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PENNULAR AND NON-PENNULAR JURASSIC SCLERACTINIANS — SOME EXAMPLES

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Four Malmian corals of different microstructures have been described: *Thamnasteria concinna*, *Dimorphastraea* sp., *Actinaraeopsis exilis* and *Isastraea* cf. *bernensis*. Aragonite coral tissue being preserved, histological observations have been initiated. Taxonomical value of microstructure and histology, as decisive for supra-generic division, is confirmed. In four discussed species, trabeculae are of a branched morphology and non-sclerodermitic structure. Each species represents a different variety of trabecular histology. A restricted significance of synapticulae for taxonomical purposes is confirmed. Are described vertical adtrabecular bars, a new skeletal element, in *Th. concinna*.

Key words: Scleractinia, morphology, microstructure, histology of skeletal tissue, taxonomy, Oxfordian, Poland.

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INTRODUCTION

Oxfordian corals are scattered as erratic boulders over a vast area S of the Baltic coast (Kegel 1918, Roniewicz *in press* and others). Colonies examined here were collected in western Pomerania, Poland. Abundant and extremely well preserved material allows the re-examination and redescription of the morphology and microstructure of four Jurassic species: *Thamnasteria concinna* (Goldfuss, 1826), *Dimorphastraea* sp., *Actinaraeopsis exilis* Roniewicz, 1968 and *Isastraea* cf. *bernensis* Etallon, 1864. These corals are of special palaeontological interest in having the original aragonitic skeleton preserved.

In describing the skeletal fabric, the following terms are used: *microstructure*, to define the arrangement, inclination and diameter of trabeculae after Alloiteau 1957 (*non* microstructure of Jell and Hill 1974); *histology*, to define the texture of skeletal tissue after the same author; *tufts*, used after Jell 1974, or *fibres*, after

Chevalier 1971, to define the aggregations of primary crystals; *clusters*, after Sorauf 1970 to define spherulitic clusters of crystallites (fasciculi of Wise 1970, 1972; fascicles of fibres of Jell and Hill 1974), *sclerodermite*, after Chevalier 1971, to define spherical aggregations made of isometric crystallites in the centre and radially disposed fibres. The structure of dissepiments in the corals examined follows the pattern typical for recent shallow-water scleractinians and consists of two layers, primary and upper, differing in histology (Wells 1969, Barnes 1970, Sorauf 1970, 1972).

Abbreviations used: c—c distance between centres of neighbouring corallites, cs or s number of costosepta or septa, d diameter of corallite, dt diameter of trabeculae, nt number of trabeculae.

Materials examined are housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated as ZPAL).

I. DESCRIPTION OF SPECIES

Family **Thamnasteriidae** Vaughan et Wells, 1943, emend. Alloiteau, 1952

Genus *Thamnasteria* Lesauvage, 1823

Type species: *Astraea dendroides* Lamouroux, 1821

Corallites of the Jurassic genus *Thamnasteria* are characterized by small diameter and densely packed morphological elements. As a rule, their structure is obliterated. Alteration of the primary skeleton and its secondary recrystallization impeded the proper recognition of corallite morphology and, above all, the microstructure.

Remarks on colonial morphotypic variability within *Th. concinna* have been completed by observations on material from the Oxfordian of the Świętokrzyskie Mts (Holy Cross Mts, Poland) and from Kimmeridgian outcrops in Pomerania, Poland.

Thamnasteria concinna (Goldfuss,1826)
(figs. 1—5; pls. 52—58; pl. 68: 1)

1826. *Astraea concinna* Goldfuss: 64, pl. 22: 1a *non* 1b.
1964. *Stereocoenia concinna* (Goldfuss, 1826); Beauvais: fig. 47B.

1976. *Thamnasteria concinna* (Goldfuss, 1826); Roniewicz: 96, pl. 25: 1*a—d*, 2*ab* (here synonymy).

Material. — Pomeranian erratic boulders, Nos ZPAL HIV/19—25, 33—215, 219—248, 305—358, 360—745.

Measurements (in mm):

colonial type	d	c—c	s	dt
large-calices	2—2,5(2,8)	2,5—3,5	24—28/30; 8/2 mm	100—150(200) μm
small-calices	1,8—2(2,3)	2—3	(16)20—26; 6—8/2 mm	

Colony and corallite morphology

Thamnasterioid colonies develop into two morphotypic growth forms: the first simple and lamellate (common in the European Upper Oxfordian and Kimmeridgian), and the second, composite and multicolumnar (rare in comparison with the first form). Colonies of the lamellate form could attain a considerable diameter or thicken up to submassive shape. A tendency to form secondary generations of lamellate floors outgrowing from the upper colony surface commonly give irregular, multistory colonial masses. In the lamellate morphotype, the calicular surface is flat and gemmation is limited to the periphery of the colony and to the temporary centres of gemmation which give rise to the secondary lamellae. Multicolumnar colony growth starts with the individualization of many growth centres on the surface of the primarily lamellate colony. Continual gemmation in limited centres results in the development of subcolonial units. The units, in the form of columns, are fused with each other by their sides and protrude with their tops on the colony surface in the form of mamillae (Roniewicz *in press*). Mamillae are delimited by furrows or large depressions (fig. 1). In the furrows corallites of two adjacent columns fuse together. The tops of the mamillae are crowded with new individuals, this zone being a zone of intense intercalicular and intracalicular gemmation. New individuals displace the older ones toward the sides. As a result, corallites in columns are arranged in a fan like manner, with individuals in the centre of the column oriented subvertically and others inclined toward the sides. Natural internal cavities are in-
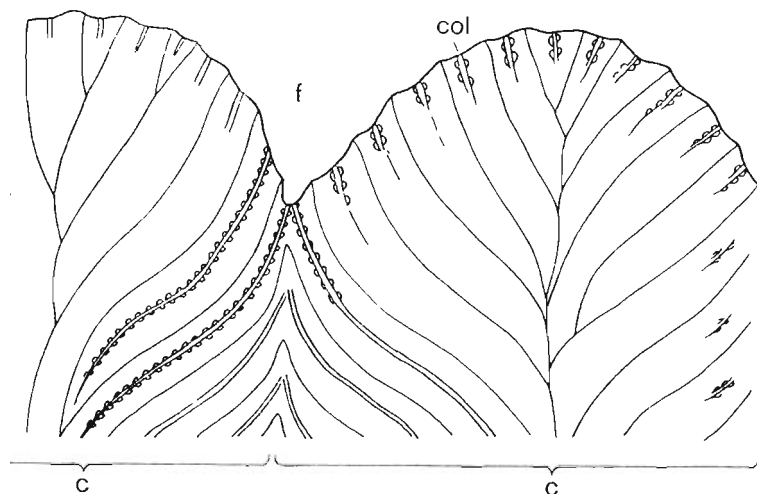

Fig. 1. *Thamnasteria concinna* (Goldfuss). Arrangement of corallites in subcolonies seen in longitudinal section: *c* columns (subcolonies), *f* furrow developed on the contact line between the columns, *col.* columella; an imiginary line delimits the corallites in the thamnasterioid colony which, in reality, is devoid of walls.

corporated into multicolumnar colonies (fig. 2). Their sides and ceiling are epithecate, whilst the floor is formed by part of an ancient calicular surface and is covered with perfectly preserved calices (pl. 56: 1). Cavity formation begins in depressions of the colony surface which become surrounded by rapidly growing areas and are then closed over at higher levels. A thin pellicula overlays the floor (pl. 56: 3ab, 4).
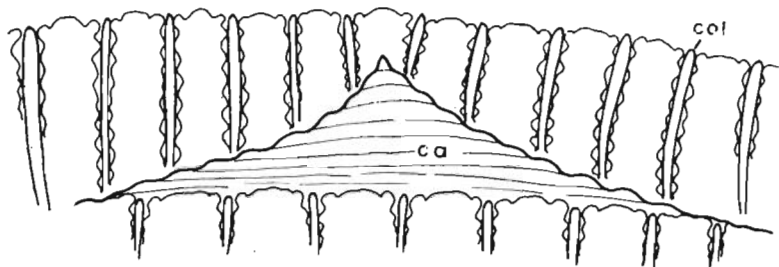

Fig. 2. *Thamnasteria concinna* (Goldfuss). Schematic drawing showing internal cavity, triangular in longitudinal section, incorporated into the corallum (compare pl. 56: 1). *Note* calices on the floor and wrinkled epitheca on the cavity walls; *ca* cavity, *col.* columella.

Corallite diameters vary depending on the colony type. This permits two (extreme) colony types, characterized respectively by small or large calices, to be distinguished.

The skeleton is built of septa, a styliform columella, vertical interseptal elements and dissepiments. Septa are confluent. Short septa anastomose with the flanks of the longer ones. The longest septa reach the columella. Dissepiments are either large and vesicular in the axial and, rarely, in the peripheral region or subtabular — in other parts of the corallum (pl. 56: 5, 6). They form, together with the inner ends of septa and the columella, a large axial structure which can be seen in transverse sections of the colony and on abraded surfaces. Vertical interseptal elements (a.b.) are developed in the extracalicular zone, including the wall region.

Microstructure and histology

Before describing the original skeletal structure a picture of altered structure which one encounters whilst studying fairly well preserved palaeontological material and using thin sections is presented.

Altered skeleton. — Two types of skeletal preservation, which give two different pictures of corallite structure, are observed in *Thamnasteria*. Remarks presented here are based on *Th. concinna* and *Th.* cf. *concinna* colonies from Oxfordian and Kimmeridgian beds of the Świętokrzyskie Mts.

First type (pl. 52: 1a, 1d): septa do not show traces of trabecular structure; septal ornamentation and outline of synapticulae are visible; central columella and "wall structures" quite distinct (= third type of skeleton preservation according to Talbot 1972).

Second type (pl. 52: 1b, 1c): thick trabeculae are revealed and a row of their dark "centres of calcification" indicate the course of septa. In contrast to the first type, ornamentation of septa, interseptal elements and "wall structures" are not visible. Both types of preservation may occur in

one colony. Naturally, neither of these patterns corresponds to the primary structure of the skeleton. What is worse, the first reveals a wall between corallites, whilst the other denies its existence. Neither of them shows the existence of a rich endotheca nor of the vertically oriented interseptal elements.

In such cases, descriptions state that such elements of high taxonomic value as the columella, endotheca or the wall occur in some parts of the colony, but are absent elsewhere in the same colony. This shows how, due to differences in the preservation of palaeontological material, wider or narrower ranges of variability can be attributed to taxa at the generic level. Such variable generic ranges do not occur in Recent corals.

It can be assumed that the two types of skeletal preservation are due to the different ways aragonite can be altered in the early stages of the transformation processes. The differences were emphasised during subsequent stages of recrystallization. In the first type, the whole skeleton in both its trabecular and fibrous parts was altered in the same way. In this case the skeleton resembles the one presented by Sandberg et al. (1973), in which aragonite inclusions within neomorphic calcite crystals are preserved. Through an optical microscope, the skeleton has distinct contours and being optically slightly denser stands out against the cement background (pl. 52: 1d). As to the second type, the trabecular and fibrous parts of skeleton were altered differently. The trabeculae apparently underwent an intense axial chalkification (James 1974, Cuif 1977, Sorauf 1981). Chalkified and unchalkified fragments differ optically: the axes of trabeculae are optically denser whilst the outer parts of the trabeculae and the entire fibrous skeleton ultimately recrystallized into clear calcite crystals. There are no optical differences between the crystals of skeletal calcite and the cement. Therefore, the lateral contours of septa are hardly visible. As a result, through an optical microscope the axes of the trabeculae are visible against a background of clear crystals (pl. 52: 1c).

