Microstructural disparity between Recent fungiine and Mesozoic microsolenine scleractinians

ELŻBIETA MORYCOWA and EWA RONIEWICZ

Morycowa, E. & Roniewicz, E. 1995. Microstructural disparity between Recent fungiine and Mesozoic microsolenine scleractinian. *Acta Palaeontologica Polonica* **40**, 4, 361–385.

The Mesozoic families Microsolenidae, Latomeandridae, Synastreidae and Cunnolitidae basically differ from the Recent fungiids, with which they had traditionally been classified due to their having synapticulae and porous septa. We propose a new suborder Microsolenina for these families because their members possess collar-like structures (pennulae of Gill 1967) spaced along the trabeculae, tending to merge into more or less continuous flanges parallel to the septal distal margin, distributed on each face of the septa. The fungiids, having trabeculae with granulations set off from the trabecular axis towards interseptal space (vepreculae of Jell 1974), are closest to the faviids from which they probably derived.

Key words: Anthozoa, Scleractinia, Fungiina, Microsolenina, microstructure, pennulae, Mesozoic, Eocene, Recent.

Elżbieta Morycowa, Instytut Nauk Geologicznych UJ, ul. Oleandry 2a, 30-063 Kraków, Poland.
Ewa Roniewicz, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

Increasing knowledge of fossil coral microstructure and microarchitecture, especially the observations by Gill (1967, 1968, 1970, 1977a, 1981, 1993, and other papers) and Cuif (1973, 1975a, b, 1976, 1977 and other papers) makes microstuctural/microarchitectural criteria increasingly important in the taxonomy of the Scleractinia. Although it is still not possible to establish a complete classification of the Scleractinia consistently based on microstructural data, some improvements can be offered. The superfamily Montlivaltioidea has been already redefined on the basis of development of trabeculae of the *Montlivaltia*-type (Gill & Lafuste 1971), the family Stylinidae is now diagnosed by the presence of microarchitectural elements named auriculae (Gill 1977), and the family Fungiidae by development of fulturae and incomplete porosity of septa (Gill 1981). Corals having pennular septal ornamentation have been excluded from the Fungiina and classified in the superfamily Pennulacea (Gill 1967). This last group will be discussed in the present paper.

The attempts to fit Mesozoic scleractinians into the classification scheme established for Recent corals have appeared unsuccessful in most cases and have resulted in artificial groupings of families. Mesozoic and Cenozoic faunas seem to have little in common with one another, having essentially different microstructures (Roniewicz & Morycowa 1993). The suborder Fungiina embracing corals differentiated on the basis of macroscopic features is an example of such an artificial group. In this paper we attempt to find a solution to that problem.

Diagnoses of the suborder Fungiina in all modern classifications (Vaughan & Wells 1943, with its more recent version by Wells 1956, Alloiteau 1952, and Chevalier 1987) always refer to the same characters: 'Solitary and colonial. Septa fenestrate, formed by simple or compound trabeculae united by simple or compound synapticulae, margins beaded or dentate' (Wells 1956). Septal porosity and synapticulae have been thus considered to be the essential features of the fungiines. We question the reliability of this foundation of the suborder.

Acronyms of Institutions: FGGUB — Faculty of Geology and Geography, University of Bucarest, Romania; UJ — Institute of Geological Sciences, Jagiellonian University, Cracow, Poland; ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Terminological notes

Some ambiguity in the meaning and/or spelling of Latin names calls for clarification of the terms of pennula, maenianum, synapticula, and trabecula.

Pennulae and menianes. — *In this paper, the terms are defined as in* Gill (1967), except restricted use of pennula as a non-corniform ornamentation in preference to Gill's (1967: p. 72) much extended original diagnosis. Up to now, the term meniane has been mostly used in its morphologic sense (e.g. Gill & Russo 1980: text-fig. 1). Due to increasing use of microarchitectural details in taxonomy, the development of menianes becomes important. Are they of a pennular origin, or do they derive from a fusion of spiniform lateral expansions growing out from a minitrabecular median septal zone, or do they develop in another, unknown way (e.g. in Ordovician *Tjanshanophyllia* Erina & Kim 1981 or various other Paleozoic corals — see p. 374)?

The terms were introduced by Gill (1967); the Latin for them is pennula (feminine, in plural — pennulae) and maenianum (neuter, pl. — maeniana); in French they are known as pennule (feminine, pl. — pennules) and meniane (feminine, pl. — menianes); in English they are known as Latin pennula (pl. — pennulae), but anglicized meniane (pl. — menianes, or —

incorrectly – menianae). The proper usage should be with Latin spelling: pennula (pl. -ae) and maenianum (pl. -a), or otherwise the correct, non-Latin ones.

Synapticulae. – The term was introduced by Milne Edwards & Haime (1857: p. 35). The ambiguity of its original meaning is caused by the fact that the skeletal features concerned are described as developing from the 'granulations ou des petites pointes coniques' on septal faces. This implies axial transverse structures growing horizontally, while the illustration cited (Milne Edwards & Haime 1857: pl. D: 1d) indicates fungiid-type vertical structures. When dealing with synapticulae in paleontological practice, uncertainty is commonly aggravated by a lack of information on the structure of interseptal elements which can all look alike in transverse section, and be scarcely discernible in longitudinal sections. That a coral exhibits structures connecting its septa, i.e. synapticulae (in the broad meaning given by Milne Edwards & Haime 1957), by itself has no taxonomic significance. In view of their being structurally heterogeneous (e.g. fulturae, adtrabecular bars, rod-like synapticulae – see p. 365) and associated with particular septal microstructures, synapticulae can only be considered as taxonomically valuable if their different structures and origins are known.

The term 'compound synapticulae' has lost its taxonomic value as it evidently lumps together supposed multicentred fungiid fulturae, centreless thamnasteriid adtrabecular bars and multisynapticular wall structures. The term can only be used reliably either within the family Fungiidae as synonymous with fulturae, or as a descriptive morphological word without any taxonomic implication.

There seems to be no regularity of organization and distribution of synapticulae in their broadest sense. For this reason, recognition of a pseudo-synapticular category among interseptal structures, proposed by Pratz (1882) and later accepted by various other authors, though rejected by others, is of little value.

Trabeculae. – To be precise about the meaning of the term trabecula, we accept the view of Bryan & Hill (1941) as well as that of Gill & Lafuste (1971) that a trabecula is a 'rod' with a radial or fanwise, fibrous structure, not segmented into sclerodermites.

Compound trabecula is a term proposed by Ogilvie (1897) and introduced to common usage by Vaughan and Wells (1943). This is a trabecula in cross section displaying multiple centres, and embraces trabeculae with regular lateral off-sets from the trabecular body such as spines, granulations, pennulae etc. The authors include in this term structurally centred trabeculae (with mono- and polyaxial trabecular body bearing lateral secondary trabeculae; for explanation of this latter term see Jell 1969) as well as trabeculae displaying many dispersed centres of calcification and lateral more or less centred structures (polycentric trabeculae: Fig. 4).

Fungia versus other 'Fungiina'

The trabeculae, synapticulae and septal porosity in *Fungia* and related genera belonging to the well delimited family Fungiidae are not comparable to those in other corals currently classified with them in the suborder Fungiina. What is even more surprising, the septal microstructure of *Fungia* itself, and the undoubted fungiid *Cycloseris*, is rather similar to that known in the Montlivaltioidea (Gill 1970, 1977b, 1981; Gill & Lafuste 1971) in the suborder Faviina.

Fungiid trabeculae. — In *Fungia*, septal trabeculae set off what Jell (1974) calls 'secondary trabeculae' that emerge on the septal flanks (*Fungia* sp. — Gill & Lafuste 1971: pl. 10: 2, pl. 11: 4, 5; *Fungia scutaria* — Jell 1974: text-fig. 1c, 2b; *Fungia fungites* — Jell 1974: text-fig. 4c; *Fungia* sp. — Gill 1981: pl. 1: 2–4, pl. 2: 3, 4; *Cycloseris cyclolites* — Gill 1981: pl. 2: 3) as regularly disposed granulations (vepreculae: Jell 1974). Similar septal ornamentation characterizes Mesozoic and early Tertiary montlivaltioid corals (*Montlivaltia*, *Thecosmilia* — Gill 1970, Gill & Lafuste 1971: pls 1–12; *Complexastraeopsis* — Morycowa 1974: text-fig. 6C; *Isastrea* — Roniewicz 1983: pl. 69: 1b, c and Morsch 1994: pl. 4: 1d; *Kobyastraea* — Roniewicz 1970: pl. 4: 2; *Cyclastrea* — Gill & Lafuste 1971: pl. 9, pl. 10: 3–5 and Gill & Russo 1973: pls 8, 9; Tertiary genus *Trochosmilia* — Gill & Russo 1973: pls 2–5; *Cyclolitopsis* — Russo 1974: pls 3–5) and Recent corals from the faviine families. In a longitudinal section of septal denticulation of *Fungia*, the shape of trabeculae and their arrangement resembles those in faviid, pectiniid or mussid corals (*Fungia* sp. — Gill & Lafuste 1971: pl. 11: 1, 2; *Fungia fungites* — Jell 1974: text-fig. 5b; compare to *Symphyllia*, *Echinopora*, and *Oxypora* in Chevalier 1971: text-figs 171, 174, 229 and 243); Jell has remarked on the resemblance between the microstructure of *Fungia* and *Favites* (1974: p. 312).

Fungiid synapticulae. — Based on microscope studies, Gill (1981) has demonstrated that *Fungia* skeletal elements, interpreted up to now as compound synapticulae, differ in structure and origin from other structures previously known as synapticulae. Contrary to common belief (Vaughan & Wells 1943) that *Fungia* has multicentred compound synapticulae growing perpendicularly to septa, those elements, named fulturae by Gill (1977b — unpublished thesis cited by Gill in later papers), grow upward, parallel to the septal plane as highly autonomous, monoaxial structures (Gill 1981: pl. 3: 2, 5, 6, pl. 4: 1–5). These are skeletal elements of a structural pattern 'regarded as a half of a trabecula with rounded end' (Gill 1981: p. 307). As fulturae grow subsequent to septal formation, they incorporate septal spiniform ornamentation which results in their apparent multicentred nature when they are observed in a section tangential to the septal blade (a fact understood by Ogilvie 1896). The distribution of fulturae is not related to the arrangement of trabeculae (Gill 1981: pl. 1: 3, 4). That kind of synapticula is confined to the family Fungiidae (Milne Edwards & Haime 1857: p. 66).

