins of the septa of both groups display auricular ornamentation.

The supposition presented in this paper that some rhipidogyrinans can be related with Pachythecaliina is partly in agreement with a classification scheme of Scleractinia proposed by L. Beauvais (1981), who classified some amphiastreids, heterocoeniids and pruvosastraeines together. Possibility of phylogenetic relationships between rhipidogyrinans and pachythecaliinans was considered also by the present author (Kołodziej, 1997, 2003). L. Beauvais & M. Beauvais (1975) considered phylogenetical relationships between Heterocoeniina, Amphiastreina (where they included most of rhipidogyrinans) and Stylinina represented by their new family Agatheliidae. According to Stolarski and Russo (2001), "pachythecaliinan" characters of agatheliids are either shared with other scleractinians or are not homologous with those in Pachythecaliina.

### PACHYTHECALIINA V. RHIPIDOGYRINA: CONVERGENCE OR PHYLOGENETIC RELATIONSHIPS?

The discussion presented above shows, in opinion of author, that rhipidogyrinans share with pachythecaliinans several characters which are absent or rare in other scleractinians. Aulastraeoporidae are the most unusual rhipidogyrinans because of their skeletal structures close to those in heterocoeniids and amphiastreids.

These similarities can be explained by convergence. However, because of "mixed" features of Aulastraeoporidae, it is tempting to speculate about phylogenetic link between Pachythecaliina and Rhipidogyrina. This hypthesis needs to be verified by more detailed studies, especially on early blastogeny of rhipidogyrinans, wall microstructure of pachythecaliinans and internal septal margins of heterocoeniids. Vestiges of microstructure in some discussed here pachythecaliinans suggest that the microstructure of Jurassic–Cretaceous pachythecaliinans is indeed more differentiated (*cf.*, Eliášová, 1976b, 1978; Roniewicz & Stolarski, 1999, 2001).

Existing differences, in septal microstructure and in overall morphology (particularly if zardinophyllids and rhipidogyrids are compared), justify the necessity of distinguishing of the suborders Pachythecaliina and Rhipidogyrina.

Changes of biomineralization style (modular *vs.* trabecular) during blastogeny e.g., *Qunestedtiphyllia fritschi* casts light on possible relationships between corals with different types of skeletal microstructures and suggest that borders between microstructural groups may not be so strict as suggested before (Roniewicz & Stolarski, 2001).

## SYSTEMATIC PALAEONTOLOGY

The classification of Scleractinia used below follows Alloiteau (1952), modified by L. Beauvais (1970), Eliášová (1976b, 1990), Kołodziej (1995), Krasnov (1970), Melnikova & Roniewicz (1976), Roniewicz (1976) and Roniewicz & Stolarski (2001).

The terms *main (cardinal) septum* and *main (cardinal) sector* are used here in the descriptions of pachythecaliinans, following their general meaning. The term *cardinal septum* is placed in the English translation of terms used in descriptions of Scleractinia (L. Beauvais *et al.*, 1993). It is neccessary to create new terms for descriptions of peculiar septal apparatus in Pachythecaliina, because the above mentioned terms can be used properly only for Rugosa (e.g., Rosen, 1993).

Measurements used in the descriptions are abbreviated as follows:
d – corallite diameter,
d cor$_l$ – large diameter of corallite,
d cor$_s$ – small diameter of corallite,
d cal – diameter of calice lumen,
d int – diameter of internal calice,
d ser – series width,
d wall – wall thickness,
den end – density of endothecal elements, in cross section,
c–c – distance between corallites centres,
s – number of septa,
c – number of costae,
S1, S2 – septa of succeeding size orders,
6S1, 12S2 – number of septa of succeeding septal orders,
( ) – less frequent values are given in brackets.

Class ANTHOZOA Ehrenberg 1834
Subclass ZOANTHARIA Blainville 1830
Order SCLERACTINIA Bourne 1900
Suborder PACHYTHECALIINA Eliášová 1976
Family Amphiastreidae Ogilvie 1897

### Genus *Amphiastrea* Étallon 1859

Type species: *Amphiastrea basaltiformis* Étallon 1859

**Remarks:** According to Alloiteau (1950: p. 106–107; 1957: p. 357), holotype of *A. gracilis* Koby 1888 corresponds with holotype of *A. basaltiformis* Étallon 1859. Alloiteau found that the specimen described by Koby (1888) as *A. basaltiformis* Étallon 1859 is the type specimen of *A. basaltiformis*. On the other hand, holotype of *A. basaltiformis* established by Étallon (1859) has been placed by Koby in the synonymy list of *A. gracilis* (see L. Beauvais, 1964; Turnšek, 1972). In consequence, some authors give *A. basaltiformis* Étallon 1859 as the type species of *Amphiastrea*, and others *A. basaltiformis* Koby 1888. According to IRZN, species established before 1930 are valid, even if they were not illustrated or were not properly described (as in the case of *A. basaltiformis* distinguished by Étallon).

Polygonal columns in the colony of *Amphiastrea* (*basaltiformis* type of colony) are an important feature and distinguishes this genus from *Amphiaulastrea* Geyer 1955. The latter displays well developed marginarium. However, it is worth noting that marginarium, although very rare, is developed in some corallites of *Amphiastrea* (see description and remarks to *Amphiastrea* sp. 1). Wide marginarium which is visible in *A. basaltiformis* illustrated by Koby (1888: pl. 65, figs 1, 1a) seems to be the result of a mistake of the draughtsman. My examination of the thin section from Koby's collection (thin section marked as "type"), does not confirm the presence of marginarium (see also L. Beauvais, 1964: text-fig. 43, pl. 22, fig. 1b).

Budding type in *A. basaltiformis* determined by Turnšek (1972) as septal budding was not correctly interpreted (Dr. D. Turnšek, pers. comm., 1996). Among pachythecaliinans this type of an increase occurs only in the Heterocoeniidae (Kołodziej, 1995).

Bilateral symmetry of adult corallites is considered as diagnostic feature of the Amphiastreidae. However, quasi-radial symmetry has been recently recognized by Morycowa (Morycowa & Marcopoulou-Diacantoni, 2002) in newly established *Mitrodendron parnassus*.

### *Amphiastrea* sp. 1
Figs 7 (A–C), 8B

?v1888. *Amphiastrea basaltiformis* Étallon: Koby, pp. 433-434, pl. 115, figs 1, 1a, 2a.
?1955. *Amphiastraea basaltiformis* Étallon: Geyer, pp. 187-188, pl. 24, figs 6-7.
v1964a. *Amphiastraea basaltiformis* Koby, non Étallon: Morycowa, pp. 500-502, pl. 22, fig. 1a-c.
?1972. *Amphiastraea basaltiformis* Étallon: Turnšek, pp. 42, 98-99, pl. 24, figs 3, 4.
?1985. *Amphiastraea basaltiformis* Étallon: Rosendahl, p. 54, pl. 5, fig. 9.
v1995. *Amphiastraea basaltiformis* Étallon: Kołodziej, fig. 4a-f.

**Material:** 1 specimen: UJ 140 P/2; 2 thin sections: UJ 30/11, 12.

**Dimensions** (in mm): d cor$_l$ = (5) 7–8 (9); d cor$_s$ = 4–5 (6); s = ca. 20–30; density of horizontal trabeculae in wall in transversal section = 7–8/2 mm.

**Description:** Colony cerioid. Corallites polygonal, slightly prolonged. Septal apparatus displays bilateral symmetry. The main septum clearly longer and thicker than other septa of the main sector. Septal faces of largest septa, particularly the main septum, ornamented with small, regular granules. Claviform inner edge of main septum. The inner edge of other septa is club-shaped or strongly thinner and zigzag. Marginarium developed sporadically; as a result "internal calice" is present. Taschenknospung budding.

**Microstructure:** The microstructure of this species described previously (Kołodziej, 1995) was based on the specimen from the Kruhel Klippe (Morycowa, 1964a). The specimen from the Lipnik Hill described herein is poorly preserved.

**Remarks:** The studied specimen differs from *A. basaltiformis* collected from the Kruhel Klippe (Morycowa, 1964a) in more prolonged corallites. In the latter specimen, well developed marginarium occurs in few corallites (see remarks on *Amphiastrea*). Recrystallization of most of the corallites does not allow estimate the number of septa. In my previous paper (Kołodziej, 1995), I placed both specimens in *A. basaltiformis*. However, later observations of thin section of the holotype (the thin section marked as "type") of *A. basaltiformis* from the Koby's collection (Muséum d'Histoire naturelle, Genève) revealed a feature not given before. The main

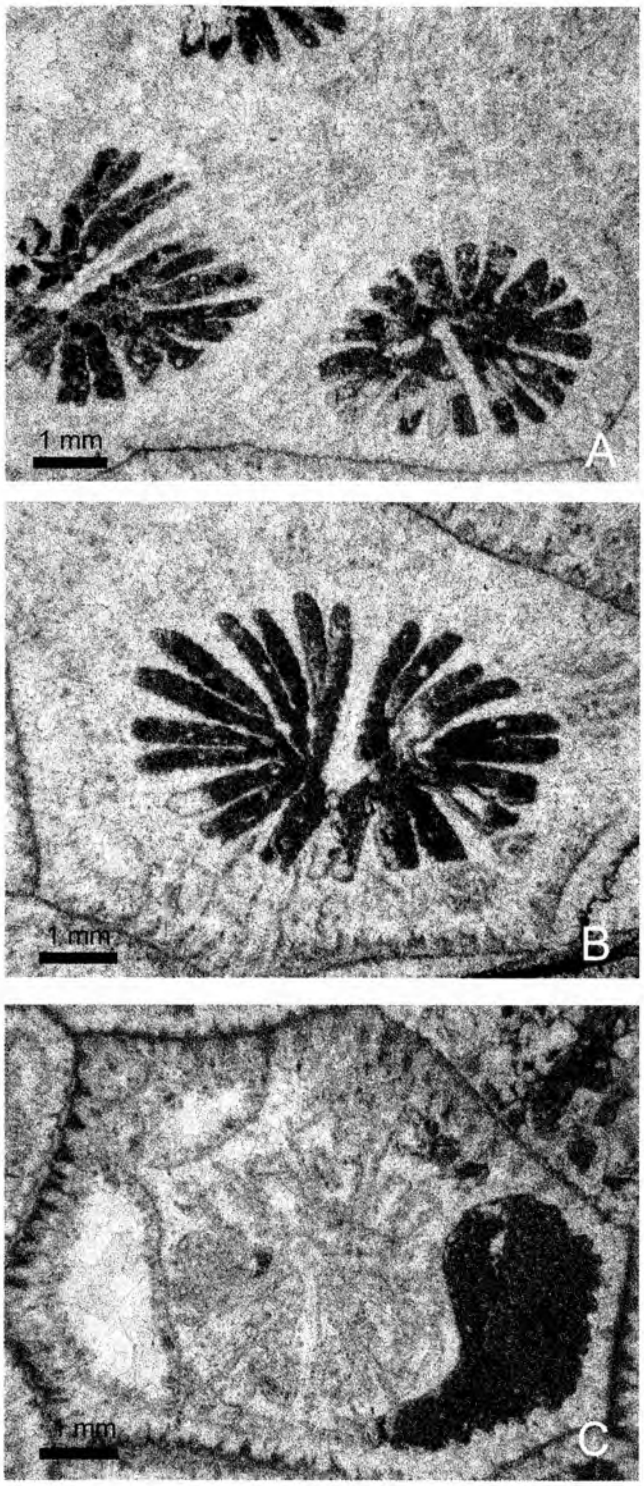

**Fig. 7.** **A–C.** *Amphiastrea* sp. 1; transverse section; Fig. 7C presents corallite with marginal zone. A–B – Tithonian–?Early Berriasian, Lipnik Hill (UJ 30/11; UJ 30/12); C – Tithonian–?Early Berriasian, Kruhel Wielki (UJ 38)

