

Considerations on most Rugosa and the Dividocorallia from de Groot's (1963) collection

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Fedorowski, J. Considerations on most Rugosa and the Dividocorallia from de Groot's (1963) collection. *Scripta Geologica*, **127**: 71-311, 1 fig., 54 pls.; Leiden, May 2004.

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Key words — Rugosa, Dividocorallia, Bashkirian-Moscovian, Spain.

Rugose corals reinvestigated herein constitute the main part of the collection described by de Groot (1963). The taxonomy proposed herein differs in several instances from that accepted originally by de Groot. Some changes, such as *Petalaxis* for *Lithostrotionella* and *Calophyllum* instead of *Polycoelia*, were already introduced in de Groot's unpublished catalogue. Others were introduced in order to match the recent advances in rugose coral systematics. Most systematic changes were based on new microstructural, diagenetic and hystero-ontogenetic studies. These are described in detail for individual species and briefly discussed in the concluding considerations. Trabecular microstructure of septa and its diagenetic alteration was documented for most species. Presence of two kinds of intercorallite walls (partition and dividing walls) was documented on the basis of their difference in microstructure. This was especially important for the genus *Petalaxis*, allowing proof of a distinction between species representing its nominative subgenus and that distinguished by de Groot as *Hillia*. A new name *Degrootia* was proposed for *Hillia*, which is preoccupied by a lepidopteran.

Two genera, one new (*Arctocorallium* gen. nov.), represented by two species, were transferred to the Calyxcorallia (Dividocorallia), the order and subclass not distinguished by de Groot. Both those species were investigated and documented in particular detail, especially their hystero-ontogeny. The restudied material allowed proof of a distinction between the Calyxcorallia and the Rugosa in the insertion of major septa. Also, an uncertain status of minor-like septa that may replace the major septa was demonstrated. Both those determinations are based on the hystero-ontogeny.

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Introduction

The paper by Dr. G.E. de Groot (1963), excellent for its time of publication, requires supplementary information and systematic revision. Several of the revised names were introduced in de Groot's unpublished catalogue. The present reinvestigation is based on the type material supplemented with few new thin sections and several long serial sections with peels. Up to ten offsetting corallites were investigated from each of those series in order to study the hystero-ontogeny and their bearing on the taxonomy of colonial corals. Unfortunately, the poor preservation of some colonies precluded

photographic illustration of an adequate quality for illustration. In consequence, illustrations of the hystero-ontogeny of such species were not included in this paper. Nevertheless, the hystero-ontogeny, the microstructure of septa and inter-corallite walls, with remarks on the diagenetic alterations, supplemented by the reinterpretation of some main macro-morphological features, form the main basis of the revision.

The microstructure of septa and diagenetic alterations in individual structures were described on the basis of conventional thin sections. Results achieved by that method are easily comparable to those supplied by the ultra-thin sections method introduced by Lafuste (1970). Scanning electron micrography (SEM), very useful for the study of the Recent and some perfectly preserved fossil Scleractinia, does not add very much information in the case of the Rugosa. I achieved closely comparable results applying both the SEM and traditional methods for the study of the microstructure in some Permian genera (Fedorowski, 1974a, pl. 66, figs. 2-3). The cathodoluminescence method is useful for proving individual steps of diagenetic alteration, but only when organic matter is shown to be totally absent, which is often difficult to prove. Besides, cathodoluminescence is not elaborate enough to make results either truly different from those obtained by classical methods (e.g., Mas & Rodriguez, 1990) or absolutely trustworthy. In the present paper I did not intend to describe step by step diagenetic processes, but wanted to document diagenesis as an important process for altering microstructure that must be considered when skeletons of the rugose corals are studied. Thus, cathodoluminescence methodologies were used only for comparing some results achieved from regular thin sections. Colour plates, i.e., the only illustrations that can truly show distinction in brightness and colour, are not published.

Microstructure and diagenesis are summarised below. Here I would only like to stress the following points:—

Each rugose coral skeleton described in this paper was diagenetically altered. This alteration was advanced to different degrees, resulting in better or worse preservation of remnants of the original microstructure. Differences mentioned can often be observed within a given specimen.

Microstructures described below as trabeculae are commonly recrystallized artifacts that preserved the original or enlarged shape and size of trabeculae, but most probably consist of diagenetic crystals not of original crystalline fibrils.

All species described by de Groot (1963) were reinvestigated, but treatment of them was different. Some were omitted from the present paper due to either inadequate preservation or a very limited collection that did not provide new data, e.g., *Amplexo-carinia wagneri* was represented only by several incomplete specimens. The original description by de Groot (1963) of "*Polycoelia*" (= *Calophyllum cantabrica*), represented in the original collection by a single, very thick thin section, was supplemented by Rodriguez & Kullmann (1990), who had 50 specimens at their disposal. Those authors have proven all morphological characters of the species originally established by de Groot (1963). Unfortunately, the state of preservation of the holotype did not allow an examination of the microstructure of septa described by those authors. Thus, it may only be stated that such a microstructure as described by Rodriguez & Kullmann (1990) does not exist in any specimen of that genus investigated by Schindewolf

(1942), Ilina (1984) and Fedorowski & Bamber (2001), and is here considered a diagenetic alteration of the trabecular microstructure.

Specimens included by de Groot (1963) in *Cyathaxonia* Michelin belong undoubtedly to that genus. On the basis of the available material I was not able to confirm or reject the specific identification. Thus, they were omitted from the main discussion, but were briefly treated in an Appendix.

Euryphyllum hispanicum and species included in the genera *Amygdalophylloides* Dobrolyubova & Kabakovich, *Carcinophyllum* Thomson, *Koninckocarinia* Dobrolyubova, *Arachnastraea* Yabe & Hayasaka, *Ivanovia* Dobrolyubova and *Lonsdaleoides* Heritsch were omitted from this revision for various reasons. I had almost nothing to add to the original description of *E. hispanicum* and fully agree with its identification. *Amygdalophylloides* and *Koninckocarinia* are represented in the collection by single, incomplete specimens, providing no data for further discussion. The identifications agree with the present knowledge of those genera, whereas species identifications, especially in the case of *Amygdalophylloides*, may be questioned.

Carcinophyllum (= *Axophyllum* according to the present taxonomy) was omitted for two reasons.

Some taxonomic problems concerning this and related genera were discussed by Rodriguez (1985). I agree with most of his conclusions.

Several other questions concerning, particularly, the microstructure of septa were impossible to solve on the basis of the restudied material. Species within the genera *Arachnastraea* and *Ivanovia* require comparison with the type specimens. *Lonsdaleoides hispanicus* and *Ivanovia freieslebeni* are nevertheless treated briefly in the Appendix.

The restudy of corals included by de Groot (1963) in the family Lonsdaleiidae was originally the only topic of this revision. It was extended to other taxa after recognition that the original material provides easily available data for supplementing in several aspects the monograph of de Groot (1963). Supplementary collections have not been studied, however, resulting in the unequal treatment of individual taxa. For most taxa new illustrations are provided. Rarely, some remarks are supported with reference to the original illustrations (de Groot, 1963).

The following remarks are necessary in order to avoid any misunderstandings in the following descriptions:—

Individual corallites of massive colonial corals differ in shape, with some being either elongated artificially because of the obliqueness of transverse sections or naturally due to temporary changes within a colony. Such an elongation camouflages their real diameters and, to some extent, the width of the dissepimentarium. In order to make my measurements consistent, the shortest diameters between two points on one side and one or two points on the opposite side of a corallite were measured. Thus, diameters listed in this paper may differ from those established by de Groot (1963).

Following Hudson (1936) and my own study (Fedorowski, 1997), I consider only the cardinal and the counter septum to be protosepta. Thus, the term 'protosepta' is not applied to the alar and counter-lateral septa as it is in many papers dealing with the Rugosa. The reader should remember this wherever the term 'protosepta' is used.

A structure that develops in some corallite axes is differently treated and bears different names. In this paper a term 'axial structure' is used in a general sense, applied to any structure that appears in the middle part of a tabularium, whereas 'median lamella' is a specific kind of an axial structure, formed from the inner end of either a cardinal or a counter septum with or without septal lamellae incorporated. Thus, the term 'columella,' commonly applied to such a simple axial structures, is not used herein.

Following Fedorowski & Jull (1976), two names of intercorallite walls within massive colonies were used; the 'partition' for a wall secreted by a common tissue of adjacent corallites and the 'dividing wall' for that secreted by each polyp separately. The first of these walls consists of three and the second of four main layers of crystalline fibrils.

Some terms used in the present paper require additional explanation. Prefixes "atavo" and "neo" used for septa and a wall of offsetting corallites were modified from Smith & Ryder (1927, pp. 339-340), who wrote: "For the epitheca and septa thus common to both parent and daughter corallite we here propose the term "atavo" epitheca and "atavo" septa to distinguish them from the "neo" epitheca and "neo" septa which belong to the daughter corallite alone.... This does not necessarily assume any fundamental difference between the "atavo" and "neo" tissue. Such an explanation is misleading. Thus, it was modified herein as follows; any morphological structure inherited by an offset from its parent corallite bears the prefix "atavo," whereas structures developed by an offset itself are "neo" structures.

Prefix "hystero" was modified from Smith & Ryder (1927), who introduced it in order to distinguish the development of offsets or "daughter corallites" from the corallite of a parent. In the sense accepted herein, this prefix was applied to early hystero-ontogenetic stages; brephic and neanic. The mature growth stage of an offset does not need a prefix because the individual resembles other mature clones.

The following terms are newly proposed for the Calyxcorallia. 'Minor-like septa' in the Calyxcorallia occupy a position comparable to minor septa in the Rugosa. They may either have originated by splitting of major septa or may have given rise to major septa either by split or by a simple elongation and inclusion in heterocoralloid pattern major septa. A 'symmetry septum' appeared first, was situated in the symmetry plane of an offset and led to an increase of its septa. It may be continuous or divided into an outer part attached to the atavotheca and an inner part at the neotheca. First major septa of an offset appeared on both sides of that septum.

Terms adopted from the Rugosa, but used in the Calyxcorallia in a different sense include the following. 'Major septa' are longer septa arranged in a heterocoralloid pattern or free; most are derived from preceding major septa by a peripheral split, some by a split of minor-like septa or by their elongation or some, especially in "diphyphylloid" corallites, may be inserted independently. 'Quadrants' are a group of major and minor-like septa inserted on one side of a peripheral and inner fragment of the symmetry septum. Sequence in increase of major septa in each quadrant began at the symmetry septum and ended next to the adjacent quadrant. As a result the neighbouring septa of adjacent peripheral and inner quadrants are the youngest. This is opposite to the sequence present in the Rugosa. In rare instances the first septum in a quadrant frames its periphery and the next septum was inserted between it and the symmetry septum.

Systematic palaeontology

Class Anthozoa Ehrenberg, 1834

Subclass Rugosa Milne Edwards & Haime, 1850

Order Stauriida Verrill, 1865

Family Hapsiphyllidae Grabau, 1928

Subfamily Antiphyllinae Ilina, 1970

Genus *Actinophrentis* Ivanovsky, 1967

Type species — *Actinophrentis donetziana* Fomichev, 1953, by subsequent designation; Upper Moscovian, Donets Basin, Ukraine.

Diagnosis — Small, solitary corals without dissepimentarium; major septa pinnately arranged up to calice floor, united axially by stereocolumn; cardinal septum shortened from early maturity; counter septum permanently elongated, distinctly or moderately; cardinal fossula meets or almost meets corallite axis; minor septa underdeveloped (after Fedorowski, 1987, p. 36).

Actinophrentis sp.

Pl. 1, fig. 1; Pl. 2, figs. 1-3.

e.p. 1963 *Zaphrentites paralleloides* de Groot, p. 40, text-fig. 29a-c.

Material — A single specimen, RGM 112574, with calice crushed by compaction and proximal end missing.

Description — An external wall, approximately 0.5 mm thick, bears shallow, but distinct, septal furrows. In the ontogenetically earliest growth stage preserved (Pl. 1, fig. 1a), with n:d ratio 16:4.9 × 4.1, thick, slightly rhopaloid, almost radially arranged major septa extend close to the corallite axis. The cardinal septum is slightly longer than the adjacent major septa. The counter septum already dominates in length and thickness. The triangular cardinal septal fossula is distinguishable. Most characters described remain similar during next 1.5 mm of growth up to n:d ratio 18:5.1 (Pl. 1, fig. 1b), but the cardinal septum thins distinctly without being shortened.

In the mature growth stage with n:d ratio 18:6.5 (Pl. 1, fig. 1c) major septa, except for the newly inserted pair in counter quadrants, remain rhopaloid. Some septa in counter quadrants and one alar septum reaches the clearly elongated and thickened counter septum; others only approach it. Some major septa in cardinal quadrants are already shortened a little and stereoplasm is lacking from here, but it remains present between inner margins of major septa in counter quadrants. The cardinal septum became distinctly shortened, reaching less than half of the axially open cardinal fossula. Minor septa remain absent from the corallite lumen, but swellings present in some loculae suggest an appearance of their initials in the external wall.

In the section made above the calice floor in cardinal quadrants, and in the peripheral part of counter quadrants and above in remaining part (Pl. 1, fig. 1d), major septa are differentiated in length and thickness, with those sectioned above the last tabula

being shortest and non-rhopaloid. The cardinal septum become very short whereas the counter septum remains rhopaloid and elongated, reaching the corallite axis. Swellings of minor septa remain, but septal blades are absent.

The microstructure of septa is trabecular with individual trabeculae *c.* 0.15 mm wide, arranged in a single row. Some irregularity in the arrangement at the periphery (Pl. 2, fig. 1) is herein interpreted as diagenetic. Such an interpretation is confirmed by the recrystallization and alteration of growth lamellae of the external wall into a zig-zag pattern. A slightly out of line arrangement of trabeculae in the inner parts of some septa (Pl. 2, figs. 2, 3) may have a similar diagenetic origin although a zig-zag pattern is not obvious in lateral parts of septa, i.e., in their diagenetically altered, secondary sheets.

Remarks — Several doubts remain from Fomichev's (1953) descriptions and illustrations of morphology of *Actinophrentis donetziana* and other Donets Basin species, preventing precise identification of the single corallite studied herein. Its morphology beneath the calice (Pl. 1, figs. 1a-c) corresponds to that of the early mature growth stage of the holotype of *A. donetziana* (Fomichev, 1953, pl. 1, fig. 23b), but the diameter and number of septa in the Spanish specimen are much smaller. Also, a strongly elongated counter septum in the calice of the Spanish specimen, that makes it similar to *Soshkineophyllum*, cannot be checked against the Ukrainian holotype that lacks a corresponding part of the corallite. With all those doubts and due to an occurrence restricted to the single, incomplete corallite, a formal species name was not proposed and the Spanish specimen was left in open nomenclature.

The corallite discussed was originally identified as *Zaphrentites*. It differs from the latter genus by its distinctly elongated counter septum, a character absent from both "*Zaphrentis*" *parallela* Carruthers, 1910, the type for that genus and its evolution leading not towards elongation, but towards shortening of the counter septum. This single specimen was described herein to document an occurrence of the genus *Actinophrentis* in Spain that may be important for palaeogeographic reconstructions.

Range — Sierra Corisa Limestone, Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Genus *Bradyphyllum* Grabau, 1928

Type species — *Bradyphyllum bellicostatatum* Grabau, 1928 (by original designation); Moukouan (Middle Carboniferous), Kansu Province, southwest China.

Diagnosis — Antiphyllinae having cardinal septum long in early ontogeny, shortened in maturity below calice floor; cardinal fossula triangular, not reaching corallite axis, located on various sides; counter septum slightly elongated, at least in early ontogeny; major septa radially arranged, shortened to form free axial area; tabulae highly rising adaxially, sagging in axial portions (after Fedorowski, 1987, p. 42).

Remarks — A comprehensive discussion of the genus *Bradyphyllum* was not pub-

lished since the paper by Fedorowski (1987) and the number of species referred to that genus afterwards was restricted. Thus, the brief discussion that follows concerns only Spanish specimens included in *Bradyphyllum* (de Groot, 1963; Rodriguez, 1984; Rodriguez & Kullmann, 1999). These specimens are restricted in number to less than ten and all vary greatly in morphology. Most of them show characteristics that are not typical for the genus. Some atypical features occurring in the specimen included by de Groot (1963) in *B. oppositum* are discussed below with remarks on that species. The same remarks can be applied to *Bradyphyllum*(?) sp. no. 2 de Groot, omitted from this revision.

Both *B. oppositum* and *Bradyphyllum*(?) sp. no. 2 of de Groot (1963) expose rotiphyloid characteristics such as cardinal septa remaining long up to a calice floor and major septa meeting at a corallite axis in early stages. At the same time both of them possess axial areas free from septa in mature growth, i.e., the character typical for *Bradyphyllum*. Specimens exposing such mixed characters may suggest a distinct generic or subgeneric status. This question will not be solved in the present paper because the material revised is inadequate for creating a new taxon of that rank.

Bradyphyllum(?) sp. no. 1 de Groot, 1963, is here definitively excluded from both the family and the genus although its exact taxonomic position remains doubtful (see discussion below).

From two species included in *Bradyphyllum* by Rodriguez & Kullmann (1999), *Bradyphyllum* sp. with its rhopaloid and elongated counter septum and major septa differentiated in length seems to be related to Polycoeliidae (*Soshkineophyllum* ?) rather than to *Bradyphyllum* in Hapsiphyllidae (Antiphyllinae). *B. rectum* Rodriguez & Kullmann possesses two important characters atypical for *Bradyphyllum*. These are:—

The permanently long cardinal septum, dominating over other major septa, the counter septum included.

Counter-lateral minor septa forming a triad. These two characters made that species similar, most probably related, to "*Fasciculophyllum*" *tripus* described by Schindewolf (1952) from the early Namurian A strata of Upper Silesia (Poland). Weyer (1977) conditionally included that species in *Rotiphyllum*, but suggested its probable separate generic status. The specimens from the Upper Carboniferous of Spain exhibit similar characteristics, strengthening Weyer's (1977) supposition, and should allow introduction of a new genus when more material is available.

Concluding those brief remarks I would like to point out that the occurrence of *Bradyphyllum* in the Cantabrian Mountains is uncertain. Only specimens included by de Groot (1963) in *B. oppositum* Fomichev, 1953, may with some restrictions be included in that genus, but their generic status should be treated as tentative for the time being (see remarks below).

***Bradyphyllum? oppositum* Fomichev, 1953**

Pl. 1, fig. 5; Pl. 2, figs. 4-7.

1953 *Bradyphyllum oppositum* Fomichev, p. 130, pl. 5, figs. 6-7.

1963 *Bradyphyllum oppositum*: de Groot, p. 12, text-fig. 4, pl. 1, fig. 5.

1984 *Bradyphyllum oppositum*: Rodriguez, p. 133, text-figs. 42, 43, pl. 1, figs. 8-9.

Material — A single specimen, RGM 112514, with calice slightly deformed by compaction, with proximal end missing. For illustrations of early growth stages, see de Groot (1963, pl. 1, fig. 5a, b).

Diagnosis — *Bradyphyllum*(?) with 24-26 radially arranged, slightly rhopaloid major septa at 7-10 mm corallite diameter; cardinal septum equal to major septa in length; cardinal fossula indistinct; minor septa as swellings on external wall.

Additional description — Only description of the microstructure of septa, with some considerations on the diagenesis, are added herein to supplement the description by de Groot (1963, pp. 12, 13). As indicated by some rudiments in de Groot's (1963) specimen, the microstructure is finely trabecular, with individual trabeculae reaching c. 0.01 mm in width and being rather widely spaced (Pl. 2, figs. 5 [right], 7). Such a narrow diameter of trabeculae is confirmed by rudiments of "dark lines" seen in some septa and interpreted as longitudinally or very obliquely sectioned trabeculae. Diagenetic alterations lead to the formation of "mésoplasme" with (Pl. 2, fig. 6) and without (Pl. 2, fig. 5, left) rudiments of trabeculae. Rudiments of trabeculae, surrounded by only slightly altered secondary sheets of septa, may remain in middle parts of some major septa (Pl. 2, fig. 4), whereas fans of secondary crystals may have uniformly replaced both the originally trabecular primary septa and originally fibro-lamellar sheets in other septa of the same specimen (Pl. 2, figs. 6-7). Diagenetic alterations in some primary parts of septa lead to an appearance of disorderly oriented crystals framed by recrystallized secondary sheets of septa (Pl. 2, fig. 5 left). Fairly distinct versus weakly marked "Stirzonen" (Pl. 2, fig. 7) depend perhaps on the advancement of diagenesis. Almost all trabeculae were altered in the left septum in that picture, whereas some slightly altered ones remain in the right one making the "Stirzzone" border clear. It is worth mentioning that diagenetic alteration in individual septa differ, sometimes considerably (e.g., Pl. 2, figs. 5 [left], 6).

Remarks — The diagnosis proposed by Fomichev (1953, p. 130) in his original description as a 'short characteristic' was translated and repeated in full by Rodriguez (1984, p. 135). Such a short description does not fulfill the demands of diagnosis. Thus, a new diagnosis is proposed herein.

From two Spanish specimens included in *B. oppositum* by Rodriguez (1984), only that derived from the Upper Bashkirian of Nueva in Asturias was illustrated by that author and taken into consideration in this paper. Its similarity to the specimens described by de Groot (1963) is close enough to consider them co-specific. The taxonomic position of the specimen not illustrated by Rodriguez (1984) is not discussed.

Only four specimens identified as *B. oppositum* were illustrated in the literature. The cardinal septum, very slightly shortened or not shortened, but thinner below a calice than in earlier growth stages, forms the main character of the type specimen allowing it to be distinguished from remaining representatives of *Bradyphyllum*. In contrast to the type, the cardinal septum remains long up to the calice floor on Spanish specimens. The cardinal septum is hardly distinguishable by its length and is atypical for that genus, being diagnostic for *Rotiphyllum*. Thus, an evaluation of such a character versus formation of an axial area free of septa is a matter of debate. In this paper I accept

the withdrawal of septa as slightly more important, but the opposite solution is almost equally acceptable. An occurrence of species showing a mixture of diagnostic features of *Bradyphyllum* and *Rotiphyllum*, accentuated a very close relationship of those genera. See Fedorowski (in press) for discussion of Spanish ?*Bradyphyllum oppositum*.

Range — Upper Bashkirian-Kasimovian of the Donets Basin in Ukraine and Upper(?) Bashkirian to Upper Moscovian of Cantabrian Mountains in Spain.

Occurrence — Upper Cheremshanskian (Upper Bashkirian), Limestone H-1; probably Vereiskian (Lower Moscovian), Limestones K5 - K9; probably Myachkovskian (Upper Moscovian) or Kreviakinskian (Lower Kasimovian), Limestones N2, N3 in Donets Basin; Upper Bashkirian (Nueva), Kasimovian (Gamonedo), Podolskian/Myachkovskian (Upper Moscovian), Sierra Corisa Limestone in Spain.

Genus *Rotiphyllum* Hudson, 1942

Type species — *Densiphyllum rushianum* Vaughan, 1908; Upper Viséan of Ireland.

Diagnosis — Antiphyllinae with cardinal septum reaching corallite axis along cardinal fossula in all growth stages; counter septum thicker and slightly longer than adjacent major septa; tabularium normal (not biform); microstructure of septa trabecular.