Synapticular elements in other corals previously classified in the same suborder as *Fungia* differ in their microstructures as follows:

(1) Adtrabecular bars in *Thamnasteria* (Thamnasteriidae, Jurassic: Roniewicz 1983) morphologically resemble fulturae, but differ from them microstructuraly in developing as unorganized (i.e. lacking axes) fascicles of fibres growing out along the trabeculae from one septum toward the adjacent septum. Their distribution parallels that of trabeculae. They can constitute a wall between densely packed corallites.

(2) Rod-like subhorizontal synapticulae in Recent Siderastraeidae (*Siderastrea* – Sorauf 1972: pl. 15: 1, and Sorauf 1981: pl. 5: 1–3), Mesozoic Haplaraeidae (*Actinaraeopsis* – Roniewicz 1983: pl. 62: 4, pl. 64: 4), and Synastreidae (coral described as *Fungiastraea* – Morycowa 1964: text-figs 17, 18) display well defined, slightly eccentrically situated axes. So, those elements fall into the category of trabecula-like structures. Rod-like synapticulae of Microsolenidae (e.g. *Chomatoseris* – Gill 1967: text-fig. 2a, c, pl. 7: 3, pl. 10; *Dermoseris* – herein: Fig. 1A; *Meandraraea* – Morycowa 1971: text-fig. 35) are supposed to have the same microstructure. They are oblique and directed slightly upward (*Chomatoseris* – Gill 1967: text-fig. 2a; 1982: pl. 2: 1, 2 and *Polyphylloseris* – Gill 1982: pl. 2: 3, 4). Similar structure in synapticulae is observed in cunnolitids (*Cunnolites* – Fig. 5A).

In the above families, the synapticulae are distributed over the whole septal surface (e.g. Siderastraeidae: *Siderastraea* – Alloiteau 1952: text-fig. 122; Chevalier 1962: fig. 150a–c; Roniewicz 1983: pl. 64: 6; Microsolenidae: *Chomatoseris* – Gill 1967: pl. 10: 1, *Dermoseris* – herein: Fig. 1A; Cunnolitidae: *Cunnolites* – herein: Fig. 5A; Haplaraeidae: *Actinaraeopsis* – Roniewicz 1983: pl. 63: 2, pl. 64: 1).

It is noteworthy, that rod-like synapticulae as listed above resemble synapticulae in other suborders. Examples are the somewhat flattened and directed upwards synapticular projections in the calicular periphery of Triassic caryophylliines (Reimaniphylliidae: *Retiophyllia* – Roniewicz 1989: pl. 8: 7, pl. 14: 1b), the synapticulae of circular section of the Triassic Astreomorphidae, a family of somewhat unclear position (*Astraeomorpha* and *Parastraeomorpha* – Roniewicz 1989: pl. 28: 5 and pl. 30: 2, 3b) as well as Mesozoic to Recent faviines (Jurassic Kobyastraeidae: *Kobyastraea* – Roniewicz 1970: pl. 3: 1; Recent Faviidae: *Diploastraea* – Chevalier 1975: figs 28, 31, poritids and others). In colonial forms, rod-like axial structures situated one upon another along calicular margins can fuse vertically into a more or less continuous synapticular wall. Such walls are observed in colonies of the thamnasterioid type of corallite fusion (e.g. *Kobyastraea* – Roniewicz 1970: pl. 3: 1). They also occur in cerioid colonies with tectiform walls, where rod-like structures appearing on peripheral septal edges link neighbouring septa together to form a zigzag wall (*Isastrea* – Roniewicz 1983: pl. 68: 2a, b; similarly also in the tectiform collines of meandroid colonies, e.g. *Alpinophyllia* – Roniewicz 1989: pl. 25: 2a).

Porosity of septa. — Much diagnostic value is commonly attributed to the porosity of septa in *Fungia*. However, this feature is confined to young septa (Duncan 1884) where the perforation is 'sporadic and due to lack of material in early stages of formation; it cannot be compared to the structural perforation in many pennular corals' (Gill 1981: p. 308). It is not homologous to the structural porosity of the other 'fungiines', such as microsolenids, latomeandrids, haplaraeids, actinacidids or poritids. In these corals, septal perforation is an intrinsic structural character due to the regular reticulate pattern of their structures. Their trabeculae are primarily separated from each other in the interpennular portions while connected by pennulae which grow simultaneously and in regular intervals along the neighbouring trabeculae (Figs 1A, 3A). Irregular septal porosity in these corals results from calcium carbonate secretion in proximal parts of the calice, the process being better developed, or even normal in some groups (latomeandrids), more than in others.

The problem of fungiid affinities. — The above patterns of septal and synapticular structure in the Fungiidae and other families classified in the Fungiina by Vaughan & Wells (1943), Wells (1956), Alloiteau 1952, and Chevalier (1987) do not support the idea of a close phylogenetic relationship between them.

The Fungiidae with 17 genera and subgenera recognized by Hoeksema (1989), are a well defined monophyletic group. Relationships with other families remain poorly recognized. Any linking of this family with the synastreids, *Acrosmilia* being allegedly intermediate (Wells 1966; Cairns 1984; Hoeksema 1989), is contradicted by the essential dissimilarity in their microstructure and skeletal architecture (compare p. 372). Instead, the fungiid microstructure has much in common with that of the Faviina (p. 364). In fact, the Fungiidae may represent a lineage evolved from the Faviidae early in the Tertiary (Roniewicz & Morycowa 1993).

The suborder Fungiina should be thus restricted, if used at all, to the nominative family. 'The suborder Fungiida has therefore to be split and other systematic units, based on different characters, should be proposed to receive its genera' (Gill 1981: p. 308). L. Beauvais (1981, repeated in Chevalier 1987) has already excluded the superfamily Archaeofungioidea from the Fungiina and raised it to the subordinal rank — as Archaeofungiina. At least some of the remaining superfamilies of the 'Fungiina' deserve the equal rank.

Characteristics of the microsolenine corals

Corals from the families Microsolenidae and Latomeandridae have many growth forms in common. They share with the apparently less morphologically variable Synastreidae and the mostly uniformly shaped Cunnolitidae, very specific, compound pennular trabeculae and regularly perforated septa, which indicates their common descent. The septal apparatus con-

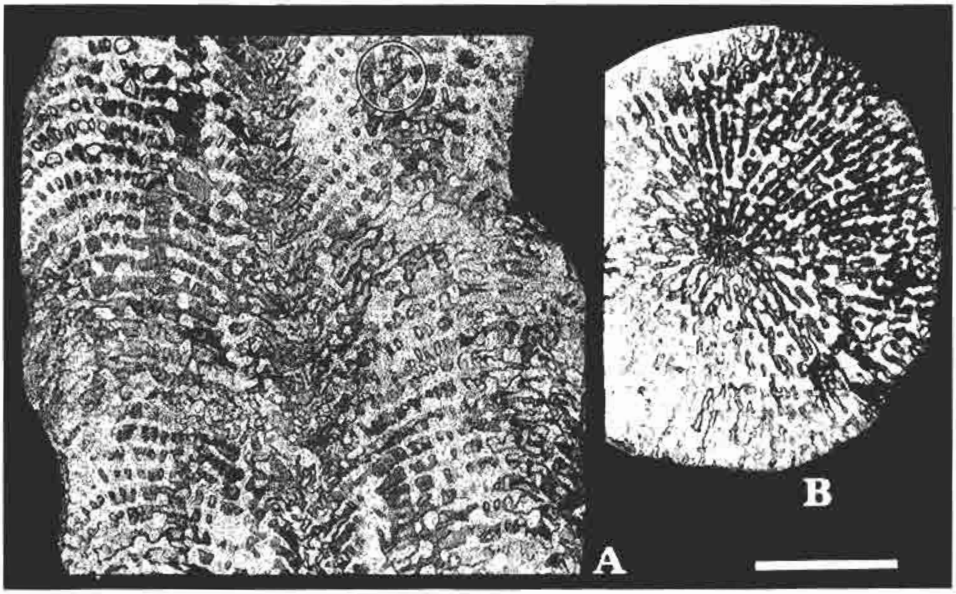

Fig. 1. *Dermoseris delgadoi* Koby 1887 (Microsolenidae), Lower Kimmeridgian, Dobrogea, Roumanie. Regularly perforated microsolenid septa in longitudinal (A) and transverse (B) sections, FGGUB. 235. ❑A. Menianes of pennular origin are regularly distributed along the septa; trabeculae are connected with each other by pennulae while remaining free in the interpennular segments, causing regularly perforated structure of septal blades. Rows of synapticulae circular in section (encircled) follow the course of trabeculae. ❑B. Perforated septa are connected with each other by abundant synapticulae (from Roniewicz 1976: pl. 32). Scale bar — 3 mm.

sists of numerous, closely arranged septa (except for small-corallite forms) and abundant vesicular endotheca. Together, they form a well defined group, easily distinguished from other corals. We propose a subordinal rank for it as Microsolenina subordo n.

High diversity of pennular structures makes the mere presence of pennulae of limited significance in classification. Because of the apparently convergent origin of pennulae and menianes in different coral groups, we propose to distinguish a separate high rank group of corals based on a uniform trabecular pattern. The four families concerned are discussed below.

Microsolenid corals. — The microstructure typical of the new group is best exemplified by the skeletal structures of the Microsolenidae.