Attempts at interpretation of recrystallized microstructure. — Having examined the recrystallized topotype material of *Th. lamourouxi* Lesauvage, Alloiteau (1957) stated that in *Thamnasteria* septa are porous with simple, fine (20—22 µ) trabeculae arranged into 1 or 2 rows; trabeculae are composed of sclerodermites of uneven height and the columella is either monotrabecular or composed of 2—3 trabeculae. Alloiteau's drawings show: fig. 146 — a strongly altered example of *Th. lamourouxi*; figs 145 and 147 — idealized drawings of septal flanks of *Th. lamourouxi* and *Th. haueri* de Fromentel, on which he showed round pores and round sections of synapticulae. The ornamentation of the septal flanks may represent a schematic drawing of pennulae (arranged into menianae), which he identified as "sclerodermite heads". Fig. 145 shows a feather-like arrangement of trabeculae in the septum.

The drawing of the microstructure in *Th. concinna* given by Beauvais

(1964: *Stereocoenia concinna*, fig. 47B) shows a monolinear row of thick, scarce trabeculae in the septum. This is an example of type two preservation, and it corresponds to some extent to the situation observed in Pomeranian specimens.

Unaltered skeleton of Pomeranian specimens. — Trabeculae display a continuous growth and sclerodermites are lacking. Fibres are oriented in relation to the trabecular axis (pl. 58: 1a). The diameter of trabeculae is 100—150 (200) μm (measured in the median septal plane). Short, secondary axes, several (generally 4—5) on each level, rhythmically branch from the main trabecular axis. They form pennulae (see Gill 1967, 1968). The tips of the secondary axes are visible on the pennular edge in the form of regular denticles. Pennulae are arranged either opposite or alternately on the septal flanks and some of them fuse laterally (pl. 53: 1, 2, 4, 9; pl. 57: 2; pl. 58: 2; figs 3ABC). The septal surface shows the distal parts of clusters, a coarse micro-ornamentation (pl. 68: 1, compare with pl. 68: 3).

The denticles on the internal edges of the septa (observable only in higher order septa as the first order septa are fused with the columella) resemble pennulae in their ornamentation (pl. 53: 8). They are also of similar size and are arranged at the same intervals as subsequent generations of pennulae. The distal edges of the septa are regularly ornamented with rounded distal trabecular terminations bordered below by pennular collars (pl. 53: 3, 4; fig. 5). The orientation of the trabeculae is distinguished on the septal flank and sutures between them are somewhat depressed (pl. 56: 3a). In a longitudinal median (= radial) section of a septum sutures are well marked (pl. 58: 1a). The only regular discontinuity in the septal blade is a sinus on the distal edge of the 1st order septa (pl. 53: 3, 4). It separates several adaxial trabeculae from the rest of the septal blade. Usually, the sinus becomes filled with skeletal tissue; however, incomplete calcification occasionally leaves lacunae here in the septal blade. Trabeculae are vertical in the peripheral parts and slightly inclined towards the centre in the adaxial parts of the septa. Trabeculae arise by offsetting.

The dissepimental primary layer consists of centripetally growing clusters of small dimensions. It shows growth lines and a central junction line (pl. 53: 1; compare pl. 65: 2ab). The upper, spherulitic layer, of strongly variable thickness, is composed of interferring clusters growing upwards from the primary layer (fig. 3A). The upper layer, at least in thick dissepiments, is contiguous with the tissue of vertical skeletal elements, i.e. of the septa and vertical interseptal elements (fig. 3; pl. 57: 3).

A particular skeletal element is developed in the natural cavities. It is a delicate pellicula closing the free space between distal terminations of skeletal parts of calices crowded on the cavity floor (pl. 56: 3ab, 4). Morphologically, the pellicula appears as a continuation of the epithecal tissue which covers the cavern wall. It must have originated, however, in a quite different way as its mode of growth shows analogies to that of the dis-

sepimental primary layer, whilst the epithecal mode of growth has its own laws (Barnes 1972, Sorauf 1972). The growth of the pellicula extends from all protruding calicular elements, radially, and centripetally into the free space. The pellicula surface shows very delicate growth wrinkles (pl. 56: 3b). In its centripetal mode of growth it resembles the primary dissepimental layer. But, in contrast to the latter, no fibres are seen on its surface. Its microstructure has not yet been observed. The only traces of its tissue organization are delicate micro-ridges on its surface, perpendicular to the growth wrinkles and resembling the epithecal surface structures (pl. 56: 2, 3b). Its centripetal growth and the overlapping of skeletal parts suggest that precipitation might have taken place at a considerable distance from the living tissue, in a liquid which covered the naked skeleton.

Vertical interseptal elements — adtrabecular bars (a.b.) — which follow the course of trabeculae (pl. 54: 1ab, 2ab; pl. 56: 5, 6; pl. 55: 2, 3—b; bars figs. 4 and 5) and are attached to them (as opposed to fulturae in *Fungia* and *Cycloseris:* Gill 1981), are a significant skeletal component. A.b. touch the opposite septum with a suture (pl. 54: 3). Generally, the bars are vertically continuous. The growth zone of a bar is situated below the distal edge of a septum (pl. 55: 2, 3); the distal extremity of the bar is in form of a sharp ridge. A.b.overlap pennulae. In cross section, a.b. show their complex structure — with diverging clusters from their broad bases on the trabecular side. In some places, the fibrous tissue is organized into clusters having a short axis. The axis appears in cross-section as an eccentric dark patch — "a center of calcification" — adhering to the trabecula. The a.b. tissue is contiguous with the thickened spherulitic dissepimental layer. A.b. take part in the formation of a thick false wall: they form a ring at the periphery of the corallite (pl. 53: 6). The ring appears in cross-section as a thick compact wall. In corallite morphology, however, it is marked as a faint element on the bottom of the shallow calice and not as a partition between the corallites. A.b. are numerous and regularly distributed starting from the wall region outwards. Usually, they divide the interseptal space and reduce it to narrow, regularly distributed "hollows". The possibility of their being developed along the inner septal edge is not excluded.

The columella is trabecular in structure. Its central, primary part which fills the axial calicular cavity, seems to be monotrabecular (pl. 53: 3, 6). At the bottom of the calice, the columella fuses with periaxial trabeculae of the 1st order septa and convex axial dissepiments (pl. 56: 6). Thus, a complex axial structure develops which in cross section takes up most of the corallite diameter. At times, the lacunae — spaces cut off by incorporated vesicular dissepiments — are visible in cross section, and in vertical section (pl. 56: 5 — 1 lacunae). The columellar trabecula is branched like the other trabeculae.
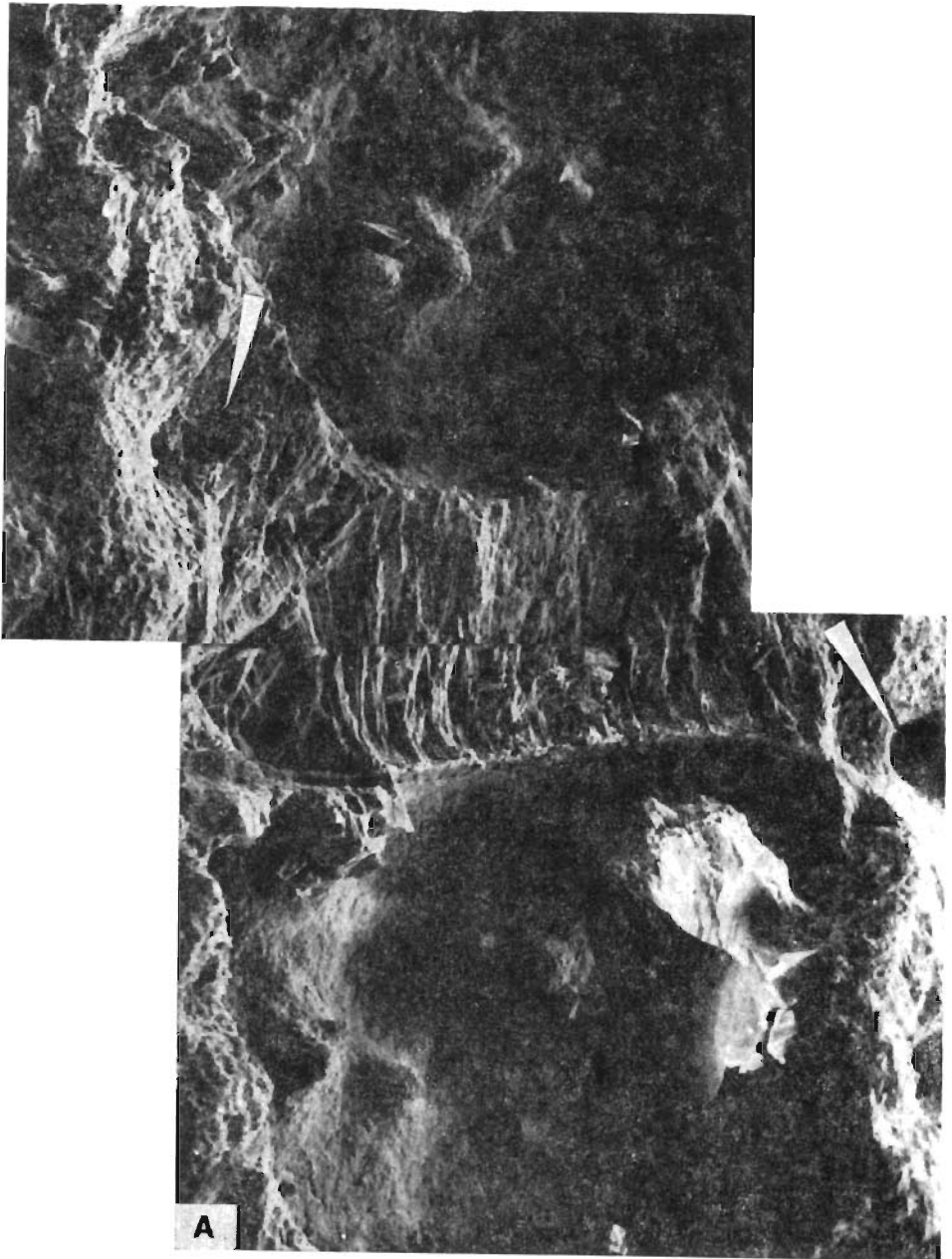
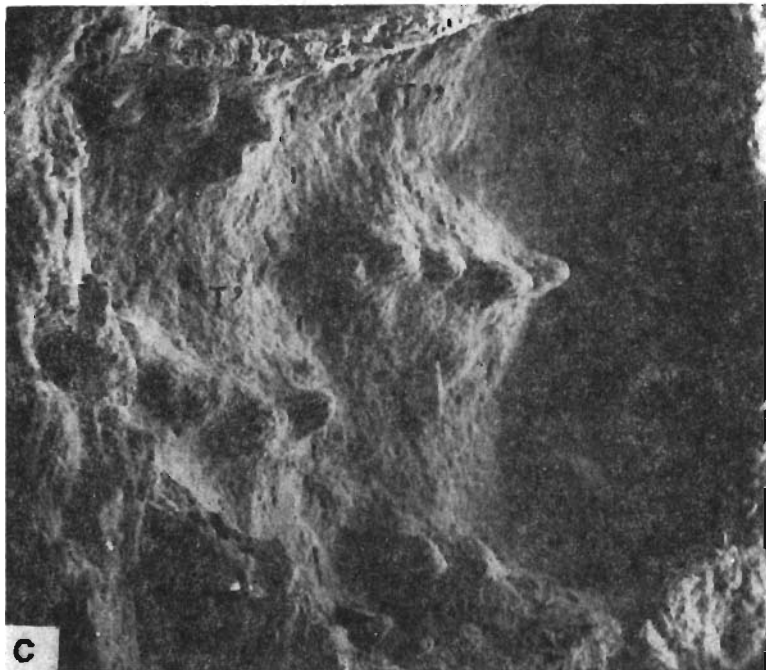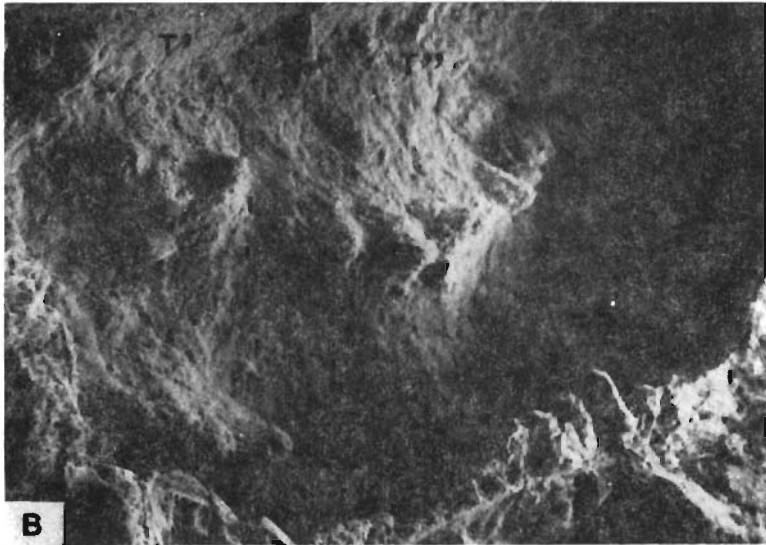Fig. 3. *Thamnasteria concinna* (Goldfuss). Specimen ZPAL HIV/33: septal face with pennulae, dissepiments and adtrabecular bars. Trabecular ornamentation is irregular, lateral trabecular axes appearing in variable number from two (A: lower left corner) to six (B: at the middle). Pennulae of neighbouring trabeculae (T' and T'') can be disposed on the same level (B) or may alternate in position (C). Dissepiments