Remarks — The concept of the subfamily Antiphyllinae Ilina, 1970, is not discussed herein, and the reader is referred to Fedorowski (1987) and Fedorowski & Bamber (2001). The concept of the genus *Rotiphyllum* Hudson, 1942, and its content varies greatly, being different in almost every paper dealing with *Zaphrentites*-like corals that possess a counter septum more or less elongated and a cardinal septum slightly shortened or not shortened in the late maturity. Such a differentiated attitude may have partly resulted from inadequately supported concept of the genus by Hudson (1942). He selected *Densiphyllum rushianum* Vaughan, 1908, the type species of his new genus despite the laconic and incomplete description and illustration of an unknown part of a corallite published by Vaughan (1908, p. 459, pl. 29, fig. 6a, b). Like in the case of the subfamily I follow the concept of *Rotiphyllum* introduced earlier (Fedorowski, 1987) and supported by Wang (1994).

In addition to earlier discussion on *Rotiphyllum*, included in remarks on *Monophyllum* and devoted mostly to the diagnostic value of the early versus late shortening of the cardinal septum (Fedorowski, 1987, p. 67), two obvious trends in the development of the counter septum in *Zaphrentites*-like corals should also be discussed. In the type species of that genus, i.e., "*Zaphrentis*" *parallela* Carruthers, 1910, the counter septum is equal to counter-lateral septa, as it is in most species belonging to *Zaphrentites sensu stricto*. Slight shortening of that septum, shown already by Carruthers (1910, pl. 37, figs. 7, 8) and further expressed by Hudson (1944), leads towards *Ufimia* and forms the first of the two trends. One may argue against placing *Zaphrentites shunnerensis* Hudson, 1944, in *Zaphrentites* instead of *Ufimia*, but an occurrence of a trend cannot be denied. Whether the genus *Ufimia* is monophyletic or represents a morphotype derived from *Zaphrentites*-like corals is outside the scope of this paper. Historical and phylo-

genetic value of shortening of a counter septum in the ontogeny is widely discussed by Fedorowski & Bamber (2001, p. 66).

A slight to considerable elongation of a counter septum, without forming an upwards sticking columella, is the second trend observed. It leads towards *Monophyllum* Fomichev, 1953, as discussed in Fedorowski (1987).

The above remarks on diagnostic value of length of the cardinal and counter septa in ontogeny are introduced mostly because neither of the Spanish specimens included in *Zaphrentites* by de Groot (1963) and Rodriguez & Kullmann (1990) exhibits the main characteristics of that genus, i.e., shortening of a cardinal septum comparatively early in the ontogeny and lack of elongation of a counter septum. Both de Groot (1963, pp. 40, 42) and Rodriguez & Kullmann (1990, p. 28) recognized elongation of the counter septum, but neither paid adequate attention to that character. Also, it remains unclear from earlier papers dealing with Spanish material when (in terms of an ontogeny) a shortening of the cardinal septum may have taken place.

The reinvestigation of the type material shows that shortening of the cardinal septum, pointed out by Rodriguez & Kullmann (1990, p. 28) as present in a corallite illustrated by de Groot (1963, text-fig. 31), occurs only well above a calice floor. As demonstrated by a strange fabric which infills the peripheral parts of cardinal fossulae, the cardinal septa reach or approach corallite axes below and just above calice floors, where they are elongated along the cardinal fossula floor. This was established during my revision in all earlier illustrated and non-illustrated corallites, identified as *Z. paralleloides* by de Groot (1963, pl. 4, figs. 1-5). This morphology is typical for *Rotiphyllum*. At the same time counter septa in those corallites dominate in counter quadrants. The morphology of *Z. clithria* (de Groot, 1963, pl. 4, figs. 6, 7; Rodriguez & Kullmann, 1990, pl. 1, figs. 9-13) is similar to that in *Z. paralleloides* and is not discussed.

A pinnate arrangement of major septa is demonstrated by all specimens included by de Groot (1963) in both *Z. paralleloides* and *Z. clithria*. That character and a domination of the counter septum may point towards *Actinophrentis* Fomichev, 1953, emended by Fedorowski (1987). However, a shortening of the cardinal septum in the type species of *Actinophrentis* was proven by Fedorowski (1987) on the basis of the reinvestigation of the type material. Moreover, the pinnate arrangement of septa occurs in the type species of *Rotiphyllum* (Vaughan, 1908, pl. 49, fig. 6a). Thus, all main diagnostic characters of the Spanish specimens, originally included in both *Zaphrentites* and *Rotiphyllum*, are in agreement with the diagnosis of the latter, but not the former, genus.

Rotiphyllum exile de Groot, 1963

Pl. 1, figs. 2-4; Pl. 4, figs. 1-4.

1963 *Rotiphyllum exile* de Groot, p. 8, text-fig. 1, pl. 1, figs. 1-2.

1963 *Rotiphyllum equabilae* de Groot, p. 9, text-figs. 2-3, pl. 1, figs. 3-4.

? 1984 *Rotiphyllum exile*: Rodriguez, p. 122, text-figs. 33-34, pl. 1, figs. 1-2.

1999 *Rotiphyllum exile*: Rodriguez & Kullmann, p. 80, text-figs. 37-40, pl. 8, figs. 1-12.

Material — Thirteen specimens, some almost complete, but all diagenetically altered to various degrees. See de Groot (1963, pp. 9, 11) for more details.

Diagnosis — Small, straight or slightly curved, conical *Rotiphyllum*, having very deep calices, about 19-27 major septa and diameter of 6-9 mm; counter septum thicker and longer than other septa; cardinal septum located in narrow fossula, short only in calice (after Rodriguez & Kullmann, 1999, p. 80).

Additional description — The fairly complete original description (de Groot, 1963, pp. 8, 9), supplemented by an emended diagnosis and comprehensive discussion of Rodriguez & Kullmann (1999), allow reduction of the addendum to the description of the microstructure of septa and its diagenetic alterations, characters not considered by earlier authors.

The microstructure of major septa of all specimens is slightly altered diagenetically. It was observed only in the transverse sections of the holotype and all paratypes, and was established as trabecular. In the holotype the trabeculae *c.* 0.08 mm in diameter are clearly separated from each other in all well preserved septa (Pl. 4, fig. 4, middle) except for their extensions embedded in the thickened external wall, where an occurrence of trabeculae is uncertain. Inner parts of primary septa form a solid dark line of a width equal to the diameter of trabeculae (Pl. 4, fig. 4, upper). The same is true for paratypes (Pl. 4, fig. 1, upper).

Secondary sheets of septa of the holotype and paratypes are fibro-normal or fibro-lamellar (Pl. 4, figs. 2-4). They differ clearly from both the primary septa and the inorganic interseptal infillings. In the paratypes originally included in *R. exilae* by de Groot (1963), as well as in the specimens distinguished by that author as *R. aequabile*, considered herein a synonym of the former, most trabeculae were diagenetically altered (Pl. 4, figs. 2, 3). In several cases they seem much larger than those in the holotype, probably because they recrystallized at the cost of secondary sheets of septa (Pl. 4, fig. 3). In the case of more advanced recrystallization these secondarily enlarged trabeculae form units similar to growth lamellae within a septum (Pl. 4 fig. 3, lower), called "Strirnzonen" by Schouppe & Stacul (1966), and considered by those authors as well as by Schindewolf (1942) and Oekentorp (1980) to occur in the lamellar septa. An occurrence of trabeculae in another septum of the same specimen, and within the "Strirnzonen" (e.g., Pl. 4, fig. 3, middle), made that interpretation unsupported. Further alteration of trabeculae may have led to their diagenetic destruction and replacement by bunches or fans of crystals (Pl. 4, fig. 2) closely comparable to the Figure 13 of Semenoff-Tian-Chansky (1974) illustrating the "mésoplasme" of that author.

Intraspecific variability — Differences in morphology shown by Spanish specimens included in *R. exilae* and/or *R. aequabile* by de Groot (1963), Rodriguez (1984) and Rodriguez & Kullmann (1999) are not large, but concerns almost all characters. In addition to the arrangement of major septa in counter quadrants, i.e., development of the "counter pseudofossula" (de Groot, 1963, p. 10) and a slight acceleration of major septa in those quadrants, shown by the specimens included by de Groot (1963) in *R. aequabile*, the following seem important:—

Differentiation in length of the counter septum that dominates in the holotype and in some other corallites (e.g., de Groot, 1963, pl. 1, fig. 1c; Rodriguez & Kullmann, 1999, pl. 8, figs. 3, 11), but does not in several other ones (de Groot, 1963, pl. 1, figs. 2-4; Rodriguez & Kullmann, 1999, pl. 8, figs. 4, 5, 8, 9; Pl. 1, fig. 3 herein).

Extreme variation in length of the cardinal septum that may extend behind the corallite axis in some sections (Pl. 1, figs. 3, 4a).

Elongation of middle major septa in cardinal quadrants so as to meet opposite major septum in counter quadrants (Pl. 4, figs. 2, 4b).

Some morphological variants, such as the development of a distinct alar pseudofossula (Rodriguez, 1984, text-fig. 34, pl. 1, fig. 2) and counter pseudofossulae in "*R. aequabile*" as well as an irregular arrangement of septa, have most probably resulted from the attachment of larvae not on the cardinal septum side, as most larvae in the so-called horn corals do, but on the lateral and perhaps the counter septum side. De Groot (1963, p. 9) wrote "The alar septa lie on the concave and convex sides" proving to some extent the above supposition.

Remarks — The reinvestigation of the type material of *R. exile* and *R. aequabile* does not support the view of de Groot (1963) of their distinction at the species level. This conclusion is supported by individual variability of main characteristics of specimens included in both species. The stratigraphically slightly younger specimen included by Rodriguez (1984) in *R. exile* may belong to a different species. Unfortunately, its morphology based on the original illustrations and description cannot be established with adequate certainty. This specimen has not been included by Rodriguez & Kullmann (1999) in the synonymy of *R. exile*.

Two characters, apparently different from *R. exile*, led de Groot (1963) to the recognition of *R. aequabile*. These are presence of a counter pseudofossula in early growth stage and lack of an acceleration of septa in counter quadrants. Both of them appeared inconsistent and weakly or not developed, thus being inadequate for such a distinction. The arrangement and number of sections of tabulae next to the counter septum in *R. aequabile* do not prove an occurrence of the tabular, i.e., true fossula. There are only major septa in some sections, best seen in the holotype, but absent from the specimen RGM 112912, that are arranged in a way called a counter pseudofossula. An identical arrangement of septa, that occurs in a transverse section of *Bradyphyllum* sp. 1 (de Groot, 1963, pl. 1, fig. 6b), was not emphasised by that author as taxonomically valuable. Such a position is fully accepted herein and is extended to *R. aequabile*. An acceleration by one major septum in a quadrant (counter-lateral septa not counted) is not a real distinguishing character as well. The occurrence of all specimens in the same stratigraphic level and in not distant localities support their species identity rather than distinction.

Range — ?Westphalian C, Escalada Formation; Westphalian D; Sierra Corisa Limestone and Picos de Europa Formation, Upper Moscovian.

Occurrence — Northern Palencia, Spain.

***Rotiphyllum paralleloides* (de Groot, 1963)**

Pl. 3, figs. 1-4; Pl. 4, figs. 5-8.

e.p. 1963 *Zaphrentites paralleloides* de Groot, p. 40, pl. 4, figs. 1-5, text-fig. 28 [text-figs. 29a-c = *Actinophrentis* sp.].

1963 *Zaphrentites clithria* de Groot, p. 42, pl. 4, figs. 6-7, text-figs. 30-31.

1990 *Zaphrentites clithria*: Rodriguez & Kullmann, p. 26, pl. 1, figs. 9-13, text-figs. 5, 6, 12.

Material — Eleven almost complete specimens (de Groot, 1963, pp. 41, 43).

Emended diagnosis — *Rotiphyllum* commonly with 22 pinnately arranged major septa at 11 mm corallite diameter; minor septa seen only near or in calice; cardinal fossula widened at periphery; counter septum dominating near calice floor, equal to other major septa higher in calice.

Individual variation — The large corallite with n:d ratio 25:14, reported by Rodriguez & Kullmann (1990, p. 26), was not considered in the diagnosis because its illustration was not provided. Nevertheless, the species may perhaps include such large specimens. Small corallites, possessing 20 major septa at 7.5 mm diameter, were included by de Groot (1963) in "*Zaphrentites*" *paralleloides* whereas only slightly larger ones in "*Z.*" *clithria*. All of them are herein synonymized. Small specimens may either represent individuals ontogenetically underdeveloped or environmentally suppressed.

Irrespective of the original species identification by de Groot (1963), not accepted in this paper, the following variations of characters were observed:—

Domination in length and thickness of the counter septum may vary from section to section from slight to considerable (de Groot, 1963, pl. 4, figs. 1c,d, 2a,b, 6a,b; Pl. 3, figs. 1a-d herein).

The cardinal septum is slightly thinner than adjacent major septa in most corallites and may be very thin in some (de Groot, 1963, pl. 4, figs. 3, 5; Pl. 3, fig. 3 herein).

Minor septa, mostly in the form of indistinct swellings of an external wall, may be recognizable either just below a calice or only in its middle part (Pl. 3, figs. 1d, 2).

The cardinal fossula is widened at periphery, but this widening is mostly slight (de Groot, 1963, pl. 4, fig. 6; Pl. 3, figs. 1a, b, 3, 4 herein) and only very rarely considerable (de Groot, 1963, pl. 4, fig. 7), depending in some instances on the growth stage (de Groot, 1963, pl. 4, figs. 1b, d, 2a, b). Also, the inner margin of the cardinal fossula below a calice floor may be slightly widened or narrow. The cardinal tabular fossula is deep irrespective of differences in its shape outlined by major septa.

Microstructure and diagenetic alteration — The microstructure was not mentioned by de Groot (1963). Rodriguez & Kullmann (1990, pp. 27, 28) described the microstructure of the corallite wall as lamellar and the microstructure of septa as the middle part consisting of bundles of crystals surrounded on both sides by perpendicular bands of crystals. The external wall was inadequately preserved. Thus, its lamellar microstructure cannot be either proven or rejected. In the case of septa, however, some diagenetic alterations observed herein as varying from comparatively small (Pl. 4, figs. 5, 7) to advanced (Pl. 4, fig. 8) are closely comparable to that described and illustrated by Rodriguez & Kullmann (1990, text-fig. 12:3).

It is obvious from the better preserved parts of septa investigated for the purpose of this paper that the original microstructure was trabecular (Pl. 4, figs. 5-7). Diameters of trabeculae are uncertain and were estimated as approximately 0.06 mm. Also, their image in a transverse section differs, pending on their position in relation to the section. Clearly separated trabeculae were sectioned nearly perpendicularly (Pl. 4, fig. 5,

bottom), the adjacent "Stirnzone" obliquely (Pl. 4, figs. 5 [middle], 6) and a dark line (Pl. 4, fig. 5, top) represents longitudinally sectioned trabecula, perpendicular to the vertical inner margin of the septum.

Individual trabeculae in some septa are surrounded by diagenetic halos of altered crystals and their originally straight row may be shifted aside (Pl. 4, fig. 7, right). Sheets of septa may be diagenetically rearranged in a way suggesting destruction of the primary, trabecular septum axialwards (Pl. 4, fig. 6). Also, the diagenesis may have resulted in a total destruction of trabeculae. Middle parts of such altered septa form solid "dark lines," surrounded by obliquely arranged crystals oriented under narrow angles of both "dark lines" of their own septa and equally recrystallized sheets of adjacent septa (Pl. 4, fig. 8). Several items described are comparable to the picture by Rodriguez & Kullmann (1990, text-fig. 12:3). Unfortunately, this comparison must remain rough, because the drawings provided by Rodriguez & Kullmann are inadequate for further analysis. The microstructure of septa and its diagenetic alterations are closely comparable in specimens of both species synonymized herein.

Remarks — Following Carruthers (1910), de Groot (1963) accepted a diagnostic value to the shape of a cardinal fossula and discussed that character widely in the context of several *Zaphrentites* species. Also, this character was one of main reasons for distinguishing two species derived from the same stratigraphic level and geographical area. The discussion and comparisons made by de Groot (1963) appeared unwarranted when both those "species" were transmitted to *Rotiphyllum*. Besides, peels produced for the purpose of this papers and the restudy of all original thin sections allowed demonstration that differences pointed out by de Groot (1963) resulted commonly from ontogenetically different parts of the specimens compared. The arrangement of major septa in cardinal quadrants seen in calices of corallites identified as "*Z.*" *clithria* (Pl. 3, fig. 2) does not differ from that seen in calices of "*Z.*" *paralleloides* (Pl. 3, figs. 1d). Also, their ontogenetically earlier growth parts are closely comparable (e.g., Pl. 3, figs. 1a, 3, 4). Keeping in mind such a striking similarity in morphology, similar n:d ratio and identical microstructure, I did not find any worthwhile arguments for distinguishing between those two species.

Range — Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Family Polycoeliidae Roemer, 1883
Genus *Soshkineophyllum* Grabau, 1928

Type species — *Plerophyllum artiense* Soshkina, 1925; Lower Permian (Artinskian) of the southern Urals, Russia.

Diagnosis — Polycoeliidae with cardinal septum shortened at or near floor of deep cardinal fossula in calice; counter septum elongated most distinctly, alar septa less so; microstructure of septa finely trabecular with closely spaced centres (after Fedorowski & Bamber, 2001, p. 59).

Soshkineophyllum corisense de Groot, 1963

Pl. 7, figs. 1-4.

1963 *Soshkineophyllum corisense* de Groot, p. 20, pl. 2, figs. 5-6, text-figs. 13-14.

Material — Three almost complete, diagenetically altered specimens (de Groot, 1963, p. 21).

Emended diagnosis — *Soshkineophyllum* with maximum number of septa 30 at 12.5 mm corallite diameter; cardinal septum in deep fossula, shortened early in ontogeny; counter quadrants dominate in volume and number of septa; elongation of metasepta inconstant; minor septa distinctly underdeveloped, recognizable in upper part of calice.

Additional description: individual variation — Strong thickening of septa early in the ontogeny, deep cardinal fossula with the cardinal septum distinctly shortened already in late neanic stage and domination of the counter and alar septa throughout the ontogeny, are main characters of the holotype. These characters are not obvious in paratypes. Morphology of an axial part of the paratype RGM 112533 (de Groot, 1963, Pl. 2, fig. 6) is especially misleading as it resembles that in the genus *Leonardophyllum* Moore & Jeffords, 1941. In contrast to the latter, however, the median lamella, strongly thickened in its middle part, does not incorporate septal lamellae. Inner margins of four major septa only reach it and the fifth long major septum terminated at axial part of a tabula or axial tabella. The polished surface made slightly above the thin section discussed (de Groot, 1963, pl. 2, fig. 6) confirms the described median lamella/septa relationship. Calcitic infillings and presence of sections of tabulae (tabellae?) in the inner part of the transverse section versus sediment infillings of its peripheral part indicate a fairly high elevation of the inner part of the calice. This character is absent from both the holotype and the paratype RGM 112534 of *S. corisense*. Also, the cardinal septum in the specimen RGM 112533 remains unshortened until early maturity and its counter-lateral septa are indistinguishable from other major septa in length. Characters mentioned may appear adequate for a separation at the species level.

The paratype RGM 112534 differs from the holotype in its smaller difference in volume and number of septa in quadrants, and in the cardinal septum being less distinctly shortened. All quadrants in the upper part of the calice of the paratype are equal in terms of volume and number of septa. Shortening of major septa in counter quadrants of the paratype, recognizable also in the holotype (de Groot, 1963, pl. 2, fig. 5a), have probably resulted from the position of the cardinal septum on the convex side. A very early growth stage is missing from the holotype, whereas in the paratype discussed the major septa are laterally contiguous for approximately 5 mm of the corallite growth in counter quadrants and for some millimetres longer in cardinal quadrants.

Microstructure of septa and diagenetic alteration — The microstructure in all specimens restudied was deeply altered diagenetically. The recrystallization may camouflage the original microstructure almost completely (Pl. 5, fig. 2). Isolated structures, observed in rare septa as showing radial arrangements of crystallites (Pl. 5, fig. 3) or dark

middle lines, straight (Pl. 5, fig. 4) or curved (Pl. 5, fig. 1), are considered remnants of trabecular microstructure.

Remarks — Only three specimens were included by de Groot (1963) in *S. corisense*. Such restricted material cannot support the introduction of a separate species for the morphologically most distinct specimen, RGM 112533 (see intraspecific variability). Its treatment as a variant within the species discussed seems more proper for the time being. Remarks by de Groot (1963, p. 21) on the difference between the Spanish Middle Carboniferous and Russian Lower Permian species are fully accepted herein.

S. accelerans Rodriguez & Kullmann, 1990 from the Westphalian D of Casavegas, Palencia, differs from *S. corisense* in the smaller number of septa at comparable diameters, and in thinner major septa that are less differentiated in length. A difference in number of septa between cardinal and counter quadrants varies from specimen to specimen, becoming identical with *S. corisense* in the corallite no. 13 of Rodriguez & Kullmann (1990, p. 31). Thus, its diagnostic value may be overestimated. Restricted collections of both Spanish taxa do not allow their closer comparison although their synonymy seems probable.

Range — Sierra Corisa limestone, Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Family Plerophyllidae Koker, 1924

Genus *Ufimia* Stuckenberg, 1895, emended Fedorowski, 1973

Type species — *Ufimia carbonaria* Stuckenberg, 1895, by original designation; Lower Permian (Artinskian) of the Ural Mountains, Russia.

Emended diagnosis — Plerophyllidae with zaprentoid early stages; alar and counter lateral septa dominating in late stages; cardinal and counter protosepta shorten progressively; longest and strongest metasepta commonly midquadrant; tabular floors tall, axially depressed; microstructure of septa trabecular, uniseriate.

Remarks — The genus was discussed most recently by Fedorowski & Bamber (2001, pp. 49-50).

***Ufimia alternans* de Groot, 1963**

Pl. 3, figs. 5-6; Pl. 5, figs. 5-8; Pl. 6, figs. 1-3; Pl. 7, fig. 6.

1963 *Plerophyllum* (*Ufimia*) *alternans* de Groot, p. 22, text-figs. 15-16, pl. 2, figs. 7-10.

1990 *Ufimia alternans*: Rodriguez & Kullmann, p. 32, text-figs. 9, 12, pl. 2, figs. 7-9.

Material — Five incomplete specimens. Proximal ends lacking. Internal structures diagenetically variously altered (de Groot, 1963, p. 24).

Emended diagnosis — *Ufimia* with biform tabularium; early in ontogeny cardinal

septum approached counter septum behind corallite axis; cardinal fossula narrow, peripherally widened; in maturity major septa alternately long and short, accelerated in counter quadrants in number; minor septa underdeveloped, except for adjacent to counter septum.

Additional description: intraspecific variability — A strong peripheral widening of the triangular cardinal fossula in the middle neanic stage of the holotype and one paratype (Pl. 7, fig. 6a) is perhaps characteristic only for this growth stage. The similar shape of the fossula in the corresponding growth stage of the specimen illustrated by Rodriguez & Kullmann (1990, text-fig. 9d-g) confirms this deduction. The latter specimen possesses the cardinal fossula bordered by parallel walls in its earlier growth (Rodriguez & Kullmann, 1990, text-fig. 9b, c). The distinctly triangular shape of the cardinal fossula remains in the holotype and some paratypes up to advanced maturity (Pl. 3, fig. 5; Pl. 7, fig. 6b), but may be hardly recognizable in some other specimens (e.g., Pl. 3, fig. 6).

