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MICROSTRUCTURE AND TAXONOMY OF AMPHIASTRAEINA (SCLERACTINIA)

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Abstract: A new classification of the suborder Amphiastraeina Alloiteau, 1952 is proposed based on microstructure. It is supposed, that the distinguishing of the suborder Heterocoeniina Morycowa, 1964 (not Beauvais, 1977) is not justified in consideration of microstructural and morphological features. Two superfamilies: Amphiastraeoidea and Heterocoenioidea which display differences in the microstructure of radial elements are introduced into the suborder Amphiastraeina. The development of skeletal elements in both groups is characterized by the wall developed prior to the septa. The wall is composed of medium-sized and thick, compound (branching) polyaxial main trabeculae giving secondary trabeculae. Septa are formed by minitra- beculae which are in microstructural continuity with trabeculae of the wall.The distinctive development of secondary septal trabeculae in taxa of the superfamily Heterocoenioidea is reflected by the spiniform septal ornamentation. The occurrence of intracalicular budding (Taschenknospung, septal division) is noted in some heterocoeniids. Three species: *Confusaforma carpathica* sp.n., *Preverastraea tenuiseptata* sp.n., and *Thecidio- smilia morycowae* sp.n. (family Heterocoeniidae) are described from the Upper Jurassic and Lower Cretaceous of the Polish and Romanian Carpathians.

Abstrakt: Opierając się na interpretacji mikrostruktury zaproponowano klasyfikację koralowców z podrzędu Amphiastraeina Alloiteau, 1952. Ze względu na cechy mikrostrukturalne i morfologiczne podrzędu Heterocoeniina Morycowa, 1964 (nie Beauvais, 1977), uznano, że jego wyróżnianie jest nieuzasadnione. Do podrzędu Amphiastraeina wprowadzono dwie nadrodziny: Amphiastraeoidea and Heterocoenioidea, wykazujące różnice w mikrostrukturze elementów radialnych. W rozwoju szkieletu ściana powstawała wcześniej niż septa. Ścianę budują średnie i duże wieloosiowe trabekule główne, od których odchodzą trabekule wtórne. Drobne trabekule septalne stanowią kontynuację trabekul ściany. Rozwój wtórnych trabekul septalnych u Heterocoenioidea odzwierciedla ostroguzkowa ornamentacja septów. U niektórych heterocenidów zaobserwowano występowanie pączkowania wewnątrzkielichowego (Taschenknospung, podział septalny). Z górnej jury i dolnej kredy Karpat polskich i rumuńskich opisano trzy gatunki: *Confusaforma carpathica* sp.n., *Preverastraea tenuiseptata* sp.n. i *Thecidiosmilia morycowae* sp.n. (rodzina Heterocoeniidae).

Key words: Scleractinia, Amphiastraeina, taxonomy, microstructure, Jurassic, Cretaceous, Carpathians.

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INTRODUCTION

Corals belonging to the suborder Amphiastraeina Alloiteau, 1952 occupy a particular position among Scleractinia because of their specific morphological features (bilateral symmetry, lonsdaleoid septa) and types of budding. The presence of these features which approximate them to Rugosa is usually explained by convergence, although the possibilities of phylogenetic relations between them have not been excluded (e.g. Melnikova & Roniewicz, 1976). Up to now, corals belonging to Amphiastraeina have been included in four families (classification according to the classification of Melnikova & Roniewicz, 1976). They range from Hettangian/Sinemurian to Cenomanian with the highest diversity in the Upper Jurassic. The more detailed discussion of these corals can be found in the papers of Alloiteau (1957), L. Beauvais (1974, 1976), Eliášová (1975, 1976b, 1978) and Melnikova & Roniewicz (1976).

In this study, taxa which, up to now, were classified among the suborder Heterocoeniina Morycowa, 1964 (not M. Beauvais, 1977) are placed in Amphiastraeina. The taxonomy of these corals, known from Oxfordian to Santonian (very rare in the Upper Jurassic) was discussed in greater detail in the paper of M. Beauvais (1977), and their microstructure was discussed by Morycowa (1971).

The suborder Amphiastraeina is poorly represented, in terms of both species and genera in Jurassic and Cretaceous coral assemblages. An exception to this is the highly diver-

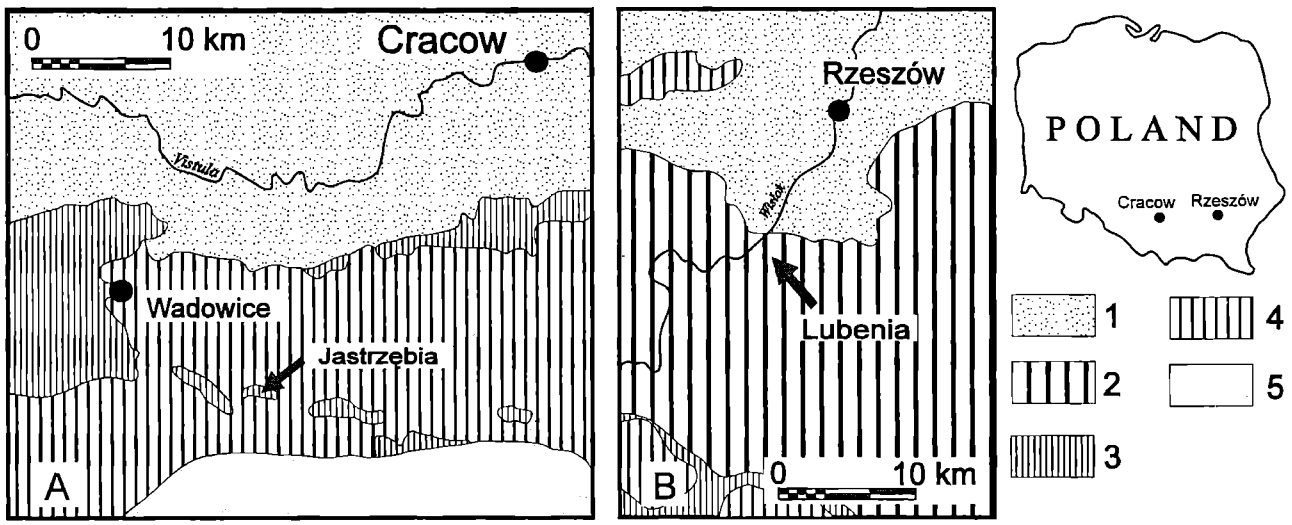


Fig.1. Map of Poland and geological sketch-maps of Polish Outer Carpathians showing type localities of *Thecidiosmilia morycowae* sp.n. (**A**) and *Confusaforma carpathica* sp.n. (**B**). *1* - autochthonous Miocene; *2* - Skole nappe; *3* - Sub-Silesian nappe; *4* - Silesian nappe; *5* - Magura nappe

sified assemblage of amphiastraeinas (many endemic taxa) known from the Štramberk Limestone (Tithonian - lower Berriasian) of Moravia (e.g. Eliášová, 1975, 1976b, 1978) and from exotics of Štramberk-type limestone from the Polish Outer Carpathians (approximately 20 species belonging to 12 genera).

The following genera discussed in this study belong to the family Amphiastraeidae Ogilvie, 1897, emend. Eliášová, 1975: *Amphiastraea* Étallon, 1859, *Amphiaulastraea* Geyer, 1955, *Mitrodendron* Quenstedt, 1881, *Pleurophyllia* de Fromentel, 1856, *Pseudopistophyllum* Geyer, 1955. The genus *Prodonacosmilia* Melnikova, 1976 belongs to the family Donacosmiliidae Krasnov, 1976, emend. Roniewicz, 1976, and the genus *Intersmilia* Eliášová, 1974 belongs to the family Intersmiliidae Melnikova & Roniewicz, 1976. The following genera are included in the family Heterocoeniidae Oppenheim, 1930, emend.: (?) *Amphimeandra* L. Beauvais & Mori, 1988, *Aulastraeopora* Prever, 1909, *Heterocoenia* Milne-Edwards & Haime, 1849, *Hexapetalum* Eliášová, 1975, *Latusastraea* d'Orbigny, 1850, *Pachycoenia* Alloiteau, 1952, *Preverastraea* L. Beauvais, 1976, *Thecidiosmilia* Koby, 1888 and *Confusaforma* Löser, 1987. The latter genus has been placed until now in the suborder Stylinina Alloiteau, 1952.

MATERIAL

The species *Confusaforma carpathica* sp.n. has been recorded from exotic of Štramberk-type limestone found in the Babice Clays (Paleocene; Rajchel, 1990) in Lubenia near Rzeszów (Skole Unit, Polish Outer Carpathians, Fig. 1B; for exact location see Kropaczek, 1917). The Štramberk-type limestone is the age and facies equivalent of the Štramberk Limestone (e.g. Morycowa, 1964a, 1974; Hoffmann, 1992). Based on the age assignments of the Štramberk-type limestone (e.g. Morycowa, *op.c.*) and the Štramberk Limestone from Moravia (Houša, 1990), obtained thus far, it is supposed that *C. carpathica* represents the Tithonian - lower Berriasian interval. According to Eliáš & Eliášová (1986), the deposition of the Štramberk Limestone in Moravia could have persisted up to the Hauterivian.

The species *Thecidiosmilia morycowae* sp.n. was recovered from conglomerates belonging to the Grodziszcze Beds (lower Aptian; see Morycowa, 1976) from Jastrzębia near Lanckorona (Sub-Silesian Unit, Polish Outer Carpathians, Fig. 1A). A rich coral assemblage from this locality has been described previously by Morycowa (1964b).