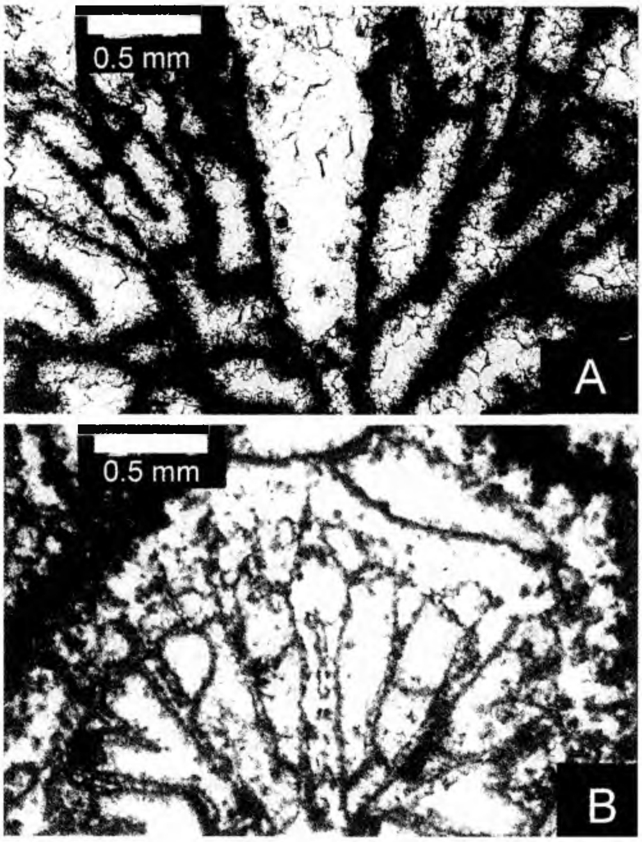

**Fig. 8.** **A.** *Amphiastrea basaltiformis* Koby 1888; transverse section showing fragment of corallite with thick main septum ("Type", coll. F. Koby, Muséum d'Histoire naturelle, Genève). **B.** *Amphiastrea* sp. 1 showing fragment of corallite with main septum; Tithonian–?Early Berriasian, Lipnik Hill (UJ 30/11)

septum is very thick, in places reaching up to 0.8–1 mm. It is much wider in the outer part, and suddenly becomes thin in the inner part. The remaining septa are much thinner (Fig. 8A). The specimen from the Koby's collection is also illustrated by L. Beauvais (1964: text-fig. 43; pl. 22, fig. 1b). It seems that such thickness of septum is not caused by recrystallization, however, more detailed studies of type specimen are necessary. Both specimens from the Štramberk-type limestones have the main septum displaying similar thickness through the length, and similar thickness attaining (0.2) 0.3 (0.5) mm (Fig. 8). Moreover, corallites in the Koby's specimen have larger diameters (d = 7–11 mm) and more numerous septa (30–40) (L. Beauvais, 1964 and personal observations). The measurements reported by Koby (1888) are different: d = 5–10 mm, s = 12–32. Specimens attributed by other authors to *A. basaltiformis* are poorly illustrated or do not have the main septum which would be similar to the one in Koby's specimen.

**Distribution:** Poland; Outer Carpathians, Skole Nappe: Lipnik Hill (Tithonian–?Early Berriasian).

### *Amphiastrea* sp. 2
Fig. 9

?1975. *Amphiastraea basaltiformis* Koby: Eliášová, p. 6, pl. 1, fig. 1.

**Material:** 1 specimen: UJ 140 P/34; 1 thin section: UJ 30/64.

**Dimensions** (in mm)**:** d = 8–12; s = ca. 20–25.

**Description:** Small, poorly preserved fragment of cerioid colony. Septa of main sector are parallel to each other. They have similar length; consequently, calicular fossa occur.

**Remarks:** The investigated specimen is close to the one described by Eliášová (1975) as *A. basaltiformis*. In *Amphiastrea* sp. 2 and in specimens described by Eliášová (1975), calicular fossa occur. Such septal pattern is not a common feature in amphiastreids and has important diagnostic value. Calicular fossa is particularly well developed in other representatives of the Amphiastreidae, namely

*Pseudopistophyllum* Geyer 1955 and *Hykeliphyllum* Eliášová 1975. The investigated specimen and the specimen described by Eliášová (1975) represent probably a new species.

**Distribution:** Poland; Outer Carpathians, Skole Nappe: Lipnik Hill (Tithonian–?Early Berriasian).

### Genus *Pleurophyllia* de Fromentel 1856
### Type species: *Pleurophyllia trichotoma* de Fromentel 1856

### *Pleurophyllia trichotoma* de Fromentel 1856
### Fig. 10

*1856. *Pleurophyllia trichotoma*: de Fromentel, p. 860.
1957. *Pleurophyllia trichotoma* de Fromentel: Alloiteau, p. 365, fig. 249.
1966. *Pleurophyllia trichotoma* de Fromentel: Roniewicz, p. 223, text-figs 13, 14, pl. 16, fig. 1.
non 1975. *Pleurophyllia trichotoma*de Fromentel: Eliášová, p. 15, text-fig. 8, pl. 7, fig. 2.
1976. *Pleurophyllia trichotoma* de Fromentel: Roniewicz, p. 38, fig. 3.
1976. *Pleurophyllia trichotoma* de Fromentel: Melnikova & Roniewicz, text-figs 1, 2, pl. 28, figs 2, 3.
non 1985. *Pleurophyllia trichotoma* de Fromentel: Rosendahl, p. 53, pl. 6, fig. 1.
1991. *Pleurophyllia trichotoma* de Fromentel: Lauxmann, pp. 143–144, pl. 6, fig. 1.
1991. *Pleurophyllia trichotoma* de Fromentel: Lebanidze, pp. 50–51, pl. 20, fig. 3a, b; pl. 21, fig. 1.

**Material:** 1 specimen: UJ 140 P/35; 4 thin sections: UJ 30/65–67, 203.

**Dimensions** (in mm): d = (5) 6–8; s = ca. 20–30.

**Description:** Phaceloid corallum. Corallites slightly elliptical. Septal apparatus displays bilateral symmetry. Main septum longer and thicker than other septa. Lonsdaleoid septa present. Taschenknospung budding.

**Remarks:** In my opinion, the specimens described by Eliášová (1975) and Rosendahl (1985) probably do not represent *P. trichotoma*. Eliášová's specimens differ from *P. trichotoma* in different septal pattern (see remarks on *Pleurophyllia* aff. *trichotoma*). The specimens illustrated by Rosendahl have a septo-parathecal wall, therefore their assignment to *Pleurophyllia* is problematical.

**Distribution:** Poland: Outer Carpathians, Sub-Silesian Nappe: Woźniki (Tithonian–?Early Berriasian); Holy Cross Mountains (Early Kimmeridgian);
Romania: Dobrogea (Late Oxfordian);
Southern Germany (Late Jurassic);
France (Portlandian);
Georgia: Abkhasia (Late Oxfordian–Tithonian).

### *Pleurophyllia* aff. *trichotoma* de Fromentel 1856
### Fig. 11 (A, B)

aff.*1856. *Pleurophyllia trichotoma*: de Fromentel, p. 860.
?1975. *Pleurophyllia trichotoma* de Fromentel: Eliášová, p. 15, text-fig. 8; pl. 7, fig. 2.

**Material:** 1 specimen: UJ 140 P/36; 3 thin sections: UJ 30/68–70.

**Dimensions** (in mm): d = 5–7 (8); s = ca. 25.

**Remarks:** The studied specimen differs from *Pleurophyllia trichotoma* in different septal pattern. Septal arrangement forms quasi-main sector, although it is less developed than in *Pseudopistophyllum* or *Hykeliphyllum*. Similar septal pattern was described by Eliášová (1975) in specimens assigned to *P. trichotoma*. It is worth noting that the presence of main sector is a feature of taxonomic value (see remarks to *Amphiastrea* sp. 2).

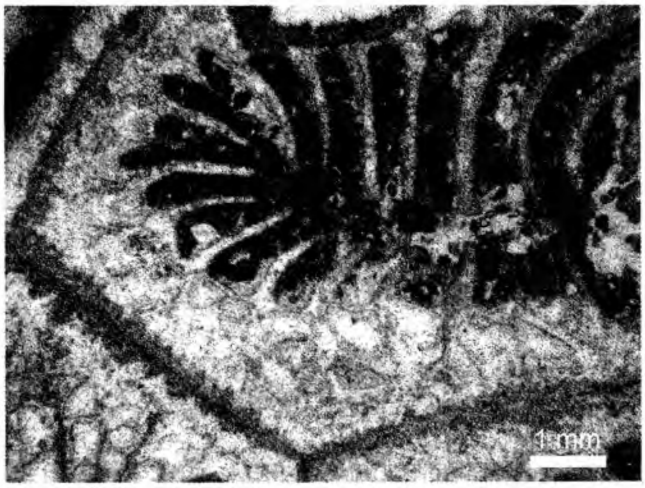

**Fig. 9.** *Amphiastrea* sp. 2; transverse section; Tithonian–?Early Berriasian, Lipnik Hill (UJ 30/64)

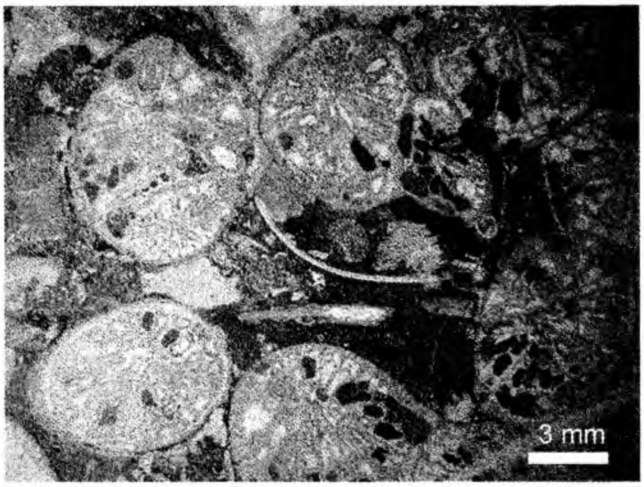

**Fig. 10** *Pleurophyllia trichotoma* de Fromentel 1856; transverse section; Tithonian–?Early Berriasian, Woźniki (UJ 30/69)

**Distribution:** Poland; Outer Carpathians, Silesian Nappe: Zamarski (Tithonian).

### *Pleurophyllia cara* Eliášová 1975
### Fig. 12

*1975. *Pleurophyllia cara*: Eliášová, pp. 15–16, text-fig. 9, pl. 8, figs 1, 2.
1976. *Pleurophyllia cara* Eliášová: Roniewicz, p. 39, pl. 3, fig. 2a, b.
1976. *Pleurophyllia cara* Eliášová: Melnikova & Roniewicz, pl. 29, fig. 1.
1985. *Pleurophyllia cara* Eliášová: Rosendahl, p. 53.

**Material:** 1 specimen: UJ 140 P/37; 3 thin sections: UJ 30/71–73.

**Dimensions** (in mm): d = 4–6 (7), s = ca. 18–25.

**Description:** Phaceloid corallum. Corallites circular or slightly elliptical. Septal apparatus displays bilateral symmetry. Lonsdaleoid septa present. Taschenknospung budding.

**Remarks**: Eliášová (1975) reported in *Pleurophyllia cara* 12 septa S1–S2 and 10–12 S3. However, figures presented by Eliášová do not confirm such regularity in septal arrangement.