Alteration in length of metasepta in counter quadrants, fairly regular in the type material (Pl. 3, figs. 5, 6; Pl. 7, fig. 6b), is hardly recognizable in some specimens illustrated by Rodriguez & Kullmann (1990, pl. 2, figs. 8a, 9a). One of those specimens (Rodriguez & Kullmann, 1990, pl. 2, fig. 9a) possesses major septa only slightly thickened and almost non-rhopaloid.

The number of major septa is invariably accelerated in counter quadrants. They are twice as many in the counter quadrants than in the cardinal quadrants of the holotype (Pl. 7, fig. 6b), but this number is reduced to 1 and 2 septa, respectively, in counter quadrants of the corallite RGM 112539 (Pl. 3, fig. 5) and to 2 major septa in the specimen illustrated by Rodriguez & Kullmann (1990, pl. 2, fig. 8a).

Minor septa became recognizable only in the mature growth when they form more or less steep, mostly non-trabecular protuberations of the external wall. Only in the paratype RGM 112538 were remnants of trabeculae recognized in these protuberations. Minor septa adjacent to the counter septum are trabecular in all specimens of the type collection except for the specimen RGM 112539. This corallite (Pl. 3, fig. 5) possesses all minor septa underdeveloped. The same is true for two corallites illustrated by Rodriguez & Kullmann (1990, pl. 2, figs. 7, 8a).

Presence of the cardinal tabular fossula was not mentioned directly by earlier authors and is not demonstrated in longitudinal sections. Transversely-sectioned tabulae that span inner margins of septa adjacent to the cardinal septum (Pl. 3, fig. 5; Pl. 7, fig. 6b) demonstrate its occurrence clearly. In some other specimens (Pl. 3, fig. 6), the cardinal fossula may either be too shallow to be demonstrated by sections of tabulae or spacing of tabulae is too large to be demonstrated by a random section.

Biformity of the tabularium was not described in this species so far. Also, its occurrence cannot be demonstrated in its longitudinal section (Rodriguez & Kullmann, 1990, pl. 2, fig. 9b). It is well demonstrated in the transverse sections, where sections of tabulae in the Position I of Sutherland (1965) form arches connecting several minor septa with the counter septum sides of adjacent major septa. This character is demonstrated best by specimens possessing the longest minor septa and is thus most obvious in specimens possessing well-developed Km septa (Pl. 3, fig. 6; Pl. 7, fig. 6b). The occurrence in all specimens examined of peripheral parts of tabulae arching

between tops of minor septal swellings and the lateral sides of adjacent major septa is proof of a diagnostic character of the biform tabularium in *U. alternans*.

Rhopaloid inner margins of several septa in some specimens may be supplemented with narrow extensions, trabecular in the microstructure (Pl. 6, figs. 2, 3). Those extensions are disconnected from trabecular parts of primary septa by stereoplasmic, non-trabecular sheets of septa. Their occurrence is interpreted herein as an additional secretion in quickly narrowing septal pockets, developed along upper margins of axial parts of tabulae.

Microstructure of septa — Despite advanced diagenetic alteration, the fine trabecular microstructure of the septa can be established in some of the better preserved fragments of the holotype (Pl. 5, fig. 5) and all paratypes restudied (e.g., Pl. 5, fig. 6; Pl. 6, figs. 1, 3). In the holotype trabeculae arranged in a single row are c. 0.06 mm wide in the early growth stage (Pl. 5, fig. 5) and are perhaps of similar arrangement in mature growth. It is difficult to establish with certainty whether their larger diameter in mature parts of some paratypes (c. 0.08–0.1 mm) is original or diagenetic (Pl. 5, fig. 6), because, in others (e.g., Pl. 6, fig. 1), they are similar to those in the holotype. The microstructure of septa in the mature part of the holotype was mostly altered to an extent preventing any closer examination (Pl. 5, fig. 7). Zig-zagging direction of growth of trabeculae described by Fedorowski & Bamber (2001, pl. 7, fig. 4; pl. 8, fig. 1c) in *Ufimia arctica* and occurring in the type species of the genus, *U. carbonaria* Stuckenbergh, 1895 (Ilna, 1984, pl. 11, fig. 5), cannot be confirmed in the species discussed, although remnants of such an arrangement may be traced in some septa (e.g., pl. 5, fig. 6; pl. 6, fig. 3).

Diagenetic alterations — The following alterations were observed:—

Partial dissolution of septa. This is best observed in the early ontogeny of the holotype, where the alar and some other septa look broken (Pl. 7, fig. 6a).

Abrupt break and shifting aside of rows of trabeculae (Pl. 6, fig. 1).

Recrystallization of some primary septa imitating remnants of fibro-normal structure (Pl. 5, fig. 8, right septum).

Alteration of primary septa into either strongly curved and partly broken (Pl. 5, fig. 7) or broken into obliquely arranged fragments (Pl. 5, fig. 8, left septum).

Zig-zag pattern in secondary sheets of septa and changes of primary septa mentioned above (Pl. 5, fig. 8).

“Stirnen” extending over the entire width of some major septa, but mostly restricted to their rhopaloid parts (Pl. 6, figs. 2, 3).

Remarks — An arrangement of major septa early in the ontogeny, late shortening of protosepta (in the sense of Hudson, 1936; Fedorowski, 1997), acceleration in number of septa and large volume of counter quadrants in *U. alternans* de Groot, 1963, closely resemble those in the holotype of the type species of the genus (Fedorowski, 1973, text-figs. 11:1a, b, 2). The close similarity to *U. schwarzbachi* Schindewolf, 1952, suggested by Rodriguez & Kullmann (1990, p. 5). is much weaker. These two species differ in the morphology of the cardinal fossula and length of the cardinal septum in the middle

neanic stage and in the absence of alternating longer and shorter major septa in counter quadrants of mature growth of *U. schwarzbachii*.

Rodriguez & Kullmann (1990, p. 5) described the microstructure of septa in their specimens as being formed of "Fassern, die schräg von der dunklen Mittellinie zur Peripherie ziehen." This suggests an absence of trabeculae, contrasting with the description above. Groups of fibres shown by those authors in their figure 12b strongly suggest the trabecular microstructure, at least similar to, if not identical with that described in this paper and by earlier authors. "Anwachslamellen" in the inner, thickened parts of major septa (Rodriguez & Kullmann, 1990, text-fig. 12a) may illustrate a simple (or simplified) microstructure of obliquely sectioned trabeculae, supplemented by stereoplasmic sheets of septa.

Range — Middle to Upper Westphalian D (Upper Moscovian).

Occurrence — Sierra Corisa Lst., Celada Limestone, Casavegas Formation, Northern Palencia, Spain.

Family Lophophyllidae Grabau, 1928

Synonym — Lophophyllidiidae Moore & Jeffords, 1945.

Remarks — Presence of a narrow dissepimentarium in addition to the columella derived from the counter septum has been erroneously identified in the genus *Lophophyllum* Milne-Edwards & Haime, 1850, since the study by Carruthers (1913). This led Moore & Jeffords (1945) to distinguish columellate and non-dissepimental corals in a new family Lophophyllidiidae. Despite the restudy by Lecompte (1955) of the types of *Lophophyllum konincki* Milne-Edwards & Haime, 1850, the type species of the genus, the family name Lophophyllidiidae was retained by most authors. Fedorowski (1990), following Lecompte (1955), demonstrated an absence of the dissepimentarium in *Lophophyllum konincki* and an occurrence of a columella in that species derived from the counter septum. He also proved the occurrence of a permanently long cardinal septum, that forms the main difference between genera *Lophophyllum* Milne-Edwards & Haime, 1850, and *Lophophyllidium* Grabau, 1928. That feature is adequate for the distinction between genera only and not between families. Consequently, the family Lophophyllidiidae was considered a junior synonym of the family Lophophyllidae Grabau, 1928 (see Fedorowski, 1990, p. 308, for more comprehensive discussion).

Professor Edouard Poty (oral information, August 2003) suggests a synonymy of *Lophophyllum konincki* Milne Edwards & Haime, 1850, with *Caninia cornucopiae* Michelin, 1840, with the former being only an early stage of the latter. Such a dramatic change of the traditional understanding of the genus *Caninia* cannot be followed without published documentation. Thus, only published data are considered in this discussion. It may appear, however, that the family name Lophophyllidiidae is valid.

Rodriguez & Kullmann (1999, p. 56) in their discussion on the genus *Lophophyllidium* did not mention either Lecompte (1955) or Fedorowski (1990), and did not follow the concept of synonymy of Lophophyllidiidae with Lophophyllidae, continuing to use the former family name without offering a discussion supporting such a point of view.

For the reasons pointed out in the first two paragraphs of this discussion, I see no reason to alter my established position.

Rodríguez & Kullmann (1999, p. 42, point 2) in the discussion of the superfamily Duplocariniacea Fedorowski, 1986, expressed their doubts as to the occurrence of trabeculae in that superfamily and in *Lophophyllidium*. They consider the microstructure of that genus to consist of "fascicles of granulo-fibres" and contrast them with "more clearly individual, cylindrical structures [in Scleractinia] composed of fibronormal tissue." However, trabeculae occur in the Rugosa, *Lophophyllidium* included (Fedorowski, 1974a, pl. 63, fig. 4; herein, Pl. 6, fig. 5; Pl. 8, figs. 2, 4, 5), although their length varies greatly being in some cases limited to short bodies, intersecting only few growth lines. Further, similar short trabeculae occur in several representatives of the Scleractinia. Thus, not the size of such structures, but continuity of their growth irrespective of growth lines, is decisive. *Lophophyllidium* and many other rugosa follow that criterion (e.g., Pl. 15, fig. 8; Pl. 18, fig. 4; Pl. 22, fig. 1).

The term "granulo-fibres" used by Rodríguez & Kullmann (1999, p. 42) was not explained by those authors. In my opinion the microstructure can be either fibrous or granular, whereas the composition of those two suggests both the diagenetic alteration and the artefact resulted from the orientation of crystals sectioned against the surface of the section. An expression "fascicles of granulo-fibres," if I understand it well, suggests composition of individual "fascicles" (i.e., trabeculae in my meaning) partly from fibres, partly from granulae. Such a composition has not been observed in any specimen of *Lophophyllidium* studied by myself and was not illustrated by Rodríguez & Kullmann (1999). Also, there occurs not a single reference to such a microstructure of septa in the Rugosa and the Scleractinia, confirmed by Professor Ewa Roniewicz in August, 2003, in her e-mail letter.

In their remarks on the genus *Lophophyllidium*, Rodríguez & Kullmann (1999, p. 56) discussed the question of the external wall in rugose corals. They refer to some early studies on the Scleractinia (e.g., Heider, 1886, and his term "pseudotheca"), but decided to follow Schindewolf (1942) who considered only a single, independent structural element of a coral to be a wall. Following partly that concept, Rodríguez & Kullmann (1999) decided to "use the term wall for the outer part of the coral and epitheca for peripheral structures which are more or less independent of the septa." Such a distinction is imprecise and disagrees with the original concept of the term "epitheca" introduced by Milne-Edwards & Haime (1848). This and other questions concerning corallite walls were discussed in a comprehensive way by Roniewicz & Stolarski (1999). Although those authors based their study on and referred mainly to the scleractinian corals, I cannot see any reason for not using for the Rugosa the terms proposed by them with the following restrictions:—

The epitheca in most Rugosa was not formed in the lappet cavity, but was probably secreted by the peripheral-most part of the lateral wall of a polyp. Phillipsastraeidae and Sestrophyllidae are the best-known exceptions among the Rugosa that form epitheca in the same way as do Scleractinia. Nevertheless, terms 'epitheca' and 'epithecal-stereomal' are applicable for the Rugosa because their origin and microstructure in both subclasses are similar.

Not all peripheral (i.e., external wall) structures present in Scleractinia (Roniewicz

& Stolarski, 1999, p. 165, glossary) are recognized so far in the Rugosa, but several are present, although some are simpler. The 'septotheca' is among the structures common for both subclasses although the term 'epithecal-septothecal' wall (Roniewicz & Stolarski, 1999, glossary) seems more proper for the Rugosa.

Genus *Lophophyllidium* Grabau, 1928

Type species — *Cyathaxonia prolifera* McChesney, 1860; Pennsylvanian (Missourian), Illinois, USA.

Emended diagnosis — Solitary, non-dissepimental corals; early growth zaphrentoid; cardinal septum shortened in early maturity; simple pseudocolumella derived from counter septum, incorporates septal lamellae when complex, may disappear in maturity; cardinal fossula triangular, open; tabularium normal or biform; microstructure trabecular.

Subgenus *Lophophyllidium* (*Lophophyllidium*) Grabau, 1928

Type species — As for the genus.

Diagnosis — *Lophophyllidium* with normal tabularium (after Fedorowski, 1987, p. 101).

Lophophyllidium (*L.*) *minus* de Groot, 1963

Pl. 6, figs. 4-5; Pl. 7, fig. 5.

1963 *Lophophyllidium minus* de Groot, p. 32, text-fig. 23, pl. 3, fig. 10.

1963 *Stereostylus* sp. de Groot, p. 35, text-fig. 26, pl. 3, fig. 11.

1990 *Lophophyllidium minus*: Rodriguez & Kullmann, p. 33, text-figs. 10-11, 12 a, b, pl. 2, figs. 10-11 (*cum syn.*).

Material — Five specimens, four identified originally as *L. minus* and one included in *Stereostylus* sp. The holotype is almost complete (de Groot, 1963, pp. 33, 36).

Emended diagnosis — *Lophophyllidium* with 18-20 thickened major septa at 6-7 mm corallite diameter; pseudocolumella monoseptal, continuous, permanently united with counter septum; minor septa in form of swellings of external wall or absent.

Remarks — The original diagnosis by de Groot (1963, p. 32) is too laconic to characterize a species whereas Rodriguez & Kullmann (1990) did not propose its emendation. In addition to the rather brief original description by de Groot (1963), the latter authors described and illustrated *L. minus* in detail. This made it possible to restrict the following remarks to some morphological changes observed in the course of the ontogeny of "*Stereostylus*" sp. The microstructure of septa and the external wall are treated in more detail.

Stereostylus sp. of de Groot has been already synonymized with *L. minus* by Rodriguez & Kullmann (1990, p. 33), but their reasons have not been discussed. Long cardinal septum early in the ontogeny (Pl. 7, fig. 5a), early disconnection of inner

margins of septa in cardinal quadrants vs. their long lasting connection in counter quadrants, simple columella, small diameters and number of septa (Pl. 7, figs. 5b, c) are closely comparable to features of the holotype of *L. (L.) minus*.

The holotype mentioned does not show the lamellar structure of the outer part of the external wall, suggested by Rodriguez & Kullmann (1990, p. 35, text-fig. 6b) for their specimens. It possesses the diagenetically altered fibro-lamellar wall, typical for all species of *Lophophyllidium* investigated in detail. Contrary to the recognition by those authors of the fibrous (“ganz aus Fasern aufgebaut”) microstructure of septa and columella, all specimens revised for the purpose of this paper possesses septa trabecular, with trabeculae of the same kind as observed in the best preserved specimen RGM 112568 (Pl. 6, fig. 5). Diagenetic alterations of primary septa may lead to the formation of irregular “dark line” as observed in the counter septum (Pl. 6, fig. 4). The recrystallization of stereoplasmic sheets of septa produced long calcitic fibrils and camouflaged their growth increments (Pl. 6, figs. 4-5).

The comparison of the here revised material to the photograph of *L. (L.) minus* published by Rodriguez & Kullmann (1990, pl. 2, fig. 10a) exhibits their obvious similarity in the microstructure despite a small magnification of that photograph. Black dots seen in several septa are most probably nothing but trabeculae typical for the genus, as established on the basis of the syntype material of *L. proliferum* (Fedorowski, 1974a). Images similar to those shown by Rodriguez & Kullmann (1999, pl. 2, fig. 10a) are seen in eight times enlarged pictures of “*Stereostylus*” sp. of de Groot (1963, pl. 7, figs. 5b, c).

Range — Wesphalian D, Upper Moscovian (Podolskian and Myatchkovskian).

Occurrence — Northern Palencia, Spain.

Subgenus *Lophbillidium* Fedorowski, 1986

Type species — *Lophophyllidium elongatum* Wang, 1947; Upper Permian, Basleo, Timor Island.

Diagnosis — Like *Lophophyllidium* (*Lophophyllidium*), but with biform tabularium (after Fedorowski, 1987, p. 212).

***Lophophyllidium* (*Lophbillidium*) *breimeri* de Groot, 1963**

Pl. 6, fig. 6; Pl. 7, figs. 1-4; Pl. 8, figs. 1-7.

1963 *Lophophyllidium breimeri* de Groot, p. 30, text-figs. 21-22, pl. 3, figs. 7-9.

1963 *Stereostylus*(?) sp. ex gr. *newelli* (Jeffords), de Groot, p. 36, text-fig. 27, pl. 3, fig. 12.

? 1984 *Lophophyllidium breimeri*: Rodriguez, p. 186, text-figs. 73-75, pl. 4, figs. 11-12.

? 1999 *Lophophyllidium breimeri*: Rodriguez & Kullmann, p. 57, text-figs. 20-21, pl. 5, figs. 1-8.

Material — Seven corallites included in the species by de Groot (1963) and one described originally as *Stereostylus*(?) sp. ex gr. *newelli* (Jeffords). Internal morphology altered diagenetically in various degree (de Groot, 1963, pp. 32, 36).

Emended diagnosis — *Lophyllidium* with 26 major septa at 12 mm corallite diameter in calice; major septa dilated up to maturity, semiradially arranged; cardinal septum slightly shortened; cardinal fossula inconspicuous; very thick pseudocolumella incorporates several septal lamellae; minor septa underdeveloped.

Additional description: intraspecific variability — All thin sections of the type material available for the study and considered mature were taken from beneath calice floors, but the distance to those floors varies. This has resulted in an artificial increasing of the intraspecific variability because not exactly the same growth stages are compared. The most important morphological differences are:—

Pseudocolumella composed of very few septal lamellae (Pl. 7, fig. 2) versus numerous, variously arranged lamellae (Pl. 7, figs. 1b, 3-4; Pl. 8, figs. 1, 3).

The cardinal septum in the holotype and in "*Stereostylus*" sp. ex gr. *neveli* (Jeffords) of de Groot (1963) reaches the columella up to the calice floor (Pl. 7, figs. 1b, 2), whereas it is slightly shortened beneath the calice in both paratypes (Pl. 7, figs. 3-4).

Biformity of the tabularium — This character can be proven by positions of minor versus major septa, shape of peripheral parts of septal loculae, shape of sections of tabulae and their positions at the periphery (Pl. 6, fig. 6; Pl. 8, figs. 6, 7). Minor septa in all corallites are laterally contiguous with cardinal septum sides of adjacent major septa. Thus, there are two minor septa contiguous laterally to both sides of the counter septum to form a kind of underdeveloped triad (Pl. 6, fig. 6; Pl. 8, fig. 7). This arrangement may be camouflaged by secondary stereoplasmic sheets and/or infillings (e.g., Pl. 8, fig. 6). Thus, it may be unrecognizable in some, but obvious in the other, loculae of the same corallite. Shape of septal loculae indicating the biformity of the tabularium depends on the mode of connection of the major and minor septa and shape of the inner margins of the latter (Pl. 8, fig. 6 vs. Pl. 8, fig. 7). The biformity of the tabularium in terms of the number and arrangement of sections of peripheral parts of tabulae is best recognizable in the transverse section of the holotype made just beneath the calice (Pl. 8, fig. 6).

Microstructure and diagenesis — The microstructure of septa and columella match those described by Fedorowski (1974a) from North American specimens of *Lophophyllidium*, the syntypes of the type species of the genus included. Individual trabeculae are c. 0.06 mm in diameter and are clearly separated from one another, fairly regular in the arrangement of fibres in each area where direction of the thin section is proper (Pl. 8, figs. 4 [right], 2, 5 [lower]), but are asymmetrical where not (Pl. 8, fig. 5, upper). The "dark lines" present in some parts of septa (Pl. 8, fig. 2, upper) are interpreted as resulting from sections oriented more or less parallel to trabeculae growth.

Diagenetic alterations are similar to those described elsewhere in this revision. Non-trabecular, zig-zag outlined part of a primary septum (Pl. 8, fig. 2, middle), following its trabecular part (Pl. 8, fig. 2, lower), and large fans of crystals or the fibronormal-like structure (Pl. 8, fig. 4, middle and left). Several variants of diagenetic alterations may appear within a single transverse section of a given septum (Pl. 8, figs. 2, 4-5).

Remarks — A single, incomplete specimen described by de Groot (1963) as *Stereostylus(?)* sp. ex gr. *newelli* (Jeffords) possesses corallites smaller in diameter than originally included by that author in *Lophophyllidium breimeri*. Its major septa are zaphrentoidally arranged with alar pseudofossulae recognizable, its cardinal septum is long and its large pseudocolumella contains only 2-3 septal lamellae (Pl. 7, fig. 2). All these features characterise a juvenile growth stage of the specimen despite of being observed up to the calice floor. Thus, I consider that specimen a probable juvenile representative of *L. (L.) breimeri*. Its microstructure of septa matches closely that character in *L. (L.) breimeri*. A weak development of biformity of the tabularium, demonstrated only by the arrangement of major and minor septa beneath the calice (Pl. 6, fig. 6) may also be a juvenile character.

Specimens included by Rodriguez (1984) and Rodriguez & Kullmann (1999) in *Lophophyllidium breimeri* de Groot were synonymized in this paper with a question mark. This is mainly because positions of the minor septa and presence of the biform tabularium was neither mentioned by those authors nor obvious from their illustrations. Simple morphology of pseudocolumellae in those specimens is comparable to *Stereostylus(?)* sp. ex gr. *newelli* (Jeffords) de Groot, included here in *L. (L.) breimeri*. As demonstrated earlier by Fedorowski (1974a, 1987) and Webb (1984), the microstructure of the pseudocolumella may vary in the course of growth of the same specimen.

Range — Westphalian D (Upper Moscovian).

Occurrence — Sierra Corisa Limestone, Northern Palencia, Cuesta Espinera, Carrera Lagos, Asturias, Northern Spain.

Incertae familiae

Remarks — Only a single specimen, described by de Groot (1963) as *Bradyphyllum(?)* sp. no. 1, is included in this category. I decided to describe that incomplete specimen in detail (see below) because of its characteristics that may help in understanding and, perhaps, subdividing the family Lophotichiidae Weyer, 1972b. Characteristics of that family were discussed by Weyer (1972b), Fedorowski (1987) and Rodriguez & Kullmann (1999), but its content and relationships remain uncertain. Main characters of the specimen in question; early growth stage rotiphylloid (de Groot, 1963, pl. 1, figs. 6a, b), i.e., pointing towards Antiphyllidae Ilina, 1970 and a biform tabularium, well accentuated in mature growth (Pl. 1, fig. 6 in this paper), pointing towards Lophotichiidae, form a mixture that distinguish this specimen from type genera of both families. *Paracania* Chi, 1937, discussed recently by Fedorowski & Bamber (2001, p. 66) in the context of its relation to *Tachylasma* Grabau, 1922, is a third genus to consider.