are of variable thickness: compare a thick dissepiment in *A* and thin ones in *B* or *C*. Contact surface between adtrabecular bars and adjacent septum shows deep imprints of pennulae (arrows). Dissepimental upper layer seems to pass without interruption into the adtrabecular bar tissue (*A*: at the middle and left). Interrupted line (*B*, *C*) marks a boundary between trabeculae *T'* and *T''*. ×300.

The fibres of the trabeculae reveal subsequent stages of growth seen as growth lines in cross section. The abundant growth of skeletal tissue causes not only the thickening of trabeculae but, above all, it promotes the widening of adtrabecular bars and the thickening of the dissepiments,
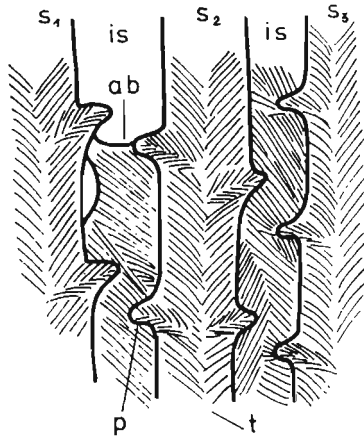

Fig. 4. *Thamnasteria concinna* (Goldfuss). Longitudinal section perpendicular to the septal blades. Schematic drawing showing septa/adtrabecular bar relationships as seen in thin section: *ab* adtrabecular bar tissue with its fibres going from the whole trabecular surface and oriented upward (compare with fibre orientation observed in different plane of section — pl. 58: *1b*; text-fig. 5), *is* interseptal space, S_{1-3} three septa, each of them showing septal trabecula in section with its main axis in the middle and secondary axes branching off and forming pennulae (*p*) on the septal (sclerodermites are lacking).

Fig. 5. *Thamnasteria concinna* (Goldfuss). Reconstruction of the distal part of septum showing septum/adtrabecular bar relationships, side view: *t* trabeculae delimited with intertrabecular boundaries and ornamented with *p* pennulae; longitudinal section of trabecula perpendicular to the septal blade at right, *ab* adtrabecular bar contact surface between its tissue and a neighbouring septum, fan-like disposition of fibres is seen as opposed to that observed in the plane longitudinal and perpendicular to the septal blade (compare fig. 4), p_1 imprints of pennulae, *dpl* dissepimental primary layer, *d* two-layered dissepiment.

i.e. the fibrous skeleton. The growth of skeletal tissue may lead to the filling up of interseptal spaces. Occasionally, as a result of weathering, the outer skeletal growth layers flake off and the primary septal face, ornamented with pennulae, is exposed (pl. 55: 2—lower right). In the flaked off skeletal layer, as in a mould, depressions made by distal edges of pennulae are visible (pl. 54: 4, 5; pl. 55: 1a, 2; fig. 3*A*).

Epitheca is present. Usually it is well preserved in the wall and ceiling regions of natural cavities (pl. 56: 1). It is thin and shows distinct growth lines (pl. 56: 2). Unfortunately, no satisfactory observations of its microscopic structure could be obtained (compare with the epitheca in cavities in colonies of *Actinaraeopsis exilis*, p. 172). On its eroded surface very delicate ridges perpendicular to the growth wrinkles, are present (pl. 56: 2).

Discussion. — The differences in opinion concerning the microstructure and architecture of the *Thamnasteria* skeleton between Alloiteau (1957) and the present author arise from the following facts: Alloiteau assumed that he observed traces of real microstructure and not, as it was in reality, a completely altered skeleton. The assumed presence of synapticulae, circular in cross-section, and regular pores in *Thamnasteria* arose from a misinterpretation of cross- sections and from the observation of the weathered colony surface (compare pl. 53: 6, 7). Alloiteau most probably did not have an opportunity to observe septal flanks, on which the details of the structure could be established. Thus, the idealized and schematic drawings presented by him can hardly be regarded as documentation. The diagnosis given by this author needs emendation.

REDEFINITION OF THE GENUS *THAMNASTERIA* LESAUVAGE, 1823

The holotype of the type species, *Thamnasteria dendroidea* (Lamouroux, 1821) from the Sequanian of Meuse, has not been preserved. The same is true of the holotype of *Th. lamourouxi* Lesauvage, 1823, from the Oxfordian of the Caen vicinity, the synonyme of *Th. dendroidea* (cf. Alloiteau 1957).

The diagnosis of *Thamnasteria* given below is based on *Thamnasteria concinna* (Goldfuss 1826), a species from the *dendroidea* group. The differences between *Th. concinna* and *Th. dendroidea* can be reduced to a dissimilarity in the colony growth form.

Emended diagnosis. — The diameters of corallites are small (a couple of mm). Radial elements are compact, confluent and anastomosing. Adaxial part of the distal edges of the 1st order septa developed as a paliform tooth. Ornamentation of septal faces is pennular. Pennulae are developed as horizontal plates with serrated borders. Internal septal edge regularly denticulate. Ornamentation of the distal edge in the form of rounded denticles bordered by a pennular collar. The vertical interseptal elements are

developed alongside trabeculae. Columella primarily monotrabecular, secondarily fused with trabeculae of the internal septal edge and with dissepiments. Dissepiments vesicular in the centre and on the periphery of corallites and subtabular in other parts. The calices are either densely packed or separated by peritheca. Epitheca developed. Gemmation intra- and extratentacular (intercalicular and peripheral). Colonies lamellate, multicolumnar or branched.

Species assigned: Th. dendroidea (Lamouroux, 1821) (= Th. lamourouxi Lesauvage, 1823), Th. concinna (Goldfuss, 1826), Th. gracilis (Goldfuss, 1826), Th. loryi M. Edwards et Haime, 1951, Th. jaccardi Koby, 1887, Th. valfinnensis Koby, 1887, Th. nicoletti Koby, 1887.

Remarks. — The minute size of the corallites is mentioned as one of the generic features. This is justified by the results of observations of Jurassic corals described as Thamnasteria of which only the group characterized by small corallites (exemplified by Th. concinna, Th. gracilis and Th. dendroidea) appears to have the set of features enumerated in the diagnosis. Corals with corallites of larger diameter represent other genera, most frequently Thamnoseris Etallon, 1854, Fungiastraea Alloiteau, 1957 or Kobyastraea Roniewicz, 1968.

Family **Latomeandridae** Alloiteau, 1952

Genus *Dimorphastraea* d'Orbingy, 1850

Type species: D. grandiflora Fromentel, 1862

The morphological and microstructural features of *Dimorphastraea* were discussed by Alloiteau (1957). Based on a re-examination of the type material (specimens from the collections of d'Orbigny and Fromentel, Hauterivian of St Dizier) and newly collected specimens (Hauterivian, Morancourt), he enumerated, among others, the following generic characters: poorly porous septa, distal edge ornamented with "thick pearls" rectangular in shape, flanks provided with granules or "bourrellets" which can fuse laterally to form horizontal ridges, synapticulae simple and compound, endotheca of scattered dissepiments and parietal columella. Observations on the microstructure were based on thin sections cut from specimens other than the type material. According to Alloiteau, centres of calcification in the septa are numerous, separate, gathered irregularly, distributed in the midline or near the septal flanks; trabeculae are simple and compound.

I had an opportunity to examine some Malmian dimorphastreas in thin section (Roniewicz 1976). In *Dimorphastraea*, the corallites are large and the septa are built of proportionally thick trabeculae, although in relation to septal dimensions they are not especially thick. Owing to the considerable size of the trabeculae and their distinct ornamentation, the main

features of the microstructure are recognizeable even in considerably altered skeletons. In the Malmian dimorphastreids, in transverse sections, septal microstructure is visible in the form of large, dark vestiges of trabeculae spaced regularly in the midline of septa. Pennulae observed in longitudinal and tangential sections are large, semilunar and fused laterally into menianae; low, large dissepiments paralleling menianae are a striking morphological feature; columella is parietal, septal porosity is irregular and scattered; synapticulae are lacking. The observations are in agreement with those made on the unaltered skeleton of Pomeranian corals. At the same time, the picture obtained from an examination of the entire Jurassic material doesn't agree with that given by Alloiteau concerning the presence of synapticulae and some statements on the histology of trabeculae (irregular distribution of centres of calcification in the septa, two categories of trabeculae).

Dimorphastraea sp.
(pls. 59, 60, 61)

Material consists of one specimen No. ZPAL HIV/27, a fragment of a colony from Resko.

Morphological features

Septa are confluent. Their axial edges are dissociated into trabeculae. In 1st order septa, trabeculae on the axial edge project into the axial cavity to form a spongy, loose, parietal columella. Septal flanks are ornamented with pennulae which are dorsally slightly concave, with semilunar distal edges slightly inclined upwards. On the trabecula, they are situated opposite or alternately to each other (pl. 60: 2). Pennulae fuse laterally into long menianae running subhorizontally. In menianae, pennular edges retain their individuality. Dissepiments are very large, rather flat and paralleling menianae (pl. 59: 4). Dissepiments can reach a considerable thickness.

Microstructure and histology

Trabeculae are 250—300 μm thick (measured in the median plane of the septum), composed of very long fibres. The intertrabecular sutures are well marked (pl. 59: 3; pl. 61: 1). Trabeculae display continuous growth, and no sclerodermitic structure. Fibres are arranged in relation to trabecular axes. Histology of trabeculae shows clusters growing out from the central area, directed radially and upwards. Compound character of trabecular histology is caused by irregularly inserted additional clusters which originate some distance from the axial area (pl. 61: 1). Clusters and sets of clusters display a common growth direction and compete for space with other sets. Some clusters are sharply delimited (pl. 61: 2). From the main trabecular axis secondary branches diverage laterally at regular intervals, several on the same level (pl. 60: 1). Each of them is composed

of fibres radially distributed in relation to the well defined axes. Those neighbouring branches on the same level, fuse with each other to form pennulae. Their tips are seen at the pennular edge as regularly distributed granules (pl. 59: 1, 2). Trabeculae are subvertical at the periphery and inclined strongly toward the corallite axis at the centre.