**Distribution:** Poland: Outer Carpathians, Sub-Silesian Nappe, Woźniki (Tithonian–?Early Berriasian);

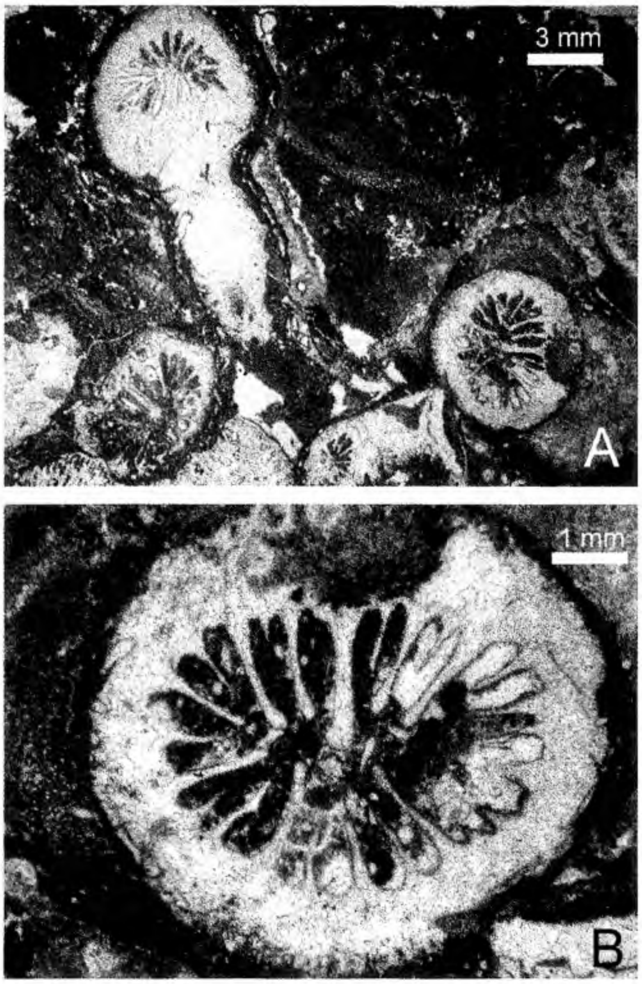

**Fig. 11.** **A, B.** *Pleurophyllia* aff. *trichotoma* de Fromentel 1856; transverse sections; Tithonian, Zamarski (UJ 30/69)

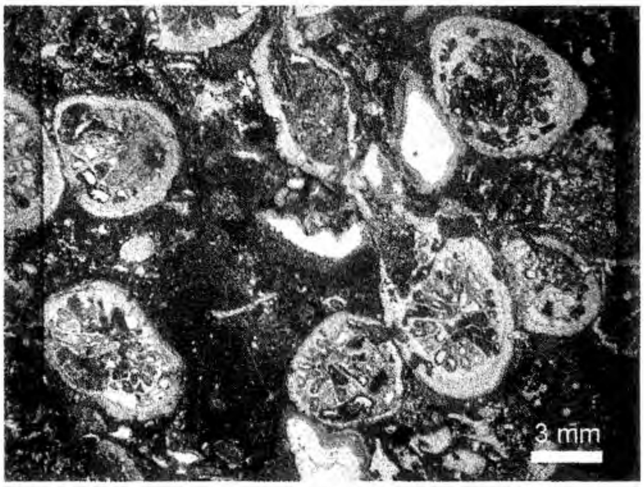

**Fig. 12.** *Pleurophyllia cara* Eliášová 1975; transverse section; Tithonian–?Early Berriasian, Woźniki (UJ 30/73)

Czech Republic: Štramberk, Skalička, Jasenice (Tithonian–Early Berriasian);
Romania: Dobrogea (Early Kimmeridgian);
Southern Portugal (Kimmeridgian).

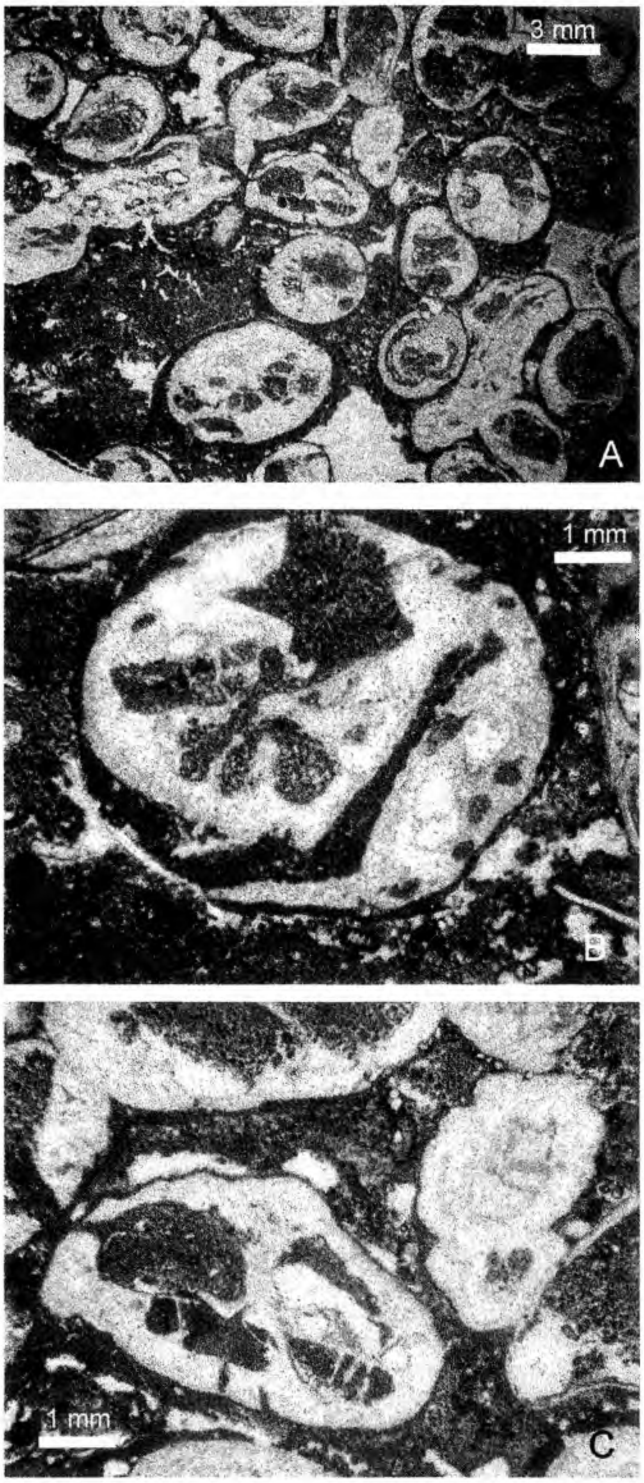

**Fig. 13.** **A–C.** *Pleurophyllia* cf. *vesiculosa* Eliášová 1975; transverse sections; Tithonian–?Early Berriasian, Jastrzębia (UJ 30/74)

### *Pleurophyllia* cf. *vesiculosa* Eliášová 1975
Fig. 13 (A–C)

cf.*1975. *Pleurophyllia vesiculosa*: Eliášová, pp. 16–17, text-fig. 10, pl. 8, fig. 3; pl. 9, fig. 1.

**Material:** 1 specimen: UJ 140 P/38; 2 thin sections: UJ 30/74, 75.
**Dimensions** (in mm): d = 3–4 (6).
**Description:** Phaceloid corallum. Bilateral symmetry of septal apparatus. Main septum clearly longer and thicker than other septa.

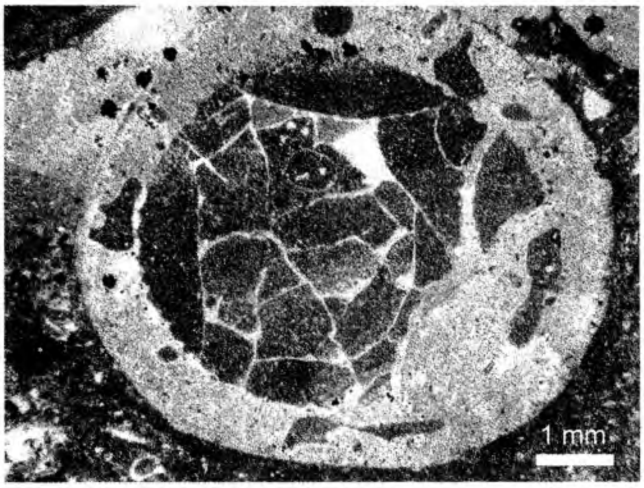

**Fig. 14.** *Mitrodendron* cf. *modicum* Eliášová 1975; transverse section, ?Valanginian, Krzywica (UJ 30/77)

Vesicles occur quite often in peripheral part of calices. Taschenknospung budding.

**Remarks:** Due to poor preservation, the number of septa cannot be estimated. The investigated specimen has much in common with *P. vesiculosa* in the diameter of corallites, thick main septum and relatively numerous marginal vesicles. *Pleurophyllia vesiculosa* was reported only from the Štramberk Limestone (Eliášová, 1975).

**Distribution:** Poland: Outer Carpathians, Sub-Silesian Nappe, Jastrzębia (Tithonian–?Early Berriasian).

### Genus *Mitrodendron* Quenstedt 1881

Type species: *Lithodendron mitratum* Quenstedt 1881

**Remarks:** Recognizing the family Mitrodendronidae Alloiteau 1952 does not seem justified, because marginarium can be present in all genera from the Amphiastreidae (Eliášová, 1975; and remarks on *Amphiastrea* sp. 1 above).

### *Mitrodendron* cf. *modicum* Eliášová 1975

Fig. 14

cf.1975. *Mitrodendron modicum* Eliášová: pp. 14–15, text-fig. 7a, b, pl. 7, fig. 1a–b.
cf.1985. *Mitrodendron modicum* Eliášová: Rosendahl; p. 52, pl. 5, fig. 8.

**Material:** 1 specimen: UJ 140 P/39/1; 3 thin sections: UJ 30/76, 77, 142.

**Dimensions** (in mm): d = 4–7; s = 8–12 S1, S2 + n S3.

**Description:** Fragments of phaceloid corallum. Septal apparatus displays bilateral symmetry. Septa very thin. Main septum is much longer than other S1, but their thickness is similar. A well developed marginarium and very thin "internal wall" occur in some corallites. Marginarium is absent in some corallites.

**Distribution:** Poland; Outer Carpathians, Sub-Silesian Nappe: Krzywica (?Valanginian).

### Genus *Amphiaulastrea* Geyer 1955

Type species: *Aulastraea conferta* Ogilvie 1897

### *Amphiaulastrea* sp. 1

Fig. 15 (A, B)

**Material:** 1 specimen: UJ 140 P/40; 2 thin sections: UJ 30/78, 79.

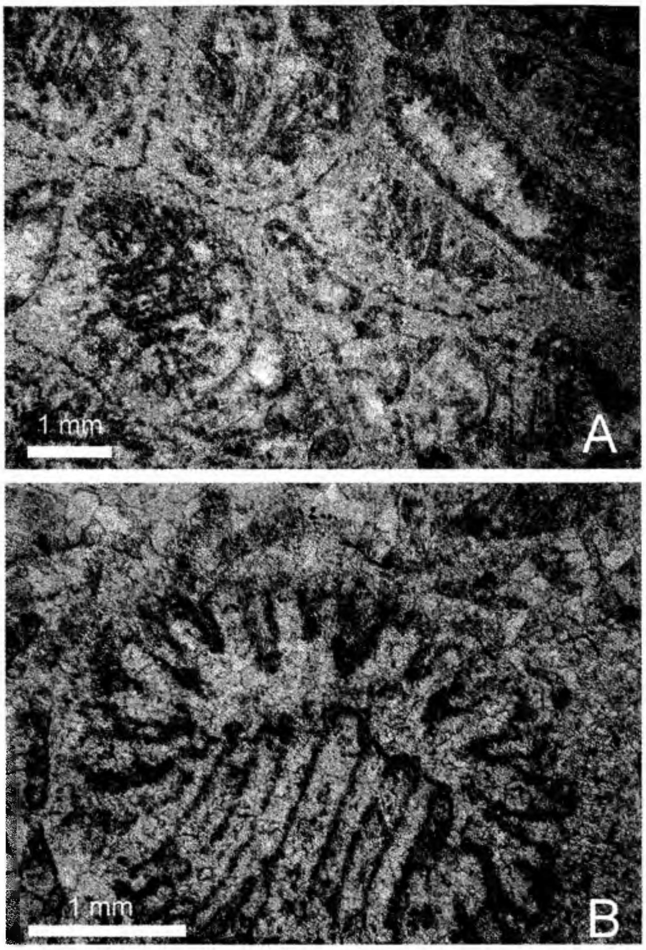

**Fig. 15.** **A, B.** *Amphiaulastrea* sp. 1; transverse sections; Tithonian–?Early Berriasian, Lipnik Hill (UJ 30/78)

**Dimensions** (in mm): d $cor_l$ = (5) 9–12; d $cor_s$ = 3–5; d int = (3) 4–5 (7); d wall = (0.5) 0.8–1 (1, 5); s = ca. 18–24 S1–S2.

**Description:** Cerioid colony. Corallites irregularly polygonal, prolonged. Marginal zone well developed. Septal apparatus displays bilateral symmetry. Main sector usually with 5 long, parallel septa of similar length and thickness. Longest septa reach up to 3/4 radius of internal calice. Short septa lying opposite the main sector are also parallel and have the same size. In consequence, fossa is well developed in calice. Inner edge of septa of claviform type. Endotheca unknown, because of poor state of preservation.

**Remarks:** The specimen represents probably a new species, but because of poor state of preservation is not distinguished formally. It differs from other species of *Amphiaulastrea* in well developed fossa. This feature occurs also in genus *Hykeliphyllum*, which, however, shows dendroid–phaceloid (in places subcerioid) shape of colony, and the inner edge is rhopaloid.