The occurrence of a biform tabularium is not unique in species included in *Bradyphyllum*. It occurs in *B. caninoideum* Huang, 1932, both in the Chinese Permian type specimen and in the Donets Basin Moscovian specimens included in that species by Fomichev (1953, p. 127). A shortened cardinal septum, and an arrangement and some differentiation in length of major septa in the latter specimens (Fomichev, 1953, pl. 5, figs. 4, 5) point towards *Paracania* to which they most probably belong. The same is true for the Chinese Permian holotype of *B. caninoideum*. A common species status of

the Donets Basin and Chinese specimens is unlikely, but further discussion on this topic is beyond the scope of the present paper.

The Spanish *Bradyphyllum*(?) sp. no. 1 of de Groot, although similar to *B. caninoideum* in its biform tabularium, differs from that species by its permanently long cardinal septum. Combination of both these mature characters point towards *Kabakovitchiella* Weyer, 1972, but such features as rotiphylloid early ontogeny, elongated counter septum in maturity and lack of elongation of counter-lateral minor septa at any growth stage available for the study, form a set of characters at least in part different from the type species of that genus, i.e., "*Amplexocarinia*" *duplex* Schouppé & Stacul, 1959. In the type and only collected specimen of that species, revised by Fedorowski (1986a), the early growth stages are not preserved. Thus, the occurrence or absence of a rotiphylloid stage in its ontogeny is almost equally likely. Early growth stages of the Upper Carboniferous specimens from the Cantabrian Mountains, investigated by Rodriguez & Kullmann (1999) and included by those authors in *Kabakovitchiella*, did not possess rotiphylloid early growth stages. This cannot be considered conclusive. Only a comprehensive study of Permian specimens from Timor - topotypes of "*A.*" *duplex* - will solve that problem. Nevertheless, the counter septum, elongated in *Bradyphyllum*(?) sp. no. 1 of de Groot and equal to adjacent septa in "*Amplexocarinia*" *duplex* and counter-lateral minor septa strongly elongated in the latter species to form a triad, but short in Spanish specimens, are adequate for considering them different at the level of genus.

The microstructure of septa in three transverse and one longitudinal thin section of the holotype of "*Amplexocarinia*" *duplex* is altered diagenetically to an extent making its recapitulation impossible. No clastic remnant of that corallite was left (Fedorowski, 1986a, p. 215). Such an unfortunate selection of the type species of the genus *Kabakovitchiella* by Weyer (1972b, p. 451) resulted in an uncertain status of the species included in it by authors. It also prevents a better identification of the Spanish specimen discussed.

Rugose coral gen. et sp. indet.

Pl. 1, fig. 6; Pl. 9, figs. 1-3.

1963 *Bradyphyllum* sp. no. 1 de Groot, p. 13, pl. 1, fig. 6, text-fig. 5.

Material — A single incomplete, corallite, RGM 112515. Diagenetic alterations advanced (de Groot, 1963, p. 13, pl. 1, fig. 6, text-fig. 5).

Description — In the ontogenetically earliest growth stage preserved (de Groot, 1963, pl. 1, fig. 6a) with n:d ratio 23:5.3 × 4.3 mm, thick, but not rhopaloid, major septa are accelerated in counter quadrants by 3 and 4 in number (alar septa not counted). "Middle dark lines" of some major septa are united near the corallite axis, the other ones are not. None of the major septa reaches the axis and a narrow axial part of the corallite is infilled solely with stereoplasm. The cardinal septum is longer than the last pair of major septa in cardinal quadrants and reaches the axial stereoplasmic infilling. Elongation of the counter septum is slight.

In the next section (de Groot, 1963, pl. 1, fig. 6b, text-fig. 5b), with n:d ratio 28:8.9 × 8.3 mm, an acceleration in number of major septa in counter quadrants increases to 9:3

(alar septa not counted). The cardinal septum is slightly thinner and shorter from adjacent major septa, but it continued to approach the axial area. The counter septum became strongly elongated and located in a kind of counter pseudofossula appeared due to the arrangement of counter-lateral septa. The cardinal fossula is indistinguishable. Minor septa appear on the inner surface of the external wall in a form of low swellings.

In the mature growth stage (de Groot, 1963, pl. 1, fig. 6c; Pl. 1, fig. 6, in this paper) with n:d ratio $30:10.8 \times 10.2$ mm, two more major septa were inserted in counter quadrants and none in cardinal quadrants. All major septa became equally thin in the corallite lumen, but strongly thickened at the periphery where they alternate with almost equally thick bases of minor septa to form a septotheca (Pl. 9, fig. 3). Radially arranged major septa withdraw from the corallite axis, leaving 4 mm wide free axial area (measured perpendicular to the cardinal/counter septa plan). Length of almost all major septa, including the cardinal septum, is approximately equal. Only the counter septum is elongated and last pairs of major septa in quadrants are slightly underdeveloped either in length or in thickness. Those adjacent to the cardinal septum are slightly deflected to its inner margin to form a triangular cardinal fossula. An occurrence of true tabular fossula is accentuated by the number of sections of tabulae larger than in adjacent loculi. Minor septa reach $1/4$ - $1/3$ major septa in length. All of them are straight and their inner margins are free. Biform tabularium is accentuated by an arrangement and number of sections of peripheral parts of tabulae in some loculi (Pl. 1, fig. 6; Pl. 9, fig. 3).

Microstructure and diagenetic alterations — The microstructure of septa was originally trabecular and uniserial, but little of it remains (Pl. 9, figs. 1, 2). Also, the diameter of trabeculae is uncertain, but they probably did not exceed 0.01-0.015 mm. Their apparently large size observed (Pl. 9, figs. 1, 2) is artificial and resulted from growth of inorganic crystals in continuation with organic ones. This process led to the formation of long crystals intersecting and/or replacing an original microstructure of stereoplasmic sheets of septa (Pl. 9, fig. 1). In other instances the recrystallization led to the disappearance of bunches of crystals and formation of rhombus-like structures that may in some instances develop so as to cover the entire thickness of a septum, the stereoplasmic sheets included (Pl. 9, fig. 2, upper). Such an advanced recrystallization is better developed in inner parts of the corallite.

Remarks — The uncertain taxonomic position of the specimen described was discussed in the remarks to the family and need not be repeated.

Range — Sierra Corisa limestone, Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Family Bothrophyllidae Fomichev, 1953
Genus *Bothrophyllum* Trautschold, 1879

Type species — *Bothrophyllum conicum* Trautschold, 1879 (by original designation); Middle Carboniferous (Upper Moscovian), Moscow Basin, Russia.

Emended diagnosis — Solitary Bothrophyllidae with well developed dissepimentarium; major septa in immature part zaphrentoidally arranged with protosepta and some metasepta joined in corallite axis; cardinal septum shortened in further growth; counter septum elongated, at least early in maturity, forming a basis for weak axial structure; in advanced growth may be equal to adjacent major septa (“caninoid” morphology); microstructure of septa finely trabecular.

Remarks — The diagnosis was emended because the original by Trautschold (1879), repeated by Dobrolyubova (1937) in her revision of the type species, does not include all main diagnostic characters of the genus, recognized in subsequent papers. The same is true for other diagnoses (e.g., de Groot, 1963; Fedorowski, 1975; Rodriguez, 1984). Brief discussion is included with remarks to *Bothrophyllum rabanaliensis* (de Groot, 1963).

***Bothrophyllum rabanaliensis* (de Groot, 1963)**

1963 *Pseudozaphrentoides rabanaliensis* de Groot, p. 72, pl. 13, figs. 1-5; pl. 14, figs. 1-2.
non 1985 *Pseudozaphrentoides rabanaliensis* Boll, p. 32, pl. 4, figs. 3a, b.

Remarks — A complete description and comprehensive illustrations of this species by de Groot (1963, p. 72, pl. 13, figs. 1-5, pl. 14, figs. 1, 2) made detailed description unnecessary. It is clear from those data that the neanic stage, critical for identification to genus, is characterized by long major septa with the cardinal and counter septa united axially and with the cardinal fossula already developed (de Groot, 1963, pl. 13, figs. 2a, 4a, 5a, b). Such a morphology is closely comparable to the early growth stages of most specimens of the type species of the genus *Bothrophyllum* illustrated by Dobrolyubova (1937, pl. 3, figs. 1-3, pl. 7, figs. 9-11, pl. 8, figs. 2-3) in her comprehensive revision. Thus, *Pseudozaphrentoides rabanaliensis* is here included in the genus *Bothrophyllum* despite of its “caninoid” mature stage. The question of achieving a *Caninia*-like or *Amplexus*-like mature morphology by the Upper Palaeozoic Rugosa belonging to various suborders has been discussed already elsewhere (e.g., Fedorowski, 1975, 1987).

The holotype of *Pseudozaphrentoides jerofoeevi* shows pathological changes in mature growth and a very short-septal, amplexoid morphology in the earliest known growth stage (Fedorowski, 1975, text-fig. 1b, c, respectively), its paratypes do not exist and topotypes were not collected. Thus, it was suggested (Fedorowski, 1975, p. 33) to abandon that generic name. Despite that revision and arguments, it was accepted as valid by Hill (1981) and was used for some specimens possessing the so-called “caninoid” mature morphology. Such an identification was introduced either irrespective of different early ontogeny (e.g., Rodriguez *et al.*, 1997) or without studying the ontogeny. The latter approach makes identifications baseless because such taxa cannot be reidentified. A lack of care in applying the generic name *Pseudozaphrentoides* has already led to increased confusion among such corals. The introduction by Kossovaya (2001) of the new genus *Alekseevella*, based on the inadequately known species *Caninia irinae* Gorsky, 1978, did not clarify the situation.

Pseudozaphrentoides rabanaliensis of Boll (1985, pl. 4, fig. 3) exemplifies the necessity of comprehensive ontogenetic studies. His specimen has nothing in common with *P.*

rabanaliensis de Groot except for the “caninoid” morphology of a probably mature growth stage. Moreover, the fragment described by Boll (1985) may well be a broken branch of a fasciculate colony as are other “species” of “*Caninia*” described by that author. All those “caninias” belong most probably to no more than two species of *Fomichevella* Fedorowski, 1975, and perhaps one species of *Heintzella* Fedorowski, 1967.

The idea of the genus *Caninia* comprising both solitary and dendroid Rugosa would have been Boll’s (1985, p. 27) subjective solution to the question if he did not refer in his generic diagnosis to diagnoses given by Hill (1938-1941, p. 105; 1981, p. F339) who did not mention branching specimens as belonging to the genus *Caninia*. Thus, the reference to those papers as a source of the idea is an obvious abuse on Boll’s side.

Other Spanish species identified as *Pseudozaphrentoides* are omitted from this discussion. It should only be pointed out that amplexoid morphology early in the ontogeny was not documented in any of them. Thus, they are not proven to belong in that genus and none can be reidentified with any credibility.

Range — Perapertu Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Family Aulophyllidae Dybowski, 1873

Subfamily Clisiophyllinae Nicholson in Nicholson & Lydekker, 1889

Genus *Mirka* Fedorowski, 1974

Type species — *Mira prima* Fedorowski, 1971, Lower Carboniferous (Upper Viséan) of the Holy Cross Mountains, Poland.

Emended diagnosis — Solitary Clisiophyllinae with incomplete axial column; axial structure united with major septa in early growth, free in maturity; median lamella monoseptal, derived from axial septum, elongated to or connected with cardinal septum in further growth; cardinal septum shortened, cardinal fossula open; lateral dissepiments common; microstructure of septa finely trabecular.

***Mirka histiophylloides* (de Groot, 1963)**

Pl. 9, figs. 4-6; Pl. 10, figs. 1-6.

1963 *Koninckophyllum histiophylloides* de Groot, p. 64, pl. 11, figs. 1-4.

non 1970 *Spirophyllum histiophylloides* (de Groot): Fedorowski, p. 575, text-fig. 11, pl. 2, figs. 6a, b, pl. 3, figs. 1-2.

Material — Six incomplete corallites, all lacking earliest growth stages and fragments or entire calices. See de Groot (1963, p. 65) for more detail.

Emended diagnosis — *Mirka* with maximum n:d ratio 41:40.0; septa in dissepimentarium very thin, carinated and/or disintegrated near periphery; major septa separated from narrow axial structure, composed of few lamelle twisting around long, thin columella connected to cardinal septum; dissepimentarium occupies more than half corallite radius.

Additional description — Morphology of the holotype and most paratypes differ in several details. Thus, the remarks included in this paragraph are based solely on the holotype. The median lamella of the axial structure is connected to the cardinal septum already at the neanic stage. This earliest morphology was not illustrated by de Groot (1963), but it closely resembles that of the paratype (de Groot, 1963, pl. 11, fig. 2a). Also it is similar to the slightly more advanced growth stage of the holotype (de Groot, 1963, pl. 11, fig. 1a), except for the incomplete dissepimentarium and more dilated major septa. It corresponds to the more advanced neanic stage of the type species (Fedorowski, 1971, fig. 52 A2) except for much more thickened major septa. As in the type species of the genus, the median lamella have most probably derived from the axial septum, but this is not demonstrated clearly.

The median lamella of the axial structure does not incorporate inner margins of major septa or septal lamellae in any thin and polished section examined and is commonly, but not permanently, connected to the cardinal septum (Pl. 10, fig. 5). It remains uncertain whether such a disintegration (de Groot, 1963, pl. 11, fig. 1c) is long or short lasting. It is likely a temporary character, resulted from the rejuvenation mentioned by de Groot (1963, p. 64) as taking place "several times in the cylindrical part."

Axial lamellae are short and very few (Pl. 10, fig. 5). There are about 5-8 elongated, thin, inner margins of septa that constitute the more peripheral part of a weak and inconstant axial structure. Median lamella may discontinuously disappear (de Groot, 1963, pl. 11, fig. 1c).

The cardinal fossula, prominent in the earlier growth stages (de Groot, 1963, pl. 11, figs. 1a, b) is hardly recognizable in some sections (de Groot, 1963, pl. 11, fig. 1c). This again may be a temporary character, resulted from the rejuvenation. As illustrated by de Groot (1963, pl. 11, fig. 1e), differences in the morphology seen in the longitudinal section, i.e., during corallite growth, may be so large as to include a caninoid stage (lower part of the picture), being rapidly replaced by a stage with comparatively dense axial structure.

In the dissepimentarium major and minor septa are very thin and most of them either bear flange-type carinae (Pl. 10, figs. 3, 4) and/or are more or less disintegrated (Pl. 10, figs. 1-4) with some forming series of plates slightly resembling the naotic septa. Disintegrated septa seen in the slightly oblique longitudinal section may form a series of short rods, resembling individualized trabeculae. All those structures occur in the middle, dissepimentarial parts of septa. Dissepiments that occur between elements of disintegrated septa either connect them (Pl. 10, figs. 1, 2) or supplement irregular structures they constitute (Pl. 10, figs. 3, 4). In addition to those "within septal" dissepiments there occur lateral dissepiments attached mostly to major septa and rectangular, irregular and pseudo-herringbone dissepiments between major and minor septa and herringbone dissepiments inwards of the latter (Pl. 10, figs. 3-5).

The partly isolated axial structure (i.e., an incomplete axial column) seen in the longitudinal section of one paratype (Pl. 10, fig. 6) occurs neither in the holotype nor in another longitudinally sectioned paratype (de Groot, 1963, pl. 11, figs. 1d, e, 4c). All remaining characters seen in the longitudinal section, i.e., the dissepimentarium composed of small, globose dissepiments, arranged in slightly oblique rows and the domed tabularium consisting of rather small, globose tabellae, are similar in all specimens observed.

Microstructures of septa are diagenetically altered, making reconstruction of their primary shape impossible. This is especially true for transverse sections. Secondary fans of fibrils may be indicative for their original finely trabecular microstructure (Pl. 9, fig. 5). Also, parallel bodies preserved in the longitudinal section of one septum (Pl. 9, fig. 6) are closely comparable to fine trabeculae described elsewhere in this paper. Thus, evidence for the trabecular microstructure of septa, although not definite, is considered supportive.

Intraspecific variation — Only the paratype RGM 112653 (de Groot, 1963, pl. 11, figs. 2a-e) does not require additional remarks. Its morphology is close to the holotype in all of the important details seen in the transverse sections. An apparent isolation of its axial structure in the longitudinal section (Pl. 10, fig. 6) was discussed above. The other two paratypes illustrated by de Groot (1963, pl. 11, figs. 3, 4a-c) differ from the holotype in several details. The corallite RGM 112655 possesses an axial structure that is comparatively wide, composed of numerous septal lamellae that are only slightly rotated around the median lamella. The latter is directly connected to the cardinal septum. Minor septa of this specimen penetrate the outer tabularium with thickened inner ends (de Groot, 1963, pl. 11, fig. 3). The paratype RGM 112657 possesses an axial area as narrow as the holotype, but its axial structure is much denser with median lamella hardly recognizable or absent from one thin section and very thin in the other one (de Groot, 1963, pl. 11, figs. 4a, b). Dissepimental parts of septa are thin and carinated, but rarely or not disintegrated. Lateral dissepiments are more common instead. Minor septa reach or, in some examples, just enter the tabularium. Despite the differences discussed, the paratypes can be accepted as illustrating intraspecific variability and not representing separate species.

Pathology? — In a part of one thin section of the holotype (Pl. 9, fig. 4) there occur several bodies that can be called “additional septa.” All those bodies possess undoubtedly septal microstructure, altered diagenetically in the same manner as regular major septa. All occur in the tabularium, but are slightly thinner than tabularial parts of the adjacent major septa. Some are continuous, others are divided into fragments. The occurrence of sections of tabulae connecting the additional septal bodies with septa indicate that these structures are original, not diagenetic, artifacts. I cannot propose any satisfactory explanation for the ephemeral occurrence of those structures.

Remarks — Fedorowski (1970, p. 575) identified some Upper Viséan specimens from Poland as conspecific with *Koninckophyllum histiophylloides* de Groot. The reexamination of the original material proved such an identification incorrect at both the species and genus level. Polish specimens possess a thick columella, that consists of both median lamella and septal lamellae, whereas it is thin and simple in Spanish specimens. This forms a substantial qualitative difference despite of the opinion of Hill (1981, p. F370) who synonymized *Mirka* with *Spirophyllum*, an opinion with which I disagree. Species of *Mirka* are very rare. In addition to the Polish and Spanish species only *Histiophyllum mediocarbonicum* Fomichev, 1953, from the Upper Moscovian of the Donets Basin can be considered as a probable representative of *Mirka* described so far.

Range — Westphalian D (Upper Moscovian).

Occurrence — Sierra Corisa Limestone and Celada Limestone, Northern Palencia, Spain.

Genus *Nervophyllum* Vassilyuk, 1960

Type species — *Nervophyllum beshevensis* Vassilyuk, 1960 (by original designation); Upper Serpukhovian, uppermost *Eumorphoceras* Zone, Donets Basin, Ukraine.

Emended diagnosis — Solitary Clisiophyllinae with mostly continuous axial column; extra septal lamellae corresponding to minor septa supplement normal septal lamellae in axial structure; simple median lamella derived from axial septum, commonly united with cardinal septum, may disappear in late ontogeny.

Remarks — Some representatives of the genus *Nervophyllum*, especially those with the number of septal lamellae corresponding to minor septa reduced, closely resemble those species of *Mirka* that display the most complex axial structure. The contemporaneous occurrence of the oldest known representatives of both genera in the Upper Viséan of Poland made their relationship in terms of ancestor/descendant uncertain. Morphology of both genera is complex, indicating advanced phylogenetic positions. Their derivation from a common ancestor (*Eostrotion*, *Koninckophyllum* or similar genus) seems more probable.

***Nervophyllum* sp. 1**

Pl. 11, figs. 1-6.

1963 *Dibunophyllum* sp. de Groot, p. 58, pl. 9, figs. 3-4

Material — Incomplete, diagenetically altered specimen RGM 112622 (de Groot, 1963, p. 59, pl. 9, fig. 3).

Microstructure and diagenetic alterations — The original microstructure was to a variable extent destroyed by recrystallization. In the better preserved parts of septa bunches of crystals (Pl. 11, fig. 1) and/or a “dark line” are recognizable. In the best preserved fragment of the longitudinally sectioned septum the bodies perpendicular to and intersecting two to several growth lines are considered remnants of obliquely sectioned trabeculae (Pl. 11, fig. 2). From all those data an original occurrence of finely trabecular microstructure of septa is predicted.

Remarks — De Groot (1963) included two specimens in her *Dibunophyllum* sp., but one of them was “longitudinally halved” (de Groot, 1963, p. 59). The latter specimen is only conditionally included in *Nervophyllum* and is omitted from the following considerations. Morphology seen in its longitudinal section (de Groot, 1963, pl. 9, fig. 4), although similar to that in other species included in *Nervophyllum*, cannot be conclusive without being supported by a transverse section.

In addition to the description by de Groot (1963) the following supplementary remarks on the morphology of the corallite RGM 112622 are introduced. Three thin sections of the specimen were originally made in sequence with the incomplete longitudinal section (Pl. 11, fig. 3) spanning two transverse sections. All sections represent the mature growth stage with n:d ratios of transverse sections being 33:17.2 and 30:15.2. Differences in the number of septa between those pointed out by de Groot (1963, p. 58) and in this paper resulted most probably from different identifications of some septa. It is suspected herein that de Groot considered minor septa the shortened septum in the larger section and two short septa adjacent to the cardinal septum in the smaller section. All those were identified as major septa in this paper.

The smaller transverse section represents the rejuvenated part of the corallite that altered its morphology. This concerns first of all the axial structure that is simplified, composed of strongly wavy, free median lamella and few septal lamellae that correspond entirely to major septa (Pl. 11, figs. 4, 6). Besides, nearly all major septa are disconnected from their lamellae, making the axial structure irregularly dibunophylloid rather than nervophylloid. Remaining characters of this section correspond closely to those of the second transverse section. Major septa are thin, only slightly thickened near the external wall. Minor septa are restricted to a quarter or less of the dissepimentarium that occupies two thirds of the corallite radius. The cardinal septum is located in the inconspicuous, open cardinal fossula, bordered by two major septa (Pl. 11, fig. 4, lower). An occurrence of true tabular fossula is indicated by a depression of the inner border of the dissepimentarium.

A small number of septal lamellae in the axial structure that were derived from minor septa (Pl. 11, fig. 5) correspond to juvenile parts of Polish specimens included in *Nervophyllum* (Fedorowski, 1971, text-figs. 46:A3, 48:A1). They are much less numerous than the number of such lamellae in the holotype of the Donets Basin type species for the genus. Unfortunately, the juvenile part of the holotype was not described and not illustrated by Vassilyuk (1960) preventing more satisfactory comparison of Spanish specimen.

The larger transverse section of corallite RGM 112622 exhibits all most important diagnostic features of *Nervophyllum*, although some of them are simplified (de Groot, 1963, pl. 9, fig. 3a). These are:—

The median lamella connected directly to the cardinal septum that is located in the cardinal fossula.

Septal lamellae corresponding to minor septa occur (Pl. 11, fig. 5), but their number is much smaller than in other species of that genus described so far, except for *N. primitivum* Fedorowski, 1971.

Major septal lamellae approaching and/or reaching the median lamella in a way comparable to leaf "nerves," typical for the genus, but the axial structure is narrow and rather inconspicuous.

Differences in characters of "*Dibunophyllum*" sp. of de Groot, 1963, discussed above are perhaps adequate for considering this specimen a new species. A formal name has not been proposed because the material available is inadequate for a comprehensive description.