The histology of the dissepiments, although typical for shallow water corals shows a trait typical of ahermatypic corals: poor clustering of the minute crystallites of the primary layer (pl. 59: 5b; compare with Sorauf and Jell 1977). The upper, spherulitic layer displays variable and often considerable thickness (pl. 60: 3). No distinct discontinuity is seen between crystal growth direction of this layer and the septal tissue.

Discussion. — Discrepancies between Alloiteau's definition of the genus and my observations can be explained as a result of the interpretation of differently preserved material. The drawing of a transverse section of *D. grandiflora* specimen (Alloiteau 1957: fig. 167) seems to show a deeply altered skeleton. In such a case a detailed discussion of histological features included in the generic diagnosis is hardly possible without examination of that material. However, vestiges of histological traits seen on the drawing have, in general, counterparts in the histology presented here.

As to the septal porosity, although in *Dimorphastraea* sp. septa are compact, in other Jurassic species pores can be developed. In *Dimorphastraea* sp. a tendency for the skeleton to thicken might obliterate porosity.

The question of the development of synapticulae needs discussion. It can be observed in Scleractinia that, considering the three interseptal elements, i.e. synapticulae, dissepiments and menianae, the intensive development of any pair of these renders unnecessary the development of the third. Narrow interseptal spaces in *Dimorphastraea* are so tightly packed with thick dissepiments and menianae, that there is no architectural need for an additional interseptal element — synapticulae. Synapticulae in the *Dimorphastraea* skeleton seem to be functionally unjustified and, according to observations on *Dimorphastraea* sp. they did not occur in the genus.

A knowledge of the microstructure of *Dimorphastraea* is important for understanding the structure in the related genus, *Fungiastraea* Alloiteau. Well preserved specimens of the Carpathian fungiastreids from the Lower Cretaceous (Morycowa 1971: fig. 15; pl. 22: 3b, 4b) are in their microstructure wholly comparable with the Pomeranian specimen of *Dimorphastraea* sp., with their thick trabeculae formed of very long fibres and with distinct intertrabecular sutures. The Pomeranian specimen confirms a slightly different appearance of the endotheca in the two genera, in *Dimorphastraea* dissepiments being large and rather flat whilst in *Fungiastraea* they display a tendency towards the development of fine and vesicular forms. Septal flank ornamentation in the Jurassic species of *Fungiastraea* strongly resembles that of the *Dimorphastraea* semilunar pennulae, which can be observed even in longitudinal sections of very

poorly preserved specimens (Roniewicz 1976: pl. 9: 2*b*,*c*). Pennulae in both genera resemble in their shape microsolenid pennulae (compare Gill 1967, 1968). At the same time, they differ from the *Thamnasteria*-type pennulae which are not semilunar, nor oriented with their edges upwards, but horizontal. The newly obtained data supports previous conclusions (Roniewicz 1976) concerning the systematics of both genera based on morphological data, *i.e.* their transfer from the family Thamnasteriidae to the family Latomeandridae.

Family **Haplaraeidae** Vaughan et Wells, 1945

Genus *Actinaraeopsis* Roniewicz, 1968, emend. Roniewicz 1976

Type species: *A. araneola* Roniewicz, 1968

The diagnosis of the genus *Actinaraeopsis* was based on the features of the type specimen and *A. exilis*, both described from the Oxfordian of the Świętokrzyskie Mts (Holy Cross Mts). The type specimens of these species have strongly porous skeletons. Specimens of *A. araneola* from Dobrogea (Romania, Roniewicz 1976) and specimens of *A. exilis* here described have, however, rather compact septa. In Pomeranian colonies differences are observed in porosity between different parts of the colony (pl. 63: 1*a*, 2). Septal blades are of uneven compactness: irregularly porous portions alternate with the compact areas (sediment penetrating the colony filled the pores and enchanced the effect of porosity). All this indicates that in this genus, skeletogenetical processes were unstable.

Actinaraeopsis exilis Roniewicz, 1968
(pls. 62, 63, 64, 65, 66: 1*ab*, 4)

1968. *Actinaraeopsis exilis* Roniewicz: 307, pl. 1: 1, 2.
  Material. — Sixty-seven colonies from Ostromice and the Baltic coast at Międzyzdroje. Nos. ZPAL HIV/216—218; 249—302, 346—352, 358—360, 748.
  Measurements (in mm):

c—c	cs	dt
2—3	26—32	100—150 μm
	20—22/5 mm	

Morphology

  Colonies massive. Calices deep (pl. 63: 1*b*). Columella on the calicular floor, in the form of a single or multi-peaked granule. Septa of the 1st order reach the columella with their trabecular projections. Septal distal edge with uneven, ornamented denticles (pl. 63: 3*ab*). Some of them strongly thickened and irregularly distributed, giving a distinctive appearance to the calicular surface of the colony (pl. 63: 3*b*). Tips of trabeculae in the form of regular denticulations are observed on the inner edge of the higher order septa (pl. 63: 1*b*). The denticles are terminally flattened and

provided with lateral spines. In the calice, at the inner septal edge, denticles can develop into long trabecular projections. Septal faces ornamented with pointed granules (pl. 63: 1b, pl. 64: 1). Synapticulae thick in relation to the septal thickness and rather regularly distributed over the whole septal surface (pl. 63: 1a, 2; pl. 64: 1, 2). The appearance and arrangement of synapticulae resemble those in *Siderastraea* (pl. 64: 6). Dissepiments are generally very thin, but in some specimens (pl. 63: 1a, 2; pl. 64: 1, 3) can thicken up to 0.1 mm. Generally tabular and wide in relation to corallite diameters, they can develop into vesicular form in the intercalicular zone. Epitheca can be observed in the ceiling areas of the natural cavities on the sides of colonies analogous to cavities developed in *Thamnasteria concinna*, p. 167. A pellicula lines the bottom of the depression, enclosing free space between the distal elements of corallite that pave the bottom.

Microstructure and histology

The trabeculae are of variable thickness. The diameter of trabeculae (measured in the median plane of the septum) amounts to 150 μm. The contours of the trabeculae can be observed on the flanks of thin septa. Trabeculae appear on the septal faces in the form of uneven ridges (pl. 63: 1a, left lower corner). The main trabecular axis is continuous; sclerodermites are lacking. Secondary trabecular axes appear laterally at rather irregular intervals and emerge as lateral spines on the septal flanks. A dark axial portion to the lateral axes is discernible in sections (pl. 62: 4). In fact, spines of two sizes are observed near the distal edge: sharp, smaller, ornamental ones and larger spines developing into synapticulae (pl. 64: 2), although it is not clear if both types are of the same, trabecular nature. Trabeculae are built of very long thin, fibres (pl. 62: 2—4). Fibres are fused into clusters (pl. 66: 3) which are distinctly individualized (? pseudocrystals of Sorauf 1970). The distribution of trabeculae is fan-shaped. They appear by offsetting: in the septal plane, the trabeculae branch at irregular intervals into 2—4 new trabeculae. Trabeculae abut lengthwise or only at the points of origin of lateral axes, where the trabecular diameter is always greater (pl. 64: 3). Synapticulae oval in cross-section, having an axis of their own (see pl. 62: 3, 4; pl. 64: 4, 5). The axis is apparently eccentric in position being situated below centre (pl. 62: 3; pl. 64: 4). Synapticulae may develop from one, or from two opposite spines which meet each other. The synapticular suture lies adjacent to the septal face or it may cut the synapticula (pl. 62: 2, 3). The dissepimental primary layer shows bundles of fibres arranged into big clusters (pl. 65: 2ab). The junction line is well marked. Broken sections show that the primary layer is formed of one row of clustered elements with cone-shaped proximal parts (pl. 65: 4). In general, its thin fibres diverge from the mid-plane either towards the upper or the lower surface. The upper dissepimental layer is composed of thick pallisade clusters (pl. 65: 3). Its tissue is in histologic continuity with the adjoining septa and synapticulae (pl. 65: 1).

Epitheca from walls of cavities displays horizontal growth wrinkles. In longitudinal broken section it reveals its fibrous structure and well mar-

ked discontinuous growth of crystallites (pl. 66: 1*ab*). Crystallite arangement confirms Sourauf's opinion (1972) concerning growth direction of epithecal tissue from the external surface inward.

Family **Isastraeidae** Koby 1889, emend. Alloiteau, 1952

Genus *Isastraea* Milne Edwards et Haime, 1851

Type species: *Astrea helianthoides* (Goldfuss, 1826).

Vestiges of microstructure in the altered skeleton of *Isastraea* are to a great extent distinguishable (resembling the second type of skeletal preservation in *Th. concinna*, p. 160). Septa in transverse section display dark bars perpendicular to the septal blade, which are situated in the position of carinae. In some parts, a dark midline is visible (pl. 69: 1*b*, *c*; fig. 9). The bars can split into several discrete points. Pelletier (1950), for the first time, analyzed and interpreted the structure of isastreid trabeculae. He recognized dark points as centres of calcification and their number as a diagnostic feature at specific level. Roniewicz (1976: 30) drew attention to the similarity between the microstructures of *Isastraea* and *Montlivaltia*.

Isastraea cf. *bernensis* Etallon, 1864
(figs. 6—11; pl. 66: 4; pls. 67, 68, 69)

Material. — Fragments of large colonies, No ZPAL HIV/303, 304, and a thin lamellar colony No. ZPAL HIV/298 in an association of colonies of *A. exilis* and *Th. concinna* overgrowing each other; Ostromice locality.

Measurements (in mm):

d	c—c	s	nt	dt
		50—60	ca. 10/2 mm	250—300 (450) µ
6.5—8	6—9	12/5 mm		

Morphology

Gemmation intratentacular with lamellar linkages. Corallites polygonal in cross-section, corners rounded (fig. 6). Septa thin. Carinae weakly developed. Internal edges of the septa ornamented with irregular denticles. Denticles of higher order septa are short, of uneven surface and sometimes bifurcated. Denticles of 1st order septa initiate the development of a few trabecular processes which penetrate into the narrow axial cavity to form a spongy, rather weak columella. Trabecular processes are subvertical, relatively thick, free or partially fused, here and there paralleling septa. Lateral outgrowths of the inner septal edges close to the centre initiate synapticulae formation. Generally, one row of synapticulae encircles the axial cavity. Synapticulae on the septal blade itself are rarely developed. External septal edges provided with synapticular expansions of peripheral trabeculae with which septa of the neighbouring corallites fuse to form a wall (figs. 7—9; pl. 67: 2*a*; pl. 68: 2*ab*). The expansions do not lie within the septal plane but grow out at an angle of up to 90°. As a result, the wall is zigzag when observed in cross-section. In longitudinal
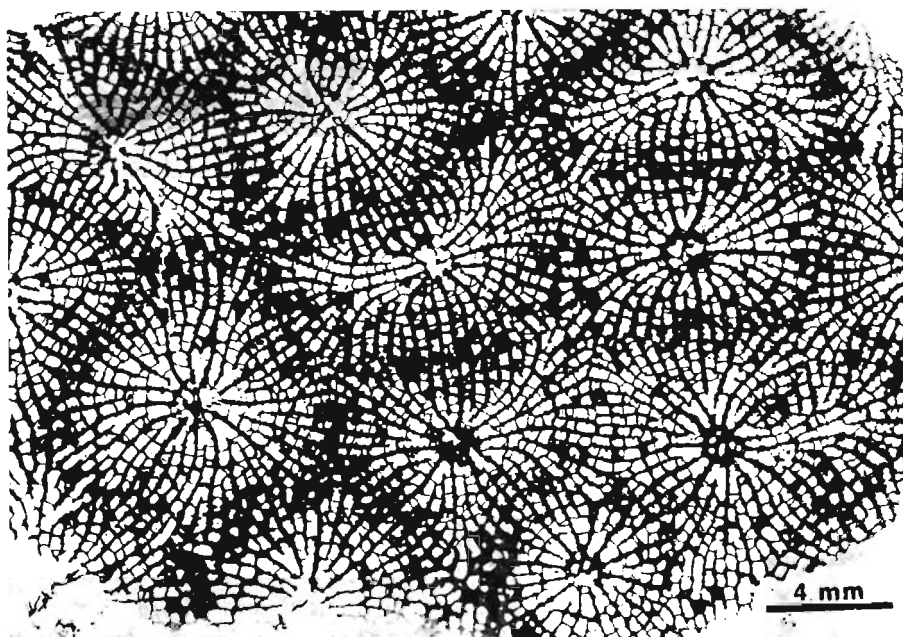
Fig. 6. *Isastraea* cf. *bernensis* Etallon. Specimen ZPAL HIV/303. Transverse section, poorly developed columella is seen.

section the wall is wavy and often discontinuous (fig. 8; pl. 67: 2). When the septa face each other with their external edges, the latter accrete, the septa become subconfluent, and a wall does not develop. Where the wall is absent, the endotheca of adjacent corallites fuses freely and joined dissepiments function as paratheca. Dissepiments are small, vesicular and steeply inclined peripherally and large, subhorizontal in the corallite axial area.