**Distribution:** Poland: Outer Carpathians, Skole Nappe, Lipnik Hill (Tithonian–?Early Berriasian).

### *Amphiaulastrea* sp. 2

Fig. 16 (A, B)

**Material:** 1 specimen: UJ 140 P/41; 3 thin sections: UJ 30/80, 81, 134.

**Dimensions** (in mm): d cal = 4–5; d int = 1.5–2.5; c–c = 2.5–5; s = 10–12 S1–S2 + n S3.

**Description:** Small fragment of cerioid colony. Corallites irregu-

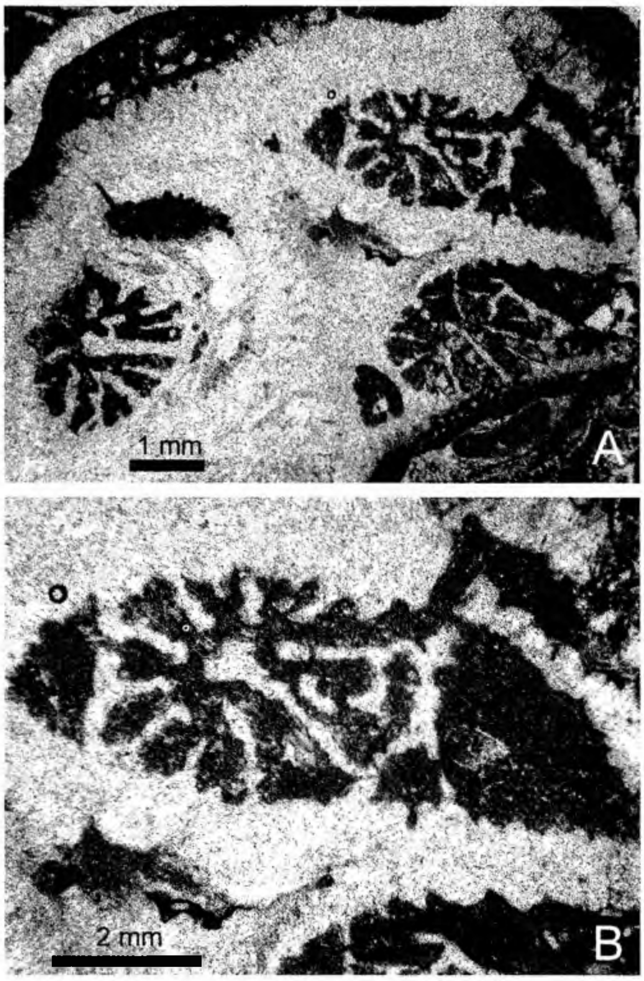

**Fig. 16.** **A, B.** *Amphiaulastrea* sp. 2; transverse sections; Tithonian–?Early Berriasian, Krzywica (UJ 30/81)

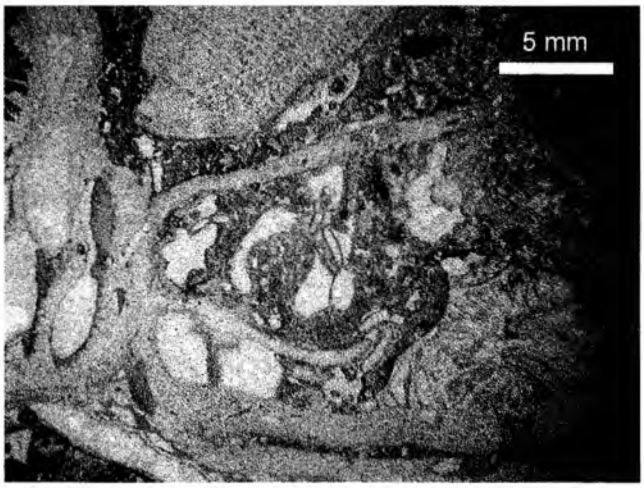

**Fig. 17.** *Aulastraea* sp.; transverse section; Tithonian–?Early Berriasian, Leńcze (UJ 30/193)

larly polygonal. Marginal zone well developed. Bilateral symmetry. Main septum distinctly longer and thicker than other septa.

**Remarks:** The described specimen is characterized by very small diameter of internal calices. In this feature, *Amphiaulastrea* sp. 2 resembles *Amphiastrea paronai* Prever 1909 from Cenomanian of Italy (Upper Aptian–Albian according to Masse & Morycowa, 1994). Discordance between figures and description of *Amphiastrea paronai* in Prever's (1909) paper do not allow to compare both species. Twelve septa are given in Prever's description, however, number of septa judged from the figure (Prever, 1909) is larger. It is possible that because of well developed marginarium, *Amphiastrea paronai* and three other new species distinguished by Prever (1909) should be assigned to *Amphiaulastrea*, not to *Amphiastrea*. In the measurable features, the examined specimen resembles *Amphiaulastrea* sp., reported (but not described and illustrated) by Löser and Raeder (1995) from Aptian–Albian of Greece. These authors noted that their specimen is similar to *Amphiastrea* aff. *gracilis*, described by Sikhuralidze (1985). However, the species described by Sikhuralidze does not have permanent marginarium, which is diagnostic for *Amphiaulastrea*; moreover, in places plocoid colony is developed.

**Distribution:** Poland: Outer Carpathians, Sub–Silesian Nappe, Krzywica (Tithonian–?Early Berriasian).

### Genus *Aulastraea* Ogilvie 1897
Type species: *Aulastraea schäferi* Ogilvie 1897

### *Aulastraea* sp.
Fig. 17

**Material:** 1 specimen: UJ 140 P/42; 2 thin sections: UJ 30/193.

**Dimensions** (in mm): d cal = ca. 25; d int = 8–9; s = ca. 40.

**Remarks:** *Aulastraea* is a genus with phaceloid-subcerioid corallum. Three studied corallites represent subceriod part of colony.

**Distribution:** Poland: Outer Carpathians, Silesian Nappe, Leńcze (Tithonian–?Early Berriasian).

## Family Donacosmilliidae Krasnov 1970

### Genus *Donacosmilia* de Fromentel 1861
Type species: *Donacosmilia corallina* de Fromentel 1861

### *Donacosmilia corallina* de Fromentel 1861
Fig. 18

*1861. *Donacosmilia corallina*: de Fromentel, p. 146.
1957. *Donacosmilia corallina* de Fromentel: Alloiteau, pp. 365–366, pl. 14, fig. 4; pl. 15, fig. 8; pl. 17, fig. 2.
1964. *Donacosmilia corallina* de Fromentel: L. Beauvais, p. 203.
?1972. *Donacosmilia corallina* de Fromentel: Turnšek, pp. 45–46, 101; pl. 27, fig. 1.
1974. *Donacosmilia corallina* de Fromentel: L. Beauvais, pl. 2, fig. 4; pl. 3, fig. 2; pl. 4, fig. 1.
1976. *Donacosmilia corallina* de Fromentel: Melnikova & Roniewicz, p. 109, text-fig. 6, pl. 27, figs 1–3.
1985. *Donacosmilia corallina* de Fromentel: Rosendahl, p. 53, pl. 6, fig. 2.
1986. *Donacosmilia corallina* de Fromentel: Russo & Sirna, p. 169, pl. 1, fig. 5.

**Material:** 1 specimen: UJ 140 P/44; 1 thin section: UJ 30/148.

**Dimensions** (in mm): d = 6–11; s = ca. 20–40.

**Description:** Phaceloid corallum. Corallites rounded. Septa of similar length, differentiated in three-sized orders. Wall very thin.

**Remarks:** Specimens described by Turnšek (1972) as *D. coralline* are here assigned with question mark to *Donacosmilia*. Septa display bilateral symmetry and the main septum is slightly longer and thicker than others in these specimens. According to Melnikova and Roniewicz (1976), septa are arranged bilaterally, not radially (see Alloiteau, 1957) in the holotype of *D. corallina*.

**Distribution:** Poland: Outer Carpathians, Silesian Nappe, Gródek upon Dunajec (Tithonian–?Early Berriasian);
Czech Republic: Štramberk (Tithonian–Early Berriasian);
South Slovenia (Upper Oxfordian–Early Kimmeridgian);
France (Oxfordian);
South Portugal (Late Oxfordian–Early Kimmeridgian);
Italy: Sardinia (Late Oxfordian–Kimmeridgian);
Tadjikistan: SE Pamir (Kimmeridgian).

## Family Intersmiliidae Melnikova & Roniewicz 1976

### Genus *Intersmilia* Eliášová 1974
Type species: *Intersmilia malveola* Eliášová 1974

#### ?*Intersmilia* sp.
Fig. 19

**Material:** 1 specimen: UJ 140 P31/2; 4 thin sections: UJ 30/82–85.
**Dimensions** (in mm)**:** d = 6–8; s = 12–24.
**Description:** Fragments of phaceloid corallum. Septal apparatus displays radial symmetry. Some corallites have regularly developed septal apparatus (6 S1, 6S2, 6 S3). Poorly developed marginal zone occurs in two corallites.
**Remarks:** The investigated specimen resembles *Intersmilia diaboli* Eliášová 1974 in the dimensions and irregular arrangement of septa. A presence of corallites with marginarium is an important feature of the studied specimen. Such a feature was not described in *Intersmilia* to date, but this does not exclude the specimen from this genus. Marginarium can be developed, although rarely; similarly like in *Amphiastrea.* In places marginarium can be present in heterocoeniids *Confusaforma carpathica* Kołodziej (Kołodziej, 1995: fig. 7b, f) and *Pachycoenia fuchsi* (M. Beauvais, 1977: pl. 2, fig. 2).
**Distribution:** Poland: Outer Carpathians, Sub–Silesian Nappe, Woźniki (?Valanginian).

## Family Heterocoeniidae Oppenheim 1930

**Remarks:** *Selenegyra*, *Hexapetalum* (previous taxonomic position is given below) and *Pachythecophyllia eliasovae* n.gen., n.sp. are assigned in this paper to the family Heterocoeniidae. These genera are characterized by branching growth form. Up to now, only one genus, *Cuneiphyllia* Eliášová (see Eliášová, 1978), having such growth form of colony, was included to this family.

### Genus *Latusastrea* d'Orbigny 1847
Type species: *Explanaria alveolaris* Goldfuss 1829

**Remarks:** Genus *Latusatrea* was a subject of detailed study carried out by Alloiteau (1957), Morycowa (1971), M. Beauvais (1977) and Morycowa *et al.* (1995). Microstructure of this genus was described by Morycowa (1971) and the present author (Kołodziej, 1995). This genus is poorly differentiated in terms of species. Up to now, only five are known from the Cretaceous (Löser *et al.*, 2002) and one species from the Upper Jurassic (*Latusastrea alveolaris* (Goldfuss 1829 – see Lauxmann, 1991).

#### *Latusastrea* sp.
Fig. 20 (A–F)

**Material:** 2 specimens: UJ 140 P/46 (Woźniki); 5 thin sections: UJ 30/89–93; UJ 140 P/47 (Lipnik Hill); 4 thin sections: UJ 30/94–97.
**Dimensions** (in mm)**:** d $cor_l$ = 1–1.5; d $cor_s$ = 1–1.5; c–c = 1.5–2.5.
**Description:** Colony massive, plocoid. Corallites oval. Main septum thick and long; attains 1/2–2/3 of corallites diameter. Other septa are thin. Variability in septal number seems to be connected with state of preservation. Up to 10 relatively well developed septa attaining up to 1/3–1/4 of corallites diameter occur in some corallites. Septa on the side opposite to the main septum are poorly developed. Septa of lower size orders are poorly developed. Budding perithecal. Extracalicular, mural budding is uncertain.