Preverastraea tenuiseptata sp.n. was found in Urgonian limestones of Barremian - early Aptian age (Popescu & Patrulius, 1964, see also Morycowa, 1971), which appear as recycled elements within the flysch deposits (Barremian - Aptian) in Valea Izvorul Alb (Rarau region, Romanian Eastern Carpathians, Fig. 2).

A new microstructure interpretation of the suborder

Fig. 2. Map of Romania showing localization of region Rarau, where *Preverastraea tenuiseptata* sp. n. was collected

Amphiastraeina is based mostly on studies of materials from Prof. Morycowa's collections (Jagiellonian University), derived from the Tithonian - Lower Cretaceous deposits of the Polish Outer Carpathians and from the Lower Cretaceous deposits of Eastern Carpathians in Romania (see Morycowa, 1964a, 1964b, 1971, 1974). All studied specimens are housed at the Institute of Geological Sciences of the Jagiellonian University.

REVIEW OF OPINIONS ON THE MICROSTRUCTURE AND CLASSIFICATION OF THE SUBORDERS AMPHIASTRAEINA AND HETEROCOENIINA

The microstructure of Amphiastraeina and Heterocoeniina has been the subject of exceptionally differing interpretations, mostly because of the poor preservation of the skeleton microstructure in these corals.

Ogilvie (1897; see also Ogilvie, 1896), who first distinguished the family Amphiastraeidae, gave the following description of their microstructure: there appear very closely situated trabeculae in the septa; the real wall is composed of septal spines ("*septaldornen*" i.e. horizontal trabeculae), which create aragonite fibres, projecting from the dark line of wall. In Ogilvie's opinion, the microstructure of the wall is similar to that of septa.

The genus *Heterocoenia* was initially included in the family Amphiastraeidae, and subsequently elevated by Oppenheim (1930) to the category of family.

Vaughan & Wells (1943) and Wells (1956) did not distinguish the family Heterocoeniidae in their classification of Scleractinia. Instead, they placed the majority of heterocoeniids in the family Amphiastraeidae, which was included in the suborder Faviina Vaughan & Wells, 1943. These authors were of the opinion that the septal microstructure of these corals is of the minitrabecular type, and the wall represents the epitheca.

Alloiteau (1952) created the suborder Amphiastraeina. In its diagnosis he emphasized the appearance of thin septal trabeculae arranged in series, and the presence of a archeotheca-type wall. This author placed the family Heterocoeniidae in the suborder Stylinina Alloiteau, 1952.

According to L. Beauvais (1974, 1976) the microstructure of amphiastraeids and heterocoeniids is similar to each other. In Beauvais' opinion, the wall and the septa are built by elementary trabeculae. L. Beauvais (1974, p. 293) wrote that: "Every small dark line of the theca is one elementary trabecula compound of small and close dark points which are centres of calcification". The appearance of elementary trabeculae in the skeleton of both groups has never been convincingly documented photographically, except in drawings given by L. Beauvais (1970, figs. 2-4). According to Ogilvie (1897) and L. Beauvais (1974) the wall and the septa of Amphiastraeina (besides the family Amphiastraeidae, this latter author placed here also the family Pruvostraeidae L. Beauvais, 1970) are of similar microstructure, and are in microstructural continuity.

In 1977, M. Beauvais created the suborder Heterocoeniina. The necessity of separating this suborder was earlier suggested by Alloiteau (1957, p. 368, 389). However, this suborder was distinguished for the first time by Morycowa (1964b), but without a diagnosis (see Morycowa *et al.*, 1995). M. Beauvais (1977) included the family Heterocoeniidae and three new families: Pachycoeniidae, Baryheliidae and Paronastraeidae in Heterocoeniina. In the opinion of this author, the microstructure of Amphiastraeina and Heterocoeniina is similar (the skeleton consists of elementary trabeculae), and the main difference between these two suborders centre on the lack the intracalicular budding in Heterocoeniina.

L. Beauvais (1981) included Amphiastraeidae and Heterocoeniidae in her new suborder Distichophyllina, characterized by the non-trabecular microstructure. The taxa from the remaining families distinguished by M. Beauvais (1977) were also accommodated in the family Heterocoeniidae. However, L. Beauvais & Mori (1988) excluded the family Amphiastraeidae from this suborder, and placed it in the suborder Pachythecaliina Eliášová, 1978. In their opinion (pp. 103 - 104) Distichophylliina is characterized by "a non-trabecular microstructure with radial elements built from a medioseptal plan displaying, on both sides, perpendicular bunches of fibres and from which lateral axes differentiate to give sclerodermites". They justified the inclusion of the Amphiastraeidae in the suborder Pachythecaliina by its "having a medioseptal plan but lacking lateral axes". Roniewicz (1989) accepted a similar systematic position of "amphiastraeid groups".

Morycowa (1971) who studied well preserved aragonitic skeletons of the genera *Latusastraea* and *Heterocoenia*, noted the occurrence of vertical and horizontal thick trabeculae in the wall, as well as the presence of thick, compound trabeculae in sclerenchymal deposits of the peritheca of *Latusastraea*. Morycowa also presumed the thick-trabecular microstructure of the septa. In the same paper she described the minitrabecular microstructure of the septa in *Amphiaulastraea rarauensis* (Morycowa, 1971), representing Amphiastraeidae, and stated that the wall is built of bundles of fibres.

Melnikova & Roniewicz (1976) accepted the fascicular structure of the Amphiastraeina wall. These authors placed in this suborder beyond the family Amphiastraeidae also the following families: Donacosmiliidae of Krasnov (1970), revised by Roniewicz (1976), Carolastraeidae of Eliášová (1976a), and the new family Intersmiliidae.

Instead, Eliášová (1976b, 1978) included these corals in four suborders, placing them in the order Hexanthiniaria Montanaro Gallitelli, 1975. In the opinion of Montanaro Gallitelli (1975), the systematic position of this order is between Rugosa and Scleractinia. According to Eliášová (*op.c*), the microstructure in particular suborders is the following: Pachythecaliina (families: Pachythecaliidae Cuif, 1975 and Hexapetalidae Eliášová, 1976) and Heterocoeniina have a fascicular microstructure (both the wall and the septa, independent of the wall); Amphiastraeina possess a fibrolamellar microstructure; Carolastraeina Eliášová, 1978

(Carolastraeidae and Intersmiliidae) - a fascicular outer wall and fibrolamellar inner wall, taking part in forming the septa.

According to Roniewicz & Morycowa (1989, 1993) the microstructure of amphiastraeids represents a phylogenetic continuity of the Triassic pachythecaliids microstructure; the heterocoeniids constitute the group of thick-trabecular microstructure; and the donacosmiliids and intersmiliids (a phylogenetic continuity of the Liassic archaeosmiliids) are the groups with minitrabecular septa microstructure.

The majority of taxonomists accepted the suborders Amphiastraeina and Heterocoeniina, but without further discussion of microstructure of the described taxa.

A good example of especially differing opinions on their taxonomic position is the genus *Latusastraea* discussed in this paper. In the papers published between 1940 and 1990, *Latusastraea* was placed in the suborders Amphiastraeina, Caryophylliina, Distichophylliina, Faviina, Heterocoeniina and Stylinina by different authors (see Turnšek & Löser, 1993).

NEW INTERPRETATION OF THE MICROSTRUCTURE OF AMPHIASTRAEINA

The interpretation presented in this paper is based mainly on the results of studies on microstructure in *Amphiastraea basaltiformis* Étallon, 1859 the representative of amphiastraeids, in *Latusastraea exiguis* (de Fromentel, 1862) and in *Thecidiosmilia morycowae* sp.n., representing the heterocoeniids.

Based on this interpretation and new data on budding, a new proposition of the taxonomy of the suborder Amphiastraeina is proposed. The features of the superfamilies and families included in this suborder are presented in section "Systematic part", and in Tab. 1. In the microstructure descriptions the following names and dimensions of trabeculae given by Morycowa & Roniewicz (in press) are used: minitrabeculae (ca 15 - 50 μm), medium-sized trabeculae (ca 50 - 90 μm) and thick trabeculae (usually more then 100 μm).

MICROSTRUCTURE OF THE WALL

The longitudinal section of the wall of *Amphiastraea basaltiformis* (Fig. 4A) shows distinct analogies with the wall of *Latusastraea exiguis* (Fig. 3A), which has a trabecular structure, as shown by Morycowa (1971) based on a study of a very well preserved aragonitic skeleton. The horizontal structures in the wall of the Amphiastraeidae have been termed "*septaldornen*" (Ogilvie, 1897), "*septes abortifs*" (Alloiteau, 1957), "elementary trabeculae" (L. Beauvais, 1974) or "fascicle of fibres" (Melnikova & Roniewicz, 1976).

Similarities in the wall microstructure among amphiastraeids and heterocoeniids are especially visible in the colonies having a cerioid form. The following position of trabeculae is characteristic then: in the centre of the wall common for two neighbouring corallites, there are medium-sized and thick trabeculae giving secondary, horizontal or oblique trabeculae (of similar dimensions) on both sides. Morycowa (1971) observed such a position of the trabeculae (60 - 120 μm in diameter) in *Latusastraea*. According to Morycowa, these horizontal or oblique trabeculae form radial elements (septa and/or costosepta) which with the exception of the largest septum, are developed as septal spines. In my opinion, these trabeculae constitute the wall element, developed prior to the septa, whereas the septa are of different microstructure (see below).