Microstructure and histology

Septa are built of relatively few, large trabeculae, generally 200—300 µm thick (measured in the septal median plane). Intertrabecular sutures well marked (figs. 9—11; pl. 69: 1a, 2). The trabeculae are arranged in series. At the external edge they are subvertical becoming gradually inclined adaxially approaching the internal edge. Trabeculae display continuous growth and no sclerodermitic structure is visible (figs. 10, 11; pl. 67: 1; pl. 69: 2). They are long and very variable in diameter. In longitudinal radial section of septa, central trabecular axes are visible (figs. 10, 11; pl. 67: 1; pl. 69: 2). Fibres are long. There is a remarkable tendency to clustering in the trabecular tissue. Some clusters become further independent branches with their own axes (pl. 67: 1). The main trabecular axis gives rise secondary axes in two planes perpendicular to each other: (1) in the plane normal to the septal plane, resulting in the formation lateral branches at very regular intervals. The branches are seen on the septal flanks as granular ornamentation. The granules are protruding and sharp (pl. 68: 2a,

Fig. 7. *Isastraea* cf. *bernensis* Etallon. Specimen **ZPAL HIV/303**. *Left*: schematic drawing of two subconfluent septa Nos 1 and 2 and a wall formed by septum No. 1, longitudinal broken section; a fragment presented in magnification is marked. *Middle*: The fragment of a wall in magnification (see also pl. 68: 2*ab*). Elements of the wall are well individualized, those having been fused with the adjacent septum are broken, one underdeveloped is not damaged. *Right*: wall structure in longitudinal thin section parallel to the septal blade. Scale bars are **250** μm.

3; pl. 69: 1a,b,c). The trabecular granulation fuses vertically to form a variably expressed carina (compare carinae in *Montlivaltia*, Gill et Lafuste 1971: fig. 19); (2) in the septal plane itself. Clusters lying in the midline individualize and develop as weak branches provided with their own axes. In transverse section, they appear as dark points or a line situated between the main axes of trabeculae (fig. 9; pl. 69: 1b,c). The midline branches of neighbouring trabeculae meet and the discontinuity between them is well expressed (pl. 69: 1b,c). Some of them give rise to new trabeculae (pl. 69: 2 and fig. 11).

The micro-ornamentation of the septal surface appears as minute granules (pl. 68: 2b, 3) and relatively large, deep depressions (pl. 68: 3). Granules represent the tips of trabecular clusters (pl. 66: 4). The depressions can be interpreted as places of attachment of the soft tissue (compare Wise 1970, Sorauf 1981). In this respect, the septal surface resembles this surface in *Siderastraea*. One can agree here with Sorauf (1972) and Sorauf and Podoff (1977) that the micro-ornamentation of the septal surface has some taxonomic importance. No similar micro-ornamentation is observed in the other coral described here.

Synapticulae differ in origin and structure (fig. 9). Those from the inner edge and septal flanks are formed from two granules, *i.e.* lateral trabecular branches which meet each other in the interseptal space. They are circular in section, with an axis subperpendicular to the septal blade. The synapticulae from the external edge, *i.e.* expansions of the peripheral
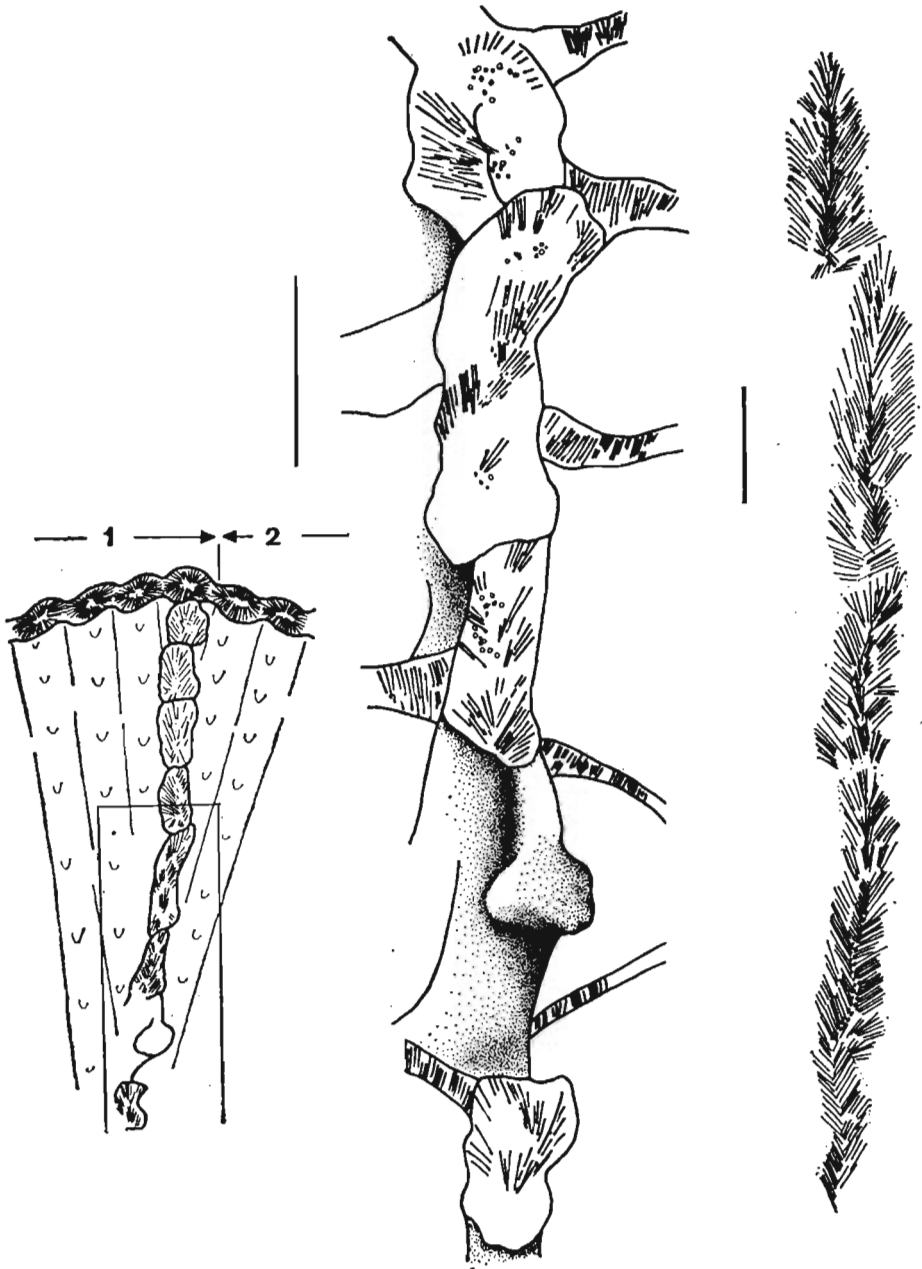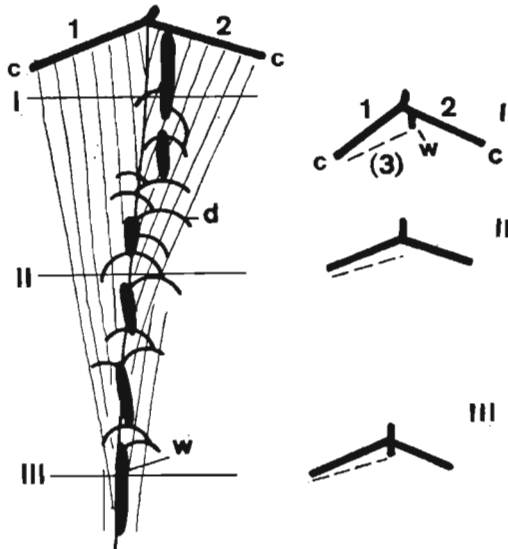

Fig. 8. *Isastraea* cf. *bernensis* Etallon. Specimen ZPAL HIV/304. No scale. Schematic drawing of two subconfluent septa Nos 1 and 2 and a wall formed by No. 3 (nonpreserved and marked with an interrupted line), in longitudinal section; c centrum, d dissepiment, w wall 1, 2, (3) septa, I—III planes of sections, showing variable development and position of the wall in cross-sections.
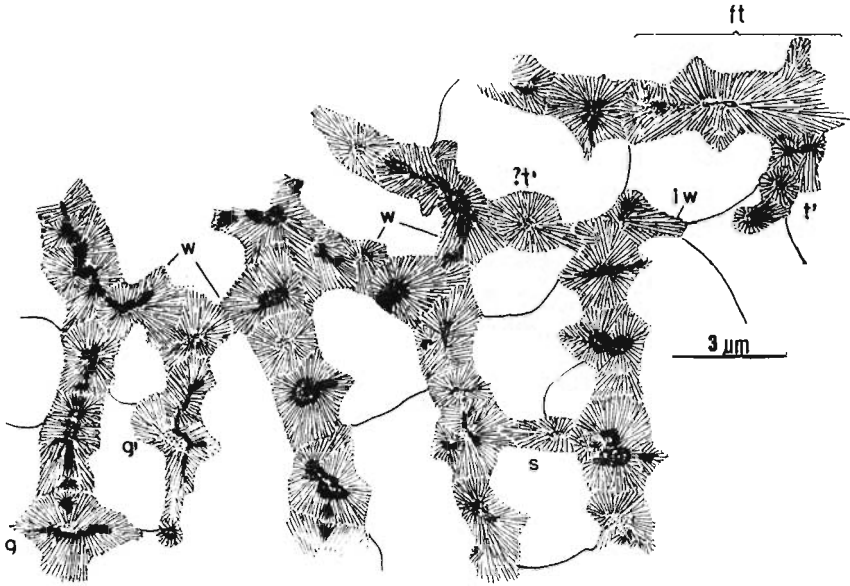
Fig. 9. *Isastraea* cf. *bernensis* Etallon. Specimen ZPAL HIV/303. Cross-section of corallites in the wall region showing multiaxial septal trabeculae with branches situated in the medial plane and those perpendicular to it, and a wall structure; *ft* flat trabecula abnormally large, with irregularities in the structure of its median zone indicating a formation of a new trabecula, *g* sharp granule, *g'* thickened granule, *iw* underdeveloped synapticular element of the incomplete wall, *s* synapticula on the septal flank, *t'* auxiliary trabeculae in the wall region, *w* trabecular apophyses — synapticular elements protruding from the septal external edge to form a wall.
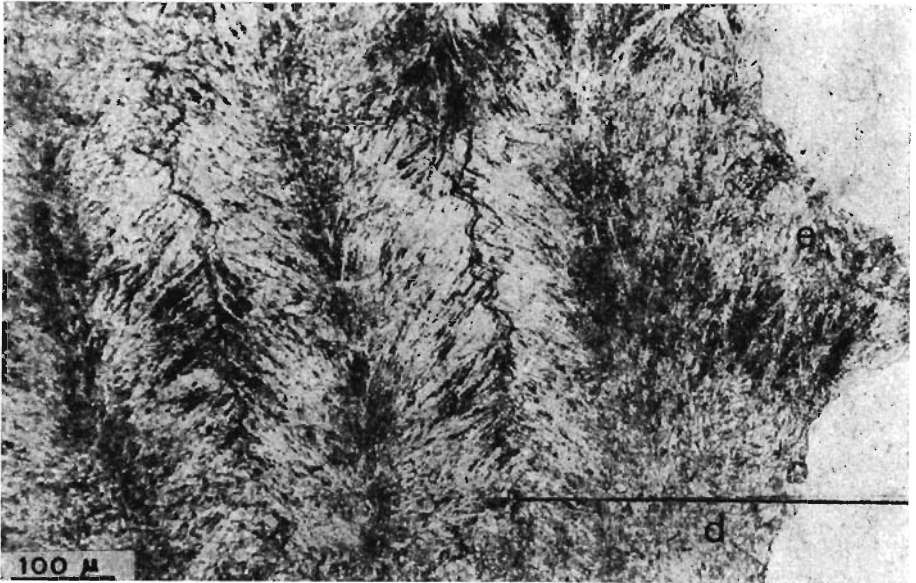