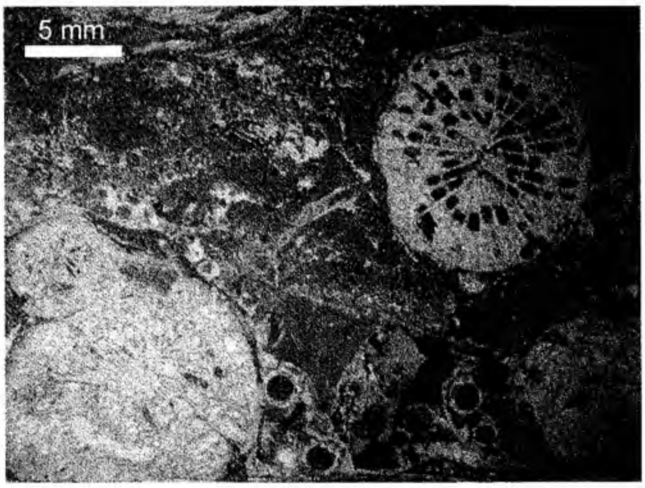

**Fig. 18.** *Donacosmilia corallina* de Fromentel 1861; transverse section, Tithonian–?Early Berriasian, Gródek upon Dunajec (UJ 30/148)

**Remarks:** The investigated species resembles *L. provincialis* (d'Orbigny 1847) in the corallites diameter, known from Hauterivian to Turonian (Morycowa *et al.,* 1995). It differs from others species in relatively well developed septa, lying opposite the main septum. Lack of proper transverse sections does not allow identify the character of septa (septal blades or septal spines). All septa, except the main septum, are developed as septal spines, as showed by Morycowa (1971) in *L. exiguis* (de Fromentel 1862). The number of septa is difficult to estimation also in other heterocoeniids, e.g., in *Thecidiosmilia morycowae* and *Pachythecophyllia eliasovae* n.gen., n.sp.
**Distribution:** Poland: Outer Carpathians, Sub–Silesian Nappe: Woźniki (Tithonian–?Early Berriasian); Skole Nappe: Lipnik Hill (Tithonian–?Early Berriasian).

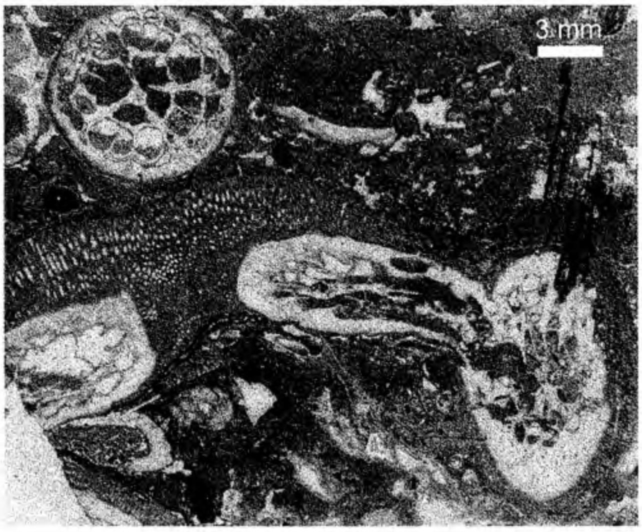

**Fig. 19.** *Intersmilia* sp.; transverse section; ?Valanginian, Woźniki (UJ 30/82, UJ 30/85)

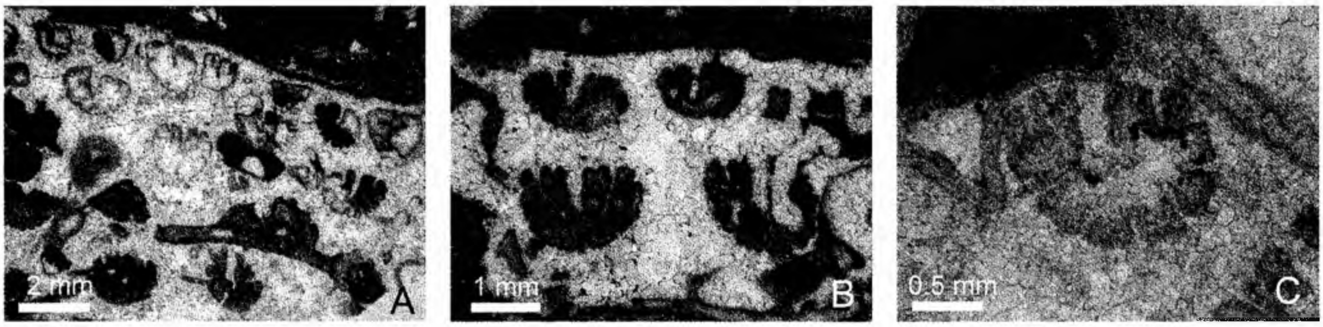

**Fig. 20.** A–C. *Latusastrea* sp.; transverse sections; A–C – Tithonian–?Early Berriasian, Woźniki (UJ 30/91, UJ 30/89, UJ 30/92)

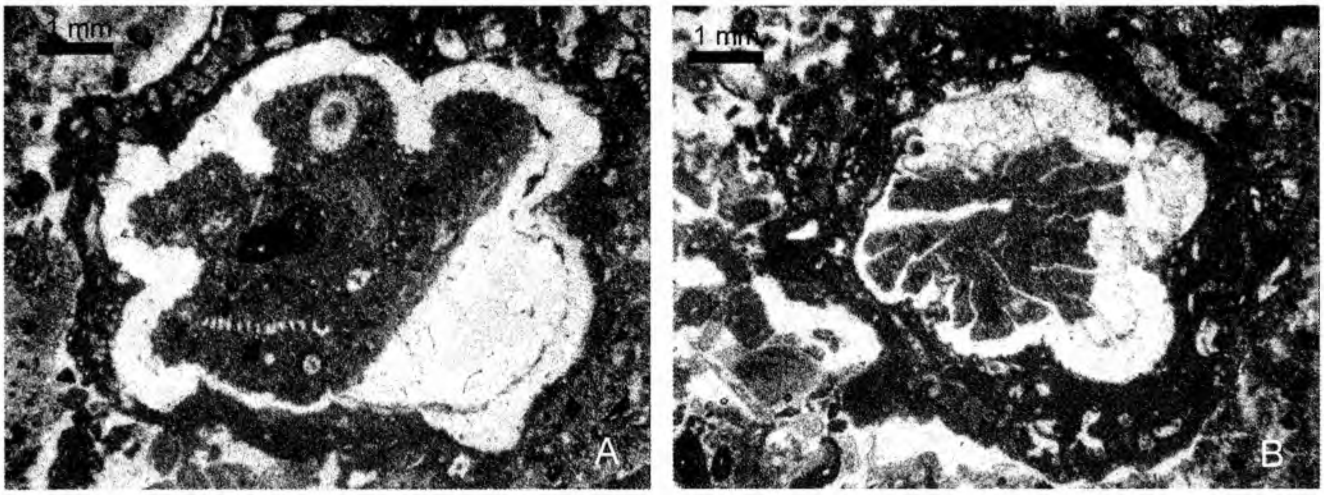

**Fig. 21.** A, B. *Hexapetalum* sp.; transverse sections; Tithonian–?Early Berriasian, Lipnik Hill (UJ 30/98; UJ 30/99)

### Genus *Hexapetalum* Eliášová 1975
### Type species: *Hexapetalum impium* Eliášová 1975

**Remarks:** *Hexapetalum* is transferred here to the family Heterocoeniidae. This genus displays characteristic wall invaginations, occurring also in *Pachycoenia*, *Confusaforma* Löser 1987 and (?) *Heterocoenia* Milne-Edwards & Haime 1848. Similarities are particularly well visible between discussed genus and *Pachycoenia,* in which between wall invaginations very thin septa can arise (*cf.*, Eliášová, 1976b; M. Beauvais, 1977: pl. 2, fig. 2). Family assignment of *Hexapetalum* is suggested among others by a presence of small granules on septal faces in the species discussed below. Such septal ornamentation seems to occur also in *Hexapetalum pium* (Eliášová, 1976b: pl. 2, fig. 3). Wall and septa in *Hexapetalum* are in structural continuity.

### *Hexapetalum* sp.
### Fig. 21 (A, B)

**Material:** 1 specimen: UJ 140 P/48; 2 thin sections: UJ 30/98, 99.

**Remarks:** Only two corallites (d = 4–6 mm) are preserved, therefore a species assignment cannot be made. Thick septa are result of wall invaginations. Very thin septa occur between invaginations (*cf.* Eliášová, 1976b). Granules cover thick septa and inner surface of wall.

**Distribution:** Poland: Outer Carpathians, Skole Nappe, Lipnik Hill (Tithonian–?Early Berriasian).

### Genus *Selenegyra* Ogilvie 1897
### Type species: *Selenegyra geikiei* Ogilvie 1897

### *Selenegyra* sp.
### Fig. 22 (A–D)

**Material:** 2 specimens: UJ 140 P/31/3 (Woźniki); 3 thin sections: UJ 30/100–102; UJ 140 P/49 (Gródek upon Dunajec); 1 thin section: UJ 30/103.

**Dimensions** (in mm)**:** UJ 140 P/31/3: thin section UJ 30/100: d $cor_l$ = 16; d $cor_s$ = 4.5; s = ca. 55; s/2 mm = (4) 5 (6); thin sections UJ 30/100–102: d $cor_l$ = 13; d $cor_s$ = 6; s = ca. 65; s/2 mm = 6. UJ 140 P/49: d $cor_l$ = 16; d $cor_s$ = 9.5; s = ca. 40; s/2 mm = 5.

**Remarks:** Single corallites of phaceloid corallum. Corallites in transverse section strongly elongated or kidney-shaped. Septa very thin, arranged in bilateral symmetry. These features suggest assignment to monotypic genus *Selenegyra.* The investigated specimens differ from *Selenegyra geikiei* Ogilvie in distinctly more numerous septa and larger diameter of corallites (in *S. geikiei*: s = 20–40; d = 2.2 × 2.0; 8 × 5 (10 × 4) – see Eliášová, 1978). Characteristic feature of the specimen UJ 140 P/31/3 are septal bifurcations of on the inner edge and the presence of lateral expansions from lateral faces of septa (Fig. 22 A, B). However, lack of proper vertical thin sections makes it impossible to define the character of these expansions (septal blades or septal spines). Eliášová (1978) did not recognize such septal expansions in *S. geikiei.* Lateral expansions on faces of S1 were reported by L. Beauvais (1976) in *Aulastraeopora* Prever. According to L. Beauvais, they resemble

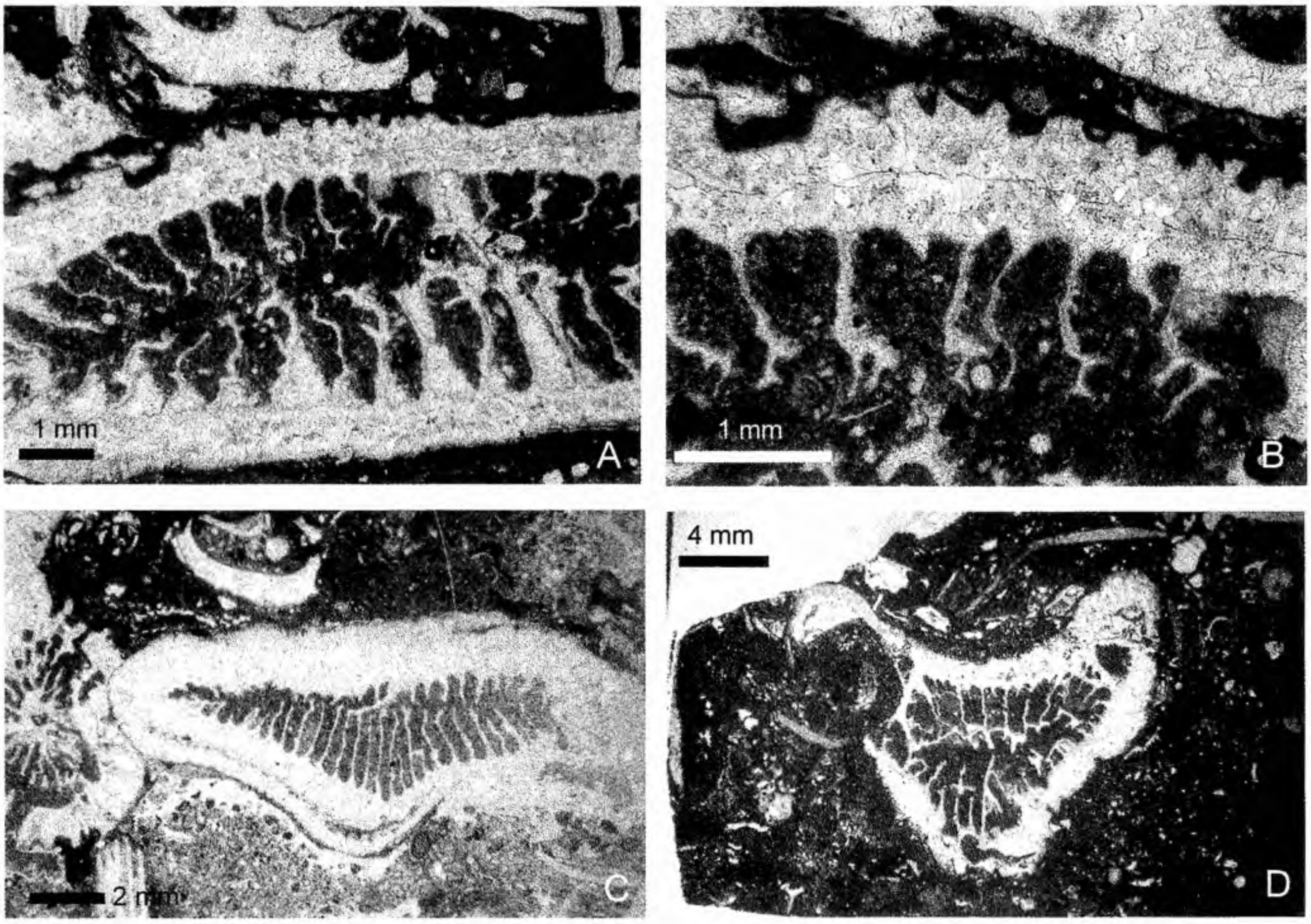

**Fig. 22.** **A–D.** *Selenegyra* sp.; transverse sections; A, B – septal bifurcations; ?Valanginian, Woźniki (A, B, C – UJ 30/100, D – UJ 30/102); Tithonian–?Early Berriasian, Gródek upon Dunajec