In his earlier papers, Gill (1966, 1967, 1968, 1982) described a then peculiar structure of septa in *Chomatoseris* and called attention to similar features in a number of Mesozoic microsolenid and latomeandrid genera, namely in *Calamoseris, Comoseris, Dimorpharaea, Dimorphastraea, Microsolena, Polyphylloseris*, and a Liassic microsolenid coral (1968) recognized later (L. Beauvais 1986) as *Proleptophyllia*. The same structure has been observed in the Jurassic genus *Dendraraea* (Lafuste 1971 — discussed as

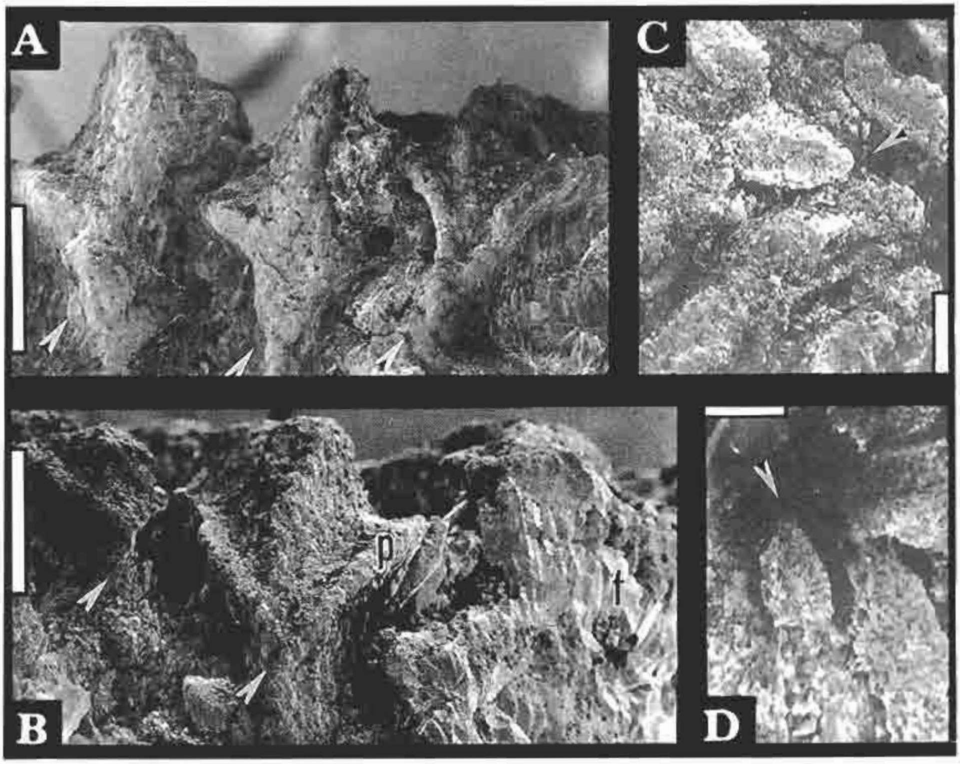

Fig. 2. *Microsolena* sp. (Microsolenidae), Callovian, Moscow region. Ornamentation of the internal septal edge in SEM, ZPAL zp/H.IV/1. V-shaped denticles (arrows) develop from (p) pennulae meeting at the internal edge of septa. ❑A. Axial view of septa showing details of a structure of adaxial trabeculae of three septa: at left, an irregular denticle of mi-pennular origin; at the centre and at right, two regularly built denticles of pennular origin. ❑B. Axial view of septa: at left and at the centre – denticles of pennular origin, at right – longitudinally broken trabecula showing subvertically arranged bundles of fibres (f). ❑C, D. Upper views of trabeculae: triangular denticles (arrows) and crenulated pennular edge (left lower corner). Scale bars in A and B – 200 µm, in C and D – 500 µm.

a pennulae-bearing Jurassic spongiomorph: Gill 1993) and in many others (*Meandraraea*, *Hydnophoromeandraraea*: Morycowa 1971, *Eocomoseris*: Melnikova *et al.* 1993).

Our review of septal microstructure in microsolenid corals is based on a series of papers by Gill (1967, 1968, 1982, 1993), to which we also add our own observations.

The trabeculae lack any traces of segmented, sclerodermitic structure (Gill 1967) and show serially arranged collar-like expansions along the trabeculae – pennulae (Gill 1966, 1967, 1968). The pennulae originate at the growing ends of the trabeculae and extend outward from them in the form of balconies (Gill 1967: text-fig. 2a–c, 1968). Mi-pennula (a half-pennular structure) appeared when a trabecular extension has developed asymmetrically on only one septal flank (Gill 1967: text-fig. 2c; Lathuilière

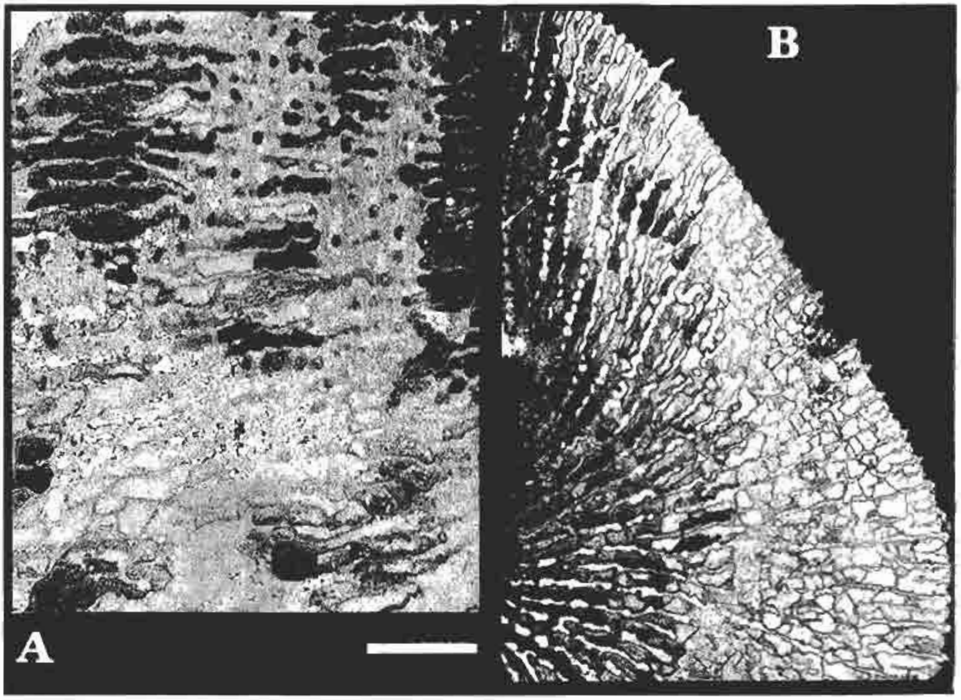

Fig. 3. *Trochoplegmopsis gregoryi* (Koby 1905) (Latomeandridae). □A. Specimen FGGUB 14 from the Upper Oxfordian, Dobrogea, Roumanie. Septum in longitudinal tangential section showing thick, vertical trabeculae (at the middle and at right), septal pores and pennulae ordered in horizontal series. □B. Specimen FGGUB 220 from the Lower Kimmeridgian, Dobrogea, Roumanie. Transverse section showing distal, porous parts of septa and solid portions of septal blades. From Roniewicz (1976: pl. 27). Scale bar – 3 mm.

& Gill 1994). Successive pennulae are regularly spaced along the trabecula (Fig. 1A). The upper surface of the pennula is concave and the distally oriented margins bear minute denticulation (Gill 1967: text-fig. 2, pl. 10: 1, 1ab; 1982: pl. 2:1–5; 1993: text-fig. 2). The pennulae within a septum can be discrete or are fused with those of the adjacent trabeculae. Pennulae merge into flanges called menianes. Menianes are developed as continuous plates (Gill 1982: pl. 1: 4) with traces of their pennular components at the margins; this is generally more distinct in the distal parts of septa. On the internal septal margin, the menianes of the opposite sides of a septum meet with each other to form a symmetrical or asymmetrical V-shape structure (Fig. 2A–D). The trabecular body is ornamented with longitudinal ridges (Gill 1993: text-fig. 2 and 3.2–3.15; Melnikova *et al.* 1993: pl. 2: 5).

The above structure can be described as pennular ornamentation of septa. The regular distribution of pennulae gives septa a regularly perforated appearance. The otherwise separate trabeculae in one septum are linked laterally with the next by pennulae. Between the pennulae, trabecular segments are not, as a rule, mutually connected (see also Fig. 1A, B).

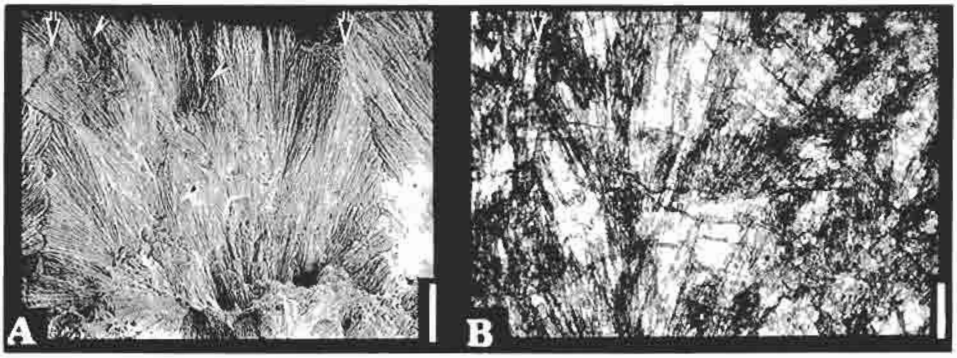

Fig. 4. Structure of polycentric trabeculae. Boundaries between adjacent trabeculae are indicated by large arrows. ❑A. *Dimorphastraea* sp. (Latomeandridae). Longitudinal section of the trabecula showing accumulation of centred bundles of fibres at the axis (at the lower right corner) and dispersed bundles at sides (arrows). Oxfordian, Poland. ZPAL H.IV/27. SEM (from Roniewicz 1983). Scale bar – 75 µm. ❑B. '*Fungiastraea*' *tendagurensis* (Dietrich) (Synastraeidae), Early Aptian, Carpathians, Poland. UJ 4P 39. Trabecula in longitudinal section. The diagenesis underlies such microstructural features as elongation of bundles of fibres and their fountain-like arrangement. Scale bar – 150 µm.

However, perforations can become completely filled with sclerenchyme, and septa then appear solid in places (e.g. *Eocomoseris* – Melnikova *et al.* 1993: pls 1, 2).

Latomeandrid corals. – Pennular ornamentation similar to that in Microsolenidae also develops in the Latomeandridae (*Dimorphastraea* – Gill 1967: pl. 8: 2a, b; *Trochoplegmopsis, Dimorphastraea, Comophyllia, Mixastrea* and *Fungiastraea* – Roniewicz 1976: pls 27–31; *Discotrochus* – Gill & Russo 1980: text-fig. 3C–F; *Aspidiscus* – Gill & Lafuste 1987: text-fig. 6–8, pl. 2: 3–9). Primary regular perforation, observed distally in the septa of latomeandrids (*Trochoplegmopsis* – Fig. 3A, B), becomes more or less obliterated proximally, as the trabeculae adhere to one another and coalesce (*Discotrochus* – Gill & Russo 1980: text-fig. 3C, D; *Dimorphastraea* – Fig. 4A). The edges of pennulae are oriented distally. The menianes in some latomeandrids are not so distinctive and continuous as in the microsolenids, their pennulae being usually discrete (examples: *Latomeandra* and *Comophyllia* – Roniewicz 1976: pl. 27: 4c, pl. 29: 3b, c; *Discotrochus* – Gill & Russo 1980: text-fig. 3c, d). However, continuous menianes are known as well (*Dimorphastraea* – Roniewicz 1976: pl. 30: 5, 6, pl. 31: 5b, c, 1983: pl. 59: 4; *Aspidiscus* – Gill & Lafuste 1987: pl. 1: 2 and pl. 2: 8, 9).