Fig. 10. *Isastraea* cf. *bernensis* Etallon. Specimen HIV/303. Septum in longitudinal radial section. At left — trabeculae of typical diameter, at right — development of multiple branches (*e*) in the median plane results in an elongation of the trabecular diameter (*d*).

trabeculae, appear as elements growing out from one septum and fusing with the septum of a neighbouring calice. Well defined simple axes inclined slightly upwards are observed in each expansion (pl. 68: 2a; fig. 7, 9). By fusing vertically, trabecular expansions form a wall, a solid element of the adtrabecular-bar type. The wall resembles the adtrabecular bars of *Thamnasteria* not only in its general appearrance but also in its being originated by particular trabeculae. It differs, however, from the adtrabecular bars in its structure which is subordinate to the structure of the trabecula. Trabecular expansions of the same pattern and rôle in skeletal architecture as that described here, are known as *trabecular apophyses* in Recent *Favites* and *Goniastrea* (Chevalier 1971).

The capability to form synapticulae seems to be different in different *Isastraea* species. Pomeranian *I.* cf. *bernensis* and *I. helianthoides* described from the Świętokrzyskie Mts (Roniewicz 1966: pl. 13: 1) can serve here as examples.

In the perimural zone a tendency to strengthen the skeleton is observed. It is expressed as overgrowth of existing, or the formation of new ele-
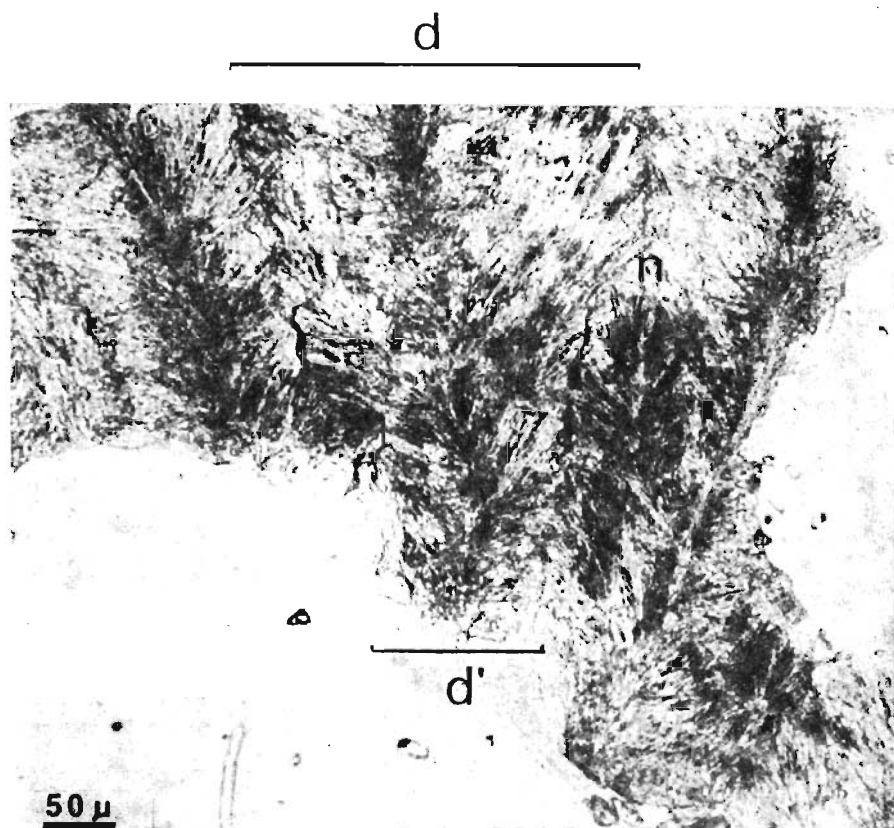

Fig. 11. *Isastraea* cf. *bernensis* Etallon. Specimen ZPAL HIV/303. Septum in longitudinal radial section. At right — a new trabecula (n) which ended its growth. At the middle — a new trabecula of a sharply rising diameter (d′ and d).

ments of the axial structure, for example, by the overgrowing of particular septal granules (up to synapticulae formation), the development of granules on the wall itself, and development of short, vertical auxiliary trabeculae originating on the dissepimental surface (fig. 9).

The dissepimental primary layer shows very minute crystallites poorly clustered (pl. 66: 2b), resembling in this respect some ahermatypic corals (Sorauf and Jell 1977). The junction line is sharp. The upper layer is built of coarse clustered tissue. A discontinuity between the septal tissue and the dissepimental upper layer is well marked.

Taxonomic remarks. — Upper Jurassic isastreids seem to be specifically diversified, judging by the lists of species described. Unfortunately, specific identifications are not verifiable on the basis of the descriptions available, which offer very generalized data. The species here described resemble *Isastraea bernensis* Etallon, 1864 from the Upper Oxfordian of Romania (see Roniewicz 1976: 67, pl. 13: 2, 3) in corallite shape, dimensions, gemmation, and number of septa. However, it differs in having a considerably lower trabecular density in the septa, a lower density of granules on the carinae and in having a distinctly developed parietal columella. At this moment, it is impossible to evaluate the taxonomical meaning of those differences and resemblances.

II. COMMENTS ON THE SYSTEMATIC POSITION OF THE CORALS CONCERNED

Ornamentation and histology as taxonomical criteria

The past fifteen years has brought numerous papers in which the histology and ornamentation of the skeleton are put forward as criteria for the recognition of higher-level taxa. Gill (1967, 1970, 1977) and Gill and Lafuste (1971), working on Jurassic corals, stress the introduction of histology and ornamentation as primary criteria for systematics. The analysis of relationships between septal histology and ornamentation in Triassic Scleractinia (Cuif 1972, 1974, 1975, 1976, 1977, 1981) showed the unquestionable superiority of histology over ornamentation. Systematic revisions in the Scleractinia proposed by these authors directly or indirectly disagree with the systematic schemes of Wells (1956) or Alloiteau (1952). The use of histology in the recognition of phylogenetic lines applies to Triassic rather than to Jurassic or more recent corals. This is because Triassic corals show a strong histologic differentiation, whilst displaying striking homoeomorphy in skeletal ornamentation and corallite architecture. In the Jurassic, a distinct impoverishment in diversity of histological types and the domination of trabecular histology is observed. However, we cannot as yet satisfactorily differentiate the forms of the latter. Histological observations are hardly possible due to the bad state of preservation of these corals. That is why, in relation to these corals,

the criteria of ornamentation (including micro-ornamentation) and morphology of the skeletal elements must do.

The corals discussed represent four varieties of trabecular microstructure which are featured by particular families and groups of families. They all belong to the group of microstructures with branched trabeculae, so common in the Jurassic (at least 3 of them have lateral axes branching off at regular intervals from the primary trabeculae). To this group of microstructures belong, apart from (1) pennular Thamnasteriidae, Latomeandridae, Microsolenidae, (2) corals with granular ornamentation (trabeculae rhomboidal in cross section), i.e. the families Kobyastraeidae Roniewicz 1978 (see: Roniewicz 1978: 56), Montlivaltiidae and Isastraeidae, and (3) corals with a neorhipidacanth-type trabeculae (Roniewicz 1976: 80), which include: corals from the suborder Rhipidogyrina Roniewicz, 1976, at least some genera presently ascribed to Stylinina (compare *Agathelia asperella* (Reuss) *in* L. et M. Beauvais 1975: pl. 1: 2, pl. 2: 1) and the genera *Diplocoenia* (*D. stellata in*: Morycowa 1964: pl. 14: 1c) and *Placophyllia* (*P. dianthus in* Eliášová 1976: 338, pl. 2: 2). The latter type of trabeculae displays long, thin, numerous secondary branches of a thickness similar to that of the primary axis, analogous to the rhipidacanth type found in the Devonian family Phillipsastraeidae (Jell 1969). This type resembles the Cretaceous type known in *Latusastraea* and *Heterocoenia*, but the latter displays less intense branching of the trabeculae which are very thick, unlike the neorhipidacanths and, at the same time, shows a correlation with a peculiar corallite architecture and wall structure (Morycowa 1971: figs 19, 21). These differences preclude, in my opinion, their assignment to the same taxon with the neorhipidacanth-type corals.

The comparison of the trabeculae of *Thamnasteria* (Thamnasteriidae) and *Dimorphastraea* (Latomeandridae) with those of *Chomatoseris* (Microsolenidae) studied by Gill (1967, 1968) shows that their pennulae are formed identically — from lateral branches (= lateral axis = secondary trabecula) of the primary trabecula. The distal endings of the branches appear in the form of denticles on the pennular edges. These genera, however, differ in the following way: (1) in *Thamnasteria*, the pennulae are flat, with a distal edge in the plane of the pennular platform, whilst *Dimorphastraea* (pl. 60: 1, 2) and *Chomatoseris* (Gill 1967: fig. 2; pl. 10: 1a) display, in side view, pennulae with a raised, crescent-shaped edge; (2) the primary trabeculae in the two latter genera show a narrowing of their diameter in between the pennular "nodes" — hence the tendency to regular septal porosity, which may be fully expressed, *e.g.* in the family Microsolenidae, or hardly developed as in the case of the Latomeandridae (Roniewicz 1976: 95). In *Thamnasteria*, the skeleton is compact; (3) In the Latomeandridae, as opposed to the Microsolenidae, synapticulae have not been recorded. In *Thamnasteria* the adtrabecular-bar type synapticulae are observed.

Trabeculae in the Latomeandridae and Microsolenidae show such similarity in their structure that these families can be regarded as phylogenetically closely related. Their affinity is supported by the corallite architecture: septa with an internal edge dissociated into trabeculae, a parietal columella, and dissepimental endotheca. These families are not in close relationship with the Thamnasteriidae. The differences in the formation of pennulae and interseptal elements as well as the dissimilarity of the morphology of the internal septal edge and columellar structure prove the above statement.