septa of lower orders. Similar expansions are also visible in ?*Aulastraeopora deangelisi* Prever (Baron-Szabo & Steuber, 1996: pl. 9, fig. 1 and Fig. 6 herein). Such expansions have been recognized in *Preverastraea tenuiseptata* Kołodziej (Kołodziej, 1995: fig. 7g, h), however, this species does not represent *Preverastraea* (Löser, 1998a). Discussed septal expansions are similar to apophysal septa, known in Rhipidogyrina. According to L. Beauvais (1976), such expansions result from off-sets of septal trabeculae. Strongly bifurcated septa occur in heterocoeniid species described by Schöllhorn (1998: p. 80) as cf. *Comalia* sp.

**Distribution:** Poland: Outer Carpathians, Sub–Silesian Nappe, Woźniki (?Valanginian); Silesian Nappe: Gródek upon Dunajec (Tithonian–?Early Berriasian).

## Genus *Pachythecophyllia* new genus

### Type species: *Pachythecophyllia eliasowae* n.gen., n.sp.

**Etymology:** Because of pachytheca dominated corallite architecture of the new genus.

**Diagnosis:** Phaceloid corallum. Septal apparatus displays bilateral symmetry. Main septum well-developed; remaining septa reduced to small granules on the inner surface of the wall. Endotheca tabular. Budding mural, extracalicular.

**Species included:** *Pachythecophyllia eliasowae* n.gen., n.sp.

**Stratigraphic and geographical distribution:** ?Valanginian; Polish Outer Carpathians (Krzywica, Gródek upon Dunajec).

**Remarks:** Very weakly developed septal apparatus is a distinctive feature of a new genus. Except the main septum, the remaining septa (if developed) are reduced to small granules on the inner surface of the wall. These granules are possibly septal spines, like in *Latusastrea exiguis* (de Fromentel) described by Morycowa (1971). Such poor development of septa was not known in other branching genera of the former suborders Amphiastreina and Heterocoeniina. Weak development of septal apparatus is known in some other heterocoeniids e.g., *Latusastrea exiguis*, *L. provincialis*, *Heterocoenia exiguum* Michelin 1847, *H. dendroides* Reuss 1854 and *Thecidiosmilia morycowae* Kołodziej (e.g., Kołodziej, 1995; Baron-Szabo, 1998). In the Triassic *Protoheterastraea leonhardi* (Volz 1896), septa are mostly represented by protosepta, which are discontinuous, sometimes reduced to septal spines or even entirely lacking on long extension (Montanaro-Gallitelli, 1973). However, two septa lying in the neighbourhood of the main septum are usually well developed in this species. Because of tabular endotheca, extracalicular, mural budding (septal budding uncertain), and in places marked spiniform septal ornamentation, the new genus is assigned to the family Heterocoeniidae. *Pachythecophyllia* is a good example of pachythecaliinan wall-based corals (see Cuif & Stolarski, 1999).

## *Pachythecophyllia eliasovae* new genus et new species

### Fig. 23 (A–L)

**Holotype:** UJ 140 P/39/2; thin sections: UJ 30/104–112, 114, 140.

**Etymology:** Patronymic, in honour of Dr. Helena Eliášova.

**Material:** 2 specimens: UJ 140 P/39/2; 11 thin sections: UJ 30/104–112, 114, 140.

**Dimensions** (in mm): d = (1) 1.5–2.5 (3.5); d wall = 0.2–0.4 (0.6); den end = 4/2 mm; s – cannot be counted.

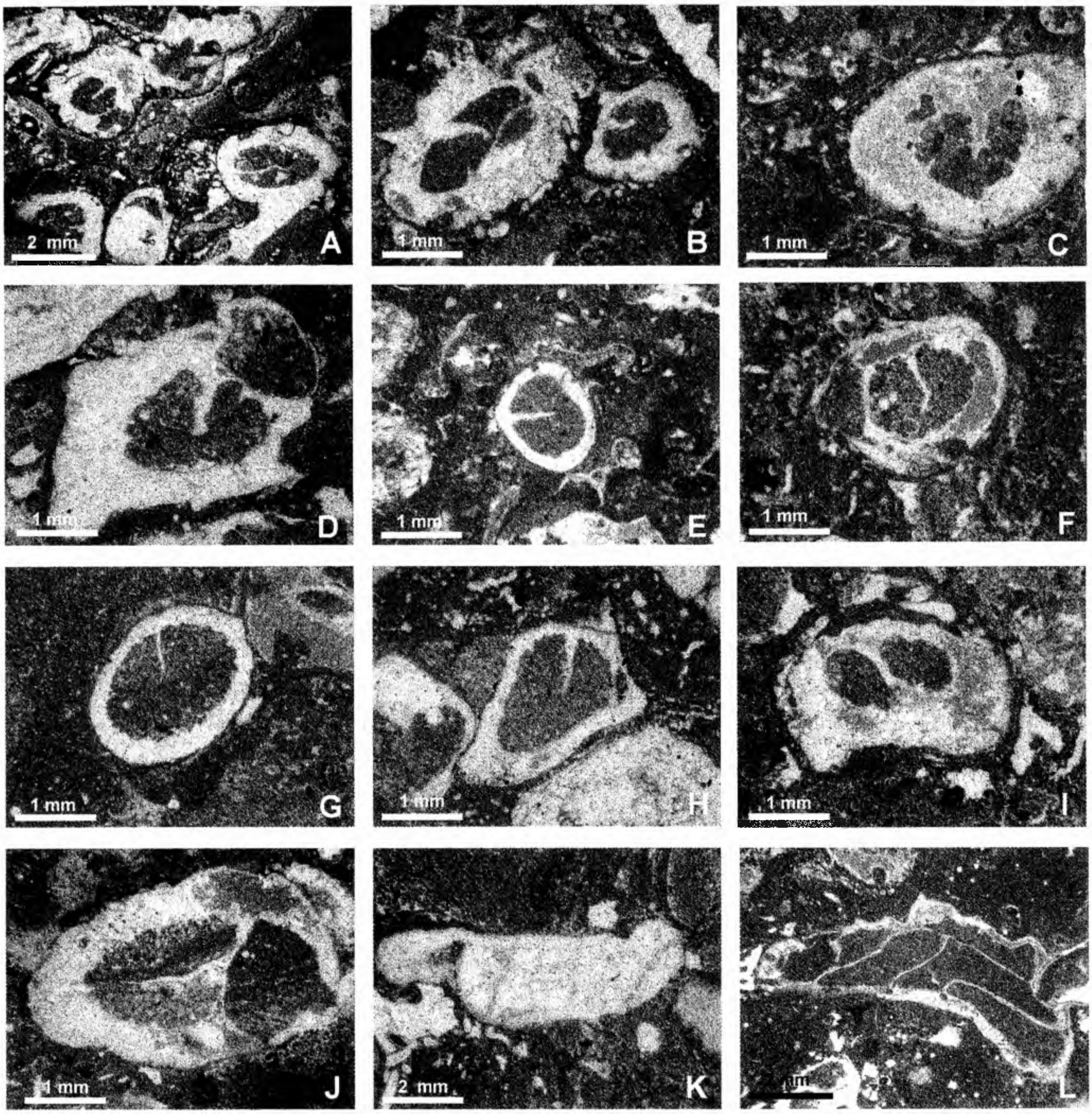

**Fig. 23.** **A–L.** *Pachythecophyliia eliasovae* n.gen., n.sp.; A–J – transverse sections, K, L – longitudinal sections; ?Valanginian, Krzywica (A, D – UJ 30/108, B – UJ 30/110, C, E, H – UJ 30/109, D, G – UJ 30/107, F, I – UJ 30/140, J – UJ 30/104, K – UJ 30/106, L – UJ 30/114)

**Diagnosis:** Species with corallites diameter 1.5–2.5 mm, wall thickness 0.2–0.4 mm and density of tabulae 4/2 mm.

**Description:** Phaceloid corallum. Branches are distributed loosly or densly. Corallites are rounded or slightly prolonged in the direction perpendicular to the main septum. Septal apparatus displays bilateral symmetry. Only main septum occurs in most of corallites. It is usually very thin and attains up to 3/4 of the diameter of calice. Remaining septa, if present, are very poorly developed. They occur usually as small granules (septal spines?) on the inner surface of the wall. In some corallites, main septum is irregularly ornamented with granules. Pachytheca is thick; endotheca is tabular; tabulae are rare. Budding is extracalicular, mural. Buds are initiated within the wall, and their subsequent developing was outside of the mother individual.

**Remarks:** It can not be excluded that some vesicles occurring in peripheral parts of corallites represent in fact the new buds. However, very poorly developed septal apparatus makes it impossible to confirm this interpretation. Septal arrangement in two corallites suggests septal budding.

**Type locality:** Poland: Outer Carpathians, Sub–Silesian Nappe, Krzywica.

**Type level:** Štramberk-type limestones.

**Stratigraphic distribution:** ?Valanginian.

**Deposition of holotype:** Institute of Geological Sciences, Jagiellonian University, Kraków; collection UJ 140 P.

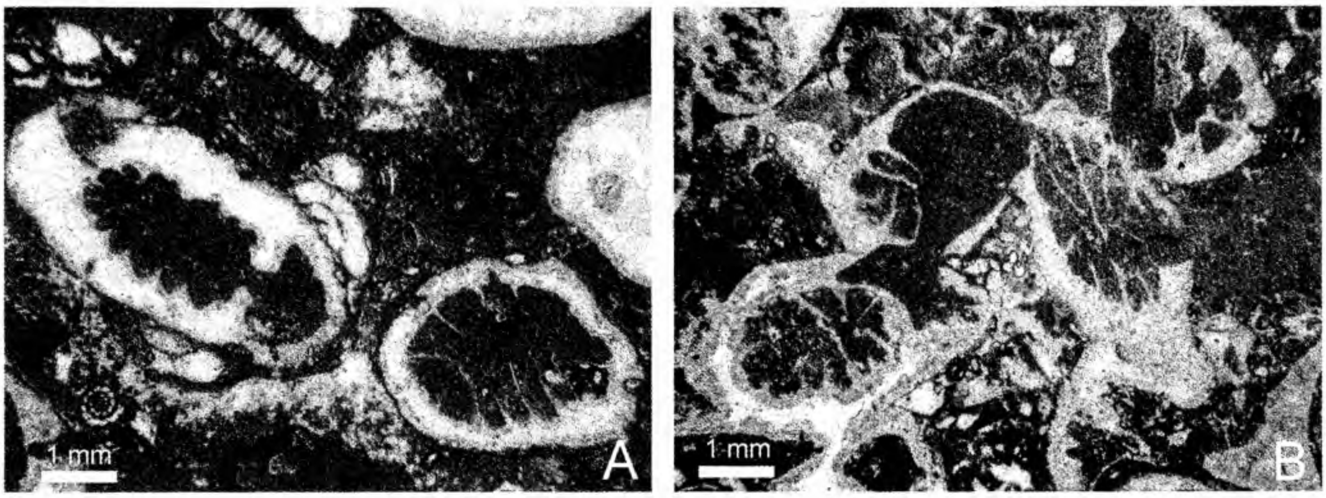

**Fig. 24.** **A, B.** *Simplexastraea* cf. *archaea* Eliášová 1976; transverse sections; Tithonian–?Early Berriasian, Leńcze (UJ 30/88)

### Incertae family

### Genus *Simplexastraea* Eliášová 1976

Type species: *Simplexastraea archaea* Eliášová 1976

### *Simplexastraea* cf. *archaea* Eliášová 1976

Fig. 24 (A, B)

cf.v*1976b. *Simplexastraea archaea*: Eliášová, pp. 360–361, text-figs 2, 5–7, pl. 3, figs 3, 4.