Range — Santa Maria Limestone, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Genus *Asturiphyllum* Rodriguez, 1984

Type species — *Asturiphyllum semenoffi* Rodriguez, 1984, by original designation; Upper Carboniferous (Upper Bashkirian to Lower Moscovian - Vereian), Asturias, northern Spain.

Emended diagnosis — Solitary dissepimental corals; axial structure of monoseptal median lamella connected permanently or temporarily to cardinal septum, septal lamellae corresponding to major and minor septa twisting around median lamella and numerous arching axial tabellae; dissepimentarium complex, including lateral dissepiments and disintegrated septa; tabularium biform; microstructure of septa probably multitrabecular.

Remarks — *Asturiphyllum* resembles *Nervophyllum* Vassilyuk, 1960, in possessing the axial structure composed of septal lamellae corresponding to several minor septa, in addition to those corresponding to major septa, and in the median lamella that elongates towards the cardinal septum. Shortening of the cardinal septum, biform tabularium and lamellae twisted in the axial structure of in *Asturiphyllum*, but not imitated leaf 'nerves' like in *Nervophyllum* are the main distinguishing characters established between these genera. Unfortunately, early ontogeny of their type species has not been studied. Thus, their true distinction or synonymy remains an open question. In this paper *Asturiphyllum* is accepted because *Clisiophyllum* sp. 2 of de Groot, 1963, closely resembles *A. semenoffi* Rodriguez, 1984, but not *Nervophyllum beschevensis* Vassilyuk, 1960.

***Asturiphyllum semenoffi* Rodriguez, 1984**

Pl. 11, fig. 7; Pl. 12, figs. 1-7.

1963 *Clisiophyllum* sp. no. 1 de Groot, p. 56, pl. 9, fig. 1.

1963 *Clisiophyllum* sp. no. 2 de Groot, p. 57, pl. 9, fig. 2.

1984 *Asturiphyllum semenoffi* Rodriguez, p. 264, pl. 10, figs. 9-12, pl. 11, figs. 1-6, text-figs. 119-124.

Material — Single, incomplete, diagenetically altered specimen RGM 112621 (see de Groot, 1963, p. 57 pl. 9, fig. 2, for more details).

Additional description — Major septa approach the axial structure, but stop at its border with thick, rounded inner margins (Pl. 12, fig. 1). Thus, the axial structure is well separated when seen in transverse section (Pl. 12, fig. 6), although an oblique and eccentric longitudinal section does not prove that separation (Pl. 12, fig. 5). It is constituted of numerous, short, flat, adaxially elevated tabellae and numerous septal lamellae twisting around the thin, long, monoseptal medial lamella (Pl. 12, figs. 2, 6) that penetrates the cardinal fossula, but does not meet the shortened cardinal septum. Extra septal lamellae, corresponding to minor septa, occur in many loculae of the axial

structure (Pl. 12, fig. 1). Their presence may not be established, however, if only the total numbers of septal lamellae and major septa are compared. Both extra and regular septal lamellae are absent from some loculae (Pl. 12, fig. 2, lower right).

The tabularium is biform. This is shown by a different distribution of sections of tabulae between many, but not all, inner margins of minor septa and lateral sides of adjacent major septa (Pl. 11, fig. 7). This phenomenon is confirmed by some details seen in the longitudinal section (Pl. 12, figs. 3, 4). Lower part of the left side of the longitudinal section with globose, dissepiment-like plate attached to sinuous tabula and two other, oriented down sections of tabulae represent Position I (Pl. 12, fig. 3, left). The same Position I represents declined, clinotabellae-like plates that are transparent through the stereoplasmic thickening of a septum (Pl. 12, fig. 4, right). The restricted material does not allow description of this biformity in more detail.

Microstructure and diagenetic alterations — Although the microstructure is mostly altered diagenetically, remaining rudiments allow an interpretation as trabecular. Several parallel bodies seen in the oblique longitudinal sections of septa (Pl. 12, fig. 7) confirm that interpretation. Dissepimental parts of several septa look either carinated or disintegrated into oblique fragments (Pl. 12, fig. 6). This may have been either primary disintegration and/or carination of septa camouflaged by recrystallization or originally continuous septa that were diagenetically broken.

Remarks — Rodriguez (1984, p. 264) included the specimen discussed herein in the synonymy of *A. semenoffi*. I follow that decision despite the differences in stratigraphic occurrence because the mature morphology of this specimen closely resembles that illustrated by Rodriguez (1984) in some of his specimens.

Range — Upper Bashkirian to Lower Moscovian - Vereian and Orbó Limestone (?Upper Moscovian).

Occurrence — Asturias and northern Palencia, Spain.

Subfamily Dibunophyllinae Wang, 1950
Genus *Dibunophyllum* Thomson & Nicholson, 1876

Type species — *Dibunophyllum muirheadi* Nicholson & Thomson, 1876, in Thomson & Nicholson (1875-1876); Upper Viséan of the British Isles.

Diagnosis — Large, solitary, with variable axial structure typically one-third as wide as corallum and consisting of long medial plate, a few (commonly four to eight) septal lamellae on either side, and numerous axial tabellae declined steeply at its periphery; less commonly lamellae may be convolute, median plate shortens towards fossula or disappears and biradial arrangement is lost; minor septa discontinuous so that dissepiments of wide dissepimentarium inosculate; cardinal septum shortens in open, commonly parallel-sided fossula that indents dissepimentarium; periaxial tabellae less steeply declined outward than axial tabellae; in early stages cardinal and counter septa and median plate continuous (after Hill, 1981, p. F361).

Dibunophyllum(?) gentisae (de Groot, 1963)

Pl. 13, figs. 1-6.

1963 *Koninckophyllum gentisae* de Groot, p. 61, pl. 10, figs. 2-3.1963 *Koninckophyllum gentisae minor* de Groot, p. 62, text-figs. 35-36, pl. 10, figs. 4-7.

Material — Eleven variably preserved specimens, mostly incomplete and diagenetically altered (de Groot, 1963, pp. 62, 64).

Emended diagnosis — Solitary dissepimental corals with maximum n:d ratio 38:20 mm; axial structure irregular; median lamella temporarily disappearing, elongated towards, commonly connected with cardinal septum when present; septal lamellae sparse, irregularly curved when median lamella absent; minor septa restricted to complex dissepimentarium that occupies up to one third corallite radius.

Microstructure and diagenetic alterations — None of the thin sections examined allows study of the unaltered microstructure of septa. This character is perhaps best preserved in the "holotype" of *K. gentisae minor*, and in its early growth stage in particular. An almost amorphous, thin, light middle line seen in the peripheral parts of some septa, and narrow bunches of calcite crystals bordering it on either side (Pl. 13, fig. 3), represent the most advanced diagenetic alterations observed. In other septa (Pl. 13, fig. 4) densely packed bunches of crystals, occupying middle parts of entire major septa, are most common. Recognizable trabeculae were not found in the transverse sections. Dark bodies seen in the longitudinal section (Pl. 13, fig. 7, lower and upper) as perpendicularly intersecting few to several strong incremental lines, are interpreted as recrystallized trabeculae. The diagenetic recrystallization followed perhaps the original matrix of crystalline fibrils and produced an image similar to original trabeculae when longitudinally sectioned.

Remarks — The slightly smaller diameter and number of septa in "*Koninckophyllum gentisae minor*", which shows similar characteristics and morphological variation to "*Koninckophyllum gentisae*", suggests there is no necessity to distinguish that subspecies. Holotypes of both "subspecies" illustrated by de Groot (1963, pl. 10, figs. 2b, 4b) prove that well. The holotype of the subspecies ("*forma*") *minor* is almost as large as the holotype of the nominative subspecies and possesses only three major septa less. It looks smaller in de Groot's (1963) illustrations because its enlargement is smaller.

As shown in several papers dealing with Lower Carboniferous dibunophylla (e.g., Hill, 1938-1941; Vassilyuk, 1960; Fedorowski, 1971; Semenoff-Tian-Chansky, 1974), the size of specimens (that is, the main reason for distinguishing "*K. gentisae minor*") cannot be treated as a first rank character of species and subspecies within the genus *Dibunophyllum*. Hill (1938-1941) established differences in morphology of the axial structure most important for the subspecies division of the common and widely distributed Upper Viséan species *D. bipartitum* (McCoy, 1849). Three subspecies, the nominative, *D. bipartitum konincki* (Milne-Edwards & Haime, 1851) and *D. bipartitum craigianum* (Thomson, 1874), were accepted by Fedorowski (1971), but rejected by Semenoff-Tian-Chansky (1974) who found those changes random. It is premature to judge whether

differences in morphology of the axial structure in *D.(?) gentisae* (de Groot, 1963, pl. 10, figs. 2-7; Pl. 13, figs. 1-2, 5-6 herein), based on few specimens, are linear or random, i.e., are suitable or not for distinction of subspecies, but its presence may prove to be the best criterion available.

The original identification by de Groot (1963) of the species discussed as belonging to *Koninckophyllum* Thomson & Nicholson, 1876, cannot be accepted. Its complex, dibunophylloid axial structure is absent from the type species of that genus. A large width of the axial structure when compared to the specimen diameter and a thin, elongated median lamella do not occur in another morphologically similar genus, *Arachnolasma* Grabau, 1922.

The generic position of "*Koninckophyllum*" *gentisae* is uncertain because its earliest ontogeny is unknown and a typically dibunophylloid axial column was not documented in its longitudinal section. The ontogenetically earliest thin section present in the collection is known from the holotype of "*K.*" *gentisae minor* (de Groot, 1963, pl. 10, fig. 4a and Pl. 13, fig. 5 in this paper). Having n:d ratio 24:8.2, the specimen possesses a well-developed dissepimentarium, most major septa approaching and some reaching the axial structure. The inner margins of the cardinal and counter septa are united to form a slightly curved and thickened median lamella (Pl. 13, fig. 5). Except for the shape of the median lamella that may be incidental, the axial structure of this stage is closely comparable to typical dibunophylla. However, it may also be compared to such Bashkirian and Moscovian species as, for instance, "*Neokoninckophyllum*" *arcuatum* Moore & Jeffords, 1945, representing perhaps a new genus, and to the earliest known growth stage of the holotype of *Clisiophyllum carnicum* Heritsch, 1936, the type species of *Amandophyllum*, recently reexamined by myself in Graz. Thus, the character mentioned may be typical for the subfamily. An absence of the cardinal fossula, permanently long cardinal septum and lonsdaleoid dissepiments occurring in late maturity of the holotype of *A. carnicum* eliminate *Amandophyllum* as a potential genus for including "*K.*" *gentisae*.

Morphology of the axial structure in the mature transverse section of "*K.*" *gentisae* s.l. (de Groot, 1963, pl. 10, figs. 2b, 4b; Pl. 13, fig. 6 in this paper) remains typical for *Dibunophyllum*, being closely comparable to undescribed Bashkirian species of the Donets Basin from my collection. However, the axial column, present in the longitudinal section of all typical representatives of the genus *Dibunophyllum*, cannot be documented in longitudinal sections of *D.(?) gentisae* (de Groot, 1963, pl. 3c, 4c, 6b; Pl. 13, fig. 2 in this paper). It remains uncertain whether an absence of the axial column is real or resulted from the obliqueness and eccentric orientation of all sections available for the restudy. With all those uncertainties a questionable position of "*K.*" *gentisae* within the genus *Dibunophyllum* seems most proper for the time being.

Range — Socavón Limestone, Cotarraso Limestone, Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Genus *Corwenia* Smith & Ryder, 1926

Type species — *Lonsdaleia rugosa* McCoy, 1849; Upper Viséan, British Isles.

Emended diagnosis — Fasciculate Dibunophyllinae with continuous axial column; dibunophylloid axial structure in transverse section based on axial septum; simple median lamella stronger connected with cardinal septum; cardinal fossula open; dissepimentarium well developed, dissepiments interseptal.

Remarks — The genus *Corwenia* was introduced by Smith & Ryder (1926) in order to distinguish the fasciculate *Dibunophyllum*-like specimens from the solitary type species of that genus. Although Smith (1916) transferred *Lonsdaleia rugosa* McCoy, 1849, to the solitary genus *Dibunophyllum* Thomson & Nicholson, 1876, they had selected that species as the type of their new genus. Strikingly enough, McCoy (1849) had already distinguished between the solitary and colonial growth form at the generic level. He included solitary, *Dibunophyllum*-like corals in his new genus *Clisiophyllum* and colonial taxa in another new genus, *Lonsdaleia*. McCoy's (1849) opinion, i.e., the distinction between the solitary versus the colonial growth form, was accepted by the great majority of coral students. An opposite view, that combining in one genus both solitary and colonial corals, found a much smaller number of followers, but lasted up to the paper by Boll (1985). Also, de Groot (1963, p. 66) started her emended diagnosis of *Corwenia* with the phrase "Solitary or phaceloid aulophyllinae corals..."

Variable growth form accompanied by consistent skeleton morphology is exceptional in the rugose corals. Thus, the relationship on a genus or even a species level of solitary and colonial growth forms have been documented in very few instances. Devonian *Heliophyllum* Hall in Dana, 1846, summarized by Oliver (1976) and Oliver & Sorauf (2002), is perhaps the best example of that kind, comprising species from solitary through fasciculate and cerioid to astreoid colonies. Permian "*Heritschioides*" sp. analysed by Fedorowski (1978) was shown to comprise solitary specimens and fasciculate to cerioid colonies within a single species. The extreme examples cited do not disprove the idea that the growth form constitutes one of the best diagnostic characters on the genus level.

De Groot (1963, p. 66), following the opposite approach, synonymized with *Corwenia* three solitary genera (*Amandophyllum* Heritsch, 1941, *Dibunophylloides* Fomichev, 1953, and *Sestrophyllum* Fomichev, 1953) and one colonial coral genus (*Heritschioides* Yabe, 1950). None of those genera is here accepted as a synonym of *Corwenia*. The first three are discounted because of their solitary growth form, with *Sestrophyllum*, additionally, possessing everted calices, a character exceptional within the Rugosa. *Heritschioides* is actually revised on the basis of topotypes recollected recently by Dr. E.W. Bamber (GSC, Calgary, Canada). Its very complex morphology, unknown so far from the published data, but examined by me with courtesy of Dr. E.W. Bamber, does not resemble the morphology of *Corwenia* closer than on the family level.

Disregard for the distinction between solitary and colonial growth form did in some instances approach the species level. Rodriguez (1984, p. 246) began his diagnosis of *Corwenia* with "Corales faceloides..." and did not mention solitary forms were included, but then identified his fasciculate colonies as belonging to the solitary species *Dibunophylloides longiseptatus* Fomichev, 1953.

Fomichev (1953, p. 396) clearly distinguished between the solitary and colonial growth form when introducing his new genus *Dibunophylloides* for solitary, *Dibunophyllum*-like, Middle and Upper Carboniferous corals. He began its generic diagnosis

with "Small, solitary, slightly curved corals." He also wrote "*Dibunophylloides* gen. nov. differs from *Corwenia* St. Smith et Ryder, mainly by its solitary corals" (both citations translated herein from Russian), leaving no doubts about his understanding of his new genus. *Dibunophylloides* was afterwards considered (Hill, 1981, p. F395) a possible younger synonym of *Amandophyllum* Heritsch, 1941. Such a position cannot be proven because one of the most important diagnostic criteria, i.e., presence or absence of the axial column in the longitudinal section of *A. carnicum*, is unknown.

Following de Groot's (1963, p. 66) generic diagnosis and her descriptions of three Spanish species included in the genus *Corwenia*, one cannot exclude a possibility of those species comprising both the solitary and colonial growth forms. Such a divergence was not established in the type material revised. Thus, I attribute a fasciculate colonial growth form to all species described by de Groot (1963), and to *Corwenia longiseptata* (Fomichev) of Rodriguez (1984) and Boll (1985), although not all specimens illustrated and/or restudied confirms such a position undoubtedly.

In the corallites of most Spanish specimens the cardinal fossula is either absent or less well developed than that in the type species *Corwenia rugosa*. Also, cardinal septa in Spanish specimens are usually long, reaching the axial structure. The median lamella is commonly met by two opposing major septa, although it is the counter septum that is more obviously prolonged into it.

All three species distinguished by de Groot (1963) are synonymized and included in *Corwenia cantabrica*, the only species that does not refer to the solitary growth form, characteristic for holotypes of the other two. Such a wide approach is in part supported by my own restudy of the material described by de Groot (1963) and in part by the study of Rodriguez (1984, pp. 249-253, fig. 110), who established a very large diversity in n:d ratios observed in Spanish colonies and synonymized *C. cantabrica* with *C. longiseptata* irrespective of differences in that character. I accept Rodriguez's (1984) position in a sense that Spanish specimens are conspecific, but I do not consider them members of the solitary Russian and Ukrainian species. Consequently, *C. cantabrica* is here accepted as the only species available for all Spanish specimens of *Corwenia* described so far. This is despite its smallest diameter of corallites and moderate number of septa. *Corwenia symmetrica* de Groot, 1963 (but not the Russian *Cyathoclisia(?) symmetrica* Dobrolyubova, 1937), comprising the largest corallites with comparatively less numerous septa, forms the opposite extremity. The introduction of a new name for colonies comprising the largest corallites is unsupported.

***Corwenia cantabrica* de Groot, 1963**

Pl. 14, figs. 1-6; Pl. 15, figs. 1-8.

1963 *Corwenia symmetrica* (Dobrolyubova, 1937): de Groot, p. 67, pl. 12, figs. 1-3

1963 *Corwenia cantabrica* de Groot, p. 69, pl. 12, fig. 10.

1963 *Corwenia longiseptata* (Fomichev): de Groot, p. 68, pl. 12, figs. 4-9.

1984 *Corwenia longiseptata* (Fomichev): Rodriguez, p. 249, text-figs. 108-111, pl. 9, figs. 1-7.

? 1985 *Corwenia longiseptata* (Fomichev): Boll, p. 24, pl. 3, fig. 2.

Material — Nineteen fragments of fasciculate colonies. Morphology of corallites well preserved. Microstructure altered diagenetically to various degree (de Groot, 1963, pp. 68-70).

Emended diagnosis — *Corwenia* with n:d ratio varying between 22:6.5, 22:9.5, 26:9.5; major septa approach, some included in narrow axial structure composed of thin median lamella, few septal lamellae, some inner margins of septa and axial tabellae; cardinal fossula indistinct; minor septa extend to outer, biform tabularium; dissepimentarium one quarter to one third corallite radius in width.

Additional description: morphology — In her otherwise comprehensive description, de Groot (1963) failed to mention the structure of median lamella which does not incorporate septal lamellae that are only attached to its surface. It is strongly curved in most specimens with sharp curves corresponding in several places to the attachment of short septal lamellae (Pl. 14, figs. 1, 4). Morphology of the axial structure is not characteristic to any species distinguished by de Groot (1963). Also, it does not depend on the hystero-ontogeny, being either more simple in earlier growth stages (e.g., Pl. 14, fig. 5; Pl. 15, fig. 1) or *vice versa* (e.g., Pl. 15, figs. 5, 6).

The tabularium is biform. This is indicated by an arrangement of sections of peripheral tabellae (Pl. 14, figs. 5-6) and by the arrangement of some tabulae and tabellae in longitudinal section, recognizable where the section exposes loculae on both sides of a given minor septum. Most parts of the longitudinal section of a corallite of the holotype colony (Pl. 15, fig. 2) exhibit Position II. Its apparently uniform morphology consists of dissepiment-like tabellae obliquely inclined towards the more dense axial structure. This morphology changes when the section exposes Position I (Pl. 15, fig. 2, upper left). A triangle seen in this area is formed by tabulae in two positions. The declined arm of the triangle illustrates Position I, whereas its inclined arm ends Position II. A similar arrangement of tabellae, although not distinguished in so sharp a manner, is observed in the specimen included by de Groot (1963) in *C. symmetrica* (Pl. 15, fig. 4, middle and upper left). Bulbose structures located between the oblique section of a septum and the dissepimentarium are tabellae in the Position I.

Hystero-ontogeny — Detailed study based on serial sections with peels was not conducted. Four offsets in a different stage of growth, present in the transverse thin section of the holotype (Pl. 15, fig. 1), provided all data for the description that follows.

An offset is formed in the peripheral part of a parent corallite, causing changes in its dissepimentarium and peripheral parts of septa, but not in its tabularial region that remains unaltered (Pl. 14, fig. 2). Peripheral parts of major and minor septa inherited from the parent corallite constitute the main part of a septal apparatus of the offset investigated. Those inherited fragments of septa, corresponding more or less clearly to major and minor septa of the parent's corallite, were perhaps all transformed into first major septa of the offset (Pl. 14, fig. 2).

All structural elements in the common parent/offset area are distinctly thickened with stereoplasm. These are parts of parent's major and minor septa, and few neosepta, altogether forming an incomplete partition, supplemented by first dissepiments of an offset (Pl. 14, figs. 2-3). Unfortunately, the sequence in increase of septa could not be established.

The long median lamella, formed by the united cardinal and counter septum, is oriented parallel to the partition (Pl. 14, fig. 2). This may well be an individual and not a species character. The counter septum, attached to the partition in the upper corner of the offset (Pl. 14, fig. 2), was most probably derived from a minor septum of the parent,

whereas the cardinal septum is attached to the atavo-theca and its origin is unknown. Individual quadrants differ slightly in size and number of septa (Pl. 14, fig. 2).

A position of the counter septum close to a parent corallite is observed in two other offsets (Pl. 15, fig. 1, upper right). In the specimen formerly included in *C. symmetricum* (Pl. 14, fig. 5, upper) the counter septum is attached to the atavo-theca opposite to the neotheca. Thus, any rule in the position of protosepta cannot be proposed. It may well be predicted, however, that the cardinal septum is a rudiment of a parent's septum, divided at the beginning of an offsetting process, i.e., when an offset's calice was formed.

All offsets observed, irrespective of the original species designation by de Groot (1963), remain strikingly long connected to a parent's corallite (Pl. 14, fig. 5; Pl. 15, figs. 1, 3). Moreover, a fairly strong partition present in the youngest stage of the hystero-ontogeny observed (Pl. 14, figs. 2, 3) may be replaced by a net common for the parent and the offset corallite, composed of slightly thickened dissepiments and peripheral parts of septa of both individuals (Pl. 15, fig. 3). The dividing wall invades into that net from the periphery to separate the daughter from the parent corallite the same way as in all fasciculate rugose corals that produce peripheral offsets.

Microstructure and diagenetic alterations — The microstructure of septa is finely trabecular. This is most clearly demonstrated by the specimen RGM 112667, included by de Groot (1963) in *Corwenia longiseptata* (Pl. 15, fig. 7), but is also recognizable in the holotype of the species (Pl. 15, fig. 8). Individual trabeculae or, more probably, their recrystallized pseudomorphoses are very thin, reaching *c.* 0.015 mm in width. Their length is uncertain because only fragments are seen, but trabeculae more than 1 mm long were measured.

Trabeculae were not distinguished in the microstructure of transverse sections of septa. Dark bodies, arranged invariably perpendicular to growth lines in the longitudinal section of septa and the columella (Pl. 15, fig. 7) cannot be incidental shades. I interpret them herein and elsewhere as recrystallized trabeculae retaining a radial arrangement of crystals. Longitudinal sections of such bodies absorb most light in their axial parts, i.e., where crystals are sectioned perpendicular to their C-axes. Identical image is achieved in the case of crystalline fibrils in original trabeculae.