Gill and Lafuste (1971) drew attention to the principal differences in microstructure between the Microsolenidae (up to now assigned to the suborder Fungiina), and the genus *Fungia*. At the same time, they stressed a certain similarities between genus *Fungia* and the family Montlivaltiidae (the latter up to now in the suborder Faviina). The principal characteristics of the microstructure, micro-ornamentation and histology of different skeletal elements in *Fungia* were described by Sorauf (1972), Jell (1974) and Gill (1981), and in the closely related genus *Cycloseris* by Gill (*op. cit.*). The trabeculae are branched. The septal flanks are covered with strong granulations — vepreculae, which originate as relatively strongly ornamented branches of the primary trabeculae. Sorauf stated (1972) that the wall is not of synapticular structure. The so called "compound synapticulae" are in fact structures genetically independent of the trabeculae. They are distinguished as a separate element — fulturae (Gill 1981). The septal flank surface has an imbricated ornamentation (Sorauf 1972, Jell 1974). On the basis of the above facts it is safe to say that the Microsolenidae, Latomeandridae and Thamnasteriidae should, obviously, be excluded from the order Fungiina. Gill (1967) proposed a new taxon, the Pennulacea, for the pennular corals. However, Cuif's observations of pennular Triassic corals (1975) showed that pennulae can develop in corals of different skeletal histology, and pennular criterion has a restricted significance for taxomonical purposes.

The examination of the skeleton of *Actinaraeopsis* (Haplaraeidae) provides the first information on the histology of non-pennular synapticular Jurassic corals. Unfortunately, as the microstructures of those representatives of this group so far described were not recognized, any comparison within it is as yet impossible. Phylogenetic relationships and links with earlier and later corals of this numerous group remain unknown. The group includes, at least, *Actinaraeopsis, Haplaraea, Meandraraea, Meandrophyllia, Actinaraea, Kobyastraea* and *Mesomorpha*. Assigned to four families of the suborder Fungiina, they show such similarities in structure that their grouping into a single taxon seems only a matter of completion of documentation. At the same time, in the light of research on *Fungia* (e.g. Jell 1974) or *Fungia* and *Cycloseris* (Gill 1981) it is clear that those Jurassic genera should be excluded from the order Fungiina.

Isastraea, by its trabecular histology and ornamentation, belongs to the *Montlivaltia* group (compare *Montlivaltia* microstructure *in* Gill 1970, Gill and Lafuste 1971). The difference in microstructure between these genera lies in more frequent branching of lateral axes from the primary trabecula in *Isastraea*. An important difference in the microstructure of radial elements is their being formed as septa in *Isastraea*, and as costosepta in *Montlivaltia* and in related genera together with synapticulae formation and a strong division of internal septal edge in *Isastraea*, lacking in *Montlivaltia* group. This justifies the differentation of the family Isastraeidae.

The latter is the closest to the Recent Faviidae, especially to the genus *Favites* (compare Chevalier 1971: trabecular histology, wall structure, type of radial elements, development of columella in diverse species of the genus *Favites*), *Goniocora* (Chevalier *op. cit.*: trabecular histology and some characters of the wall) and to some Paleogene faviids (Eliášová 1974: septal microstructure in *Favia* and *Plavecia*).

The phylogenetic relationships between the Montlivaltiidae and Isastraeidae can be considered as very close. The montlivaltid type of trabeculae is characteristic of many genera of the suborder Faviina and is similar to the main trabeculae in representatives of the suborder Fungiina. The specificity of this type of microstructure allowed Gill and Lafuste (1971) to suggest the recognition of the group Montlivaltioidea.

Homoeomorphy, a phenomenon encountered usually in scleractinian colony and corallite morphology, is also observed at the septal structure level. Pennular Triassic corals (Cuif 1975) exemplify this. In the corals studied here, similarities between the Haplaraeidae (*Actinaraeopsis*) and Siderastraeidae (*Siderastraea*) in the structure of synapticulae and in the morphology of septa and endotheca are homoeomorphic. The differences are visible only on the histological level and thus in the trabecular micro-ornamentation.

The corals examined here represent two histological types of trabeculae: coarse- and fine-fibred. The former is found in pennular and montlivaltioid skeletons whilst the latter occurs in *Actinaraeopsis*.

Taxonomical significance of synapticulae

I accept the first definition of the term *synapticula* (Milne-Edwards 1857), that is I regard it simply as an element which joins septa. The subdivision of synapticulae into "true" and "false" depending on whether they possess centres of calcification, suggested by Pratz (1882) and followed by Ogilvie (1896) is not confirmed by the results of new research.

Similarly the term "compound synapticula" proposed by Vaughan and Wells (1943) and meaning a synapticula with many centres of calcification of its own has become meaningless (Gill 1981). The term cannot be applied

to any of the types of synapticulae studied here, not even to the synapticulae in *Fungia*, which were considered the model for this structure.

Sorauf's (1972) observations on contemporary *Siderastraea*, Gill's research on contemporary *Fungia* and *Cycloseris* (1981) and the observations on Jurassic material presented here indicate that synapticulae are skeletal elements of varied structure and origin. The differences between them are much more significant than those recognized by Pratz (1882). Synapticulae in *Fungia* (= fulturae of Gill 1981) are independent of the septa in their formation and are not related to the trabeculae; they emerge after the insertion of the septa. Another type — adtrabecular bars — are, to a great extent, similar to fulturae. They overlap the septal surface, but as opposed to fulturae, they remain genetically related to the trabeculae (p. 163).

Fulturae of *Fungia* and adtrabecular bars of *Thamnasteria* seem to be initiated not by the septogenic zone of the ectoderm but by the unfolded zone, resembling in this the formation of dissepiments. Their relatioship to the septa justifies this supposition. An interpretation of the relationship between synapticulae and the skeletogenic zone in *Fungia* was given by Ogilvie (1896: fig. 36).

The adtrabecular-bar type elements can be found in different genera. They are either similar in their origin and histology, as are bars in *Thamnasteria* and a wall in *Fungia* or *Siderastraea* (see Sorauf 1972: pl. 15: 1 and pl. 18: 1 and the present paper pl. 64: 7), or different in this respect, as are the structures just mentionned and a wall in *Isastraea*.

Synapticulae in *Actinaraeopsis* are analogous in their appearance, arrangement and structure to the synapticulae in *Siderastraea* (and, to some extent, to microsolenid synapticulae) (pl. 69: 1, 6). They form horizontal beams (= "simple synapticula"), in which their relationship to the trabeculae is of a different nature to that of adtrabecular bars. They are trabecular branches with a well individualized axis diverging from the primary trabecula. In *Siderastraea*, synapticulae penetrate the soft tissue over the entire septal surface (pl. 64: 6): from the distal edge to the calicular bottom. They are initiated not by the pedal zone but, at the distal edge, by the same tissue as the trabeculae and simultaneously with them. The pedal zone overlies the dissepiments, which are placed at a considerable depth as compared with the distal ends of the septa. Taking into account a striking similarity in the arrangement of the synapticulae and the endotheca, one should assume that analogous relationships prevailed in *Actinaraeopsis*. In *Isastraea*, synapticulae are homologous of those in *Actinaraeopsis*, their arrangement, however, being quite differnt.

In the case of the three types of synapticulae discussed, we encounter three different modes of formation of similar elements. It should be expected that further studies will reveal a still greater diversity as these elements occur in many different groups of corals. Gill (1981) questioned the

systematic importance of synapticulae. The facts presented here seem to support his doubts, since synapticulae are identical in corals of such different histology as *Actinaraeopsis* and *Siderastraea* and *Isastraea*, and since adtrabecular elements develop similarly in pennular (*Thamnasteria*) and nonpennular corals (the wall in *Fungia*, or in *Siderastraea*).

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PRZYKŁADY JURAJSKICH KORALI PENNULARNYCH I NIEPENNULARNYCH

Streszczenie

Jurajskie korale znalezione w osadach lodowcowych na Pomorzu (Roniewicz *in press*) przedstawiają interesujący materiał paleontologiczny, gdyż ich aragonitowy szkielet nie uległ kalcytyzacji. Doskonały stan zachowania szkieletu pozwolił na nowe zbadanie czterech gatunków: *Thamnasteria concinna* (Goldfuss, 1826) i *Dimorphastraea* sp. spośród pennularnych oraz *Actinaraeopsis exilis* Roniewicz, 1968 i *Isastraea* cf. *bernensis* Etallon, 1864 spośród niepennularnych. Nowe dane morfologiczne i mikrostrukturalne pozwalają na przeprowadzenie rewizji dotychczasowej diagnozy rodzaju *Thamnasteria* Lesauvage, 1823. Generalnie, przeczą też one panującemu poglądowi na mikrostrukturę korali, który mówi, że trabekule są zbudowane z porcji

szkieletowych — sklerodermitów. Natomiast dane te potwierdzają pogląd Gilla 1970 oraz Gilla i Lafuste'a (1971), że trabekule mają przyrost ciągły.

Mikrostruktura szkieletu (a gdy ta nie jest zachowana, to w ograniczonym zakresie, jej odbicie w postaci ornamentacji septalnej) wysuwają się jako główne kryteria wydzieleń taksonomicznych na poziomie ponad-rodzajowym. Wśród korali o rozgałęzionych trabekulach uzasadnione wydaje się wydzielenie kilku różnych grup korali pennularnych, grupy niepennularnych z ostrymi guzkami (którym Gill 1967, potem Gill i Lafuste 1971 proponują, odpowiednio, nazwy Pennulacea i Montlivaltioidea), niepennularnych z cienkimi i długimi odgałęzieniami typu neoripidakantowego, i in. Przeprowadzono przegląd budowy elementów typu synaptikularnego, która okazuje się bardzo różnorodna, lecz niezwiązana z określonym typem mikrostruktury septów. Ze względu na to zakwestionowano przydatność synaptikul dla systematyki.

EXPLANATION OF PLATES 52—69

SEM micrographs if not stated otherwise
Specimens in the plates 53—69 are from Middle Oxfordian erratic boulders,
Pomerania

Plate 52

Thamnasteria cf. *concinna* Goldfuss, 1826, Middle Oxfordian, Bałtów,
ZPAL HIII/363

Illustration of two different states of preservation of skeleton (1ab after Roniewicz 1966); a, d trabecular structure obliterated, septal outline, dissepiments and "wall structure" visible; b, c vestiges of trabeculae are the only structural features preserved.

All seen in light microscope

Plate 53

Thamnasteria concinna Goldfuss, 1826, Ostromice

1, 2. Transverse sections. Multidentate, elongated pennulae seen from the lower side. Specimens ZPAL HIV/35 and 33, respectively.

3.   Calice with septal distal edge ornamentation preserved and columella in the centre. Septal blade is divided into adaxial paliform portion and the main blade. Specimen ZPAL HIV/35.

4.   Adaxial portion of distal septal edge provided with sinus (arrow) delimiting the internal paliform lobe. The same specimen.

5, 6.   Undamaged (5) and damaged (6) portions of the same calicular surface. Inter-
        septal elements (arrow) constituting the "wall structure" are visible in the
        portion where the distal edge is slightly eroded. The same specimen. Seen in
        reflected light.
7.   Colony preserved as a pebble displaying calicular surface in different state
        of preservation: in the middle — undamaged, to the right — slightly damaged
        with interseptal elements visible, peripherally extremely damaged, showing
        the thick central organ. Specimen ZPAL HIV/20. Seen in reflected light.
8.   Inner edge of high order septum with ornamented denticles developed (com-
        pare with pennulae). Specimen ZPAL HIV/228.
9.   The same specimen and magnification. Septal flank. Pennulae of one trabecula
        can be fused (in the middle) or remain discontinuous. Dissepiments are based
        on vertical adtrabecular bars (b).

Plate 54

Thamnasteria concinna Goldfuss, 1826, Ostromice

1, 2.   Vertically discontinuous (*1*) and continuous (*2*) adtrabecular bars. Growth
        direction is from the trabecular surface (*1a*, *1b*, *2a*) toward the neighbouring
        septum. *2b* clusters directed toward the interseptal space. Specimen ZPAL
        HIV/231 and 35, respectively.
3.   Suture (arrow) between the septum (left) and adtrabecular bar (right). Spe-
        cimen ZPAL HIV/35.
4, 5.   Moulds of the septal face with imprints of pennulae (arrow) in the adtrabecu-
        lar bar tissue. Dissepiments in the interseptal space (double arrow) developed
        as thin or thick structures; *b* adtrabecular bar, *s* longitudinal section of the
        septum, perpendicular to the septal blade. Specimen ZPAL HIV/33.