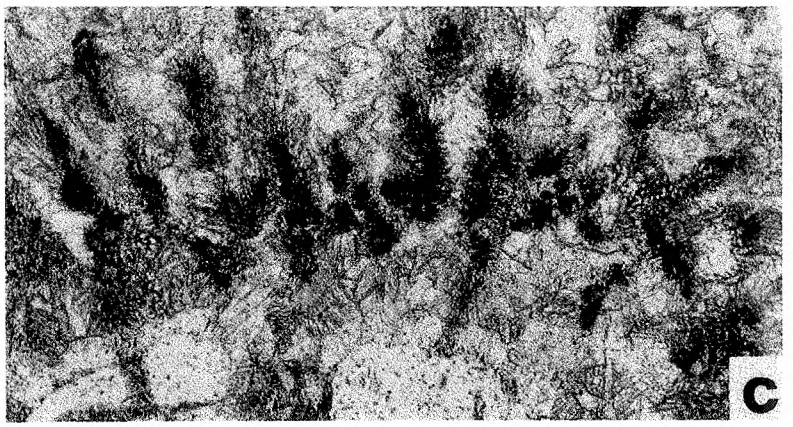
The presence of vertical trabeculae is very clearly visible in the wall of *Latusastraea exiguis* (Morycowa, 1971, text-fig. 23; and Figs. 3A, C of this paper). Despite strong recrystallization of the skeleton, they are also present in the wall of *Confusaforma carpathica* sp.n. (Fig. 7E). Horizontal and oblique trabeculae are in places clearly marked in transversal sections of *Amphiastraea basaltiformis* and *Thecidiosmilia morycowae*, whereas vertical trabeculae are undistinguishable. This part of the wall is usually preserved as a straight, dark intramural line or a narrow fissure. The presence of epitheca on the wall surface of *Amphiastraea* indicates that in this genus during the colony development, the separation of individuals occurred lengthwise along the intramural line. In consequence, the neighbouring corallites posses independent walls (the pseudocerioid type of colony). Vertical trabeculae appear in better preserved parts of the wall in the amphiastraeid coral *Amphiaulastraea rarauensis* (Morycowa, 1971, pl. XXVI, fig. 1d; and Fig. 4H, this paper), whereas, horizontal trabeculae are very poorly marked. This can be explained by the state of preservation, because in studied *Latusastraea exiguis* with well preserved microstructure, both vertical and horizontal or oblique trabeculae are visible, but sometimes these two latter types are not preserved. The occurrence of horizontal trabeculae in *A. rarauensis* may be, however, manifested by the appearance of regularly arranged granules on the inner surfaces of the wall (see Morycowa, 1971, pl. XX, fig. 1g).

Similarities between the wall structure of *Latusastraea* and *Amphiastraea* are also observable in sections transversal to the trabeculae arrangement. Trabeculae of sclerenchymal deposits of the peritheca of *Latusastraea exiguis* (Figs.

Fig. 3. *Latusastraea exiguis* de Fromentel, 1862; coll. E. Morycowa; **(A-C, E-F, G, I):** Jastrzębia, lower Aptian; **H:** Trzemesna, Barremian - lower Aptian; **D:** Valea Izvorul Alb, lower Aptian. **(A)** Longitudinal section of wall, UJ 6/41, ×40. **(B)** Transverse section of wall; trabeculae arrangement on one side of intramural line and branching of trabeculae, UJ 6/38, 80. **(C)** Transvere section of wall, UJ 6/40, ×40. **(D)** Compound trabeculae of peritheca, UJ 124P/70a, ×100. **(E)** Trabeculae of peritheca; horizontal trabeculae of wall are visible in the lower - left corner, UJ 6/39, ×40. **(F)** Trabeculae of peritheca; particular centres of calcification are not visible, UJ 6/39, ×80. **(G)** Transverse section of wall; poorly marked centres of calcification of trabeculae are visible (arrow), UJ 6/40, ×40. **(H)** Budding by septal division, UJ 6/42, ×30. **(I)** Transverse section; largest septum (below) and rudimentary one (above), UJ 6/38, ×80


A


B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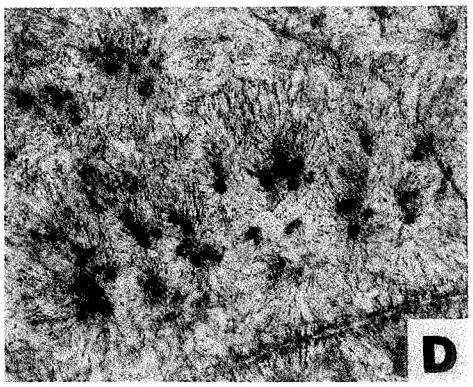
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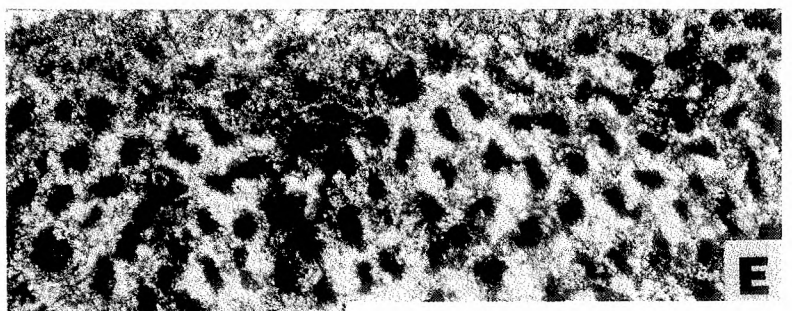
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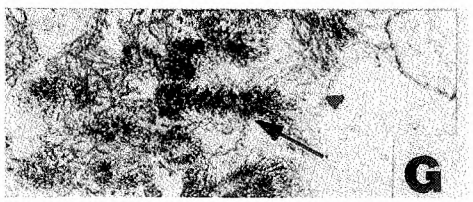
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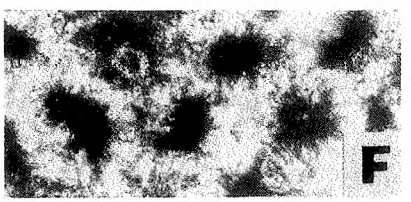
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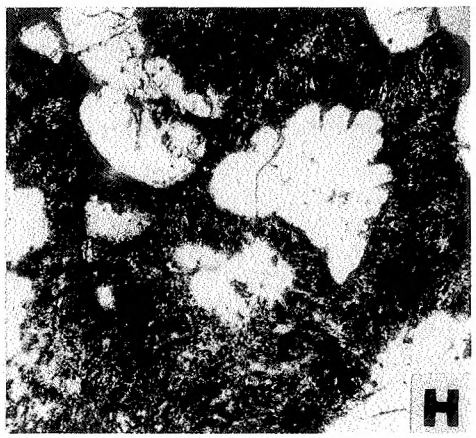
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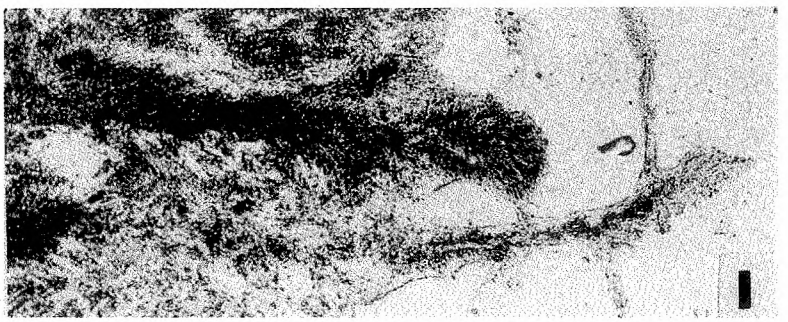
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3E - F) are of similar dimensions and appearance as the wall trabeculae in *A. basaltiformis* (Fig. 4C).

Morycowa (1971, pl. XIV, fig. 1b; also Fig. 3D in this paper) observed in very well preserved sclerenchymal deposits of the peritheca the presence of large, compound trabeculae, approximately 160 - 320 μm in diameter. Several dark centres of calcification have been found in the centre of such trabecula. In my opinion, the wall forming trabeculae in amphiastraeids and heterocoeniids are of the same nature, although of smaller size then the trabeculae of the peritheca. However owing to diagenesis, calcification centres are either not preserved in the trabecula (*cf.* Figs. 3E-F, 6A) or are faintly marked within the dark central part of trabecula (Figs. 3G, 6B). Following the classification of trabeculae proposed by Morycowa & Roniewicz (in press), the described type of compound (branching) trabecula should be qualified as the polyaxial main trabecula giving secondary trabeculae.

Characteristic branching of trabeculae is visible in transverse sections of the wall in *L. exiguis* and *A. basaltiformis* (Figs. 3B, 4B; both figures show the arrangement of trabeculae on one side of the intramural line).

Roniewicz (1970) observed in the wall of *Pseudodiplocoenia oblonga* (Fleming, 1827) (included within incertae sedis group) the presence of serial, obliquely arranged trabeculae which strongly resemble the wall structure in Amphiastraeina. However, in opposition to amphiastraeinas, the septa are of thick-trabecular microstructure.

The inner surface of the wall is thickened by stereome, which continues on the septal faces (Fig. 6C). Then, two parts of the wall can be distinguished: the external trabecular part and the inner, generally fibrous one (Figs. 4D-E, 6D). Such structure appears to favour the divergement ("*décollement*") of the wall layers and forming marginal vesicles (Fig. 6D).