Cunnolitid and synastreid corals. – Although pennulae of corals from these groups were actually the earliest to have been presented in the literature (Late Cretaceous *Cyclolites* recte *Cunnolites* and *Leptophyllia* – Pratz 1882: pl. 1: 3, 3a, b, 9), their microstructures are still poorly known. Some details can be observed in two Urgonian synastreid corals described by Morycowa as *Fungiastraea* (Morycowa 1964: text-fig. 17, pl. 22: 3a, and

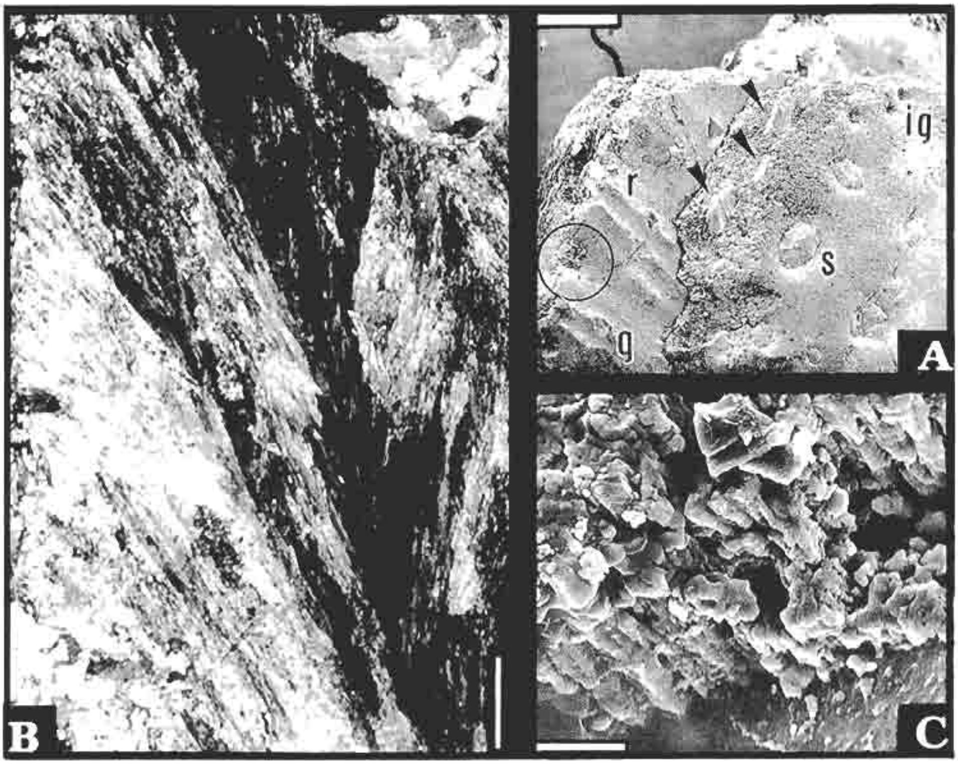

Fig. 5. *Cunnolites* sp. (Cunnolitidae), Late Cretaceous, Gosau. Structure of polycentric trabeculae. UJ P-1. ❑A. Lateral view: at left, septal blade of a low-order septum built of large trabeculae and provided with rare pores (encircled), and thin, flat trabeculae (black arrows) of a regularly perforated high-order septum; at right, interseptal marly deposit pierced by regularly distributed rod-like synapticulae (s). Trabeculae show longitudinal ridges (r) continuing into rudimentary pennular ornamentation developed in the form of horizontal rows of large granulations (g), here broken off; imprints of granulations are preserved in the form of pits in the interseptal deposit (ig). ❑B. Longitudinal radial thin section of a trabecula displaying a complex arrangement of bundles of fibres and their subvertical orientation. ❑C. Transverse broken section of a central part of a trabecula displaying subvertical, parallel, lateraly striated bundles of fibres constituting trabecular body. A and C: SEM. B: transmitted polarized light. Scale bars in A — 500 µm, in B — 127 µm, in C — 5 µm.

text-fig. 18, pl. 22: 4b, respectively; herein: Fig. 4B) and *Fungiastraeopsis* (Morycowa 1971: text-fig. 34). Some illustrations of septal ornamentation in genera close to *Synastraea* or *Cunnolites* have been published (Late Cretaceous: Gill 1967, Turnšek 1978, M. Beauvais 1982; Late Eocene: Eliášová 1974; for details see p. 380). Synastreid septa display a general similarity of their ornamentation to that in the microsolenid corals. Some cunnolitids [*Cunnolites (Paracunnolites)* — Turnšek 1978] show the same structure, however, the shape of pennulae is different from that in microsolenids and latomeandrids (upper surface being concave in a typical microsolenid, *Chomatoseris*, while flat or descending in *Cyclolites* — Gill & Russo 1980: text-fig. 1D and E, respectively). Pennular margins in some synastreids show highly individualized granulations (Morycowa 1964: text-fig. 17). Similarly, denticles on cunnolitid pennular edges are individualized (*Cunnolites* – Pratz 1882: pl. 1: 3), or are completely dissociated into individual secondary trabeculae emerging on the septal sides as large granulations arranged in horizontal rows (Fig. 5A).

Complex nature of trabeculae in the Microsolenina

In the microsolenines, trabeculae do not show a singular structurally delimited axis. In the family Latomeandridae, the trabecular body is composed of fascicles of fibres that originate partly in the central part but some of them arise at various distances from it (*Dimorphastraea* – Roniewicz 1983: pl. 59: 3; pl. 61: 1, 2; synastreid described as *Fungiastraea* – Morycowa 1964: text-fig. 17; herein Fig. 4A and B, respectively). This results in complex features of their microstructure when observed in transverse and longitudinal sections. These trabeculae were named 'polycentric' earlier in this paper (p. 363).

Gill & Lafuste (1971: pp. 27–28, text-fig. 17b) emphasised that the microstructure of distally rounded or moniliform trabeculae (exemplified by microsolenid corals) is fountain-like. We have noted that in *Cunnolites* the trabeculae can show subparallel bundles of fibres with a diameter ca. 2 µm, dividing at an acute angle (Fig. 5B). In SEM, the cross sections show bundles of fibres in the form of subvertical micro-rods with a minutely striated lateral surface (Fig. 5C). Longitudinal ridges on the surface of the trabecular body are characteristic of the microsolenine corals and express the complex structure of trabeculae (*Cunnolites* – Pratz 1882: pl. 1: 3–3b and Gill & Russo 1980: text-fig. 1E; herein Fig. 5A; *Chomatoseris* – Gill 1967: pl. 9: 1a and 1968: text-figs 2 and 3; *Dendraraea* – Gill 1993: text-figs 3.2, 3.3, 3.8, 4.7, 4.11; *Eocomoseris* – Melnikova *et al.* 1993: pl. 2: 5).

Among Triassic corals an apparently analogous structure has been reported in *Silesiastraea* (Morycowa 1988: text-fig. 9A, B). In transverse and longitudinal sections of interpennular trabecular sectors, an ornamentation has been observed which can be interpreted as an equivalent of longitudinal ridges of the microsolenine coral trabeculae (Morycowa 1988: text-fig. 9C).

Origin of the microsolenine compound trabecular structure

Septal structure in the Microsolenina differs from that in other flange-bearing corals because of the distinct structure of their compound trabeculae and in their regular septal primary porosity. Although its development is not yet known, it is likely that their structure evolved in the

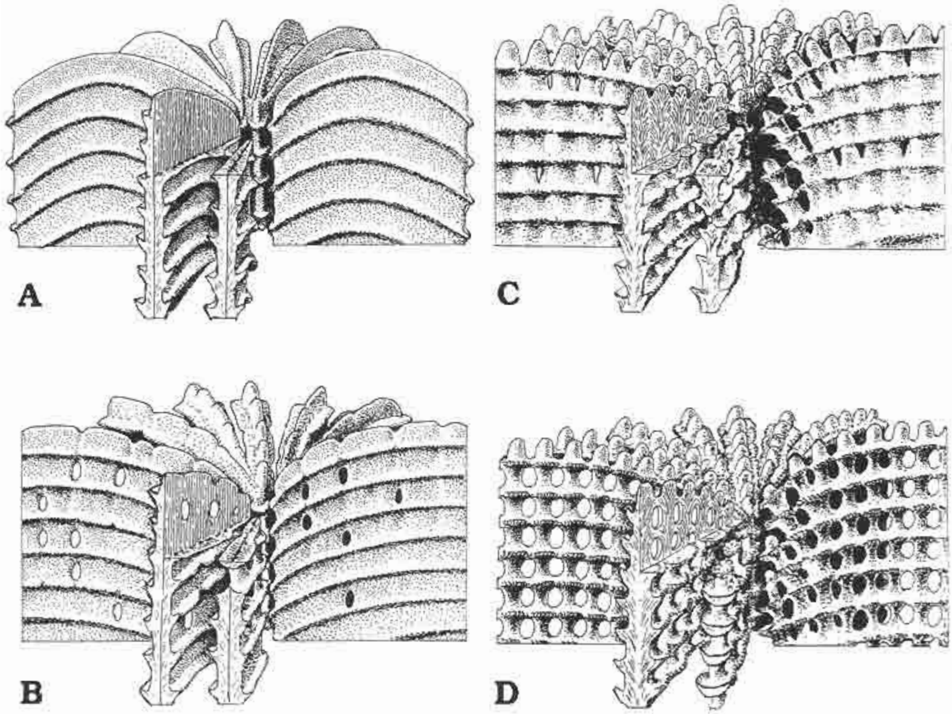

Fig. 6. Possible stages of development of latomeandrid and microsolenid patterns of pennular septal microstructure (for the sake of clarity, columellar structures and dissepiments are omitted). ❑A. Triassic *Astraeomorpha* (Astraeomorphidae) – a precursor structure showing solid, minitrabecular septa with menianes. ❑B. Triassic *Seriastraea* (Astraeomorphidae) — a pattern in which aggregations of minitrabeculae cause development of septal lobes initiating formation of pennular trabeculae; perforation embryonic. ❑C. Jurassic *Fungiastraea* – latomeandrid pattern with well differentiated pennular trabeculae associated with irregular porosity of septa; parietal columella is formed by free adaxial trabeculae. ❑D. Jurassic/Cretaceous *Microsolena* – microsolenid pattern with individualized trabeculae linked with each other by their pennulae to form regularly perforated septal blades.