Remarks — Most remarks on the genus apply to the species discussed and are not repeated. The colony included by Boll (1985) in *Corwenia longiseptata* was conditionally included in *C. cantabrica*. The very poor description and inadequate illustration by Boll (1985, p. 24, pl. 3, fig. 2) do not allow identification of his specimen with confidence. It seems to resemble specimens identified by de Groot (1963) and Rodriguez (1984) in n:d ratio, but differs from them in the morphology of the axial structure illustrated. The lack of any comparison to specimens described by earlier authors from Spain made identification of Boll's (1985) specimen even more difficult.

Range — Cotarraso, Sacavón and Verdiana limestones, Westphalian C, D, Moscovian (Kashirskian and Podolskian).

Occurrence — Northern Palencia, Spain.

Subfamily Amygdalophyllinae Grabau in Chi, 1935
Genus *Spirophyllum* Fedorowski, 1970

Type species — *Spirophyllum santaecrucense* Fedorowski, 1970 (by original designation); Upper Viséan of the Holy Cross Mountains, Poland.

Emended diagnosis — Solitary dissepimental corals or incipient colonies; septa tend to disintegrate into pseudonaotic structure at periphery; columella composed of median plate and septal lamellae, elongated towards or united with shortened cardinal septum, may disintegrate in advanced maturity; cardinal fossula open, parallel-sided, indented into dissepimentarium; axial column may occur, but cyclic systems of axial tabellae and septal lamellae most common in longitudinal section; microstructure of septa trabecular.

***Spirophyllum multilamellatum* (de Groot, 1963)**

Pl. 16, figs. 1-3.

1963 *Koninckophyllum multilamellatum* de Groot, p. 60, pl. 9, figs. 4-7, pl. 10, fig. 1.

? 1970 *Spirophyllum multilamellatum*: Fedorowski, p. 575, text-fig. 10, pl. 1.

1984 *Spirophyllum multilamellatum* (de Groot): Rodriguez, p. 257, pl. 10, figs. 3-8, text-figs. 114-118.

non 1985 *Koninckophyllum multilamellatum*: Boll, p. 21, pl. 2, fig. 4a, b.

Material — Fifteen corallites, but only some cut and two thin sectioned (de Groot, 1963, p. 61).

Emended diagnosis — *Spirophyllum* with 30×2 septa at 21 mm corallite diameter; major septa approach, but most of them not reach, axial structure; number of septal lamellae almost or fully corresponds to number of major septa; minor septa enter peripheral tabularium; dissepimentarium reach approximately half corallite radius; lateral dissepiments common.

Microstructure and diagenetic alterations — The microstructure of primary septa was trabecular. Size of trabeculae uncertain, all most probably having been enlarged by recrystallization. Remnants of more or less regular trabeculae are sparse (Pl. 16, figs. 1 [middle], 3 [right septum]). Many trabeculae were diagenetically altered into half-moon bunches of fascicles, resembling "Stirnen" (Pl. 16, figs. 1 [upper], 2, 3 [right septum]). Further diagenetic deformations caused smearing of boundaries between individual trabeculae and formation of "dark lines" (Pl. 16, figs. 1 [lower], 3 [lower left septum]). Diagenetic alterations are random in distribution, being differently accentuated in adjacent septa (e.g., Pl. 16, figs. 2, 4). More obvious diagenetic alterations, such as broken septa, calcitic veins, etc., are omitted from consideration.

Remarks — The species discussed was illustrated by de Groot (1963, pls. 5-7, 10, fig. 1) mostly by polished sections. It has been established, however, that the columella invariably incorporates septal lamellae. Numerous septal lamellae twisting around the complex columella and systems of tabulae seen in the longitudinal section of the holotype (de Groot, 1963, pl. 9, fig. 5d) are characteristic for *Spirophyllum*.

I now question the Polish specimen (Fedorowski, 1970) because a single, incomplete corallite cannot provide data adequate for the unquestionable identification. The Polish specimen possesses ten major septa more than the holotype at a corresponding diameter, but its morphology is similar to the holotype more obviously than it is to most paratypes of *S. multilamellatum* (Fedorowski, 1970, p. 575). In some Spanish paratypes major septa form a part of the axial structure, whereas that structure is simplified in the others (e.g., de Groot, 1963, pl. 10, fig. 1a, b). Such considerable differences between paratypes themselves, and between them and the holotype, may be indicative for an artificial grouping. The restricted sectioned material does not allow a more comprehensive discussion in this matter.

Boll (1985) included in *Koninckophyllum multilamellatum* de Groot two incomplete specimens with only the mature part of one illustrated (Boll, 1985, pl. 2, figs. 4a, b). Morphology of the sections suggests that the specimen is probably a member of *Spirophyllum* that possesses a compact columella disintegrated in maturity into a few individual septal lamellae. *Spirophyllum perditum* Fedorowski, 1970, may serve as an analogy. The latter species (Fedorowski, 1970, p. 596, text-fig. 20, pl. 10, figs. 1-4) possesses a typical, compact, amygdalophylloid median lamella in premature growth stages, strongly suggesting its generic relationship, whereas taxonomic status of Boll's (1985) specimen is uncertain and prevents closer comparison. Its mature growth stage differs from the holotype of "*K.*" *multilamellatum* in morphology of the axial structure, in a more complex dissepimentarium and in n:d ratio.

Range — ?Upper Viséan (Lower Brigantian), Perapertu Formation (Lower Moscovian).

Occurrence — Northern Palencia, Spain; ?Holy Cross Mountains, Poland.

Family Lithostrotionidae d'Orbigny, 1852
Genus *Thysanophyllum* Nicholson & Thomson, 1876

Type species — *Thysanophyllum orientale* Nicholson & Thomson, 1876; Lower Carboniferous (Upper Viséan), Scotland.

Emended diagnosis — Cerioid corals with lonsdaleoid dissepimentarium; weak, strongly interrupted axial structure may occur; both protosepta may temporarily elongate; tabulae mostly complete, slightly domed and/or trapezoid; offsetting lateral.

Remarks — Hudson (1926, p. 149) overlooked designation by Gregory (1917, p. 238) of *Thysanophyllum orientale* Nicholson & Thomson, 1876, as the type species of the genus. He also mentioned missing the holotype, an absence of topotypes and did not choose a lectotype specimen. *Thysanophyllum orientale* was restudied in detail by Hill (1938-1941, p. 162), who chose a lectotype. Jull (1967) made brief remarks on new topotypes and studied the hystero-ontogeny of this species (see *T. grootae* sp. nov., below). The morphology of the lectotype was restudied recently by Fedorowski *et al.* (in prep.). Thus, all main characters of this genus, apart from the microstructure of septa, are well established. The latter character remains unknown because the lectotype is

recrystallized, making such a study impossible. The same is true for the specimen reinvestigated in the present paper.

All earlier authors agreed that one septum is or can be elongated early in the hystero-ontogeny. It remains controversial, however, which septum is elongated. Hudson (1926, p. 150, pl. 8, fig. 4b), introducing a new species *T. praedictum*, close to *T. orientale* in stratigraphic and geographic distribution, considered the elongated septum attached to the atavo-theca (position not mentioned by Hudson, 1926, but established here on the basis of his illustrations) to be the counter septum. He also pointed its potential to meet the cardinal septum, a character also found in *T. grootae* sp. nov. The youngest offset illustrated by Hudson (corallite b), resembling closely a comparable growth stage of the here studied offsets (Pls. 18-20), is especially convincing.

Hill (1938-1941) considered the elongated septum to be the counter septum, whereas Jull (1967) claimed it to be the cardinal septum, a position maintained by Hill (1981) in the revised *Treatise*. Details of the hystero-ontogeny and a question of the elongated major septum are described below. Here I would point out that both the counter and the cardinal septum may be elongate. Elongation of these septa is mostly alternate, but both may extend simultaneously up to the short-lasting meeting. The above characters were established on the basis of the specimen investigated herein. Thus, there can always be an argument that characters of a species distant both in age and space from the type cannot be conclusive. However, a close similarity of the British Upper Viséan type and other species to the Spanish species in all substantial morphological characters allows extending the above observations to the genus level.

There are several Upper Carboniferous and Lower Permian species included in the genus *Thysanophyllum* by authors. All those species were proven by Fedorowski *et al.* (in prep.) to be members of different genera. A comprehensive discussion included in that paper made wider remarks on that problem unnecessary. *Thysanophyllum grootae* sp. nov., exposing all characters typical for the genus, appears the stratigraphically youngest representative of *Thysanophyllum* known so far.

***Thysanophyllum grootae* sp. nov.**

Pl. 16, figs. 4-6; Pls. 17-20.

1963 *Stylastraea* [*Thysanophyllum*] *trimorpha* de Groot, p. 51, pl. 6, fig. 2.

Holotype — RGM 112600 (Pl. 16, figs. 4-6, Pls. 17-20) (de Groot, 1963, p. 51, pl. 6, figs. 2a-c).

Type locality — Locality 35 of R.H. Wagner, southwest of Perapertú, Northern Palencia, Spain.

Derivation of name — Named in honour of the late Dr. G.E. de Groot, an outstanding student of rugose corals.

Diagnosis — *Thysanophyllum* with 13-15, exceptionally 16 major septa and 4.5-5.5 mm, exceptionally up to 6.3 mm corallite diameter; minor septa mostly absent; lons-

daleoid dissepiments rarely form complete peripheral ring; dissepimentarium occupies less than one third corallite radius.

Description; mature morphology — Intercorallite walls are complete and look thick when compared to extremely thin major septa, but their thickness does not exceed 0.15 mm (Pl. 17, fig. 6). Major septa are wavy, equally thin in the dissepimentarium and the tabularium, almost equal in length within individual corallites, extend into the tabularium for a third to half of its width. Most of them are interrupted and restricted to the inner dissepimentarium and the tabularium, some occur only in the tabularium. A small number of continuous, major septa occur in nearly each mature corallite (Pl. 17, fig. 1). Continuous septa and rarely occurring peripheral strips of septa are attached to inner surfaces of external walls without penetrating their thickness (Pl. 17, fig. 6). Positions of some septal strips indicate they are minor septa. In the late neanic stage (Pl. 20, figs. 7, 8) the minor septa may be almost complete in number, but they are always incomplete in mature parts of corallites. The cardinal fossula was either absent or was not established.

The dissepimentarium occupies up to one third of a corallite radius and consists of 1-3 rows of dissepiments, seen in longitudinal section (Pl. 17, fig. 2). All dissepiments are thin-walled. Thus, the inner thickened wall is absent. Lonsdaleoid dissepiments in the transverse section are commonly few, but may occasionally form an entire peripheral ring (Pl. 17, fig. 1). Most of them are small and flat. The interseptal dissepiments occur between continuous major septa and form various structures inside the ring of lonsdaleoid dissepiments either spanning the adjacent major septa or forming short, oblique plates attached to lateral surfaces of septa and the underlying lonsdaleoid dissepiments.

The tabularium is comprised of mostly complete, slightly domed tabulae with inner parts flat or slightly sagging (Pl. 17, fig. 2). Additional, elongated tabellae rarely occur. Some short tabellae inclined towards inner end of a temporary elongated counter or, less commonly, the cardinal protoseptum are occasionally present (Pl. 17, fig. 2, middle).

Hystero-ontogeny — This process, investigated more or less completely in 10 corallites, invariably began with an elongation of 2-4 septa that meet the external wall and became thickened (Pl. 18, fig. 1; Pl. 19, fig. 1). Those thickened septa are restricted to the dissepimentarium of the parent corallite and are commonly disconnected from their inner parts, attached to a lonsdaleoid dissepiment-like section of a tabula (Pl. 18, figs. 1-4; Pl. 19, figs. 5-6). As shown in the longitudinal section (Pl. 16, figs. 5-6; Pl. 17, fig. 2), the dissepimentarium is lacking from the sector of offsetting, being replaced by tabulae of various shape, size and arrangement. Those tabulae and thickened parts of parent's septa mentioned above, form a strengthened basis for the offset. Formation of such a construction was confirmed in silicified, etched specimens (Fedorowski, 1978, pl. 14, figs. 3b, 4a, b, 5b).

The thickened parts of septa became divided into inner and peripheral segments (Pl. 18, fig. 2) initiating formation of a new calice to host an offset's polyp. This again can be compared to etched specimens (Fedorowski, 1978, pl. 14, fig. 5a). An interruption of thickened parts of septa, seen in transverse sections, resulted from their continuous

upwards growth in peripheral and inner segments, but not in their middle parts. The arrangement of tabulae in the longitudinal section (Pl. 16, figs. 5-6; Pl. 17, fig. 2) indicates a full integration of the parent and offset polyps during this early stage of the offsetting.

Irrespective of the number of thickened parts of septa that began the offsetting (two to four), only one atavoseptum remains at the atavotheca of an offset. This short strip of the atavoseptum (Pl. 18, figs. 3-4; Pl. 19, fig. 2) developed afterwards into the protoseptum of an offset.

Inner parts of thickened septa remaining in the common parent/offset area are connected by a tabula. The position of that tabula, attached to a complete parent's septum on at least one side (Pl. 17, figs. 4-5), makes an impression of the incomplete wall. This structure is here called an apparent wall because it may perhaps incorporate fragments of true neotheca if the latter approaches the tabula closely (e.g., Pl. 16, fig. 5) and the transverse section cuts both structures obliquely. A position of the neotheca distant from a tabula documented in another longitudinal section (Pl. 16, fig. 6) shows isolation of those two structures clearly.

The inner fragments of atavosepta, connected by the apparent wall, underwent atrophy at the offset's side at the time of the formation of first fragments of neotheca. This atrophy is commonly total (Pl. 18, figs. 3-4; Pl. 19, fig. 2). Only in one offset investigated did a possible atavoseptum remain at a neotheca. However, this determination is uncertain and is not illustrated.

The identification and positions of the protosepta was possible due to the step-by-step observations in closely spaced peels (Pl. 18, figs. 3-6; Pl. 19, figs. 7-10; Pl. 20, figs. 3-7). First, major neosepta in the offset were inserted either simultaneously at the atavotheca and the neotheca (Pl. 18, figs. 4-5), or the former slightly preceded the latter (Pl. 20, figs. 3-4). Irrespective of the model, first neosepta at the atavotheca were inserted on both sides of the remaining atavoseptum that became the protoseptum of the offset. In both offsets illustrated and in most remaining ones this is the cardinal septum. I cannot confirm this rule, however, because identification of the cardinal septum in some offsets was impossible. Insertion of alar neosepta and next neosepta in cardinal quadrants may be so rapid that the sequence was impossible to establish (Pl. 18, figs. 4-5, upper), or the process was slower, the alar neoseptum was inserted first (Pl. 18, fig. 6, lower) and the next neoseptum soon after (Pl. 19, figs. 7, lower). Both of these neosepta were hardly recognizable at the beginning and their poor development was prolonged for c. 0.3 mm.

An insertion of several neosepta at the neotheca was sometimes so rapid that a sequence in their appearance is impossible to establish. In the corallite "a" (Pl. 18, Pl. 19, figs. 7-10), four neosepta appeared at the neotheca (Pl. 18, fig. 5) almost simultaneously with the second alar septum at the atavotheca. The counter septum in this corallite was delayed in its appearance and was inserted at the neotheca within 0.1 mm of further corallite growth (Pl. 18, fig. 6, middle right). An acceleration in the increase of septa in counter quadrants at the beginning of the septogenesis is common in the species described (Pl. 19, figs. 7, 8 [counter quadrants left]; Pl. 20, figs. 5, 6 [counter quadrants upper]), but not the delay in the appearance of the counter septum.

In the corallite "b" (Pl. 19, figs. 1-2; Pl. 20, figs. 1-7) the cardinal septum remains at the atavotheca next to the lonsdaleoid dissepiment (Pl. 19, fig. 2). It disappeared from

the offset (Pl. 20, fig. 3, bottom) for c. 0.2 mm growth, i.e., when the alar neoseptum in the left cardinal quadrant and two first septa in the right cardinal quadrant were inserted (Pl. 20, fig. 3). It reappears next to or on the lonsdaleoid dissepiment mentioned (Pl. 20, fig. 4, lower) prior to the insertion of the second major neoseptum in the left cardinal quadrant and first minor septa in the right cardinal quadrant (Pl. 20, fig. 5). Only two more major neosepta were inserted in cardinal quadrants of that offset afterwards (Pl. 20, figs. 6, 7, lower).

The counter septum of the corallite "b" was inserted as the first neoseptum at the neotheca in a form of a very short strip (Pl. 20, fig. 3). The counter-lateral septa inserted next were extremely short as well (Pl. 20, fig. 4). All three septa increased their length rapidly (Pl. 20, fig. 5) making an impression of being inserted simultaneously with the next neosepta in counter quadrants.

Both forms of offsets are good examples of variability of the protosepta in *T. grootae* sp. nov. and, perhaps, in the genus. In the offset "b" the cardinal septum is the longest in some part of growth (Pl. 20, fig. 6, lower), but became slightly shortened within 0.9 mm of further growth when the counter septum became elongated so as to cross the corallite axis (Pl. 20, fig. 7). The corallite "a" exhibits similar, although less spectacular, change in length of the protosepta (Pl. 19, figs. 9-10), but in addition to the elongation of the counter septum, it shows a septal lamella oriented perpendicular to that septum and attached to its inner margin (Pl. 19, fig. 10). Both phenomena described are very short lasting. The septal lamella is ephemeral and the protosepta are equal to other major septa in most of a corallite growth. Thus, elongation of the counter septum, although prevailing greatly in number of instances over elongation of the cardinal septum, does not constitute a firm support for the identification of *Thysanophyllum* as a lithostrotionid coral genus as proposed by Hill (1981).

Major septa in many immature corallites are all or mostly continuous (Pl. 19, fig. 10; Pl. 20, figs. 7-8). Minor septa in corallites possessing continuous major septa are in almost full number, but there is a similar number of immature corallites that possess mostly lonsdaleoid dissepiments and the minor septa strongly reduced in number (Pl. 17, fig. 1). The sequence of insertion of minor septa is not quite clear. They always follow the insertion of major neosepta, but their appearance seems almost random (Pl. 19, figs. 7-10; Pl. 20, figs. 5-7).

The mode of formation of the neotheca is uncertain. In all corallites studied by means of serial transverse peels the neotheca replaces the apparent wall (Pl. 18, figs. 2-3; Pl. 19, fig. 2; Pl. 20, figs. 3-4) by a quick thickening and a possible change of the microstructure. The neotheca is incomplete for a different, but rather short, period of growth (Pl. 18, figs. 4-5; Pl. 20, fig. 4). It is extended on both sides to an atavotheca within 0.1-0.4 mm growth of an offset (Pl. 18, fig. 6; Pl. 20, fig. 5). Evidence for the microstructure of the transition from an apparent wall to the neotheca is restricted to a single thin section (Pl. 17, fig. 5). It demonstrates a simultaneous occurrence of remnants of an apparent wall, i.e., the tabula and the neotheca that incorporates fragments of septa. Such an image was mentioned above as resulting from an arrangement of individual structures against the transverse section and may thus be incidental.

The only detailed analysis of the hystero-ontogeny in unquestionable *Thysanophyllum* until now is that by Jull (1967), who studied topotypes of *T. orientale*. Unfortunately,

spacing between individual growth stages illustrated by that author are sometimes too large to make some details certain, one series is incomplete, lacking the earliest stage of the hystero-ontogeny, and hand drawings instead of photographs published by Jull (1967) create some doubts concerning his interpretation. A rather laconic description leaves several important details unexplained. Also, the examples illustrated therein show very large variability in substantial characters.

The variability mentioned and some gaps in illustrations provided by Jull (1967) made a simple comparison impossible. It may only be stated that a total atrophy of atavosepta on the offset's side of the neotheca is well documented in both *T. orientale* and *T. grootae* sp. nov. The following characters of *T. grootae* sp. nov. find their counterparts in some examples provided by Jull (1967).

Position of the cardinal septum at the atavotheca, at least very common and perhaps typical for *T. grootae* sp. nov., is well documented in two examples, but unknown in the third illustrated by Jull (1967, text-fig. 5:1e, 3a, 2a-e, respectively).

All parental septa were reduced from the earliest hystero-brephic stage in two offsets illustrated by Jull (1967, text-fig. 5: 1a-d, 2a, b), whereas this phenomenon was omitted from the analysis of third example of that author. Thus, in contrast to *T. grootae* sp. nov., the cardinal septum in both examples must be the neoseptum. However, it was inserted at the atavotheca in two cases (Jull, 1967, text-fig. 5:1e, 3a), i.e., in the position characteristic for *T. grootae* sp. nov.

Some septa, including the cardinal septum, were perhaps inherited by offsets shown in the third example illustrated by Jull (1967, text-fig. 5:3a). This cannot be considered certain, however, because earliest hystero-ontogeny was not illustrated.

Jull (1967, p. 626) claimed that first dissepiments inserted are interseptal, i.e, like in *T. grootae* sp. nov. This is more or less clearly confirmed in two offsets illustrated by that author, but not exactly so in drawings illustrating the third example (Jull, 1967, text-fig. 5:2b, c). Formation of lonsdaleoid dissepiments in this offset seems to precede an insertion of first septa. The same example exhibits the development of the parent/offset dividing wall to begin from one side, but not in the middle of the common parent/offset area as it does in both other examples illustrated by Jull (1967, text-fig. 5:1c-e, 3a) and in *T. grootae* sp. nov.

Elongation of the cardinal septum early in the hystero-ontogeny in *T. orientale* is also inconsistent, but seems more common than in *T. grootae* sp. nov. Nevertheless, this character can be found in both species.

The comparison of most substantial characteristics in the hystero-ontogeny of *T. orientale* and *T. grootae* sp. nov. indicates a close similarity of these two species. Large differences in the hystero-ontogeny of individual offsets in *T. orientale* prevent such a conclusion being considered fully proven. Thus, the reinvestigation of the latter taxon is required.

Microstructure and diagenetic alterations — The primary microstructure of the septa is not preserved. Indications of an originally trabecular structure are inconclusive, so this problem is left open.

The microstructure of intercorallite walls is important evidence for a level of

integration of some massive colonies. Polyps of such colonies are integrated if walls are of the partition kind (Fedorowski & Jull, 1976). The diagenetic alteration prevents an indisputable demonstration of a particular kind of intercorallite walls in the colony under consideration. Bunches of crystals developed in most of the thickness of the wall (Pl. 17, fig. 6) can be interpreted either as a result from diagenetic alteration of a partition or the dividing wall.

Intracolony variation — The intracolony variation observed is manifested in an acceleration versus a delay in achieving mature morphology, and in a different development of individual characters in immature and mature corallites. The first is especially important because size of corallites and their number of septa is commonly and correctly considered a diagnostic character of species. This is not quite true for the colony discussed. Small and most probably immature corallites may possess the same number of septa as large and completely developed corallites (Pl. 17, fig. 1).

Differences in morphology of individual corallites within the colony may appear in the course of their growth. Morphology is most variable in middle and late hysteroneanic stage. Following the similar early hysteroneanic stage, i.e., up to formation of a complete ring of dissepiments, there are two opposite extremes in further development of young corallites.

Towards development of a complete number of major and minor septa with continuous major septa accompanied by interseptal dissepiments.