MICROSTRUCTURE OF SEPTA

In *Latusastraea*, which has a much thinner wall than *Amphiastraea*, the thick trabeculae reach the inner wall surface forming rudimentary septa. The poor development of the septal apparatus composed mainly of rudimentary septa and poorly marked on the surface of the inner wall is a characteristic feature of some heterocoeniids. In such a case it is difficult to determine the number of septa (*cf.* Figs. 5A, C-E). The Figure 3I ilustrates the relation between the rudimentary septum and the largest ("cardinal") one formed by small, oblique trabeculae. The differences in dimensions of the trabeculae forming the wall and the septum in *Thecidiosmilia morycowae* are shown in Fig. 6A. Septal trabeculae (approximately 20 - 30 μm in diameter) are arranged vertically (Figs. 6H-I) or obliquely, and are so compacted that, as a rule, they are not distinguishable in the mid-septal zone. It appears that medium-sized and thick trabeculae are present within the septa of *Thecidiosmilia morycowae* (Fig. 6G). The mid-septal zone is preserved in different ways in the representatives of the discussed suborder (*cf.* Figs. 4F-G, 6H-I). Similarly, as in the case of the wall, a narrow fissure may be formed along mid-septal zone.

A fundamental, commonly noticeable difference between the amphiastraeids and heterocoeniids is observed in the microstructure of the radial elements. Well developed but not regular lateral septal trabeculae (secondary trabeculae - Jell, 1969) appear in the septa of heterocoeniids. Their presence is expressed by locally very strong, irregular septal ornamentation (*cf.* Figs. 6C, 6F, 7G-H). The ornamentation in amphiastraeids is generally poor or not marked, probably due to the absence or poor development of secondary trabeculae.

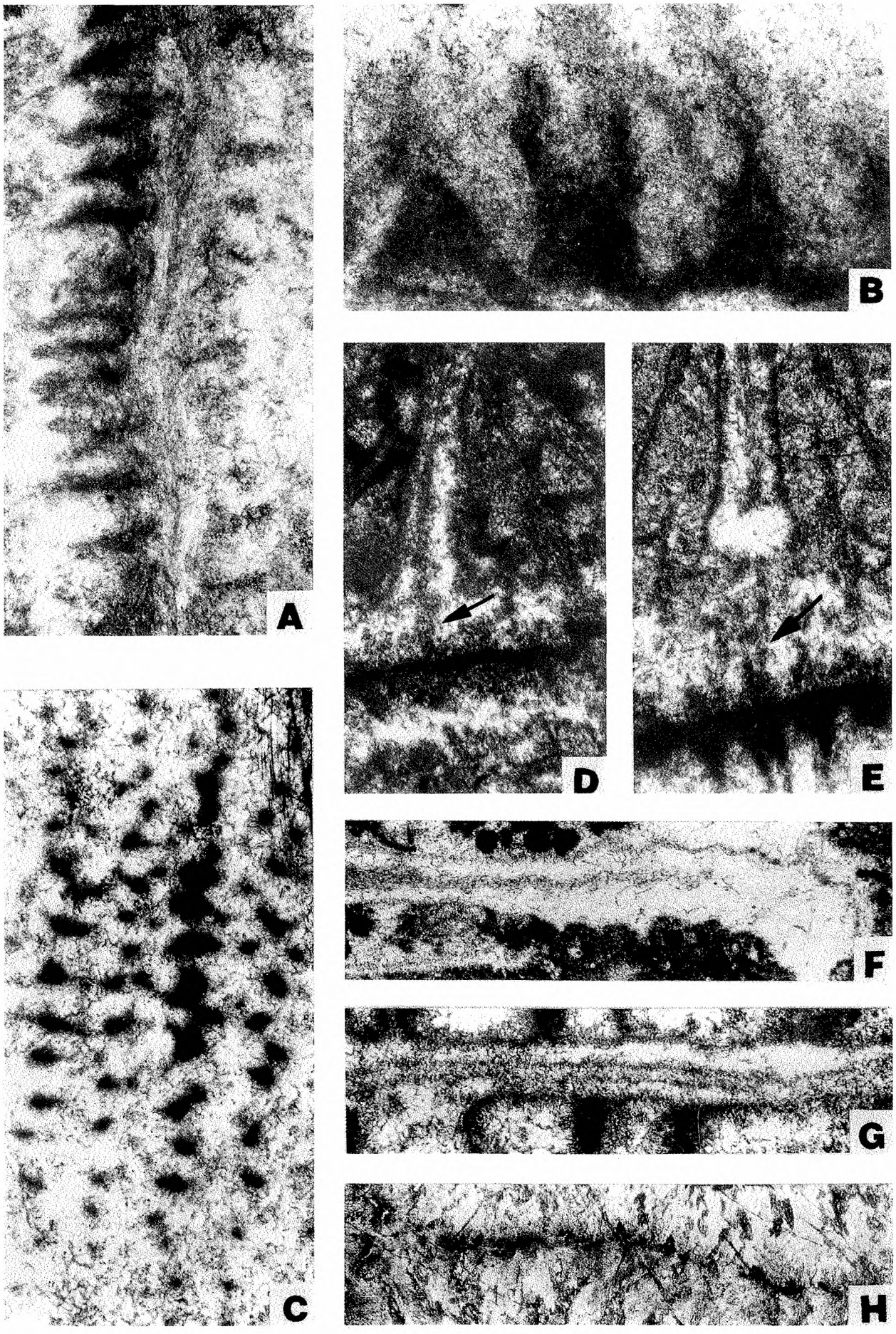
A specific skeletal structure is seen in some heterocoeniids, termed compound septum ("*septes composés*") by Alloiteau (1957). According to Alloiteau (p. 368), these septa "*constitué de septes simples dont la presence se manifeste extérieurement sur les faces latérales et sur tout le bord axial arrondi, par des lignes réguliérement espacées de fines granules quidistants*". The definition of this term is not quite clear, especially since the author did not refer to drawings or photos. In my opinion, the skeleton structure of that type is connected with the particular wall development. Eliášová (1976b) described such structures in *Hexapetalum pium* Eliášová, 1976. She termed this structure "wall invagination" whereby septa subdivide the primary calice into open segments. According to Eliášová (1976b., text-fig. 12) the real septa are formed on top of and between these invaginations. A similar arrangement is visible in *Pachycoenia fuchsi* (Felix, 1903) (see M. Beauvais, 1977, Pl. II, Fig. 2). The thick "septa" in *Confusaforma* (*cf.* Fig. 6A) are probably of identical origin. Their tops may be pointed by thin, "filiform" septa, which also appear independently.

Growth layers are visible in stereome covered septal faces of *Thecidiosmilia morycowae* (Fig. 6C). This stereome is the continuation of the stereome covering the inner part of the wall.

WALL - SEPTA RELATION

In the skeleton development the wall is developed prior to the septa (Melnikova & Roniewicz, 1976), similarly as in Pachythecaliina (*cf.* Cuif, 1975; Roniewicz, 1989). In the opinion of the present author, the trabeculae forming septa

Fig.4. **(A-F)** *Amphiastraea basaltiformis* Étallon, 1859, Kruhel Wielki, upper Tithonian - lower Berriasian, coll. E. Morycowa, UJ 38 P/5. **(A)** Longitudinal section of wall; horizontal trabeculae are visible, UJ 8/5, ×40. **(B)** Transverse section of wall; trabeculae arrangement on one side of intramural line; branching of trabeculae, UJ 8/4, ×80. **(C)** Wall in longitudinal (tangential) section; horizontal trabeculae in transverse section are visible, UJ 8/5, ×40. **(D, E)** Contact of the mid-septal zone with horizontal trabeculae of wall (arrow), UJ 8/4, ×40. **(F)** *Amphiastraea basaltiformis* Lipnik Hill near Przemyśl, Tithonian - lower Berriasian, UJ 140 P/2. Mid-septal zone, UJ 30/12, ×100. **(G)** *Pseudopistophyllum woznikensis* Morycowa, 1974, Woźniki, upper Tithonian, coll. E. Morycowa, UJ 40 P/20. Mid-septal zone, UJ 10/30, ×100. **(H)** *Amphiaulastraea rarauensis* (Morycowa, 1971), Valea Izvorul Alb, lower Aptian, coll. E. Morycowa, UJ 124 P/120. Transverse section of the wall; vertical trabeculae are seen, UJ 124 P/120a, ×25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are the continuation of the wall trabeculae. It is visible in *Amphiastraea basaltiformis* that the mid-septal line is in touch with the thick trabeculae forming the wall (Figs. 4D-E). Also according to Ogilvie (1897) the dark line appearing in the septum (formed by densely compacted trabeculae) goes off the wall.

CONCLUSIONS

Generally two types of trabeculae should be distinguished in the skeleton of amphiastraeids and heterocoeniids: medium-sized and thick trabeculae forming the wall and minitrabeculae, appearing in septa.

In connection with the similarities in microstructure of amphiastraeids and heterocoeniids further distinguishing of the suborder Heterocoeniina seems to be unjustified. The existing differences in microstructure of septa in both groups are in turn the basis for distinguishing of two superfamilies: Amphiastraeoidea and Heterocoenioidea within the suborder Amphiastraeina (their diagnoses are given below). It may be presumed, that if the septal ornamentation appears in the representatives of the superfamily Amphiastraeoidea, then it has also trabecular foundations. Therefore the boundary between these two superfamilies is in certain degree arbitrary.

Despite the differently interpreted microstructure, the above presented data seem to confirm the concept of structural continuation of the wall and septa (Ogilvie, 1897; L. Beauvais, 1974).

REMARKS ON BUDDING

A characteristic feature of the family Amphiastraeidae is the occurence of specific types of intracalicular budding: Taschenknospung-type, which was considered hitherto as restricted to this family, and parricidal budding (rarely, in some genera). Melnikova & Roniewicz (1976) placed among the Amphiastraeina the families Donacosmiliidae, Carolastraeidae and Intersmiliidae, in which the Taschenknospung-type budding is absent. The Taschenknospung is a type of intramural budding (Eliášová, 1978). In both cases, it is extratentacular gemmation (intra- or extracalicular) in which the septa of parent individuals do not take part in forming the septal apparatus of descendant individuals (Vaughan & Wells, 1943; Alloiteau, 1957; Roniewicz, 1966).