Triassic from flange-bearing corals derived from the astreomorphid stem (Fig. 6). The structure could have derived from astreomorphids, with their minitrabecular meniane-bearing septa and rod-like synapticulae (Melnikova 1971; Roniewicz 1989; Roniewicz & Morycowa 1993). There, the minitrabeculae already tend to disrupt the close arrangement and to cluster into isolated larger units, thereby initiating the formation of compound trabeculae and porous structure of septa. This step in microstructural evolution is represented by *Seriastraea* Schäfer & Senowbari-Daryan *1978* (Roniewicz *1989*: pl. *31*: *1*c, d, pl. *32*: *1*a–c). *The next step* achieved by some Triassic pennular corals, i.e. a structure of integrated, compound trabeculae, with longitudinal micro-ridges, seems to be represented by *Silesiastraea*. Typically microsolenine trabeculae appeared at the very beginning of the Jurassic (Hettangian/Sinemurian *Eocomoseris* – Melnikova *et al.* 1993) and persisted beyond the Cretaceous boundary up to the Late Eocene (*Discotrochus* — Gill & Russo 1980; *Leptophyllon* and others — Eliášová 1974).

Other flange-bearing scleractinians

Flanged septa vary surprisingly in structure in different non-microsolenine corals. Apparently, septal ornamentation similar to that discussed above is known in some fossil and Recent coral groups with permanently compact septa.

Although subhorizontal flanges already occurred in solitary Palaeozoic corals from the Ordovician (*Tjanshanophyllia*) through the Permian (Devonian *Metriophyllum*, Devonian-Carboniferous *Lopholasma*, Permian *Asserculinia* — compare Hill 1981), they are most typical of many scleractinian groups, especially in the Mesozoic. In Triassic genera with minitrabecular microstructure, corals with continuous menianes are known (Astraeomorphidae: *Astraeomorpha* — e.g. Cuif 1975, and *Seriastrea* — Roniewicz 1989; Procyclolitidae: *Craspedophyllia* and *Procyclolites* — Cuif 1975), as well as some with short menianes (Reimaniphylliidae: some *Retiophyllia* — Roniewicz 1989: pl. 12: 1b, d, h). Beginning in the Anisian (e.g. *Silesiastrea* — Morycowa 1988), more or less continuous menianes are known in the families characterized by thick and apparently monoaxial coalesced trabeculae, such as the Cuifastraeidae (Melnikova 1983), tropiastraeid corals (Cuif 1976), the guembelastraeid group of genera (Cuif 1976), and the Alpinophylliidae (Roniewicz 1989), amounting in total to more than 10 genera (*Karachastraea*, *Tropiastraea*, *Tropiphyllum*, *Tropidendron*, *Thamnotropis*, *Stuoresia*, *Andrazella*, *Guembelastraea*, *Cuifastraea*, *Gillastraea*, *Chevalieria*, *Alpinophyllia*, *Stuoresimorpha*). Pennular structures resembling free pennulae of Jurassic *Dendraraea* (Gill 1993) are known in the Spongiomorphidae (*Spongiomorpha*), a group apparently close to Astraeomorphidae and recently re-established within the scleractinian taxonomy (Gautret *et al.* 1992; Cuif & Gautret 1993).

In thick-trabecular corals with non-coalesced simple trabeculae and perfectly compact septa, flat pennular structures are developed which either constitute sets paralleling distal septal edges and resembling menianes (in omphalophylliids — Cuif 1975: pl. 6: 1, 3, pl. 7: 2, 3) or are disposed randomly (in *Pamiroseris* — Roniewicz 1974: pl. 10: 1c).

Only a few post-Triassic corals with compact thick-trabecular septa show pennular ornamentation. In the Middle Jurassic, long menianes are observed in a genus characterized by massive to irregularly porous septa — *Periseris* (Lathuilière 1990). Another coral, *Thamnasteria* (Thamnasteriidae), common especially in the Middle and Late Jurassic, displays short and denticulate pennulae with horizontal edges which rarely coalesce into two- or three-pennular units (Morycowa 1971: text-fig. 31A, B; Roniewicz 1983: text-fig. 3B, C). The Oxfordian to Cenomanian *Thamnoseris* has similar pennulae. In the Recent fauna, Chevalier (1987) mentioned pennular ornamentation in rare genera of the following non-microsolenine families: Agariciidae (*Pavona*, *Pachyseris*, *Leptoseris*), Siderastreidae (*Coscinaraea* and *Meandroseris*) and Psammocoridae (*Psammocora*).

Among Cenozoic mini-trabecular corals, i.e. caryophylliids, particular species in few genera show short menianes parallel to the distal septal margin (*Caryophyllia* – Cuif 1968a: pl. 2: 6; Zibrowius 1980: p. 60, pl. 22: M; Russo 1981: pl. 54: 3a; *Sclerhelia* – Zibrowius 1974; *Paracyathus* – Zibrowius 1980: pl. 44: K; *Acanthocyathus* – Stolarski 1991: p. 43), homologous to those in the Triassic genus *Retiophyllia* mentioned above.

Function of flange-like ornamentation

Pennulae and menianes might have provided support for polyp tissue during coral growth (Gill 1967, 1982). However, the Recent deep-water filtering agariciid zooxanthellate coral, *Leptoseris fragilis*, has symmetrical menianes on septal sides (Schlichter 1992), that support tubular ramifications of the coelenteron arranged into a particular gastrovascular system. This coral is also known for its fungiform colonial coralla developing by irregular circumoral budding. The mode of life of *Leptoseris fragilis*, with its expanded thin coralla, seems to correspond closely to that of many pennular fossil corals. This applies especially to the microsolenid and latomeandrid corals of fungiform or lamellate colonies expanded over several square decimetres, abundant in late Jurassic biomicritic limestones (e.g. Roniewicz & Roniewicz 1971: p. 410, pl. 1: 1, 2; Morycowa 1974: text-fig. 2 and 1985: p. 55) or to corals adapted to unconsolidated substrates, such as the Jurassic *Chomatoseris* (Gill & Semenoff-Tian-Chansky 1971, Gill & Coates 1977) and *Genabacia* (Gill 1972), Cretaceous *Aspidiscus* (Gill & Lafuste 1987) and the cunnolitids (Turnšek 1978), and Tertiary *Discotrochus* (Gill & Russo 1980). The same can be said about meniane-bearing Triassic corals, especially to the expanded lamellate colonies of *Thamnotropis* (Turnšek 1986), *Seriastraea* (Schäfer & Senowbari-Daryan 1978), the fungiform solitary or colonial *Procyclolites* (Frech 1890), and others.

From the beginning it was clear that the taxonomic significance of pennulae (Gill 1967) was likely to increase with increasing knowledge of their structural details. Subsequently, recognition of various pennular structures permitted to discriminate numerous pennular coral genera amongst homeomorphic taxa (especially in the Triassic, e.g. *Tropiastrea* – Cuif 1968b, *Guembelastraea*, *Andrazella*, *Stuoresia* – Cuif 1976) as well as helped to make more precise diagnoses of other genera (*Thamnasteria* – Roniewicz 1983) and to designate new families (e.g. Cuifastraeidae Melnikova 1983). From the taxonomical point of view, the most significant characters appear to be the detailed structures of trabeculae and septa, the outward expression of which is microornamentation.

Diagnoses of new and emended taxa

Suborder Microsolenina subordo n.

Diagnosis. – Radial elements costoseptal or biseptal in type, densely arranged, formed by compound trabeculae and structurally fenestrate. Trabeculae with longitudinal striation. Septal faces ornamented with pennulae which can fuse into menianes, or dissociate into lateral axes. Pennular edges ornamented. Synapticulae trabecular in origin, rod-like. Columella parietal or monotrabecular, if developed. Dissepiments vesicular, isometric or flat and wide, depending on family.

Families included. – Microsolenidae Koby 1890, Latomeandridae Alloiteau 1952, Synastreidae Alloiteau 1952, Cunnolitidae Alloiteau 1952.

The range of our new suborder is narrower in comparison to that of the superfamily Pennulacea Gill 1967. Gill (1967: p. 73) placed the latter in the suborder Fungiina and encompassed within it all pennular corals regardless of differences in other features of their skeletal structure. Thus, he included not only the Synastreidae, Latomeandridae, Microsolenidae and Cunnolitidae, but also the Siderastreidae and Agariciidae, together with genera from the families Thamnasteriidae, Astraeomorphidae, and others.

Stratigraphical range. – Frequent from the Sinemurian to the Campanian; rare in the Eocene.

Remarks. – The families Microsolenidae and Latomeandridae show complete morphogenetic spectra evolving in parallel. In both families, solitary and all possible colonial growth forms and colony types are present. In this respect, the families Synastreidae and Cunnolitidae are different, the former embracing only solitary and thamnasterioid forms while the latter are predominantly discoidal solitary corals.

The diagnoses and ranges of the families Synastreidae and Cunnolitidae are awaiting emendation. Having no possibility to execute any revision of these groups, we limit ourselves to remarks on the structure of septa based chiefly on literature and completed by our observation of some species.

It is noteworthy, that synastreid and cunnolitid groups represent a new tendency in the evolution of the structure of trabeculae – individualization of lateral axes forming pennulae. This process reaches culmination in a kind of granular lateral ornamentation observed within the genus *Cunnolites*.

Family Microsolenidae Koby 1890

Figs 1, 2, 6; Table 1.

Emended diagnosis. – Solitary and colonial. Radial elements regularly fenestrate, anastomosing. Pennular edges directed upwards, ornamented with rounded, equal dentation. Synapticulae abundant, regularly distributed. Columella parietal or styliform – monotrabecular, if present. Dissepiments in the form of flat and wide, thin-walled dissepiments.

Table 1. Published sources of information on microsolenid septal microstructure and/or ornamentation (ideograms, drawings, legible micrographs).