**Material:** 1 specimen: UJ 140 P/45; 3 thin sections: UJ 30/86–88.

**Dimensions** (in mm): d $cor_l$ = 2–3.5 (4); d $cor_s$ = 1.5–2; s = up to 20.

**Description:** Phaceloid corallum. Corallites in transverse section oval, elongated in the direction perpendicular to main septum. Septa thin, arranged in bilateral symmetry. Two slightly smaller, parallel septa occur on both side of main septum. Budding mural, extracalicular.

**Remarks:** The investigated species differs from *S. archaea* described by Eliášová (1976b) in slightly smaller diameter of corallites. My own observations of two transverse thin sections of this species from the collection of Dr. H. Eliášová showed that the septal pattern is like that of the specimen described above (*cf.* Eliášová, 1976b: pl. 3, fig. 4). As a result, the septal pattern resembles the main sector.

**Distribution:** Poland: Outer Carpathians, Silesian Nappe, Leńcze (Tithonian–?Early Berriasian).

## Suborder RHIPIDOGYRINA Roniewicz 1976

## Family Rhypidogyridae Koby 1905

### Genus *Ogilvinella* Eliášová 1973

Type species: *Ogilvinella elegans* Eliášová 197

### ?*Ogilvinella morycowae* new species

Fig. 25 (A–D)

**Holotype:** UJ 140 P/52; thin sections: UJ 30/121–125, 193.

**Etymology:** Patronymic, in honour of Professor Elżbieta Morycowa.

**Material:** 1 specimen: UJ 140 P/52; 6 thin sections: UJ 30/121–125, 193.

**Dimensions** (in mm): d cal = 3.5–8; d per = 1–2.5; c–c = 4–10; s = 12–35 S1–S3 + n S4.

**Diagnosis:** Calice diameter 3, 5–8 mm, width of peritheca 1–2, 5 mm, distance between corallite centres 4–10 mm, number of septa 12–32.

**Description:** Colony massive, plocoid. Corallites elliptically elongated or circular. Columella lamellar, well developed. Septa in four-sized orders. Septa S1 and S2 long and of subequal length and thickness. Septa S3 thin, attain 1/3–2/3 of S1 length. Septa S4 often developed, short and very thin. Inner margins locally rhopaloid. Septal ornamentation granular, regular. Costal parts of radial elements of the first three-sized orders thick and similar in thickness. The number of costae related to septa S4 difficult to estimate due to poor preservation. Vestiges of neorhipidacanth trabeculae visible in radial elements. Septal budding. Features of endotheca of the investigated specimen poorly visible in longitudinal section.

**Remarks:** New species is assigned with a question mark to *Ogilvinella* Eliášová 1973 (previous name *Ogilviella*; see Eliášová, 1976c) from the Štramberk Limestone. Septal budding occurs in the studied specimen, while in *Ogilvinella* budding is extracalicular. It could indicate that the new species represents a new genus. However, both septal and extracalicular budding occur in *Ogilviella parelegans* that was established by Sikhuralidze (1976) from Albian of Georgia (*O. parelegans* was not illustrated by Sikhuralidze).

A new genus is not established here, because the studied material is scarce (only one specimen) and the septal budding can be intrageneric variability. In some rhipidogyrids, both septal and extracalicular budding occur.

The new species differs from the species described by Sikhuralidze (1976) in larger diameter of corallites, smaller number of septa and costae. Moreover, Sikhuralidze mentioned the occurrence of extracalicular budding (apart from septal budding), which is not present within this species.

**Type locality:** Poland: Outer Carpathians, Sub-Silesian Nappe, Krzywica.

**Type level:** Štramberk-type limestones.

**Stratigraphic distribution:** Tithonian–?Early Berriasian.

**Depositions of holotype:** Institute of Geological Sciences, Jagiellonian University, Kraków; collection UJ 140 P.

### Genus *Placogyra* Koby 1904

Type species: *Placogyra felixi* Koby 1904

### ?*Placogyra* sp.

**Material:** 1 specimen: UJ 140 P/3/3; 4 thin sections: UJ 30/115–117, 120.

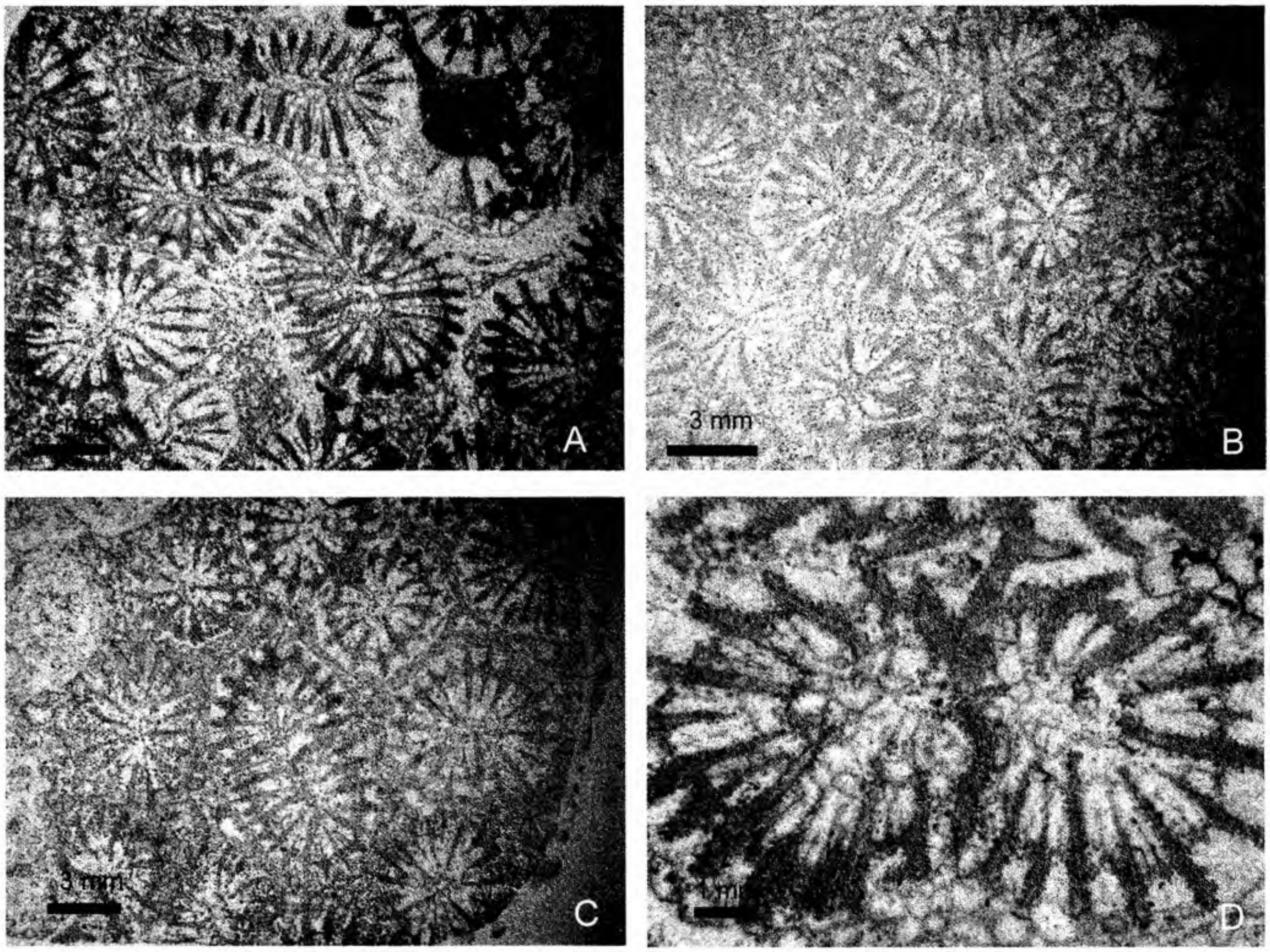

**Fig. 25.** **A–D.** ?*Ogilvinella morycowae* n.sp.; transverse sections; Tithonian–?Early Berriasian, Krzywica (UJ 30/125)

**Dimensions** (in mm): d ser = 12–14 (15); d per = 2–8; S1, S2/10 mm = 9–10.

**Description:** Colony massive, meandroid. Septa differentiated probably into three-sized orders. Septa S1 very thick, approach the centre, but usually do not reach columella. Septa S2 nearly equal S1, are similar length, but much thinner. Septa S3 very poorly preserved. Inner margin of septa rhopaloid. Locally aphophysal septa are visible. Costae nonconfluent. Columella lamellar. Wall parathecal. Peritheca well developed. Budding extracalicular.

**Remarks:** The studied specimen was assigned to *Placogyra* with a question mark, because peritheca is well developed. It differs from *Psammogyra* de Fromentel 1862 in having extracalicular budding.

**Distribution:** Poland: Outer Carpathians, Sub-Silesian Nappe: Jastrzębia (Tithonian–?Early Berriasian).

## Family Pruvostastraeidae L. Beauvais 1970

**Remarks:** According to L. Beauvais (1970, see also L. Beauvais, 1974, 1976), who assigned her Pruvostastraeidae to the suborder Amphiastreina, this family differs from Amphiastreidae in unilamellar wall, lack of marginarium and septal budding. In L. Beauvais' (1981) classification scheme, corals of this family have been classified into new subfamily Pruvosastraeinae (family Amphiastreidae, suborder Distichophylliina). *Pruvostastraea*, *Acanthogyra*, *Budaia* Wells 1933, *Columnogyra* L. Beauvais 1976, *Polymorphastraea* Koby 1906, *Glenarea* Počta 1887 and *Dichotomosmilia* L. Beauvais 1967 were included into this subfamily. However, some of these taxa need to be revised; as well their position within Pruvostastraeidae or Aulastraeoporidae is unclear (*cf.*, Löser, 1998a). In my opinion, the necessity of distinguish of the Pruvostastraeidae is justified because in contrast to Rhipidogyridae, the wall is in structural continuity with septa (rhipidotheca).

### Genus *Acanthogyra* Ogilvie 1897
### Type species: *Acanthogyra columnaris* Ogilvie 1897

### *Acanthogyra* cf. *columnaris* Ogilvie 1897
Fig. 26

cf. *1897. *Acanthogyra columnaris*: Ogilvie, p. 131, pl. 16, fig. 2.
cf. 1991. *Acanthogyra columnaris* Ogilvie: Lauxmann, pp. 139–140, text-fig. 7, pl. 5, figs 2, 3.

**Material:** 1 specimen: UJ 140 P/51; 2 thin sections: UJ 30/118, 119.

**Dimensions** (in mm): d = 5–7 × 9–11; s = 10–15 + n S3.

**Description:** Small fragment of cerioid colony. Corallite shape irregularly polygonal or elongated. Septa S1 and S2 of similar length, well developed. Septa and wall in structural continuity (rhipidotheca). Locally, wall parathecal, probably in outer part of colony. Neorhipidacanth microstructure.