Budding of the Taschenknospung-type is not universally understood. The exact course of this budding is known in *Pleurophyllia trichotoma* de Fromentel, 1856 (Roniewicz, 1966; Melnikova & Roniewicz, 1976). A bud originates in the compact wall tissue, and next moves inwards the parent calice, growing at the expense of the space occupied by the parent individual. According to Ogilvie (1897), this type of budding takes place in endothecal vesicles. L. Beauvais (1974, 1976) stated that the budding in Amphiastraeidae takes place in marginarium vesicles originated by "detaching" ("*décollement*") of the innermost layer of the wall. This "detaching" means the divergement of the wall layers related with interruption of the continuity of its vertical growth. Essential for proper definition of the Taschenknospung-type budding is determination of the place in which the buds originate. In the opinion of Prof. E. Roniewicz (pers. commun.), the term "Taschenknospung-type budding" should be restricted to cases of buds originating in the compact wall, whereas if a new individual originates in marginal pocket, budding should be termed marginal budding. It should be noted that some authors (e.g. Alloiteau, 1957; L. Beauvais, 1974, 1976, 1981) use this later term as a synonym of the Taschenknospung-type budding. In this study this term is used in a broad sense, because for many taxa, the exact place in which buds originate is not determined.

M. Beauvais (1977) recognized the lack of intracalicular budding in the suborder Heterocoeniina as a main feature differentiating the new suborder from Amphiastraeina. However, the examples described below argue that, though rarely, in some taxa of Heterocoeniina this type of budding is also present.

Observations of budding in *Thecidiosmilia morycowae* show that a new individual originated in the wall develops, as a rule, outside the calice of the parent individual. However, the new individual can also broaden at the expense of the space occupied by the parent individual, which is a feature of the Taschenknospung budding (Fig. 5D).

It seems possible that this type of budding is also present in *Preverastraea* (see below).

Another type of intracalicular budding that occurs in heterocoeniids is septal division, observed in *Latusastraea exiguis* (Fig. 3H) and *Thecidiosmilia morycowae* (Fig. 5C). This type of budding is characteristic of *Confusaforma*, hitherto placed in the suborder Stylinina (see systematic part). It is possible that septal division is also present in *Heterocoenia* (*cf.* M. Beauvais, 1977, Pl. I, Figs. 1, 2). According to L. Beauvais (1988) this type of budding occurs in the genus *Amphimeandra*, placed within Amphiastraeidae. It is possible that septal division in heterocoeniids is related to the strong development of secondary trabeculae, which give rise to some septa in new individuals originating by this type of budding (Fig. 5C). In this connection, it is possible that the genus *Amphimeandra* should be placed in the family Heterocoeniidae. It should be, however, noted that in the opinion of Prof. E. Roniewicz (pers. comm.) the microstructure vestiges suggest that this genus might be included in the suborder Rhipidogyrina Roniewicz, 1976.

Structures resembling new individuals originating as a consequence of parricidal budding (e.g. in genera *Intersmilia* and *Mitrodendron*; *cf.* Roniewicz, 1966; Melnikova & Roniewicz, 1976) have been observed in some calices of *Thecidiosmilia morycowae*.

SYSTEMATIC PART

Order Scleractinia Bourne, 1900

Suborder Amphiastraeina Alloiteau, 1952

Emended diagnosis: Trabecular wall developed prior to the septa. Trabeculae of wall (vertical and secondary - horizontal and

oblique), compound, medium-sized or thick. Septal minitrabeculae are the continuity of wall trabeculae. Septal secondary trabeculae well developed (Heterocoenioidea), poorly developed or not developed (Amphiastraeoidea). Symmetry bilateral or radial. Endotheca two-zonal (subtabuloid dissepiments in axial part of corallites and vesicular ones in marginal part) or one-zonal without vesicular elements. Columella absent or parietal (*Prodonacosmilia*). Budding intracalicular (Taschenknospung-type, parricidal and septal division) or/and extracalicular (intramural, lateral or perithecal).
Stratigraphical range: ? Hettangian/Sinemurian - Santonian.

Superfamily Amphiastraeoidae Ogilvie, 1897
Emended diagnosis: septal secondary trabeculae poorly developed or absent, which is reflected by poorly developed septal ornamentation or the lack of such ornamentation.

Family Amphiastraeidae Ogilvie, 1897, emend. Eliášová, 1975
Diagnosis: symmetry bilateral, lonsdaleoid septa present, endotheca two-zonal, budding Taschenknospung-type and parricidal.

Family Donacosmiliidae Krasnov, 1970, emend. Roniewicz, 1976
Diagnosis: symmetry radial, lonsdaleoid septa present, endotheca two-zonal, budding lateral.

Family Carolastraeidae Eliášová, 1976
Diagnosis: symmetry bilateral, lonsdaleoid septa absent, endotheca tabular, budding lateral.

Family Intersmiliidae Melnikova & Roniewicz, 1976
Diagnosis: symmetry radial, lonsdaleoid septa absent, endotheca subtabuloid, budding lateral and parricidal.

Superfamily Heterocoenioidea Oppenheim, 1930
Emended diagnosis: septal secondary trabeculae well developed, which is reflected by the distinct ornamentation of septal faces.
Remarks: The superfamily Heterocoenioidea was previously distinguished by Löser (1994). This author did not give a diagnosis of this superfamily and placed it in the suborder Stylinina.

Family Heterocoeniidae Oppenheim, 1930
Emended diagnosis: endotheca most often one-zonal, subtabuloid, budding mainly extracalicular (intramural and perithecal), rarely intracalicular (septal division and Taschenknospung).
Remarks: The emended diagnosis of the family takes into account the presence of intracalicular budding (septal division and Taschenknospung). The family Heterocoeniidae encompasses taxa differing considerably from one another with respect to morphological features (the development of endotheca, presence or lack of lonsdaleoid septa, type of symmetry) and the type of budding. These features were the basis for distinguishing families, which in this study are placed in the superfamily Amphiastraeoidea. It is within the realm of possibilities that within the superfamily Heterocoeniidae new taxonomical units of family or subfamily rank could be distinguished. M. Beauvais (1977) based on the nature of the septa (compound *sensu* Alloiteau (1957), "*composés ramifiés*", rudimentary) included among Heterocoeniina, in addition to the family Heterocoeniidae, three new families: Pachycoeniidae, Baryheliidae and Paronastraeidae. In her classification of Scleractinia L. Beauvais (1981) distinguished only the family Heterocoeniidae with two new subfamilies: Heterocoeniinae and Baryheliinae. In the classification presented herein only the family Heterocoeniidae (including also taxa from the remaining families) is distinguished. In my opinion, there are no unequivocal criteria that allow the distinction of particular types of septa. Classification and features of the suborder Amphiastraeina are presented on Tab. 1.

DESCRIPTIONS

Abbreviations used in the descriptions: D - diameter of colony; H - height of colony; dk - diameter of corallites; dc - diameter of calices; ds - thickness of septum (in middle of length); s - number of septa; e - density of endothecal elements; ( ) - values encountered rarely.

Superfamily Heterocoenioidea Oppenheim, 1930, emend. herein
Family Heterocoeniidae Oppenheim, 1930, emend. herein
Genus *Thecidiosmilia* Koby, 1888

Type species: *Thecidiosmilia valvata* Koby, 1888
Emended diagnosis: Colony cerioid. Septa arranged in bilateral symmetry. Spiniform, irregular septal ornamentation. Lonsdaleoid septa rare. Endotheca subtabuloid. Budding extracalicular, rarely intracalicular (Taschenknospung-type and septal division).
Stratigraphical range: Upper Jurassic ("Astartian") - lower Aptian.
Remarks: Birenheide (1969) included *T. valvata* in *Latusastraea*. These genera have many common features, but *Thecidiosmilia* contrary to *Latusastraea*, does not possess a peritheca, Taschenknospung-type budding can be present locally, and corallites do not display the typical "swallow's nests" shape.

Alloiteau (1957) ranked this genus among Amphiastraeidae on the grounds that buds may originate in marginal pockets. But considering the strong septal ornamentation reflecting the microstructure of septa observed in *T. morycowae*, this genus can not be placed in this family.

The emended diagnosis of *Thecidiosmilia* takes into account the presence of strong septal ornamentation and reproduction by Taschenknospung and septal division. This genus was until now represented only by the holotype of *T. valvata* from the "Astartian" (Oxfordian) of the Jura Mountains (Switzerland).