Genus	Author	Illustrations
Chomatoseris	Gill 1967	text-fig. 2, 3b; pl. 7; pl. 9: 1, 1a, b; pl. 10
	Gill 1968	text-figs 1, 2, 3A–E; pl. 62; pl. 63: A3, A5–A7, A9, A11, B4, B8–9, C2, C3/C11, C4, C6, C8, C11–12; pl. 64; pl. 65: D8, E1–4, F1, F7/8, F9, F11; pl. 66: 1, 3
	Gill 1982	pl. 2: 1, 2; pl. 3: 3, 4
Comoseris	Koby 1889	pl. 130: 7
	Gill 1967	pl. 9: 2
	Roniewicz 1976	pl. 34: 2a, b, 5
Dendraraea	Lafuste 1971	fig. 1–3
	Gill 1993	fig. 2; fig. 3.4–3.18; fig. 4.4–4.12
Dermoseris	Roniewicz 1976	pl. 32: 1a, b; reproduced herein Fig. 1
Dimorpharaea	Gill 1967	text-fig. 3a, 7; pl. 8: 3b; pl. 11: 1; pl. 12: 1, 1a, 3b
	Gill 1968	text-fig. 3G; pl. 65: D4, E5/E6, F5–7; pl. 66: 4
	Gill 1982	text-fig. 4; pl. 3: 1, 2
Eocomoseris	Melnikova *et al.* 1993	pls 1, 2
Hydnophoromeandraraea	Morycowa 1971	text-figs 7b, 35, 36; pl. 34
Kobya	Pandey & Fürsich 1993	pl. 6: 8
Meandraraea	Koby 1889	pl. 130: 5
	Morycowa 1971	text-figs 7b, 35
Microsolena	Koby 1889	pl. 130: 6
	Roniewicz 1976	pl. 33: 5a, b
	Gill 1982	pl. 1: 4
	Pandey & Fürsich 1993	pl. 9: 3b, 5, 12
	herein	Fig. 2
microsolenids indet.	Gill 1968	text-fig. 3F, H; pl. 63: B5–6
Polyphylloseris	Morycowa 1971	text-fig. 7b, pl. 32: 1d–f
	Gill 1982	pl. 2: 3, 4
Proleptophyllia (figured as indet.)	Gill 1968	pl. 6: 2b
microsolenid described as *Tricycloseris*	Pandey & Fürsich 1993	1993 pl. 7: 9

Genera included. – Simple: cupolate, free – *Chomatoseris* Thomas 1939; fungiform, calice convex – *Trochoplegma* Gregory 1900; fungiform, calice flat – *Trocharaea* Etallon 1864; cylindrical, calice flat – *Proleptophyllia* Alloiteau 1952; simple passing into incipient meandering colonies

— *Tricycloseris* Tomes in Gregory 1900. Phaceloid: calice convex — *Dermoseris* Koby 1887. Thamnasterioid: cupolate — *Genabacia* Milne Edwards & Haime 1849; surface flat, calices chaotic and flat, columella lacking or parietal — *Microsolena* Lamouroux 1821 and *Gosaviaraea* Oppenheim 1930; calices convex — *Polyphylloseris* de Fromentel 1857; circumoral series — *Dimorpharaea* de Fromentel 1861; calices in series — *Kobya* Gregory 1900; branching, axial corallites lacking, columella monotrabecular — *Dendraraea* d'Orbigny 1849. Thamnasterioid-cerioid: columella monotrabecular — *Eocomoseris* Melnikova, Roniewicz, & Löser 1993. Meandroid: uniserial, calices distinct, collines tholiform or tectiform — *Meandraraea* Etallon 1858; calices indistinct — *Michelinaraea* Alloiteau 1952; uni- and multiserial — *Comoseris* d'Orbigny 1849. Meandroid to hydnophoroid: *Hydnophoromeandraraea* Morycowa 1971.
Stratigraphical range. — Hettangian/Sinemurian through Campanian, ?Maastrichtian.

Family Latomeandridae Alloiteau 1952

Figs 3, 4A, 6; Table 2.

(corrected from Latomeandriidae Alloiteau 1952)

Emended diagnosis. — Solitary and colonial. Radial elements anastomosing, compact or regularly fenestrate at the distal or distal/internal region. Pennular edges directed upwards and ornamented with rounded, equal dentation. Synapticulae scarce. Columella parietal, composed of trabecular lobes. Dissepiments vesicular, abundant.

Genera included. — Simple: fungiform, calice flat — *Protethmos* Gregory 1900; infundibuliform, lobate — *Trochoplegmopsis* Roniewicz 1976; turbinate — *Neothecoseris* Eliášová 1994; *Latohelia* Loeser 1987; discoid, minute — *Discotrochus* Milne Edwards & Haime 1948. Phaceloid: lamellar linkages — *Latomeandra* Milne Edwards & Haime 1848; ?lack of lamellar linkages — *Calamoseris* Alloiteau 1957. Cerioid: nonconfluent, lack of lamellar linkages — *Latiastraea* Beauvais 1964; non- and subconfluent, lamellar linkages — *Mixastraea* Roniewicz 1976. Cerioid-meandroid: nonconfluent in collines, valley-septa — *Microphyllia* d'Orbigny 1849; nonconfluent in collines, valley-septa, series centrifugal — *Comophyllia* d'Orbigny 1849; confluent in collines, valley-septa — *Vallimeandra* Alloiteau 1957. Thamnasterioid: calices chaotic — *Stylomeandra* de Fromentel 1857, *Fungiastraea* Alloiteau 1952, and *Astreofungia* Alloiteau 1952; circumoral series — *Dimorphastrea* de Fromentel 1857; concentric series, collines tholiform — *Koilomorpha* Alloiteau 1952 and *Brachymeandra* Alloiteau 1957; serial to chaotic, subcerioid, collines tholiform — *Brachyseris* Alloiteau 1957. Discoid, meandroid-hydnophoroid, collines tectiform — *Aspidiscus* Koenig 1825. Subplocoid — *Baryphyllia* de Fromentel 1857. Plocoid — *Ovalastraea* d'Orbigny 1849.

Genera *Aspidiscus* and *Discotrochus* have been shifted to the family Latomeandridae due to their having upward-directed pennulae and proximally diminishing septal perforation. Up to now, *Discotrochus* has been

Table 2. Published sources of data on latomeandrid septal microstructure and /or ornamentation (ideograms, drawings, legible micrographs).

Genus	Author	Illustrations
Aspidiscus	Gill & Lafuste 1987	text-figs 6–8; pl. 1: 2; pl. 2: 3–9
Astreofungia	Eliášová 1994	pl. 2: 1, 2
Brachyseris	Eliášová 1994	pl. 4: 1c, 1d
Calamoseris	Gill 1967	text-fig. 1; pls 5, 6, pl. 12: 4, 5
Chorisastrea	Gill 1967	pl. 12: 2b
Comophyllia	Roniewicz 1976	pl. 29: 3b, c
Dimorphastrea	Gill 1967	text-fig. 3a; pl. 8: 2a; pl. 11: 2a, b
	Roniewicz 1976	pl. 30: 6, 7; pl. 31: 5b, c, 6
	Roniewicz 1983	pl. 59: 1, 4; reproduced herein Fig. 4A
	Eliášová 1994	pl. 1: 2a, 2b
Discotrochus *	Gill & Russo 1980	fig. 3A–F
Fungiastraea (as *Thamnasteria*)	Koby 1889	pl. 130: 3, 3a
Microphyllia (as *Latimeandra*)	Koby 1889	pl. 130: 1, 2
	Eliášová 1993	pl. 2: 3b
Neothecoseris	Eliášová 1994	pl. 3: 5; pl. 7: 4
Ovalastrea	Eliášová 1994	pl. 5: 1, 2c, 3
Protethmos	Pandey & Fürsich 1993	pl. 8: 6, 8a, 10
Trochoplegmopsis	Roniewicz 1976	pl. 27: 1a–c, 3a, b; reproduced herein Fig. 3

* The septal ornamentation of the Miocene form described by Chevalier (1962: fig. 153a–c) as *Discotrochus* seems to differ from a typical pennular latomeandrid ornamentation.

included in the Fungiidae (Vaughan & Wells 1943; Wells 1956; Chevalier 1987), while the position of *Aspidiscus* has wandered from the Synastraeidae in Vaughan & Wells (1943), through the Cyclolitidae in Wells (1956), to Funginellidae in Alloiteau (1952) and Chevalier (1987).

Stratigraphical range.— Pliensbachian to Eocene.

Family Synastreidae Alloiteau 1952

Fig. 4B; Table 3.

Remarks. — The pennulae in some Late Eocene synastreids have concave upper surfaces and denticulated edges resembling in this regard latomeandrid & microsolenid corals (Eliášová 1974: pl. 4: 1b), while in others they are not so regularly developed (Eliášová 1974: pl. 4: 3); septal perforation is imperceptible. Some individualization of particular lateral axes observed on the edge of pennulae of other synastreid corals (Aptian corals described as *Fungiastrea* — Morycowa 1964) indicates that in this group there is initiated a tendency to decompose the pennulae.

The endotheca is vesicular, abundant.

Stratigraphical range. — Aptian to Eocene.

Table 3. Published sources of information on (I) synastreid and (II) cunnolitid septal microstructure and/or ornamentation (ideograms, drawings, legible micrographs).

Genus	Author	Illustrations
I. Synastreidae		
Fungiastraeopsis	Morycowa 1971	text-fig. 34
Hydnophyllon	Eliášová 1974	pl. 4: 3
Leptophyllia *	Reuss 1854	pl. 6: 4, 5; pl. 7: 2, 3
	Pratz 1882	pl. 1: 9
	Koby 1889	pl. 129: 17–19
	Eliášová in press	pl. 3: 1
Leptophyllon	Eliášová 1974	pl. 4: 1b; pl. 6: 1
Synastrea	Gill 1967	pl. 11: 3
Synastreid coral described as *Fungiastraea tendagurensis*	Morycowa 1964	text-fig. 17; pl. 22: 3b; text-fig. 18; pl. 22: 4b
	herein	Fig. 4B
II. Cunnolitidae		
Cyclolites (recte *Cunnolites*)	Pratz 1882	pl. 1: 1–8
	Gill 1967	pl. 8: 1a
	Gill & Russo 1980	fig. 1E
Cunnolites	Turnšek 1978	pls 18, 19
	M. Beauvais 1982	pl. 22: 1b; pl. 67: 3, 4; pl. 68: 1, 2
	herein	Fig. 5
Paracunnolites	M. Beauvais 1982	pl. 42: 4
Plesiocunnolitopsis	M. Beauvais 1980	fig. 1B

* Eliášová in press indicated that the type species of *Leptophyllia* is a pennular coral. As such, this genus cannot link the Fungiidae with the microsolenines.