Plate 55

Thamnasteria concinna Goldfuss, 1826, Ostromice, ZPAL HIV/33

1.   *a* Surface of a skeletal lining of a septal flank seen in longitudinal section
        and showing imprints of pennulae; *b* a fragment of this surface.
2.   Distal portion of a corallite with distal septal edge preserved, longitudinal
        section. Adtrabecular bars (*b*), four in number (*1—4*), show either imprints of
        pennulae (left) or pennulae protruding from under the skeletal cover (lower
        right).
3.   The same specimen. Distal portion of a corallite. Adtrabecular bars (*b*) termi-
        nally pointed, thickened in their upper parts, connected with a thickened dis-
        sepiment. Other dissepiments thin.

Plate 56

Thamnasteria concinna Goldfuss, 1826, Ostromice

1.   Natural cavern incorporated into the corallum in longitudinal section. Thick
        growth wrinkles covered with epitheca and a floor covered with extremely
        well preserved calices are seen. The walls of the cavity are inclined towards
        each other until they meet to roof the cavity, completely cutting off contact
        with the external environment. The closure is situated in the uppermost

part of the cavity ceiling (arrow). Specimen ZPAL HIV/35. Seen in reflected light.

2. Slightly eroded surface of epitheca with growth wrinkles and perpendicular minute striation (arrow). The same specimen.

3. Fragment of calice from the bottom of the cavity: *a* septal face in front and terminal portion of trabeculae in the upper part of the picture. A pellicula (arrows), partially broken, fills the free space between the terminal septal elements; *b* the pellicula upper surface with growth wrinkling and delicate perpendicular striae (arrow). The same specimen.

4. Two trabecular tops from which pellicula growth has been started concentrically to close the free space. Growth wrinkles well marked. The same specimen.

5, 6. Two longitudinal broken sections to show differences in appearance of the skeleton depending on differences in calcification potential; *5* represents a specimen with thickened skeleton: thick columellar structure which includes thick-walled dissepiments (expressed as lacunae, *l*) and internal edges of septa, is visible; *6* represents a specimen of low calcification potential: vesicular dissepiments are thin-walled, columella (*c*) underdeveloped. Adtrabecular bars (*b*) appear as longitudinally continuous (*5*) or discontinuous (*6*) structures. Vertical structures closest to the columella may represent either adtrabecular bars (?) or inner edges of septa of a higher order anastomosing with septal blades of first order septa reaching the columella. Specimens ZPAL HIV/22 and 231. Seen in reflected light.

Plate 57

Thamnasteria concinna Goldfuss, 1826, Ostromice

1. Lower surface of the primary layer of a dissepiment with growth lines and junction suture (arrow) well expressed. Specimen ZPAL HIV/35.

2. Trabecula in transverse (slightly oblique) section, intertrabecular sutures marked with arrows. Lower side of pennulae visible. Trabecular diameter is elongated in the direction of the septal plane. Pennulae from the two trabecular sides are not exactly opposite each other. Specimen ZPAL HIV/33.

3. Contact of dissepiment (*d*) and adtrabecular bar (*b*) in longitudinal section. Skeletal tissue of both elements is contiguous. The same specimen.

Plate 58

Thamnasteria concinna Goldfuss, 1826, Resko, ZPAL HIV/19

1. *a, b* Longitudinal-tangential section of the septal blade. *1a* Lower part of the picture: longitudinal radial section showing well delimited trabeculae (*t*), each with main axis in their centre. Upper part of the picture: left side — section passing near the septal face, cutting the pennular branches (*p*), right side — section passing through the adtrabecular bar (*b*). *1b* A fragment magnified showing the adtrabecular bar with its fan-like disposition of fibres and distal portions of pennulae (*p*) incorporated into the adtrabecular bar structure (lower left), or free (upper left). The fibres display weakly clustered or non-clustered arrangements.

2. Longitudinal section (perpendicular to the septal blade) cutting two septa and interseptal space filled with the adtrabecular bar tissue (*b*). In both septa the

trabecular main axis (*ma*) and secondary (lateral) axes (*la*) are seen that give rise to the pennulae (*p*). General direction of growth of fibres of the adtrabecular bar tissue is from the right to the upper left.

All in light microscope

Plate 59

Dimorphastraea sp., Resko, ZPAL HIV/27

1. Thick dissepiment paralleling menianae, in longitudinal broken section.
2. Top of one of the denticles of the pennular distal edge ornamentation in broken section; radial arrangement of crystallites is visible.
3. Trabecula in transverse section with well marked sutures and a distinct clustering of fibrous tissue. Fibres are thin.
4. Dissepiments paralleling menianae, in longitudinal section.
5. *a* Transverse section with lower side of pennulae and of a primary dissepimental layer shown. Junction line marked; *b* a fragment magnified to show nonclustered crystallites of the lower dissepimental surface.

Plate 60

Dimorphastraea sp., Resko, ZPAL HIV/27

1. Septum in longitudinal section perpendicular to the septal blade: main axis (*ma*) and lateral axes (*la*) are well marked; *pe* pennular edge.
2. Longitudinal thin section to show the disposition of pennulae and their shape with their distal edges directed upwards. Inner septal edge of a higher order septum, dissociated into free trabeculae, seen in the middle of the picture. Seen in light microscope.
3. Longitudinal section showing a dissepiment with the primary layer built of minute crystallites seen at the lower right corner and a thick upper clustered layer. Thick tufts are discernible in the clusters. The lower surface is covered by a secondary deposit.

Plate 61

Dimorphastraea sp., Resko, ZPAL HIV/27

1. Trabecula in longitudinal oblique section showing sutures at the contacts with neighbouring trabeculae (arrows) and multiple centres from which clusters originate. Fibres are thin.
2. Longitudinal section of trabecula showing its axial part. Fibres are thin, clustered.

Plate 62

Actinaraeopsis exilis Roniewicz, 1968, Ostromice
1: ZPAL HIV/291; 2—4: ZPAL HIV/216

1. Transverse section of a colony with subcolonial units (*u*) delimited with a zone of deformed corallites (furrow zone).

2. Transverse section of a septum and synapticulae (*s*). Synapticular sutures indicated with arrows. Trabecular axes and intertrabecular boundaries recognizeable.
3. Longitudinal section perpendicular to the septal blade with main trabecular axis (*ma*) and irregular lateral axes diverging from it. Two synapticulae are seen (*s*); intrasynapticular suture is marked with an arrow.
4. Longitudinal section perpendicular to the septal blades of three septa; synapticulae in the centre. Lateral, synapticular axes (*la*) are visible. Axes are situated in the lower part of the synapticulae. Main axis poorly visible.

All in light microscope

Plate 63

Actinaraeopsis exilis Roniewicz, 1968, Ostromice
1—3: ZPAL HIV/348, 4: ZPAL HIV/291

1, 2.   Two fragments of the distal part of the corallite in longitudinal broken section: 1*a* and 2 irregularly distributed pores and the tabular character of the endotheca are seen. Trabeculae expressed in the form of ridges are seen on the lower left side of 1*a*. 1*b*. A fragment showing a section of the calice with regular denticulation on the inner edges and large round granules on the distal edges of septa. Irregular ornamentation in form of sharp granules.
3. Calicular surface: *a* ornamentation of septal edge — rounded tops of trabeculae with pointed lateral granules; *b* larger portion of the same surface. Irregular distal granulation with some granules overgrown (arrow).
4. Transverse thin section showing columella anastomosing with internal septal edges. Seen in light microscope.

Plate 64

Actinaraeopsis exilis Roniewicz, 1968, Ostromice

1. Septal face with synapticulae and granular ornamentation; well developed thick dissepiments are seen. Specimen ZPAL HIV/297.
2. Distal part of a septum with sharply pointed granules which give rise to synapticulae; small pointed granules of septal ornamentation visible in the middle. Specimen ZPAL HIV/351.
3. Porous fragment of a septal blade (a fragment of pl. 63: 2). Septal face with granules and synapticulae; dissepiments tabuloid. Specimen ZPAL HIV/348.
4, 5.   Synapticula in transverse (4) and in longitudinal (5) sections. The axis is seen in the lower part of the synapticula. Specimen ZPAL HIV/297 and 351, respectively.

Siderastraea sp., Cuba, Recent

6. Calicular portion of the corallite in longitudinal broken section. Visible synapticulae piercing cracked soft tissue which line the septal flanks.
7. Wall in longitudinal section. Compare with adtrabecular bars in pl. 54.

Plate 65

Actinaraeopsis exilis Roniewicz, 1968, Ostromice
1, 2, 4: ZPAL HIV/297, 3: ZPAL HIV/348

1. Contact between dissepimental and synapticular tissue seen in longitudinal section. Tissue of both elements seems to be contiguous.
2. *a, b* Lower surface of a dissepiment. Strongly clustered tissue is seen. Junction suture well marked.
3. Palisaded upper dissepimental layer in longitudinal section.
4. Broken section of a dissepiment showing a primary layer tissue clustered into conical units (arrow) with their fibres oriented toward the upper or the lower dissepimental surface.

Plate 66

Actinaraeopsis exilis Roniewicz, 1968, Ostromice

1. *a* Epitheca in longitudinal section. Septum is seen in the upper right corner. Crystallite growth is oriented from the external surface inwards. *b* Faint clustering of epithecal tissue is visible. Specimen ZPAL HIV/348.
2. A dissepiment seen from its lower side: *a* junction suture well marked, *b* primary layer (lower part of the photograph) built of poorly clustered crystallites. Specimen ZPAL HIV/297.
3. Septal surface with ornamental granulation (*g*) and cluster tops emerging. Crystallites in clusters well delimited. Specimen ZPAL HIV/348.
ZPAL HIV/303

Isastraea cf. *bernensis* Etallon, 1864, Ostromice
ZPAL HIV/303

4. Septal surface with crowded clusters. Crystallites well delimited.

Plate 67

Isastraea cf. *bernensis* Etallon, 1864, Ostromice
ZPAL HIV/303

1. Septal trabeculae in longitudinal radial section. Two trabeculae well developed with their axes recognizeable. Clustering of the trabecular tissue well expressed. At the middle — three trabecular branches (*1, 2, 3*) situated in the medial septal plane and posessing their own axes.
2, a, b Longitudinal broken sections showing endotheca, wall, parietal columella and septal ornamentation, ×5. Seen in reflected light.

Plate 68

Thamnasteria concinna Goldfuss, 1826, Ostromice, ZPAL HIV/35

1. Septal surface with clusters well seen.

Isastraea cf. *bernensis* Etallon, 1864. Ostromice, ZPAL HIV/303

2. *a* Surface of two septa and longitudinal broken section of a wall. The wall is formed of trabecular projections which are seen as a vertical row of fused elements protruding from the septal blade (see also text-fig. 7); the elements are broken with one exception (a detail magnified in the picture 2b). *b* Detail of the wall representing an underdeveloped external projection of the peripheral trabecula. Micro-ornamentation of the whole surface is to be noticed.

3.   Septal face with micro-ornamentational granulation and a deep imprint of
        a body attachment.

Plate 69

Isastraea cf. *bernensis* Etallon, 1864, Ostromice, ZPAL HIV/303

1.   *a* Transverse section of a septum. The section passes through the intergranular
        zone of trabeculae where branching is lacking. Two granulae (*g)* of an older
        generation of branching are seen. *b, c* Branching of the main axis: lateral
        axes (*la*) and those in the medial septal plane (*me*) are visible. Discontinuity
        of the medial septal line and a suture between trabeculae (arrow) well expres-
        sed.
2.   Longitudinal radial section of septum showing distribution of trabeculae, two
        new trabeculae (*n*) are to be observed.
                            All in light microscope