Thecidiosmilia morycowae sp.n.
(Figs. 5, 6)

Holotype: UJ 139 P 1, Figs. 5, 6
Type locality: Jastrzębia near Lanckorona (Polish Outer Carpathians).
Type level: Grodziszcze Beds (lower Aptian).
Derivation of name: Patronymic, in honour of Prof. Elżbieta Morycowa.
Diagnosis: Diameter of calices: 2 - 3 (3, 5) mm. Density of endothecal elements: 3 - 4/2 mm.
Material: One colony, 9 transverse sections, 2 longitudinal thin sections.
Dimensions (in mm): D – 175 x 160; H max. – 50; dc – 2 - 3 (3, 5); s – up to about 35; e – 3 - 4/2 mm.
Description: Cerioid colony with a slightly convex surface. Walls of corallites protruding. Septa arranged in bilateral symmetry. Apart from largest septum and two septa lying on both sides, the remaining septa are developed, as a rule, as rudimentary ones, poorly marked on the inner surface of the wall. For this reason, it is difficult to determine the number of septa. The largest septum attaines 3/4 of the diameter of calice and is usually ornamented by large, sharp, irregularly distributed granules (Figs. 6C, 6F). How-

Table 1

Classification and features of the suborder Amphiastraeina

Suborder AMPHIASTRAEINA Alloiteau, 1952, emend.					
microstructure of wall	medium-sized and thick, compound (branching) polyaxial main trabeculae giving secondary trabeculae				
microstructure of septa	minitrabeculae; secondary trabeculae absent or weakly developed				minitrabeculae; secondary trabeculae well developed
superfamilies	**Amphiastraeoidea** Alloiteau, 1952, emend.				**Heterocoeniidea** Oppenheim, 1930, emend.
ornamentation of septa	absent or weakly developed				spiniform; well developed
families	**Amphiastraeidae** Oglivie, 1987, emend. Eliašová	**Donacosmiliidae** Krasnov, 1970, emend. Roniewicz	**Carolastraeidae** Eliašová, 1976	**Intersmiliidae** Melnikova & Roniewicz, 1976	**Heterocoenioidae** Oppenheim, 1930 emend.
symmetry	bilateral	radial	bilateral	radial	bilateral or radial
lonsdaleoid septa	present	present	absent	absent	present or absent
endotheca	two-zonal	two-zonal	one-zonal	one-zonal	one-zonal or two-zonal (rarely)
columella	absent	absent or parietal	absent	absent	absent
budding	intracalicular (Taschenknospung, parricidal)	extracalicular (lateral)	extracalicular (lateral)	extracalicular (lateral) intracalicular (parricidal)	extracalicular (intramural, perithecal) and intracalicular (septal division, ? Taschenknospung)

ever, in places, the ornamentation is not indistinct. Lonsdaleoid septa are rare. Endotheca subtabular. Intracalicular budding mostly present: Buds originate in the wall, and their further development takes place outside the parent corallite. Taschenknospung budding is present also - the development of a new individual takes place at the expense of space occupied by the septal apparatus of the parent individual (Fig. 5D). Marginal pockets are present. These originated as a consequence of the divergement of wall layers, but it is not known whether the pockets or the compact wall is a place of origin of new individuals. Reproduction by septal division is also present: the largest septum joined to opposite septum, divides the parent calice into two parts (Fig. 5C). In some calices, structures resembling buds forming in parricidal budding have been observed (Figs. 5F-G).

Microstructure: Wall trabecular; trabeculae medium-sized and thick, compound (branching, polyaxial). Within the wall large, dark central parts of trabeculae can be distinguished (Figs. 6A-B). In places, in these trabeculae, poorly resolvable centres of calcification can be seen (Fig. 6B), whereas in dark zone of the central part of the wall common to two adjoining corallites, individual trabeculae are not distinguishable. In longitudinal section, secondary trabeculae (oblique or horizontal course) of the wall are visible (Fig. 6E). Some secondary trabeculae of the wall attain its internal surface, forming rudimentary septa. Septal spines built by thick trabeculae occur (Fig. 6G). In transverse section of the largest septum, vestiges of vertical or oblique minitrabeculae about 20 - 30 μm in diameter can be seen (Fig. 6H-I). These minitrabeculae are so close to each other, as a rule, this zone is preserved as continuous, dark mid-line or narrow fissure. A similar fissure within the wall is marked. In transverse sections of the largest septa, ramifications of the trabeculae (secondary trabeculae) are visible in places. These are reflected by sharp, rare granules (Fig. 6F). Medium-sized and thick trabeculae appear within the septa (Fig. 6G). As a consequence of specific skeletal recrystallization increasing layers can be observed. The stereome which covers faces of the septa is a continuation of the stereome covering the inner surface of the wall (Fig. 6C).

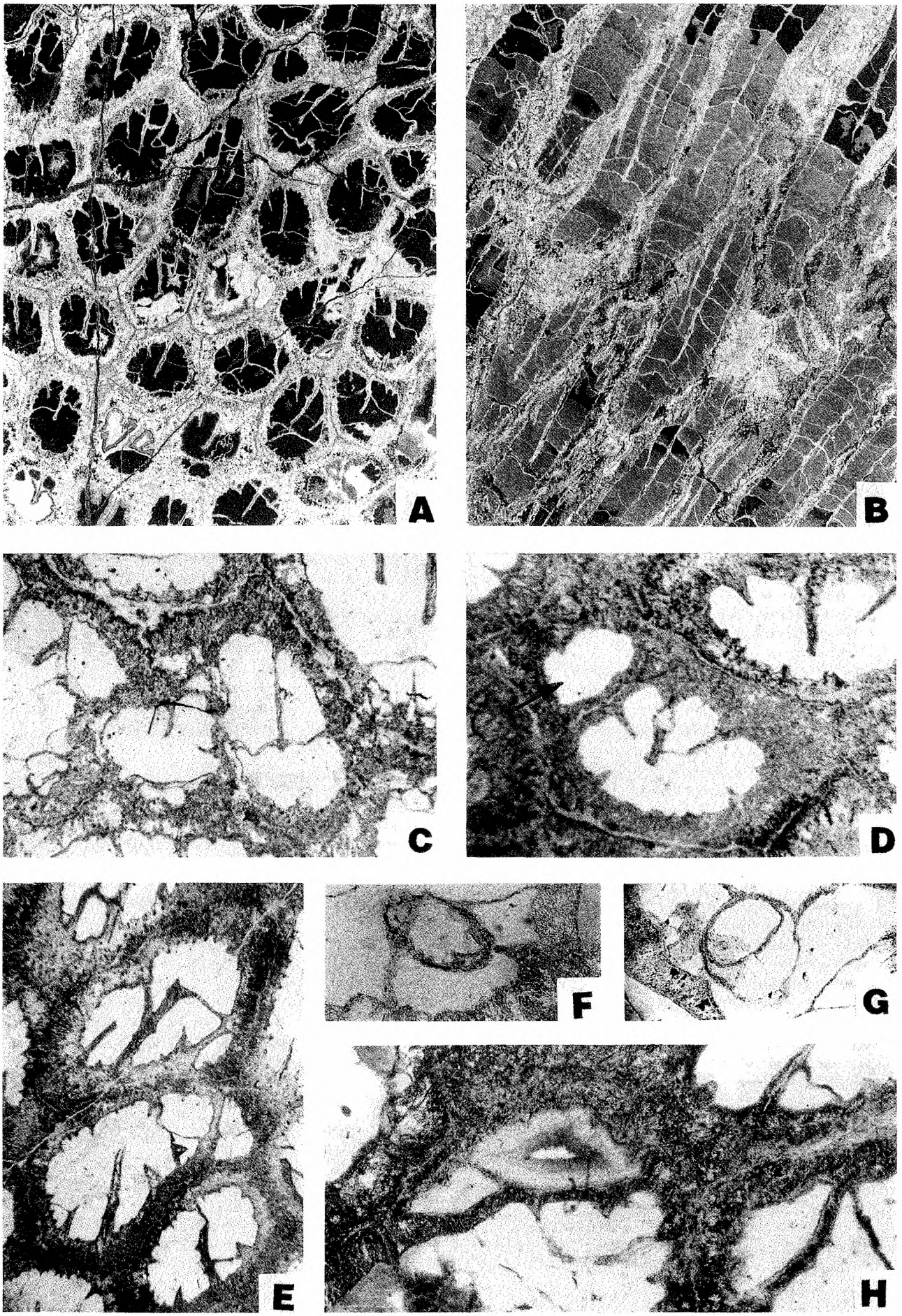
Remarks: The new species differs from *T. valvata* by having a poorly developed septal apparatus (most of the septa are rudimentary), smaller diameter of calices, and a lower density of endothecal elements. Koby (1888) noted that corallites of *T. valvata* attaine 4 -5 mm in diameter, and the density of endothecal elements is up to 2/1 mm, whereas Birenheide (1969) gave the following values for the same specimen: dc = 3 - 4 mm, e = 3/1 mm. Further remarks on microstructure of *T. morycowae* are also contained in the chapter "New interpretation of microstructure of the suborder Amphiastraeina".

Occurrence: Polish Outer Carpathians (Jastrzębia near Lanckorona): lower Aptian.

Genus *Confusaforma* Löser, 1987

Type species: *Confusaforma weyeri* Löser, 1987

Fig. 5. *Thecidiosmilia morycowae* sp.n., Jastrzębia, lower Aptian, UJ 139 P/1. **(A)** Transverse section of the corallites (negative), UJ 29/8, ×5. **(B)** Longitudinal section of corallites (negative), UJ 29/11, ×5. **(C)** Budding by septal division, UJ 29/2, ×20. **(D)** Taschenknospung-type budding (arrow shows new individual), UJ 29/1, ×18. **(E)** Marginal pockets, UJ 29/7, ×10. **(F, G)** Transverse section of corallite; presumable parricidal buds, UJ 29/2, x 40; UJ 29/4, ×45. **(H)** Marginal pocket, UJ 29/8, ×25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Emended diagnosis: Cerioid colony, plocoidal or irregular in places. Septa arranged irregularly or in bilateral symmetry. Lonsdaleoid septa not numerous. Endotheca generally one-zonal, formed by subtabular dissepiments; there are also, in places, vesicular dissepiments. Marginarium occurs rarely in some corallites. Budding extracalicular -intramural, and intracalicular - septal division.
Stratigraphical range: Tithonian - lower Turonian.
Remarks: Löser (1987, 1989) placed this genus in the family Cyathophoridae, the suborder Stylinina. However in *Confusaforma carpathica* sp.n. the lonsdaleoid septa and vestiges of microstructure typical of Amphiastraeina have been observed. This genus is close to *Latusastraea* and *Thecidiosmilia*. Besides morphological similarites, in these genera budding by septal division is present.