Family Cunnolitidae Alloiteau 1952

Fig. 5; Table 3.

Remarks. — The illustrations given by Pratz (1882: pl. 1: 3, 3a, b), Gill & Russo (1980: text-fig. 1E) and our own observations (Fig. 5A) demonstrate that pennulae are different in shape from those of latomeandrid-microsolenid-synastreid type. Cunnolitid pennulae have flat upper surfaces and horizontal or downard-directed coarsely ornamented edges, or they are dissociated into separate granulations.

Turnšek (1974) presents micrographs of a cunnolitid having regular porosity throughout the septal blades, and regularly distributed menianes. A cunnolitid specimen from the Gosau beds examined by us shows subcompact structure in low order septa, regularly perforated high order septa, regular rod-like synapticulae, striated trabeculae and pennulae dissociated into rows of granulations (Fig. 5A). Such a large structural diversity of cunnolitids as well as vague morphologic criteria to distinguish

Cunnolites from *Paracunnolites*, *Plesiocunnolites*, or *Plesiocunnolitopsis*, show that cunnolitid corals need a taxonomic revision based on microstructutral criteria.

The endotheca in the here examined *Cunnolites* sp. is formed of vesicular, isometric dissepiments.

Stratigraphical range. — Late Cretaceous.

Acknowledgments

We thank Dr. Jerzy Dzik for preparing the drawings. SEM micrographs were taken by Dr. Janusz Błaszyk in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw. We owe our warmest thanks to Dr. Bernard Lathuilière for his taxonomical suggestions, and to Dr. Ann Budd, Dr. Brian Rosen and Dr. Helmuth Zibrowius for reviewing the manuscript, discussion and information concerning recent corals as well as for the linguistic improvement of the text.

References

Alloiteau, J. 1952. Madréporaires post-paléozoïques. In: J. Piveteau (ed.) *Traité de Paléontologie* **1**, 539–684. Masson et Cie. Paris

Beauvais, L. 1981. Sur la taxinomie des Madréporaires mesozoïques. *Acta Palaeontologica Polonica* **25**, 3–4, 345–360.

Beauvais, L. 1986. Monographie des Madréporaires du Jurassique inférieur du Maroc. *Palaeontographica* **194 A**, 1–68.

Beauvais, M. 1982. Révision systématique des Madréporaires des couches de Gosau (Crétacé supérieur, Autriche). *Travaux du Laboratoire de Paléontologie des Invertébrés, Université Pierre et Marie Curie. Paris VI.* 5. Atlas — Figures.

Bryan, W.H. & Hill, D. 1941. Spherulitic crystallization as a mechanism of skeletal growth in the Hexacorals. *Proceedings of the Royal Society of Queensland* **52**, 78–91.

Cairns, S. 1984. An application of phylogenetic analysis to the Scleractinia: Family Fungiidae. *Palaeontographica Americana* **54**, 49–57.

Chevalier, J.P. 1962. Recherches sur les Madréporaires et les formations récifales miocènes de la Méditerranée occidentale. *Mémoires de la Société géologique de France (n.s.)* **40** (1961), 1–562; atlas.

Chevalier, J.P. 1971. Les Scléractiniaires de la Mélanesie Francaise. Première Partie. *Expédition Francaise sur les récifs coralliens de la Nouvelle Calédonie* **5**, 1–307.

Chevalier, J.P. 1975. Les Scléractiniaires de la Mélanesie Francaise, Deuxième Partie. *Expédition Francaise sur les récifs coralliens de la Nouvelle Calédonie* **7**, 1–407.

Chevalier, J.P. 1987. Ordre des Scléractiniaires. In: P.P. Grasse (ed.) *Traité de Zoologie. Cnidaires, Anthozoaires*. **III, 3**, 403–764. Masson. Paris–New York—Barcelone–Milan–Mexico–Sao Paulo.

Cuif, J.P. 1968a. Etude ontogénique de quelques Madréporaires Caryophylliidae actuels et fossiles. *Mémoires du Muséum National d'Histoire Naturelle (n.s.) C. Sciences de la Terre* **16**, 3, 101–156.

Cuif, J.P. 1968b. Note sur le genre *Toechastraea* Volz, 1896. *Bulletin de la Société géologique de France (7 ser.)* **9**, 903–908.

Cuif, J.P. 1973. Recherches sur les Madréporaires du Trias. I. Famille Stylophyllidae. *Bulletin du Muséum d'Histoire Naturelle, sér. 3*, **97**, *Sciences de la Terre* **17**, 211–291.

Cuif, J.P. 1975a. Recherches sur les Madréporaires du Trias. II. Astraeoidea. Revision des genres *Montlivaltia* et *Thecosmilia*. Etude de quelques types structuraux du Trias de

Turquie. *Bulletin du Muséum d'Histoire Naturelle. ser. 3.* **275**. *Sciences de la Terre* **40**. 293–400.

Cuif. J.P. 1975b. Recherches sur les Madréporaires du Trias. III. Etude des structures pennulaires chez les Madréporaires triasiques. *Bulletin du Muséum d'Histoire Naturelle. ser. 3.* **310**. *Sciences de la Terre* **44**. 45–127.

Cuif, J.P. 1976. Recherches sur les Madréporaires du Trias. IV. Formes cério-méandroïdes et thamnasterioïdes du Trias des Alpes et du Taurus sud-anatolien. *Bulletin du Muséum d'Histoire Naturelle. ser. 3.* **381**. *Sciences de la Terre* **53**. 68–194.

Cuif, J.P. 1977. Arguments pour une relation phylétique entre les Madréporaires paleozoïques et ceux du Trias. Implications systématiques et l'analyse microstructurale des Madréporaires triasiques. *Mémoires de la Société géologique de France (n.s.)* **56**. 129. 1–54.

Cuif. J.P. & Gautret. P. 1993. Evolution des Scléractiniaires: diversité des architectures poreuses au Trias supérieur. *Géobios* **26**. 405–412.

Duncan, P.M. 1884. Observations on the madreporarian family – the Fungiidae, with especial reference to the hard structures. Pt. 1. *Journal of the Linnean Society. Zoology* **17**. 137–162.

Eliášová. H. 1974. Hexacorallia et Octocorallia du Paleogene des Carpathes externes. *Sbornik geologickych ved. Paleontologie* **16**. 105–156.

Eliášová. H. 1994. Latoméandrides (Scléractiniaires) du Crétacé supérieur de Bohème (République tchèque). *Věstnik českého geologického ústavu* **69**. 2. 1–17.

Eliášová. H. (in press) Cunnolitidae du Crétacé de Bohème (Scléractiniaires. Fungiina) Cénomanien supérieur – Turonien inférieur: République tchèque. *Věstnik českého geologického ústavu.*

Erina. M.V. & Kim. A.I. 1981. On some Ordovician Scleractinia-like corals from the South Tien-Shan. *Acta Palaeontologica Polonica* **25**. 375–379.

Frech. F. 1890. Die Korallenfauna des Trias. Die Korallen der juvavischen Triasprovinz. *Palaeontographica* **37**. 1–116.

Gautret. P., Ezzoubair. F.. & Cuif. J.P. 1992. Recherche sur les affinités des Spongiomorphidae Frech. 1890. 1 – Caractéristiques microstructurales et minéralogiques de *Spongiomorpha acyclica* Frech. 1890. *Géobios* **25**. 345–355.

Gill. G.A. 1966. Quelques précisions sur les septes perforés des Polypiers mésozoïques. *Compte rendu sommaire des séances de la Société géologique de France* **5**. 19.

Gill. G.A. 1967. Quelques précisions sur les septes perforés des polypiers mésozoïques. *Mémoires de la Société géologique de France (n.s.)* **46**. 106. 58–81.

Gill, G.A. 1968. Sur les pennules de Microsolenides (Coraux). Etude complémentaire. *Revista Italiana di Paleontologia e Stratigrafia* **74**. 969–986.

Gill. G.A. 1970. La structure et la microstructure septale de *Montlivaltia* Lmx.: critères nouveaux pour la systématique des Hexacoralliaires. *Comptes rendus hébdomadaires des séances de l' Academie de Sciences* **270D**. 294–297.

Gill. G.A. 1972. Croissance vers le bas et possibilité d'un deplacement autonome chez *Genabacia*, Madréporaire en petite colonie libre du Dogger. *Comptes rendus hébdomadaires des séances de l'Academie des Sciences* **274D**. 2459–2462.

Gill, G.A. 1977a. Essai de regroupement des Stylines (Hexacoralliaires) d'après la morphologie des bords internes de leurs septes. *Mémoires du Bureau de Recherches Géologiques et Minières* **89**. 283–295.

Gill. G.A. 1977b. Problèmes de structure. de classification et d'écologie chez les Hexacoralliaires fossiles et actuels. 2ème partie: travaux inédits et résumé. 1–256. *Thèse des sciences.* Université Pierre et Marie Curie. Paris VI.

Gill. G.A. 1981. The fulturae ("compound synapticulae"). their structure and reconsideration of their systematic value. *Acta Palaeontologica Polonica* **25**. 301–310.

Gill. G.A. 1982. A supposed rhythmic mechanical process in coral skeletal growth. In E. Montanaro-Gallitelli (ed.). Palaentology. Essential of Historical Geology. *Proceedings of the 1st International Meeting on Palaeontology. Venice. 2–4 June 1981*. 445–466.

Gill. G.A. 1993. Free pennulae within *Dendraraea* sp. (scleractinian coral) from the Callovian of southern Israel. *Courier Forschungsinstitut Senckenberg* **164**. 199–204.

Gill, G.A. & Coates, A.G. 1977. Mobility, growth patterns and substrate in some fossil and Recent corals. *Lethaia* **10**, 119–134.

Gill, G.A. & Lafuste, J.G. 1971. Madréporaires simples du Dogger d'Afghanistan: étude sur les structures de type "*Montlivaltia*". *Mémoires de la Société géologique de France n.s.* **50**, 115, 1–40.

Gill, G.A. & Lafuste, J.G. 1987. Structure, répartition et signification paléogeographique d'*Aspidiscus*, hexacoralliaire cénomanien de la Tethys. *Bulletin de la Société géologique de France (8 ser.)* **3**, 921–934.