Towards interrupted major septa, reduced minor septa and lonsdaleoid dissepimentarium dominating. A number of corallites exposing various steps of intermediate morphology demonstrate the inconsistency of that morphological division. Irrespective of those differences, all septa were inserted directly on the external wall. Thus, the so-called "presepsiments," i.e., dissepiments developed prior to the insertion of septa, are absent. Temporary elongation of the counter septum and the cardinal septum, an occasionally observed axial meeting of those two septa and elongation of some metasepta occur during the neanic growth stage. It seems most likely that such inconstant length of septa resulted from their amplexoid character and its taxonomic value should not be overestimated.

Remarks — The morphological variety in all growth stages of *T. grootae* sp. nov. is similar to species from the British Viséan. However, *T. orientale* and *T. minus* differ so much from *T. grootae* sp. nov. in the diameter of corallites and n:d ratios that those species can be omitted from further discussion. *T. argylli* (Thomson) possesses those characters similar to *T. grootae* sp. nov. Hill (1938-1941, p. 164) characterized the former species as having "average diameter 3 mm, and fairly equal. The 13 or 14 major septa are about 0.5 mm long." Her poor illustrations (Hill, 1938-1941, pl. 8, figs. 35, 36) do not provide adequate data for an indisputable comparison and remeasurements, but two specimens measured expose their smaller diameter of about 3.4 mm. This fits the diameter and number of septa of the smallest mature corallites of *T. grootae* sp. nov. Despite large differences in n:d ratio of Spanish corallites pointed out above, I did not include the Spanish colony in the British species for the following reasons:—

The holotype and the only specimen representing *T. argylli* is very poorly preserved, inadequately studied and not collected *in situ* (Hill, 1938-1941, p. 164). Identification of distant specimens with such a holotype can hardly be precise.

Thysanophyllum argylli comprises corallites with mostly continuous major septa and with flat, densely packed tabulae, i.e., different in these respects from *T. grootae* sp. nov.

Only the largest mature corallites of *T. argylli* achieved n:d ratio of the smallest representatives of *T. grootae* sp. nov. With all doubts and differences mentioned, it looks safer to introduce a new species for the Spanish colony.

Range — Perapertu Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Family Petalaxidae Fomichev, 1953
Genus *Cystolonsdaleia* Fomichev, 1953

Type species — *Petalaxis (Cystolonsdaleia) lutugini* Fomichev, 1953 (by original designation); Upper Carboniferous, Lower Moscovian (Kashirian), Limestone L, Donets Basin, Ukraine.

Diagnosis — Cerioid; corallite walls four-layered; septa finely trabecular, thickened at corallite wall; axial structure joined to cardinal septum, vertically continuous; tabularium biform; tabulae subhorizontal to adaxially elevated, generally concave, some deflected distally to form periaxial cones in axial column; dissepiments ordinarily transeptal; increase lateral (after Bamber & Fedorowski, 1998, p. 72, simplified).

***Cystolonsdaleia densiconus* (de Groot, 1963)**

Pl. 21, figs. 1-3.

1963 *Lonsdaleia portlocki* (Stuckenber) *densiconus* de Groot, p. 79, pl. 15, fig. 1.

Material — A fragment of a single colony, RGM 112719. Some corallites crushed. Slight diagenetic alteration of the microstructure. See de Groot (1963, p. 80) for more details.

Emended diagnosis — *Cystolonsdaleia* with n:d ratio 16:6.0-20:8.0; thick median lamella continuous with cardinal septum; remaining major septa do not reach axial structure; counter septum equal to other major septa; periaxial cones poorly developed; axial tabellae rare.

Additional description: morphology — De Groot (1963) pointed out a temporary absence of septal lamellae and axial tabellae in the axial structure of her new subspecies. Indeed, the scarcity of those structural elements as well as considerable thickness of median lamella form a set of distinguishing characters of the Spanish specimen (Pl. 21, fig. 1). A strong underdevelopment of periaxial cones (term introduced by Bamber & Fedorowski, 1998) should be mentioned in addition (Pl. 21, fig.

2). All those characters make *C. densiconus* similar to some species of *Petalaxis*.

Like in other representatives of the genus, the tabularium in *C. densiconus* is biform. This character is not always well expressed because minor septa may be underdeveloped or absent from the tabularium. Differences between Position I and II are not large. Thus, they are not always obvious from the longitudinal section, except when a fragment of a minor septum is sectioned (Pl. 21, fig. 2, lower and upper left).

Microstructure — The finely trabecular microstructure, established by Bamber & Fedorowski (1998) for *Cystolonsdaleia*, is well documented in the longitudinal section of *C. densiconus* (Pl. 21, fig. 3). Individual trabeculae are densely packed, slightly wavy during their growth and very thin, not exceeding 0.01 mm in diameter. In the outer tabularium they are arranged at an angle of *c.* 30-45° to the periphery. The microstructure of septa and intercorallite walls was not investigated in the transverse section. That section was made from a part of the colony altered diagenetically to an extent making recognition of the original microstructure impossible.

Remarks — De Groot (1963, p. 81) considered the name *Petalaxis* Milne-Edwards & Haime, 1852, invalid. Thus, she identified species included in that genus by Fomichev (1953) as “undoubtedly a *Lithostrotionella*.” She also criticized an idea by Fomichev (1953) of *Cystolonsdaleia* as a new subgenus of *Petalaxis*, i.e., of *Lithostrotionella sensu de Groot*. Both those ideas of de Groot (1963) are not followed in the present paper.

The question of validity of the name *Petalaxis* Milne-Edwards & Haime, 1852, was for a long time controversial. Its type was designated three times; by Roemer (1883), who designated *Stylaxis maccoyana* Milne-Edwards & Haime, 1851, by Hill (1938-1941) who oversaw the earlier designation by Roemer (1883) and designated *Stylaxis portlocki* Milne-Edwards & Haime, 1851, and by Fomichev (1953) who oversaw both earlier designations and independently designated *S. maccoyana*. The situation became clear after the paper by Sutherland (1978). The genus *Petalaxis*, based on the type species *Stylaxis maccoyana* Milne-Edwards & Haime, 1851, has not been questioned since.

A restudy of the type material (Bamber & Fedorowski, 1998) and the investigation of new samples from the Ellesmere Island (Arctic Canada) documented an important distinction between *Petalaxis* and *Cystolonsdaleia*, i.e., the occurrence of axial cones in *Cystolonsdaleia* and the absence of those structures in *Petalaxis* (see Bamber & Fedorowski, 1998). A further discussion of the genus *Cystolonsdaleia* and genera included in the family Petalaxidae is given by Fedorowski *et al.* (in prep.).

De Groot (1963, p. 79) considered characters of *Stylaxis portlocki* Milne Edwards & Haime, 1851, and *Cystolonsdaleia portlocki* of Fomichev (1953) different from *Petalaxis portlocki* of Stuckenberg (1888) and Dobrolyubova (1935), and considered the Spanish specimen studied by her related to the latter two. Also, she transferred *P. portlocki* of the latter two authors and her new subspecies *densiconus* to the genus *Lonsdaleia* McCoy, 1849. This was not followed by Bamber & Fedorowski (1998), who elevated *L. portlocki densiconus* de Groot to the level of a species within the *Cystolonsdaleia*.

The Spanish specimen differs from the Russian and Ukrainian *C. portlocki* in more compact axial structure, dominated by median lamella supplemented by rare septal

lamellae, very few axial tabellae and inconspicuous periaxial cones. Also, the n:d ratio of the Spanish specimen differs from the Russian and Ukrainian specimens.

Rodríguez (1984) did not recognize a distinction of the specimen described by de Groot (1963) and included it in the synonymy with *Cystolonsdaleia portlocki* (Stuckenberg, 1888). This and the identity at the species level of the specimen of Rodríguez (1984) with Russian species is not accepted herein. Neither of the Russian and Ukrainian specimens identified as *C. portlocki* possesses the axial column constituted mostly of linking axial tabellae with median lamella (Rodríguez, 1984, text-fig. 182, pl. 18, figs. 5-6). The microstructure of septa was not illustrated by Rodríguez (1984) in photographs. His drawing (Rodríguez, 1984, text-fig. 180) showing crystals growing obliquely to the lateral surfaces of septa and sharply elongated peripherally in some places, cannot reflect the original microstructure. It may, however, have resulted from diagenetic alterations. This problem cannot be solved without a large magnification photograph.

Range — Celada Limestone, a probable equivalent of Sierra Corisa Limestone, Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Genus *Petalaxis* Milne-Edwards & Haime, 1852

Subgenus *Petalaxis* (*Petalaxis*) Milne-Edwards & Haime, 1852

Type species — *Stylaxis M'Coyana* Milne-Edwards & Haime, 1851; Upper Carboniferous (Moscovian, Myachkovsky), Moscow Basin, Russia.

Diagnosis — Cerioid, rarely subcerioid in part of colony; corallite wall trabecular early in ontogeny, replaced by four-layered; septa finely trabecular, commonly discontinuous in dissepimentarium; axial structure joined to cardinal septum, varies from simple median lamella to complex structure; tabularium biform; tabulae usually concave to subplanar, axially elevated in some; dissepimenta ordinarily transeptal, in some species mainly interseptal; increase lateral (simplified after Bamber & Fedorowski, 1998, p. 19).

Remarks — The genus *Petalaxis* was thoroughly discussed by Bamber & Fedorowski (1998; Fedorowski *et al.*, in prep.). Thus, the discussion that follows concerns mostly variability of the axial structure, not mentioned in those papers. The informal grouping of species, introduced by Sando (1983) and followed by Kossovaya (1998, 2001), is not accepted. Artificiality of such grouping is well accentuated by the so-called *Petalaxis* (*P.*) *maccoyana* Group (Kossovaya, 1998, p. 676; 2001, p. 162) comprising species with three-layered walls (*P.(D.) wagneri*, *P. (D.) intermedia*, *P. (D.) sexangulus*) and four-layered walls (*P. (P.) maccoyana*, *P. (P.) donbassica*). Composition of external wall reflects a level of integration within colonies. Thus, its taxonomic value is obvious and its rank should be evaluated higher than species. Grouping together of bearers of such distinct characters cannot be accepted from the biological point of view.

The direct relationship of the columella to the cardinal septum in the family Petalaxidae has been generally accepted and is not challenged in the present paper. Some peculiarities of the axial structure, such as a temporary disconnection of the median lamella from the cardinal septum and appearance of lateral lamellae, require more thorough investigation. The restudy for the purpose of the present paper of several specimens belonging to different species of the genus *Petalaxis* has shown, however, that not only morphology of the axial structure may differ greatly during the course of growth of particular corallites (e.g., Pl. 30, figs. 5-8), but also the position of the median lamella and its connection to major septa may change. Very thick median lamella directly connected to the cardinal septum at the beginning of serial acetate peel impressions (Pl. 30, fig. 5) became isolated from it for some distance of growth and transfers into the axial structure by incorporating few septal lamellae and axial tabellae (Pl. 30, figs. 6, 7). An arrangement of some of those lamellae, directly connected to major septa (Pl. 30, fig. 6), camouflage a true symmetry of the corallite. The median lamella joined the cardinal septum at the end of the series illustrated (Pl. 30, fig. 8), but as a part of the axial structure additionally composed of few strong septal lamellae and axial tabellae. Transfer from slightly elongated septal lamella in the axial structure (Pl. 30, fig. 9) into lateral lamella, with few axial tabellae spanned between it in the median lamella (Pl. 30, fig. 10), is shown by another corallite of the same colony.

The described and similar variance in morphology of the axial structure is fairly common in some transverse sections of the holotype colony of *Petalaxis (Degrootia) perapertuensis*, but rare in others of the same colony. Also, they were recognized in a part of the paratype colony of *P. (D.) wagneri wagneri* and are common in some transverse sections of *P. (D.) cantabrica*. An inconstant character of variance with either complex or simple model prevailing in particular parts of colonies or during different astogenetic stages is misleading. As a result, a different species or higher rank position may be proposed to different parts of a colony when studied from a single, incidental section, as commonly takes place.

An absence of the axial structure and/or an occurrence of the median lamella disconnected from the cardinal septum is another problem to be discussed. None of the corallites studied herein in adequate detail and along an adequate length of growth exhibits a total absence of the median lamella and/or the cardinal septum permanently equal in length to remaining major septa. Serial acetate peel impressions investigated along 0.5 to 1.5 cm. growth of corallites document both temporary acolumellate growth of individual corallites and its random occurrence within colonies. Thus, interruption of the axial structure in *Petalaxis*, but not its absence from some corallites, was accepted. This character may change from section to section and should be utilized for taxonomy with special care. Also, slight elongation of the thin cardinal septum instead of a formation of the thickened median lamella is rare and incidental in most species restudied, but it may be diagnostic for some others.

A comparison of the phenomena described above to individual growth levels of a colony or to periods of offsetting of individual corallites did not bring satisfactory results. Only some relationship between offsetting and isolation of a median lamella from the cardinal septum was established. It was observed in few instances of formation of an offset on the cardinal septum side of a corallite.

Petalaxis (Petalaxis) maccoyanus (Milne-Edwards & Haime, 1851)

Pl. 21, figs. 4-7.

- 1851 *Stylaxis M'Coyana* Milne-Edwards & Haime, p. 453, pl. 12, fig. 5.
 1963 *Lithostrotionella celadensis* de Groot, p. 82, pl. 15, fig. 2.
 1963 *Lithostrotionella maccoyana* (Edwards & Haime, 1851): de Groot, p. 82, pl. 16, fig. 1.
 ? 1984 *Petalaxis penduelensis* Rodriguez, p. 351, text-figs. 185-188, pl. 19, figs. 1-4.
 1985 *Petalaxis stylaxis* (Trautschold): Boll, p. 42, pl. 5, fig. 5.
 1998 *Petalaxis mcoyanus* Bamber & Fedorowski, p. 42, text-figs. 16, 24-25; pl. 1, figs. 1-10 (*cum syn.*).
 2001 *Petalaxis (P.) mcoyanus* Kossovaya, p. 163, pl. 33, figs. 10-11, pl. 33, figs. 1-2.

Material — Six fragments of colonies altered by compaction and recrystallization to a different degree. Some corallites within individual colonies crushed. Microstructure slightly altered in some (e.g., RGM 112721), deeply altered in other corallites (de Groot, 1963, pp. 82-83).

Diagnosis — *Petalaxis* having 14-19 (commonly 15-17) major septa at mean diameter 4-8 mm; minor septa extend adaxially from dissepimentarium one quarter to two thirds of tabularium radius; axial structure consists of thickened median lamella, short, discontinuous septal lamellae, one, rarely two lateral lamellae and rare axial tabellae; tabulae commonly incomplete, concave, subhorizontal; periaxial tabellae may be convex and moderately to strongly elevated adaxially, 5-12 (commonly 9 or 10) tabulae in 5 mm; tabularium to corallite diameter ratio 0.65-0.73; transeptal dissepimentarium continuous, dissepiments of medium size (after Bamber & Fedorowski, 1998, p. 44).

Remarks — *Petalaxis maccoyanus* was most recently discussed in detail by Bamber & Fedorowski (1998). Three earlier records were not considered in that discussion; *Lithostrotionella celadensis* de Groot, 1963, *Petalaxis penduelensis* Rodriguez, 1984, and *Petalaxis stylaxis* (Trautschold) of Boll, 1985. Characters illustrated and described by the latter author leave no doubt that his illustrated specimen belongs to *P. maccoyanus*. Thus, a wider discussion is unnecessary.

A reinvestigation of a single, fragmentary colony separated by de Groot (1963) as the new species *Lithostrotionella celadensis* does not prove that distinction. Colonies with corallites exposing a poor development of an axial structure and an underdevelopment of minor septa, i.e., characters considered diagnostic for "*L.*" *celadensis*, occur in specimens from the type area for *P. maccoyanus* (e.g., Bamber & Fedorowski, text-fig. 24c, pl. 1, fig. 6) and elsewhere, together with colonies possessing those structures albeit better developed. Intermediate corallites present within particular colonies and colonies with the first or second kind of morphology prevailing, allow these characters to be considered as intraspecific.

The late Bashkian occurrence of *P. penduelensis* forms the only reason for a questionable synonymy of that species with *P. maccoyanus*. Its n:d ratio and morphology, including characters pointed out by Rodriguez (1984, p. 353) as distinguishing his specimens from *P. maccoyanus*, are easily recognizable in the latter species. Thus, the specimens of Rodriguez (1984) represent probably the earliest occurrence of *P. maccoyanus* recorded so far. The stratigraphic value of that species, pointed out by Bamber & Fedorowski (1998), will be reduced if the proposed synonymy is confirmed.

Kossovaya (2001) did not accept "*Lithostrotionella*" *maccoyana* (Milne Edwards & Haime) of de Groot (1963) as a member of that species and did not indicate an alternative for its identification. Also, she included in *P. (P.) stylaxis* (Trautschold) the Russian specimens identified by Bamber & Fedorowski (1998) as *P. maccoyanus*. Canadian colonies described by those authors were omitted by Kossovaya (2001) from any discussion.

The position of Kossovaya (2001) could perhaps be considered a different attitude to the evaluation of characters if well documented and consistent. However, illustrations by Kossovaya (2001, pl. 32, fig. 10, 11, pl. 33, figs. 1, 2) of *P. (P.) maccoyanus* are incomplete and poor, being taken from very oblique sections that deforms the real morphology of corallites. Reasons pointed out by Kossovaya (2001, p. 163) for not considering specimens included in that species by Bamber & Fedorowski (1998) are inadequate. These are "...more simple axial structure [in Kossovaya's specimens], with rare additional axial septal plates and less numerous rows of dissepiments." First of those arguments cannot be judged with certainty from Kossovaya's (2001) pictures, but may be true for some colonies or particular sections. Large variability of the axial structure is discussed above with remarks on the genus. The Spanish specimen revised herein (Pl. 21, fig. 7) shows that variability well.

Despite listing few syntypes, Kossovaya (2001) restricted her investigation and illustrations to her own single colony with very few corallites sectioned, and to two corallites taken from the colony described by Fedorowski (*in* Fedorowski & Goryanov, 1973, text-fig. 20), although 15 well preserved corallites of that colony were available from the illustration cited. Thus, an axial structure of *P. maccoyanus*, described by Kossovaya (2001, p. 167) as almost identical to that of *P. (P.) stylaxis*, cannot be considered either important for the distinction between those species or conclusive for their identifications.

The difference in number of rows of dissepiments, pointed out by Kossovaya (2001, p. 163), does not exist. The number of rows of dissepiments seen in longitudinal sections of specimens investigated by Bamber & Fedorowski (1998, pl. 1, figs. 2, 3, 5, 7, 8, 10), including Russian hypotypes, is mainly restricted to two. The same is true for the Spanish specimens investigated by de Groot (1963, pl. 1b, 2b and Pl. 21, fig. 6 in this paper). An enlarged number of dissepiments seen occasionally in parts of sections is either artificial, resulting from the obliqueness of a section, or corresponds to sections through corallite corners. The number of dissepiments that fill the room between an external wall and a constant tabularium is always larger in corners, but this cannot be considered for comparisons. Oblique illustrations provided by Kossovaya's (2001) made impossible any detailed comparison of number of rows of dissepiments in her specimen.

Three items included in descriptions of species by Kossovaya (2001) should be pointed out as very doubtful or non-existing. Describing *P. (P.) maccoyanus* (p. 163) she wrote "clinotabulae rare." The term "clinotabulae" was introduced by Minato & Kato (1965) for peculiar basal structures characteristic for the family Waagenophyllidae. They are absent from the family Petalaxidae in which a bifurcated tabularium is developed.

Describing hystero-ontogeny in *P. (P.) donbassica*, Kossovaya (2001, p. 165) mentioned an "intercorallite offsetting." Such an offsetting occurs exclusively in aphyroid taxa and the term means formation of an offset on a coenosarc without connection to

any polyp that can be pointed out as its parent. Although illustrations were not provided by Kossovaya (2001), an intercorallite offsetting is by definition absent from cerioid colonies.

In the description of *P. (P.) stylaxis* Kossovaya (2001, p. 167) stated that trabeculae are "rare" (redkie). Because of the double meaning of this word in Russian it remains uncertain whether they are widely spaced or seldom occurring. Neither meaning is correct. Trabeculae in all Petalaxidae investigated so far are fine and placed next to each other as all monacanthine trabeculae do. Thus, there is no reason to believe that they differ considerably in the specimen investigated by Kossovaya (2001) unless the latter does not belong in that family. The second meaning cannot be accepted because trabeculae either are developed or not. *Tertium non datur*. The lack of illustrations in Kossovaya's (2001) paper of such important details as the microstructure of septa and external walls, the sequence in development of particular details during hystero-ontogeny, the biform arrangement of tabulae, the morphology of the axial structure and the presence or absence of channels, make the conclusions unsupported therein.

The comparison of descriptions and illustrations by Dobrolyubova (1935) and Kossovaya (2001) of *Petalaxis stylaxis* (Trautschold, 1879) has shown that some colonies included in that species are very close in all characters to colonies included herein in *P. maccoyanus*. In this paper I do not propose a synonymy of those two because the holotype of *P. stylaxis* was not investigated in the modern way. Also, the investigation of probable topotypes is incomplete, with the microstructure of their intercorallite walls unknown and their general morphology variable. Nevertheless, such a synonymy seems probable.

In these remarks I would only like to point to the specimen illustrated by Dobrolyubova (1935, pl. 1, fig. 1), possessing intercorallite channels closely resembling those in ?*P. (P.) monocyclica* (Pl. 23, fig. 4). Reinvestigation of Dobrolyubova's (1935) specimen may document a separate subgeneric or generic status of those two specimens. Such a solution is not formally proposed herein due to the unknown microstructure of the Russian specimen and poor preservation of the Spanish colony. It seems indisputable, however, that specimens exposing such an important, qualitative character cannot be included in a species possessing continuous intercorallite walls. The Early Permian *Parawentzelella* distinguished by Fontaine (1961) mainly due to possessing channels, and generally accepted by subsequent authors, may serve as a good precedent.

Kossovaya (2001) did not mention the microstructure of intercorallite walls, critical for subgeneric identification. Thus, species identified by that author as *Petalaxis s.s.* are herein accepted only by an analogy with other Russian, Canadian and Spanish specimens investigated in adequate detail. The microstructure of septa in Spanish specimens is finely trabecular with individual trabeculae approximately 0.02 mm in diameter, slightly wavy in their growth and rather widely spaced (Pl. 21, fig. 4). Well preserved trabeculae were not seen in the transverse section of septa. Their remnants were observed in one median lamella (Pl. 21, fig. 4). This appearance confirms bodies seen in the longitudinal section as trabeculae altered the same way as those discussed in slightly more detail with *Corwenia cantabrica*.

Diagenetic alterations of the intercorallite walls in all colonies reinvestigated

prevent rigid conclusions. Comparison with similarly altered walls in other colonies indicates that they consist of four-layers, established by Bamber & Fedorowski (1998) for the species discussed.

Range — ?Upper Bashkirian (Valdeteja Formation), Upper Moscovian (Podolskian and Myatchkovian).

Occurrence — Moscow Basin (Russia), Donets Basin (Ukraine), Northern Palencia (Spain), Ellesmere Island (Canadian Arctic Archipelago), ?southwest China.

Petalaxis (Petalaxis) belinskensis Fomichev, 1953

1953 *Petalaxis maccoyana* Milne Edwards & Haime var. *belinskensis* Fomichev, p. 457, pl. 31, fig. 3.

1963 *Lithostrotionella maccoyana* f. *major* de Groot, p. 83, pl. 16, fig. 2.

Material — A single, incomplete colony, RGM 112726, illustrated by de Groot (1963, p. 84, pl. 16, fig. 2).