Up to now, only one species of this genus was known (*C. weyeri*). It was recorded from the upper Cenomanian of Saxony (Germany) (Löser, 1987, 1989) and from the upper Cenomanian - lower Turonian of the Czech Republic (Löser, 1987; Eliášová, 1992).

Confusaforma carpathica sp.n.
(Figs. 7A-F)

Holotype: UJ 140 P 1, Figs. 7A-F
Type locality: Lubenia near Rzeszów (Skole Unit, Polish Outer Carpathians).
Type level: Štramberk-type limestone (Tithonian - lower Berriasian).
Derivation of name: From the region of origin.
Diagnosis: Diameter of calices (1, 5) 2 - 3 (4) mm. Density of endothecal elements 3 - 4/2 mm.
Material: One fragment of a colony, 7 transverse thin sections, 2 longitudinal thin sections.
Dimensions (in mm): dc – (1, 5) 2 - 3 (4); s – up to 8; e – 3 - 4/2 mm.
Description: Cerioid, in places plocoid colony, irregular ("subhydnophoroidal") in places in its external part (Fig. 7C). Septa arranged irregularly or in bilateral symmetry. Due to poor preservation and the fact that most of the septa are presumably rudimentary, poorly marked on the surface of the "inner wall", it is difficult to determine the number of septa. The invaginations of the wall divide calice like septa into segments. On top of these invaginations, very thin septamay be developed. Budding is by septal division, and presumably by extracalicular budding as well. Rare marginal vesicles were observed (in two calices) (Fig. 7F). As a consequence of the strong development of the marginal zone, an "inner calice" occurs (in two calices) (Fig. 7B). Endotheca is formed by subhorizontal dissepiments and in places, in the external parts of corallites, vesicular dissepiments may occur (Fig. 7D).

Microstructure: Despite the strong recrystallization of the skeleton, vertical trabeculae (80 - 100 μm in diameter) are visible in places, in the centre of the wall (Fig. 7E; for comparison see microstructure of the wall of *Latusastrea exiguis* - Fig. 3C, and *Amphiaulastraea rarauensis* - Fig. 4H).
Remarks: Löser (1987, 1989) and Eliášová (1992) observed extracalicular budding in *C. weyeri*. Because of the bad state of preservation of *C. carpathica* sp.n. it is difficult to distinguish buds originating in the wall from vesicles originating in the wall. The new species differs from *C. weyeri* by having corallites that are two times wider, and less densely distributed endothecal eléments. The occurrence of invaginations of the wall, which like septa divide the calice into open segments, resembles the case of *Hexapetalum pium* described by Eliášová (1976b). In *C. carpathica*, similarly as in *H. pium*, thin septa may be developed on top of these invaginations.
Occurrence: Polish Outer Carpathians (Lubenia near Rzeszów): Tithonian - lower Berriasian.

Genus *Preverastraea* L. Beauvais, 1976
Type species: *Aulastraeopora chelussi* Prever, 1909
Emended diagnosis: Cerioid colony. External and internal wall present. Symmetry radial and/or bilateral. Some septa run from the external wall to the "internal calice". Faces of septa ornamented by sharp, irregularly arranged granules. Lonsdaleoid septa numerous. Budding presumably of the Taschenknospung-type. Two-zonal endotheca: subhorizontal elements in axial part and vesicular ones in peripheral part.
Stratigraphical range: lower Aptian - Cenomanian.
Remarks: Prever (1909) described from Cenomanian (upper Aptian - Albian according to Masse & Morycowa, 1994) of Italy, the genus *Aulastraeopora* with 9 new species, 5 of which are colonial and 4 of which are solitary forms. L. Beauvais (1976) excluded the colonial taxa from this genus, and placed them in a new genus *Preverastraea*. This genus is very similar in morphology to *Amphiaulastraea* (family Amphiastraeidae). The place in which the buds originated (compact wall?, marginal pocket?) is unknown in both cases.

Of the five species described by Prever (1909), only *P. isseli* was recorded from the Cenomanian of Tibet (Liao Wei-Hua & Xia Jin-Bao, 1985), and *P.* cf. *isseli* from the lower Cenomanian of Westphalia (Germany) (Löser, 1994).

Preverastraea tenuiseptata sp.n.
(Figs. 7G-I)

Holotype: UJ 138 P 1, Figs. 7G-I (coll. E. Morycowa).
Type locality: Valea Izvorul Alb (Rarau region, Eastern Romanian Carpathians).
Type level: Urgonian limestones from Valea Izvorul Alb (Barremian - lower Aptian).
Derivation of name: Lat. *tenuis* - thin; from the thin septa.
Diagnosis: Corallites 2 - 5 mm in diameter. About 10 - 12 thin septa. Density of endothecal elements 4 - 6/5 mm. Distinct bilateral symmetry.
Material: One fragment of a colony, 4 horizontal thin sections, 1 longitudinal thin section.
Dimensions (in mm): dk – 3 - 5; s – ca. 10 - 12 (plus rudimentary septa); ds – 0.03 - 0.05; e – 4 - 6/5 mm
Description: Cerioid colony. The inner and outer walls are distinctly marked. The wall separating neighbouring corallites is locally very thin. Some septa run from the corallite wall to the "internal calice". As a rule, the bilateral symmetry is well marked. Septa are thin; on faces of the larger septa sharp granules are visible. These may attain considerable dimensions (Fig. 7G). The largest septum is broad at its base, and its internal margin may often

Fig. 6. *Thecidiosmilia morycowae* sp.n., Jastrzębia, lower Aptian, UJ 139 P/1. **(A)** Vestiges of thick trabeculae of wall and mid-septal zone with minitrabeculae, UJ 29/7, ×100. **(B)** Transverse section of wall; centres of calcification are poorly visible (arrow), UJ 29/7, ×100. **(C)** The biggest septum; growth layers are visible, UJ 29/1, ×60. **(D)** Marginal vesicle (dissepiment), UJ 29/2, ×25. **(E)** Longitudinal section of wall: secondary trabeculae branching from dark intramural zone are visible, UJ 29/2, ×40. **(F)** Transverse section of septum; secondary trabecula is seen, UJ 29/7, ×100. **(G)** Thick-trabeculae (?) in septum and in septal spines, UJ 29/7, ×80. **(H, I)** Mid-septal zone of two septa (H -crossed nicols), UJ 29/7, ×100