Gill, G.A. & Russo, A. 1973. Présence d'une structure septale de type "Montlivaltide" chez *Trochosmilia*, Madréporaires éocène. *Annales de Paléontologie, Invertébrés* **59**, 1–27.

Gill, G.A. & Russo, A. 1980. Recognition of pennular structures typical of Mesozoic corals in *Discotrochus orbignyanus* from the Eocene of the Gulf States. *Journal of Palaeontology* **54**, 1108–1112.

Gill, G.A. & Semenoff-Tian-Chansky, P. 1972. Analogie entre la structure du squelette chez les Coraux *Combophyllum* (Devonien) et *Chomatoseris* (Jurassique), en relation avec leur mode de vie. *Comptes rendus hébdomadaires de l'Académie des Sciences* **273D**, 49–50.

Gregory, J.W. 1900. The corals. Jurassic fauna of Cutch. *Palaeontologia Indica (9 ser.)* **2**, 2, 1–195.

Hill, D. 1981. Rugosa and Tabulata. In: C. Teichert (ed.) *Treatise on Invertebrate Paleontology* **F**, *Supplement* **1**, 1, I–xi, 1–378. Boulder/Colorado.

Hoeksema, B.W. 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen* **254**, 1–295.

Jell, J.S. 1969. Septal microstructure and classification of the Phillipsastreidae. In: K.S.W. Campbell (ed.) *Stratigraphy and Palaeontology. Essays in Honour of Dorothy Hill*, 50–73. Australian National University Press, Canberra.

Jell, J.S. 1974. The microstructure of some scleractinian corals. *Proceedings of the 2nd International Coral Reef Symposium, Brisbane* **2**, 301–320.

Lafuste, J. 1971. Présence de pennules chez un Spongiomorphide du Kimméridgien de l'Ile de Ré (Charente-Maritime). *Compte rendu sommaire des séances de la Société géologique de France* 1971, **1**, 42–43.

Lathuilière, B. 1990. *Periseris*, scléractiniaire colonial jurassique. Revision structurale et taxinomie de populations bajociennes de l'est de la France. *Géobios* **23**, 33–42.

Lathuilière, B. & Gill, G.A. 1994. Possible causes to the occurrence of mi-pennulae within pennular corals — working hypothesis. *Second European Regional Meeting of the International Society for Reef Studies, Grand-Duchy of Luxembourg, Programm and Abstracts*, 84. International Society for Reef Studies.

Melnikova, G.K. (Мельникова, Г.К.) 1971. Новые данные о морфологии, микроструктуре и систематике позднетрясовых Thamnasterioidea. *Палеонтологический журнал 1971*, **2**, 21–35.

Melnikova, G.K. (Мельникова, Г.К.) 1983. Новые позднетрясовые склерактинии Памира. *Палеонтологический журнал 1983*, **1**, 45–53.

Melnikova, G.K., Roniewicz, E., & Löser, H. 1993. New microsolenid genus *Eocomoseris* (Scleractinia, early Lias — Cenomanian). *Annales Societatis Geologorum Poloniae* **63**, 3–12.

Milne Edwards, H.M. & Haime, J. 1857–1860. Histoire naturelle des Coralliaires ou Polypes proprements dits **1** (1857), 1–346. Paris.

Moore, R.C., Hill, D., & Wells, J.W. 1956. Glossary of morphological terms applied to corals. In: R.C. Moore (ed.) *Treatise on Invertebrate Paleontology* **F**, 245–251. Geological Society of America and Kansas Press.

Morsch, S.M. 1994. Mise au point sur les genres *Confusastrea* d'Orbigny et *Complexastrea* d'Orbigny (Scleractinia, Jurassique). *Annales de Paléontologie* **80**, 213–235.

Morycowa, E. 1964. Hexacoralla des couches de Grodziszcze (Néocomien, Carpathes). *Acta Palaeontologica Polonica* **9**, 3–112.

Morycowa, E. 1971. Hexacorallia et Octocorallia du Crétacé inférieur de Rarau (Carpathes orientales roumaines). *Acta Palaeontologica Polonica* **16**, 1–149.

Morycowa, E. 1974. Hexacorallia d'un bloc exotique de calcaire tithonique à Woźniki près de Wadowice (Carpathes Polonaises Occidentales). *Acta Geologica Polonica* **24**, 457–484.

Morycowa, E. 1985. Upper Jurassic Hexacorallia in the Foreland of the Polish Carpathians. *Proceeding reports of the 13th Congress of the Carpatho-Balkan Geological Association, Poland — Cracow* **I**, 52–56.

Morycowa, E. 1988. Scleractinian corals from the Middle Triassic of the Cracow-Silesia region, Poland. *Acta Palaeontologica Polonica* **33**, 91–121.

Ogilvie, M. 1897. Microscopic and systematic study of madreporarian types of corals. *Philosophical Transactions of the Royal Society of London* **187B**, 83–345.

Pandey, D.K. & Fürsich, F. T. 1993. Contribution to the Jurassic of Kachchh, Western India. I The coral fauna. *Beringeria* **8**, 3–69.

Pratz, E. 1882. Ueber die verwandtschaftlichen Beziehungen einiger Korallengattungen mit hauptsächlicher Berücksichtigung ihrer Septalstruktur. *Palaeontographica* **29**, 81–122.

Roniewicz, E. 1970. *Kobyastraea* n. gen. genre homéomorphique de *Thamnasteria* Lesouvage, 1823 (Hexacoralla). *Acta Palaeontologica Polonica* **15**, 137–151.

Roniewicz, E. 1974. Rhaetian corals of the Tatra Mountains. *Acta Geologica Polonica* **24**, 97–116.

Roniewicz, E. 1976. Les Scléractiniaires du Jurassique supérieur de la Dobrogea Centrale (Roumanie). *Palaeontologia Polonica* **34**, 23–121.

Roniewicz, E. 1983. Pennular and non-pennular Jurassic scleractinians — some examples. *Acta Palaeontologica Polonica* **27**, 157–193.

Roniewicz, E. 1989. Triassic scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. *Denkschriften der Oesterreichische Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Kl.* **126**, 1–152.

Roniewicz, E. & Morycowa, E. 1993. Evolution of the Scleractinia in the light of microstructural data. *Courier Forschungsinstitut Senckenberg* **164**, 233–240.

Roniewicz, E. & Roniewicz, P. 1971. Upper Jurassic coral assemblages of the Central Polish Uplands. *Acta Geologica Polonica* **21**, 399–422.

Russo, A. 1974. Il genre *Cyclolitopsis* Reuss (Corallo eocenico): struttura settale e sua posizione systematica. *Bolletino della Societa Paleontologica Italiana* **13**, 3–16.

Russo, A. 1981. The psychrospheric coral fauna from the Lower Pliocene of Northern Italy. *Acta Palaeontologica Polonica* **25**, 613–617.

Schäfer, P. & Senowbari-Daryan, B. 1978. Neue Korallen (Scleractinia) aus Oberrhät-Riffkalken südlich von Salzburg (Nördliche Kalkalpen, Österreich). *Senckenbergiana Lethaea* **59**, 117–135.

Schlichter, D. 1992. A perforated gastrovascular cavity in the symbiotic deep-water coral *Leptoseris fragilis*: a new strategy to optimize heterotrophic nutrition. *Helgoländer Meeresuntersuchungen* **45**, 423–443.

Sorauf, J. 1972. Skeletal microstructure and microarchitecture in Scleractinia (Coelenterata). *Palaeontology* **15**, 88–10.

Sorauf, J. 1981. Biomineralization, structure and diagenesis of the coelenterate skeleton. *Acta Palaeontologica Polonica* **25**, 327–343.

Stolarski, J. 1991. Miocene Scleractinia from the Holy Cross Mountains, Poland; Part 1 — Caryophylliidae, Flabellidae, Dendrophylliidae, and Micrabaciidae. *Acta Geologica Polonica* **41**, 37–67.

Turnšek, D. 1978. Solitary Senonian corals from Stranice and Mt Medvednica (NW Yugoslavia). *Slovenska Academija Znanosti in Umetnosti, IV. razred. Razprave* **21**, 3, 1–68.

Turnšek, D. 1986. Carnian coral *Thamnotropis rakoveci* n. sp. from Perbla near Tolmin (NW Yugoslavia). *Slovenska Academija Znanosti in Umetnosti, IV. razred. Razprave* **26**, *Ivan Rakovec vol.*, 305–312.

Vaughan, T.W. & Wells, J.W. 1943. Revision of the suborders, families, and genera of the Scleractinia. *Geological Society of America, Special Papers* **44**, i–xv, 1–363.

Wells, J.W. 1956. Scleractinia. In: R.C. Moore (ed.) *Treatise on Invertebrate Paleontology* **F**, 328–444. Geological Society of America and Kansas Press.

Wells, J.W. 1966. Evolutionary development in the scleractinian family Fungiidae. *Symposia of the Zoological Society of London* **16**, 223–246.

Zibrowius, H. 1974. Redescription of *Sclerhelia hirtella* from Saint Helena, South Atlantic, and remarks on Indo-Pacific species erroneously referred to the same genus (Scleractinia). *Journal of Natural History*, **8**, 563–575.

Zibrowius, H. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Océanographique, Monaco* **11**, 1–284.

Streszczenie

Skleraktinie jurajskie i kredowe należące do rodzin Latomeandridae, Microsolenidae, Synastreidae i Cunnolitidae, ze względu na morfologiczne podobieństwa z dzisiejszymi koralami, były włączane do podrzędu Fungiina. Budowa mikroskopowa septów (mikrostruktura), tj. budowa trabekul — zarówno ich trzonów (typ wielocentrowy), jak też struktur bocznych, czyli ornamentacji (guzki, pennule, meniany, synaptikule; Fig. 1–5), świadczą o braku bezpośrednich powiązań filogenetycznych między wymienionymi rodzinami z jednej, a kenozoiczną rodziną Fungiidae z drugiej strony. Autorki proponują wyodrębnienie nowego podrzędu, Microsolenina, który obejmowałby wymienione rodziny jurajsko-kredowe. Przedstawiają też schemat przekształcenia budowy szkieletu septalnego typowego dla jednej z triasowych linii filetycznych korali minitrabekularnych, Astraeomorphidae, w złożone struktury występujące u korali rodzin Latomeandridae i Microsolenidae, które pojawiły się z początkiem jury (Fig. 6).