**Remarks:** *Acanthogyra parvisepta* and *A. micra*, created by Eliášová (1973) are here considered as synonyms of *A. columnaris*, similarly as Lauxmann (1991). The differences in corallite diame-

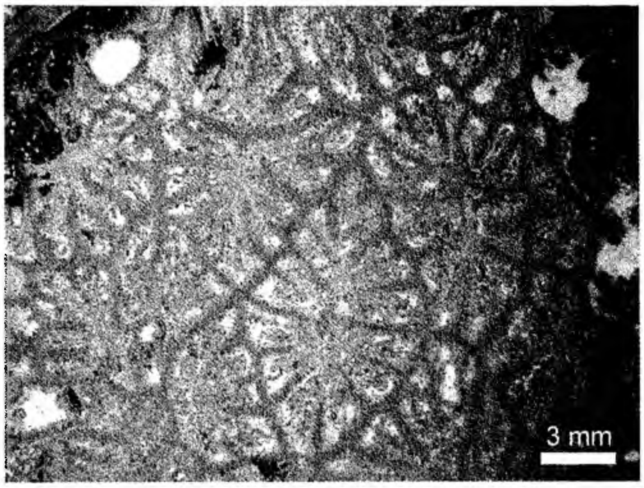

**Fig. 26.** *Acanthogyra* cf. *columnaris* Ogilvie 1897; transverse section, Tithonian–?Early Berriasian, Krzywica (UJ 30/118)

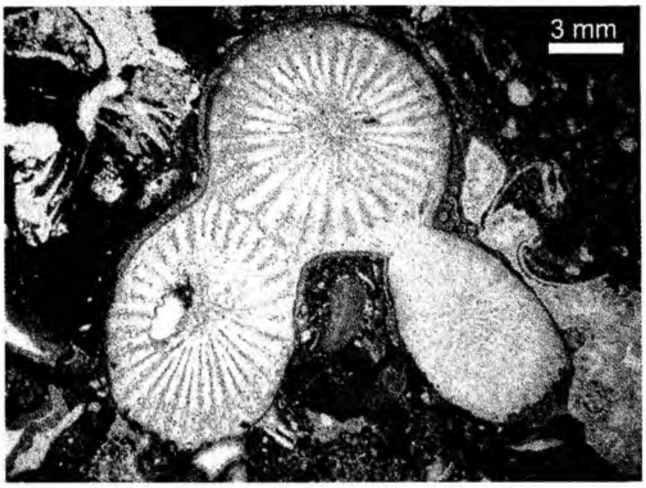

**Fig. 27.** *Placophyllia dianthus* (Goldfuss 1826); transverse section; ?Valanginian, Woźniki (UJ 30/128)

ters seem to be connected with intraspecific variability of *A. columnaris*. Parathecal wall occurring in one place is a distinctive feature of the investigated specimen.

**Distribution:** Poland: Outer Carpathians, Sub–Silesian, Krzywica (Tithonian–?Early Berriasian).

### Family Placophyllidae Eliášová 1990

**Remarks:** Eliášová (1990) has proposed to place *Placophyllia* (usually assigned to the family Placosmiliidae Alloiteau, 1952, suborder Astraeoina) and *Diplocoenia* (Stylinidae or Isastraeidae) in a new family Placophyllidae within suborder Rhipidogyrina on the basis of the neorhipidacanth microstructure. Morycowa (1997) has completed the diagnosis of this family and placed there *Pseudoironella* Sikhuralidze 1979 and also a newly established genus *Diplocoeniella*.

### Genus *Placophyllia* d'Orbigny 1849
### Type species: *Lithodendron dianthus* Goldfuss 1826

**Remarks:** Acccording to Eliášová (1976d), there is a microstructural similarity between *Placophyllia dianthus* (Goldfuss 1826) and *Diplocoenia stellata* (Étallon 1859), described by Morycowa (1964b). Roniewicz (1976) recognized neorhipidacanth microstructure in both species. In opinion of Morycowa (1997), the specimen described by her as *D. stellata* (Morycowa, 1964b) belongs to a new genus *Diplocoeniella* from the family Placophyllidae, suborder Rhipidogyrina.

Baron-Szabo (1998, 2000) again assigned *Placophyllia* cf. *curvata* Turnšek 1974 and a new species *Placophyllia bandeli* to the Placosmillidae. Unfortunatelly, her interpretation of microstructure of *Placophyllia* as faviid-type was based on poorly preserved skeleton (see photographs in Baron-Szabo, 1998, 2000). Moreover, neorhipidacanth microstructure appears to be present in *Placophyllia* cf. *curvata* (Baron-Szabo, 1998: pl. 2, fig. 6).

### *Placophyllia dianthus* (Goldfuss 1826)
### Fig. 27

*1826. *Lithodendron dianthus*: Goldfuss, p. 45, pl. 3, fig. 8.
1875-1876. *Placophyllia rugosa* Becker: Becker & Milaschewitsch, p. 140, pl. 38, figs 9, 10.
1954. *Placophyllia dianthus* (Goldfuss): Geyer, p. 193, pl. 16, fig. 2.
1954. *Placophyllia rugosa* Becker: Geyer, p. 193, pl. 16, fig. 3.
1966. *Placophyllia rugosa* Becker: Roniewicz, p. 220, text-fig. 10, pl. 12, fig. 1.
1970. *Placophyllia dianthus* (Goldfuss): L. Beauvais, p. 1122.
1972. *Placophyllia rugosa* Becker: Turnšek, pp. 184, 241, pl. 24, figs 1, 2.
1975. *Placophyllia rugosa* Becker: Turnšek, p. 12, pl. 5, figs 1-3
1976d. *Placophyllia dianthus* (Goldfuss): Eliášová, p. 338, pl. 1, fig. 3; pl. 2, figs 1, 2.
1976d. *Placophyllia rugosa* Becker: Eliášová, p. 338, pl. 1, figs 1, 2.
1985. *Placophyllia dianthus* (Goldfuss): Rosendahl, p. 49, pl. 1, fig. 10.
1985. *Placophyllia rugosa* Becker: Rosendahl, p. 121, pl. 2, fig. 1.
1990. *Placophyllia rugosa* Becker; Eliášová, p. 338, pl. 1, figs 1, 2.
1991. *Placophyllia dianthus* (Goldfuss): Lauxmann, p. 155, text-fig. 15.

**Material:** 1 specimen: UJ 140 P/31/4; 8 thin sections: UJ 30/100, 128–131, 152–154.

**Dimensions** (in mm): d = (6) 7–10 (11); s = ca. 30–40.

**Description:** Phaceloid corallum. Corallites subcircular, covered with thin epitheca. Radial elements differentiated into three-sized orders. Septa S2 slightly shorter than S1. Septa S3 rare. Some longest septa attain lamellar(?) columella. Wall parathecal, locally septo-parathecal. Budding extracalicular, marginal. Rejuvenescence occurs in one calice. Neorhipidacanth microstructure visible.

**Remarks:** *Placophyllia rugosa* Becker 1875 is regarded here as a younger synonym of *P. dianthus*, following Lauxmann (1991).

**Distribution:** Poland: Outer Carpathians, Sub–Silesian Nappe, Woźniki (?Valanginian); Holy Cross Mountains (Late Oxfordian); Czech Republic: Štramberk, Jasenice (Tithonian–Early Berriasian);
South Portugal (Early Kimmeridgian);
South Germany (Late Jurassic);
South Slovenia (Late Oxfordian–Early Kimmeridgian);
Croatia (Late Jurassic).

## CONCLUSIONS

Skeletal character of some species belonging to two scleractinian suborders Pachythecaliina and Rhipidogyrina show on similarity between them. These similarities include following features of skeletons: occurrence of lonsdaleoid septa, wall which is in continuity with septa, lateral branches in wall trabeculae of Pachythecaliina (visible in some taxa), bilateral symmetry of corallite, occurrence of marginarium, occurrence of apophysal septa, and possibly character of internal septal margin.

The similarities between these suborders can be explained by convergence. However, "mixed" rhipidogyrinan-pachythecaliinan features of the family Aulastraeoporidae (Rhipidogyrina) allow speculate about phylogenetic relationships of both suborders.

The systematic part gives descriptions of species from discussed suborders occuring in Štramberk-type limestones, the Polish Outer Carpathians (7 localities from the Silesian, Sub-Silesian and Skole nappes). Similarly as in the Štramberk Limestone (Moravia) pachythecaliinans, although not numerous in the studied material, are highly taxonomically diversified (17 species of 12 genera, including *Pachythecophyllia eliasovae* n.gen., n.sp.). On the other hand, rhipidogyrinans are represented only by 4 species of 4 genera, including ?*Ogilvinella morycowae* n.sp.

Tithonian–?Early Berriasian age is assumed for the most studied corals. Four described species, including *Pachythecophyllia eliasovae* n.gen., n.sp., came probably from the Valanginian limestones, what is suggested on the basis of foraminifera, found in the pebbles.

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# Streszczenie

## KORALOWCE Z PODRZĘDÓW PACHYTHECALIINA I RHIPIDOGYRINA (SCLERACTINIA): DYSKUSJA NAD PODOBIEŃSTWAMI ORAZ OPIS GATUNKÓW Z WAPIENI TYPU SZTRAMBERSKIEGO, POLSKIE KARPATY ZEWNĘTRZNE

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Koralowce z podrzędu Pachythecaliina Eliášová 1976 (późny trias–mastrycht) z uwagi na swoje cechy szkieletu zajmują szczególną pozycję wśród Scleractinia. Niektórzy badacze rozpatrują możliwość ich ewolucyjnych powiązań z paleozoicznymi koralowcami Rugosa. Do podrzędu tego włączono rodzinę Amphiastreidae (za Roniewicz i Stolarskim, 2001), a ponadto rodziny zaliczane tradycyjnie do podrzędu Amphiastreina (w tym Heteroceoniidae; Kołodziej, 1995). Koralowce z podrządu Rhipidogyrina Roniewicz 1976 (środkowa jura-mastrycht) uważane były najczęściej za spokrewnione z "typowymi" skleraktiniami z podrzędu Meandriniina lub Stylinina. W oparciu o literaturę oraz własne obserwacje (Figs 2–5) przedstawiono tutaj dyskusję dotyczącą obu podrzędów. Zdaniem autora, niektóre ripidogyriny, pomimo odmiennej mikrostruktury septów, wykazują znacznie większe podobieństwo do pachytekalinów niż do pozostałych skleraktinii. Koralowce z obu podrzędów posiadają septa lonsdaleoidalne, nieopisywane dotychczas u innych koralowców post-paleozoicznych. Pozostałych podobieństw można dopatrywać się w typie ścianie koralitów (pachyteka v. ripidoteka), obecności septów apofyzalnych, symetrii bilateralnej koralitów, ich marginarium oraz wewnętrznym brzegu septów. Rodzina Aulastraeoporidae wykazuje mieszane cechy, tj. charakterystyczną dla ripidogyrinów mikrostrukturę septów oraz aurikularną ornamentację brzegu wewnętrznego septów (Morycowa & Marcopoulou-Diacantoni; 1997; Morycowa & Kołodziej, 2001), a jednocześnie morfologia ich koralitów jest zbliżona do heterocenidów spokrewnionych z amfiastreidami. Podobieństwa te można tłumaczyć konwergencją, nie można jednak wykluczyć, że wynikają one z filogenetycznego pokrewieństwa obu podrzędów (por. Beauvais, 1981). Dla zweryfikowania tej hipotezy, należy przeprowadzić dalsze badania obejmujące blastogenezę ripidogyrinów (bilateralna symetria może być lepiej wykształcona we wczesnych stadiach ontogenezy; Lebanidze, 1991) oraz badania mikrostruktury pachytekalinów.

W części systematycznej pracy zamieszczono opisy Pachythecaliina i Rhipidogyrina z wapieni egzotykowych typu sztramberskiego z polskich Karpat Zewnętrznych (7 stanowisk z jednostki śląskiej, podśląskiej i skolskiej; Fig. 1). Wiek badanych koralowców nie został jednoznacznie określony. Powszechnie uważa się, że wapienie "facji sztramberskiej", zarówno na obszarze polskich Karpat jak i na Morawach, tworzyły się głównie w tytonie i lokalnie we wczesnym beriasie. Ostatnie badania otwornic z egzotyków zawierających koralowce sugerują, że lokalnie sedymentacja tych wapieni mogła trwać nawet do walanżynu (Ivanova & Kołodziej, w druku).

Pachytekaliny w badanym materiale są nieliczne, ale bardzo silnie zróżnicowane taksonomicznie (17 gatunków, 12 rodzajów, w tym *Pachythecophyllia eliasovae* n.gen., n.sp.; Figs 7–24). Ripidogyriny są reprezentowane przez 4 gatunki z 4 rodzajów, w tym ?*Ogilvinella morycowae* n.sp. (Figs 25–27). Pachytekaliny z obszaru polskich Karpat Zewnętrznych oraz te opisane z wapieni sztramberskich na Morawach (m.in., Eliášová, 1975, 1976a, b, 1978), z licznymi endemicznymi taksonami, reprezentują okres najsilniejszej radiacji w historii tej grupy koralowców.