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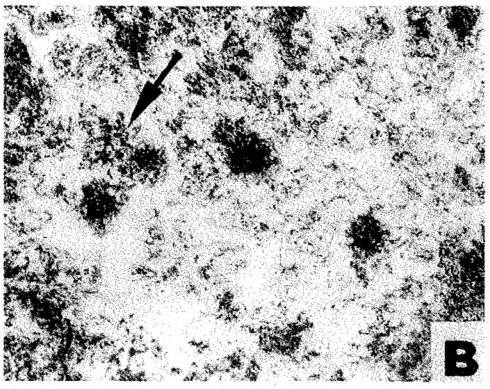
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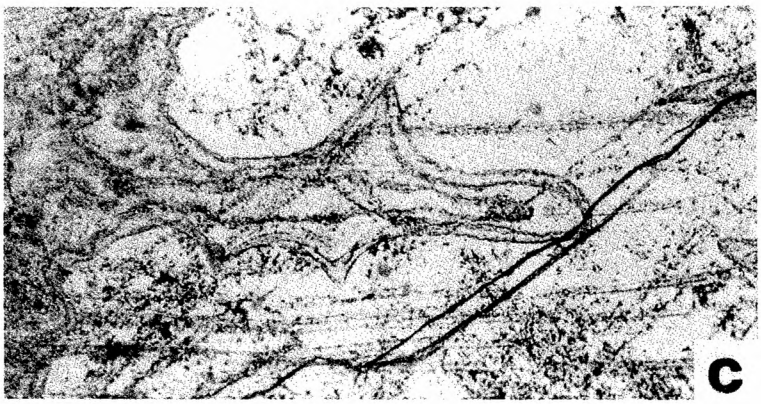
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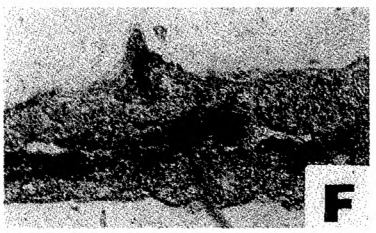
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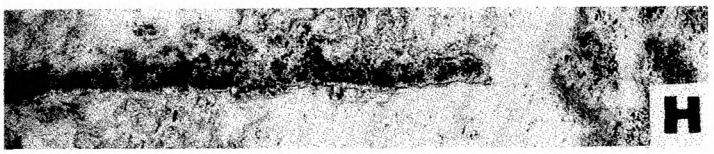
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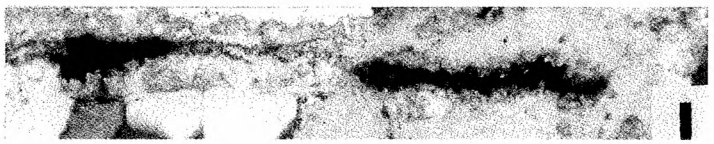
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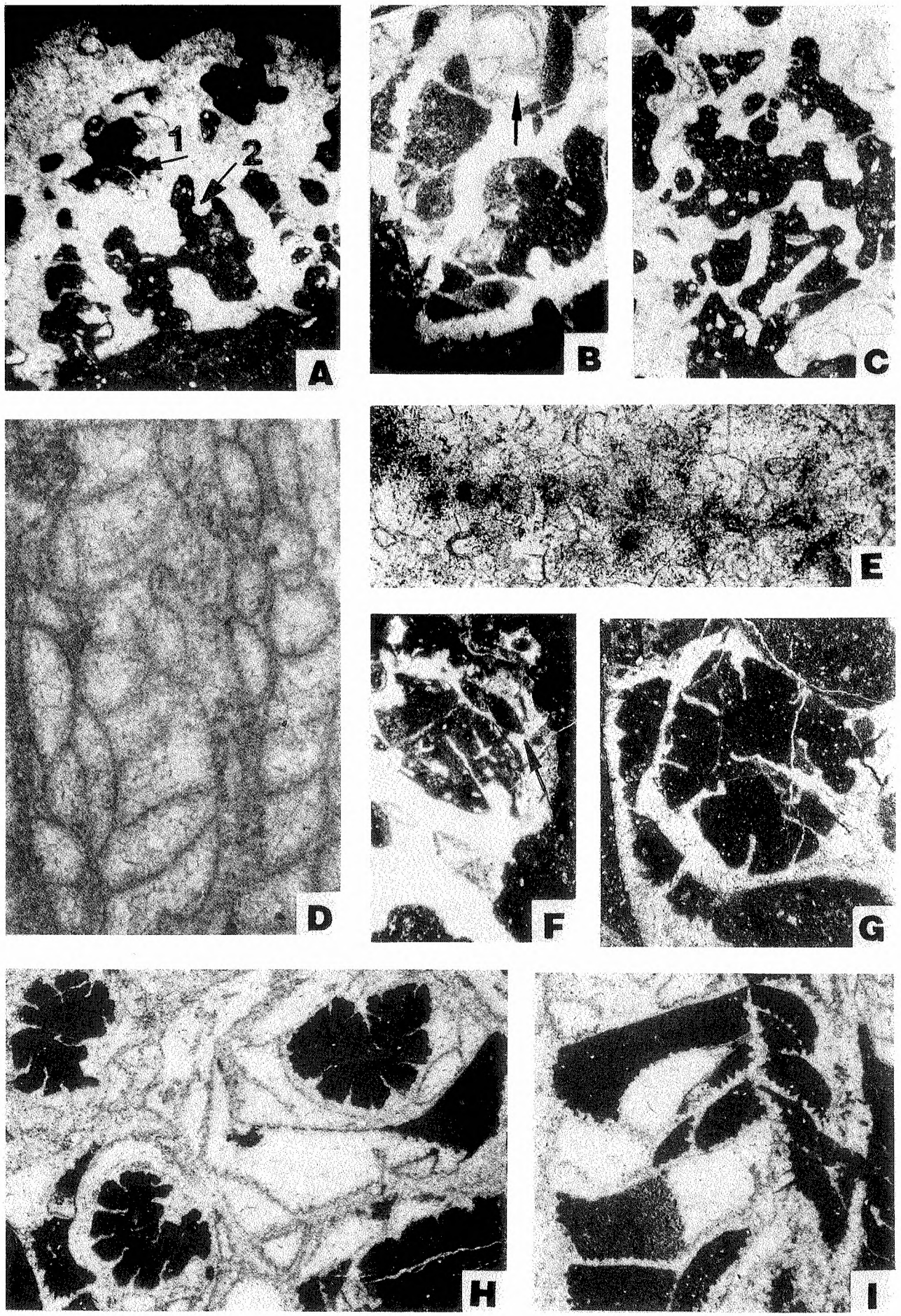
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become thinner (Fig. 7I). Endotheca two-zonal: tabuloid and subhorizontal dissepiments in the axial part, and vesicular ones in the peripheral part. Numerous lonsdaleoid septa are developed on the endothecal elements. The place in which buds originated is unknown; but one may suppose that Taschenknospunk-type budding is present (see remarks on the genus *Preverastraea*).

Remarks: The new species is similar to *P. bohemi* (Prever, 1909) both of the dimensions of corallites and in the number of septa. It possesses, however, much thinner septa, particularly in its inner part. The illustration of L. Beauvais (1976, Pl. V, Fig. 5) reveals that the septa in *P. bohemi* are two or three times broader. Distinctly marked bilateral symmetry differentiates the new species from the remaining species of the genus *Preverastraea*.

Occurrence: Romanian Eastern Carpathians (Valea Izvorul Alb): Barremian - lower Aptian.

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Fig. 7. (A-F) *Confusaforma carpathica* sp.n., Lubenia, Tithonian - lower Berriasian, UJ 140 P/1. **(A)** Invagination of wall (indicated by arrow 2) and well developed thin septum (arrow 1), UJ 30/6, ×8,5. **(B)** "Inner calice" (arrow), UJ 30/5, ×10. **(C)** Irregular shape of colony, UJ 30/1. **(D)** Longitudinal section of endotheca, UJ 30/4, ×12,5. **(E)** Transverse section of wall; vertical trabeculae are visible, UJ 30/7, ×100. **(F)** Marginarium (arrow), UJ 30/5, ×10. **(G-I)** *Preverastraea tenuiseptata* sp.n., Valea Izvorul Alb, Barremian -lower Aptian, UJ 138 P/1. **(G)** Big granules on face of biggest septum, UJ 28/3, ×20. **(H)** Transverse section of corallites, UJ 28/4, ×10. **(I)** Longitudinal section of the endotheca; two zones of endotheca and lonsdaleoid septa are seen, UJ 28/5, ×10

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Streszczenie

MIKROSTRUKTURA I TAKSONOMIA AMPHIASTRAEINA (SCLERACTINIA)

Bogusław Kołodziej

Koralowce z podrzędu Amphiastraeina Alloiteau, 1952 zajmują szczególną pozycję wśród Scleractinia z uwagi na specyficzne cechy (bilateralna symetria, lonsdaleoidalne septa, sposoby pączkowania) zbliżające je do Rugosa. Obecność tych cech tłumaczy się konwergencją, choć nie wykluczano możliwości filogenetycznych relacji Amphiastraeina z Rugosa.

Podrząd Amphiastraeina jest w jurajskich i kredowych zespołach koralowcowych na ogół słabo reprezentowany przez gatunki i rodzaje. Wyjątek stanowią zróżnicowane zespoły amfiastreinów z wapieni sztramberskich (tyton - dolny berias) na Morawach (m.in. Eliášová, 1975, 1976b, 1978) oraz z wapieni egzotykowych typu sztramberskiego z polskich Karpat zewnętrznych.

Ze względu na cechy mikrostrukturalne i morfologiczne podrzędu Heterocoeniina Morycowa, 1964 (a nie jak podawano wcześniej M. Beauvais, 1977), uznano, że jego wyróżnianie jest nieuzasadnione. Podrząd ten w randze obniżonej do poziomu nadrodziny włączono do podrzędu Amphiastraeina.

Mikrostruktura szkieletu dyskutowanych koralowców była przedmiotem wyjątkowo rozbieżnych poglądów. Przedstawioną propozycję klasyfikacji podrzędu Amphiastraeina oparto na nowej interpretacji mikrostruktury. Wykazano wyraźne podobieństwa w mikrostrukturze amfiastreidów i heterocenidów, zaznaczające się szczególnie przy porównaniu cerioidalnych przedstawicieli obu grup (patrz Figs. 3, 4). Układ trabekul jest wówczas następujący: w centrum ściany, wspólnej dla dwóch sąsiednich koralitów, występują wertykalnie ustawione średnie i duże trabekule, od których odchodzą na obie strony ściany trabekule wtórne o przebiegu horyzontalnym lub ukośnym. Uznano, że trabekule te posiadają budowę analogiczną jak opisane przez Morycową (1971) złożone trabekule warstw perytekalnych u *Latusastraea exiguis*. Stosując terminologię według Morycowej i Roniewicz (w druku) ten typ trabekuli to wieloosiowa trabekula główna, od której odchodzą trabekule wtórne. Kontynuacją trabekul ściany są drobne trabekule septalne. W rozwoju szkieletu ściana powstawała wcześniej niż przegrody. Mimo odmiennego poglądu na mikrostrukturę, przedstawiona w pracy interpretacja jest generalnie zbieżna z koncepcją mikrostrukturalnej kontynuacji ściany i septów (Ogilvie, 1897; L. Beauvais, 1974). Do podrzędu Amphiastraeina wprowadzono dwie nadrodziny (Tab. 1): Amphiastraeoidea Ogilvie, 1897, obejmującą rodziny: Amphiastraeidae Ogilvie, 1897, emend. Eliášová, 1975, Donacosmiliidae Krasnov, 1970, emend. Roniewicz, 1976, Carolastraeidae Eliášová, 1976 i Intersmiliidae Melnikova i Roniewicz, 1976 oraz nadrodzinę Heterocoenioidea Oppenheim, 1930 z rodziną Heterocoeniidae Oppenheim, 1930, emend. Obecność dobrze, ale nieregularnie rozwiniętych trabekul wtórnych w elementach radialnych u koralowców z nadrodziny Heterocoenioidea, odzwierciedlona jest przez silną, nieregularną, ostroguzkową ornamentację septalną. U niektórych heterocenidów stwierdzono występowanie pączkowania wewnątrzkielichowego (typu Taschenknospung i podział septalny), którego brak uważano dotychczas za istotną cechę diagnostyczną tej grupy.

W części systematycznej pracy zamieszczono opisy trzech

nowych gatunków należących do słabo znanych rodzajów z rodziny Heterocoeniidae: *Confusaforma carpathica* sp.n. (tyton - dolny berias, Figs. 7A-F) i *Thecidiosmilia morycowae* sp.n. (dolny apt, Figs. 5, 6) z polskich Karpat zewnętrznych (Fig. 1) oraz *Preverastraea tenuiseptata* sp.n. (barrem - dolny apt, Figs. 7G-I) z rumuńskich Karpat wschodnich (Fig. 2).