Diagnosis — *Petalaxis* with maximum n:d ratio 20:7.0 mm; major septa approach, some reach axial structure comprising thickened median lamella and 0-6 short septal lamellae; minor septa up to two thirds of tabularial parts of major septa; counter septum commonly shortened a little; complete ring of small, globose lonsdaleoid dissepiments.

Remarks — Both Fomichev (1953) and de Groot (1963) recognized and discussed differences of their subspecies from *P. maccoyanus*. De Groot (1963, p. 84) recognized a similarity of her specimen to both "subspecies" of *P. maccoyanus* distinguished by Fomichev (1953), but she accepted differences between her specimens and those "subspecies" as more important than similarities. I maintain the opposite position. All characters pointed out in the diagnosis are in common for the Spanish and Ukrainian specimens whereas differences between them are sparse and of much lesser taxonomic value. *Petalaxis maccoyanus multiseptatus* Fomichev, 1953, occurring in the same "L" set of limestones as *P. belinskensis*, belongs probably to the same species. Its very poorly preserved holotype (Fomichev, 1953, pl. 31, fig. 4) prevents a satisfactory comparison. Thus, this "subspecies" was not considered herein and was not included in the synonymy above.

De Groot (1963, p. 84) pointed out an occurrence of clinotabellae in Spanish specimen as one of main differences when compared to the Donets Basin specimens. These structures are absent from all specimens of the family Petalaxidae, including those of Spain and the Donets Basin. The problem of clinotabellae vs. tabulae (tabellae) in Position I was discussed by Bamber & Fedorowski (1998) and earlier in the present paper.

Range — Middle to Upper Moscovian.

Occurrence — Donets Basin (Limestones L1-L7), Ukraine; Northern Palencia (Vañes Formation, Westphalian C), Spain.

Petalaxis (Petalaxis) orboensis (de Groot, 1963)

Pl. 22, figs. 1-8.

- 1963 *Lithostrotionella orboensis* de Groot, p. 85, pl. 17, fig. 2.
 ? 1978 *Lithostrotionella orboensis*: Fan, p. 183, pl. 67, fig. 1.
 ? 1984 *Lithostrotionella orboensis*: Yu, p. 362, pl. 2, fig. 3.

Material — Two fragments of colonies derived from the same locality; only the holotype was thin sectioned and illustrated (de Groot, 1963, p. 86).

Emended diagnosis — *Petalaxis* with up to 20 major septa and up to 8.6 mm corallite diameter; septa thin; major septa approaching thin, irregular, interrupted median lamella; minor septa discontinuous in dissepimentarium, may reach three quarters of tabular parts of major septa; counter septum may be slightly shortened; dissepimentarium *c.* one third corallite radius in width; ring of lonsdaleoid dissepiments incomplete.

Additional description: morphology — N:d ratios measured for the purpose of this paper differ slightly from those measured by de Groot. This most probably resulted from a different method of measuring. Examples of n:d ratio: 20:7.8; 19:8.6; 19:8.0; 19:6.5; 18:6.6; 18:6.4; 18:6.2; 17:5.9. The counter septum in some corallites is slightly shortened (Pl. 22, fig. 6, left) whereas it is indistinguishable from other major septa in most corallites (Pl. 22, fig. 1). The cardinal septum is almost permanently connected to a median lamella that in most corallites forms its simple elongation often intersecting the entire axial area and approaching the counter septum (Pl. 22, fig. 7). The median lamella is monoseptal, commonly slightly thickened and straight, but may be thin and wavy or absent from some transverse sections. The latter may be a secondary character resulting from the advanced diagenesis (Pl. 22, fig. 8). The tabularium is clearly biform in some corallites or their parts, where it is documented by numerous sections of peripheral parts of tabulae on one side of a minor septum and none or very few on its opposite side (Pl. 22, fig. 6, lower). This character is not equally well demonstrated in all loculae, but was proven in the longitudinal section showing a transmission from Position II to Position I (Pl. 22, fig. 2, upper right; fig. 3, the same enlarged). The opposite side of the tabularium in the same section (Pl. 22, fig. 2, left) exhibits disturbances caused by an incorporation of a strange object.

Microstructure and diagenetic alterations — As indicated by less altered parts of septa, their microstructure was most probably finely trabecular. Unfortunately, sections available for the study do not prove this with adequate certainty. Diagenetic alterations are variously advanced, with bunches of fibrils (Pl. 22, fig. 4) documenting the lesser advancement. Fans of fibrils in sections of first offset's septa are similar to those in the neotheca (Pl. 22, fig. 4). Thus, I consider the latter a partition comparable to that described by Bamber & Fedorowski (1998) in a comparable growth stage of other *Petalaxis* species. The partition was in the Russian and Canadian *Petalaxis* replaced by the dividing wall, a process predicted for the Spanish species of that subgenus as well. Despite of uncertainty resulting from diagenetic alterations, the mature intercorallite walls seem to consist of four layers (Pl. 22, fig. 5) as they are in the mature corallites of *Petalaxis s.s.* from the type area. Thus, I consider the species discussed to represent the nominative subgenus of *Petalaxis*.

Remarks — The reinvestigation of thin sections of *P. orboensis* allowed establishment of its close similarity to *P. donbassicus* (Fomichev, 1939), restudied by Bamber & Fedorowski (1998). These two species possess a similar n:d ratio, major septa approaching axial structure, very long minor septa and the tabularium is clearly biform. Thin, interrupted and monoseptal median lamella in *P. orboensis* versus thick in *P. donbassica* and the tabularium generally convex in the Spanish species constitute the main differences between those species. Similarity of *P. orboensis* to *P. mohikana* Fomichev, 1953, discussed by de Groot (1963, p. 86) is accepted herein and omitted from this discussion.

There are two records of the occurrence of *P. orboensis* in Moscovian strata of South China (Fan, 1978; Yu, 1984). Although both records mentioned are uncertain, the specimen described and illustrated by Fan (1978, p. 183, pl. 67, fig. 1a, b) strikingly resembles the Spanish holotype. Possessing similar numbers of septa and corallite diameters it also has thin major septa approaching thin median lamella, long minor septa, the dissepimentarium of similar width and tabulae inclined towards the columella. Very sparse lonsdaleoid dissepiments in the Chinese specimen, an uncertain microstructure of its septa and morphology of its tabularium (biform or normal) make its synonymy with *P. orboensis* doubtful.

Corallites in the colony described by Yu (1984, p. 362, pl. 2, fig. 3a, b) and revised by the present author differ from the Spanish holotype in possessing better-developed lonsdaleoid dissepiments and in having major septa thicker in the tabularium. They resemble the Spanish holotype in the interruption of the median lamella, in possessing a biform tabularium and in n:d ratio.

Range — Orbó limestone, Upper Moscovian; ?Huanglung Limestone, Moscovian.

Occurrence — Northern Palencia, Spain; ?Sichuan and Jiangsu, South China.

?*Petalaxis monocyclicus* (de Groot, 1963)

Pl. 23, figs. 1-7.

1963 *Lithostrotionella monocyclica* de Groot, p. 85, pl. 17, fig. 1.

Material — One fragment of a colony. Specimen diagenetically altered, but remnants of primary microstructure preserved in places (de Groot, 1963, p. 85).

Emended diagnosis — Cerioid(?) colonies with intercorallite channels; maximum n:d ratio 22:8.3 mm; cardinal septum elongated so as to pass corallite axis; counter septum may be longer than adjacent major septa; simple, elongated columella, derived from cardinal septum, may be free; minor septa as half-moon thickenings of intercorallite walls; microstructure of septa trabecular.

Additional description: morphology — N:d ratios of corallites constitute regularly increasing values with largest differences observed in early growth stages. Measured values are following: 22:8.3; 22:8.0; 21:7.6; 21:7.1; 20:6.5; 20:6.3; 20:6.2; 20:5.3; 18:4.7; 17:3.8; 17:3.4; 17:3.0; 15:3.2; 15:3.0. Mature morphology of individual corallites is con-

stant in the moderate length of thin major septa and in the absence of blades of minor septa. The latter are represented by half-moon thickenings of intercorallite walls, equal in size with those corresponding to major septa. Neither a "dark line" nor other microstructural elements are seen in those peripheral thickenings. "Half-moons" corresponding to minor septa are absent from the intercorallite walls early in the hystero-ontogeny (Pl. 23, fig. 3, lower).

There are narrow channels present rarely between mature corallites (only two were observed in two thin sections available for the study). Rounded and slightly thickened external walls bordering these channels and an arrangement of dissepiments (Pl. 23, fig. 4) prove the natural, not diagenetic, nature of these breaks in intercorallite walls. These channels allowed direct communication of neighbouring polyps. Unfortunately, advanced diagenesis prevents detailed microstructural study of intercorallite walls and a further interpretation of the colony integration.

The development of protosepta and a median lamella is most variable and important. The earliest hystero-ontogenetic stages were not investigated, but at least some corallites possess the counter septum slightly shortened in the neanic stage when the cardinal septum is already elongated (Pl. 23, fig. 1). This shortening is not constant and in the other corallites of similar or slightly larger diameter and/or number of major septa the counter septum is equal to adjacent major septa or slightly longer from them. It is not quite certain whether the counter septum became elongated so as to meet the distinctly elongated cardinal septum or only the latter grew up to meet the former. Both options can be possible. Corallites possessing united protosepta (Pl. 23, fig. 5) are not unique. There are also sections of corallites with the cardinal septum elongated around the median lamella, almost up to meeting the counter septum, that remain equal to other major septa (Pl. 23, fig. 7). The counter septum in rare corallites is elongated without meeting the long cardinal septum. The median lamella is in such instances free from both protosepta (Pl. 23, fig. 6). In most corallites (Pl. 23, fig. 1) median lamellae form simple elongations of cardinal septa. The variability described is partly connected to growth stage, but is also observed in mature corallites. It was described in so much detail for two reasons; as being unique among species of *Petalaxis* described so far and as being so large. Several of those variants may have been considered taxonomically important if consistent for different colonies. Despite the occurrence of such an important character as channels, the single colony investigated does not permit a far-ranging extrapolation.

The development of lonsdaleoid dissepiments in individual corallites differs, but the completeness of the lonsdaleoid dissepimentarium is mostly connected to hystero-ontogeny. Only the largest mature corallites may possess a complete ring of lonsdaleoid dissepiments. Those dissepiments are very different in size within a given section of a corallite, ranging from small, globose blisters to large bodies that span the entire segment of an intercorallite wall (Pl. 23, fig. 1). Differences in the development of lonsdaleoid dissepiments are seen in all growth stages observed.

The microstructure and diagenetic alterations were insufficiently studied due to the inadequate material. The microstructure of septa is trabecular, but poorly preserved remnants of trabeculae were observed only in a single median lamella (Pl. 23, fig. 2). In the case of intercorallite walls, remnants of a single "dark line" (Pl. 23, fig. 4), may speak in favour of the fibro-normal partition, but this cannot be proven.

Remarks — Morphology of protosepta and the axial structure clearly distinguish the species discussed from all species of *Petalaxis*. The same characters, however, and an absence of rigid data concerning the microstructure of the intercorallite wall made its place within that genus doubtful. This concerns elongation of the counter septum and formation of the columella. The species discussed may be important for establishing ancestors of that genus if well represented. Unfortunately, this problem cannot be solved with data provided by the specimen discussed. A connection of the cardinal and counter septa present in some corallites points towards *Lithostrotion*, but a very well developed lonsdaleoid dissepimentarium prevents such an interpretation.

Range — Santa Maria Limestone (Upper Bashkirian to Lower Moscovian-Vereian).

Occurrence — Northern Palencia, Spain..

Subgenus *Petalaxis* (*Degrootia*) subgen. nov.

Type species — *Lithostrotionella* (*Hillia*) *wagneri* de Groot, 1963.

Etymology — Named in honour of the late Dr. Gerda E. de Groot, an outstanding student of rugose corals.

Diagnosis — *Petalaxis* with corallites divided by partitions.

Remarks — De Groot (1963, p. 86) introduced a new subgenus *Hillia* of the genus *Lithostrotionella* for corals possessing "a narrow, mainly interseptal dissepimentarium; tabulae horizontal or concave with upturned edges, some with clinotabellae; increase peripheral." She then included in that subgenus such species as, for instance, *Hillia intermedia* de Groot that obviously do not fit the diagnosis due to its wide dissepimentarium with numerous lonsdaleoid dissepiments, but left with the nominative subgenus the species or specimens, such as the paratype of "*L.*" *sexangula* de Groot, that clearly exposes diagnostic characters of *Hillia*. Also, she did not draw attention to the microstructure of intercorallite walls and misinterpreted as clinotabellae the peripheral tabulae in Position I of the biform tabularium. An imprecise statement "narrow dissepimentarium" led in turn to the inclusion in the subgenus of specimens possessing that character, but otherwise distinct, such as "*Hillia*" *radians* de Groot and the paratype, RGM 112738, of "*H.*" *wagneri*.

The question of priority of the name *Petalaxis* over *Lithostrotionella* and preoccupation of the name *Hillia* by a lepidopteran insect was discussed elsewhere (e.g., Sutherland, 1978; Hill, 1981; Yu, 1984; Bamber & Fedorowski, 1998) and will not be repeated. There remain several questions open, however, with the correctness of the introduction by Yu (1984) of the new generic name *Grootia* on the first place. Yu (1984, pp. 104, 112 [English translation]) pointed out the preoccupation of the name *Hillia*. He did not replace the invalid name in accordance to the ICZN rules, however, but introduced the name *Grootia* as *genus novum* based not on *Lithostrotionella* (*Hillia*) *wagneri*, i.e., the type species of *Hillia*, but on the Chinese species *Paralithostrotion*

ceriodium Xu in Jia et al., 1977. Creation of a new genus instead of the substitution is acceptable from the formal point of view. Also, checking in the *Nomenclator Zoologicus* shows that the name proposed by Yu (1984) is not preoccupied. Thus, the name *Grootia* is most probably valid from the formal point of view.

Grootia was accepted by Kossovaya (1998, 2001) without comprehensive discussion. Also she included *Lonsdaleia ivanovi* Dobrolyubova, 1935, in *Grootia*. This species is a potential member of *Degrootia*, but I did not consider it in the context of that subgenus. Dobrolyubova (1935, p. 31, pl. 11, figs. 1, 2) did not mention the microstructure of septa and the intercorallite wall in her species. Strong boundaries within the thickness of those walls seen in the pictures cited say nothing until three- or four-layered walls are established on the basis of microstructural studies. Thus, having no new data I follow the position of Bamber & Fedorowski (1998) who questionably included that species in *Cystolonsdaleia*.

The original characteristics of the genus *Grootia* are very incomplete in the diagnosis, description, illustration and remarks. Yu (1984, p. 122) based the diagnosis of his new genus on that of *Hillia* writing: "The diagnosis of new genus is identical with *Lithostrotionella* (*Hillia*) Groot." He further states "Septa of two orders. Lathlike columella developed. Dissepimentarium narrow." These are trivial and do not characterize any particular genus. Also, he is incorrect in such basic information as presence of well developed clinotabulae and absence of "cystosepiments" (= lonsdaleoid dissepiments). Rare lonsdaleoid dissepiments occur both in the type species of *Grootia* and in another species included in it by Yu (1984), whereas clinotabulae of that author are, in fact, tabulae in the Position I. Development of the biform tabularium in the type species of *Grootia* can only be predicted on the basis of positions of sections of some tabulae in the transverse section, but cannot be proven due to an absence of properly oriented longitudinal thin sections. However, an occurrence of the biform tabularium in *Grootia longhuoensis* (Yu, 1984, pl. 1, fig. 1b) was established by me on the basis of the original thin sections restudied.

The microstructure in both septa and intercorallite walls of the type species of *Grootia* is unknown. A thick and rather poorly preserved thin section did not provide reliable data, the stony remnants of specimens, holotypes included, are not housed by Chinese museums and the topotype material was not available for the purpose of this paper. An examination of the original illustrations (Xu in Jia et al., 1977, pl. 72, fig. 7a, b) did not throw light on those characteristics either. The restudy of *Grootia longhuoensis* did not bring satisfactory information because the material is strongly diagenetically altered.

Summing up all the reasons pointed out above and taking in mind a very poor representation of the genus *Grootia* (only two fragments of colonies were available for original studies and only four poor thin sections exist), I decided not to apply the name *Grootia* to any Spanish taxa, although some of them are comparable to the Chinese specimens in their general morphology. This concerns first of all the paratype RGM 112738 of "*H.*" *wagneri* and the paratype RGM 112728 of "*L.*" *sexangula*, both possessing the dissepimentarium incomplete. Other species and specimens are much less similar to the Chinese species.

Diagenetic alterations precluded a conclusive decision concerning the microstructure of intercorallite walls in the Chinese specimens identified as *Grootia*. Thus, the

main diagnostic character distinguishing *Degrootia* from *Petalaxis* cannot be extended to *Grootia*. In the case of the Spanish specimens fairly sophisticated data were available (see descriptions of individual species for details). It was established that intercorallite walls formed exclusively from laterally contiguous septa, common to neighbouring corallites, are absent from the corallites included by de Groot (1963) in *Hillia*. Thus, a wall comparable to that in the Permian genus *Wentzelloides* (Minato & Kato, 1965, pl. 1, fig. 3 and Pl. 24, figs. 1-3 in this paper) does not occur in *Degrootia*. In most Spanish specimens of "*Hillia*," i.e., *Degrootia*, these walls are directly comparable to another Permian genus, *Wentzellophyllum*, considered septal by Minato & Kato (1965, pl. 1, fig. 7). In this case the strongly thickened peripheral parts of septa are in a direct lateral contact, but there occurs a thin line between individual corallites (Pl. 24, fig. 5; Pl. 29, fig. 4). In some specimens there are short fibrous segments included between peripheral parts of septa (Pl. 24, fig. 4; Pl. 29, fig. 5). As shown by detailed study (see descriptions of species below) there is almost no difference in the origin of the latter two microstructures. Thus, they are considered variants that can commonly occur within the same colony (e.g., Pl. 29, figs. 4-6). First variant is here proposed to call exclusively septal and the second septo-sclerenchymal. The presence of a line, mentioned above, was recognized by Minato & Kato (1965, p. 11) who called it the "original thin wall," but its origin was not discussed.

The occurrence of a thin middle layer of crystals dividing septa in both variants and an incorporation of interseptal fibrous segments in the septo-sclerenchymal wall may be superficially compared to the middle line in the dividing wall, and interpreted as proof for the total isolation of polyps. In contrast to four-layer walls in *Petalaxis s. s.*, however, the wall structure discussed is not constituted of two dark films separated by light film of crystals of an inorganic origin (e.g., Bamber & Fedorowski, 1998, fig. 16 i-n, fig. 17a-d), but is built of uniform sets of crystals comparable to that in the "dark line" of septa (Pl. 29, fig. 4). An upwards and uniform growth of those crystals is confirmed in the longitudinal sections of such walls, which are considered partitions (Pl. 29, fig. 1).

Intercorallite walls occurring in the nominative subgenus of *Petalaxis* were considered dividing walls by Bamber & Fedorowski (1998) who discussed their origin. Despite diagenetic alterations camouflaging primary microstructure, the same kind of walls occur in the Spanish specimens included herein in *Petalaxis s.s.*

This is a matter of a subjective approach to the taxonomy whether or not the interpreted differences in colony integration (i.e., an occurrence of dividing walls vs. partitions) and, consequently, physiology of different groups of species is adequate for their separation on a genus or subgenus level. Such a subjective approach is especially obvious when an origin of intercorallite walls forms the only difference whereas all other characteristics find their counterparts in both groups as observed in the case discussed. From three options available, to ignore that difference, to recognize it but to gather all species in two informal groups and to accept subgeneric ranks, the third option was selected here. It agrees with de Groot's (1963) philosophy although it is supported by different premisses.

Despite the septo-sclerenchymal partition of "*Lithostrotionella (Hillia) wagneri*, a substitute name for *Hillia* (but not a new subgenus), based on a different type species, was proposed. Such a position accentuated a generally correct way of thinking by de Groot, whereas the basic characteristics of *P. (D.) wagneri* are adequate for its subgeneric distinction.

The intracolony variability in morphology and measurements of most species distinguished by de Groot (1963) as *Hillia* (= *Degrootia* nom. nov.) is strikingly similar, repeating most characters discussed below for the holotype colony of *P. (D.) wagneri*. Besides, only *P. (D.) sexangula* is stratigraphically younger (Upper Moscovian). All remaining species are Upper Bashkirian to Lower Moscovian-Vereian. Only *P. (D.) radians* of those four differs from all the remaining species in n:d ratio (Fig. 1) and in a wide, almost exclusively interseptal dissepimentarium that may reach more than one third of a corallite radius. Its interrupted median lamella and the cardinal septum temporary equal to other minor septa are the only characters comparable to some sections of *P. (D.) wagneri* and *P. (D.)* sp.

As shown by this discussion, I generally agree with taxonomic distinctions introduced by de Groot (1963), although a close analysis of morphological characters, hystero-ontogeny and measurements allow some corrections (see below) that may have resulted from a subjective attitude to the material. N:d ratios of *P. (D.) perapertuensis*, *P. (D.) santaemariae*, *P. (D.) intermedia*, *P. (D.) wagneri* and *P. (D.) sexangula* are strikingly similar, repeating each other in large part. This similarity may form a strong argument favouring their synonymy. Such a solution cannot be excluded in some instances, but it does not apply to all taxa listed. An analysis of Figure 1 shows that the number of septa and corallite diameters of individual species exhibit some differences when considered separately. The maximum number of major septa may be of a special value. Three constant values can be distinguished; 15 (*sexangula*), 17 (*wagneri*) and 20-21 (*intermedia*, *perapertuensis*, *santaemariae*). Such a constant character must be considered important, and it obviously is important when *P. (D.) cantabrica* and *Petalaxis (Degrootia)* sp. *versus* remaining species are compared. Thus, morphological details of pairs and/or groups of species distinguished by de Groot (1963) are discussed below in addition to the number of septa.

The field of n:d ratio of *P. (D.) sexangula* is located completely within that of *P. (D.) wagneri* and the frequency peak of both taxa occurs in the same class (Fig. 1). Also, both species closely resemble each other in most morphological characters, temporary equalization of the cardinal septum with major septa and partly septo-sclerenchymal partition included. An extremely constant number of septa and corallite diameters in mature corallites of *P. (D.) sexangula* forms, in fact, the main character distinguishing it from *P. (D.) wagneri*. From three options available, a synonymy with *P. (D.) wagneri*, a subspecies of the latter or an independent species, I arbitrarily selected the second one. Underdeveloped minor septa and monoseptal columella form a set of additional distinguishing characters, whereas close similarity in all other characteristics and in an intracolony variability prevent acceptance of *P. (D.) sexangula* as an independent species as originally proposed by de Groot (1963, p. 84).

In the case of four species possessing n:d ratios closely comparable to one another (Fig. 1), *P. (D.) perapertuense* possesses the smallest corallites and the dissepimentarium most distinctly reduced. It is considered a separate species as discussed below. The remaining three taxa are much less distinct from one another. Thus, their independent rank proposed by de Groot (1963) was reduced to a subspecies of *P. (D.) wagneri*. The later subspecies differs from the remaining two mainly by having smaller number of septa, *P. (D.) wagneri santaemariae* can be distinguished by short minor septa and *P. (D.) wagneri intermedia* by the largest frequency in the class of 4-5 mm, but not in 3-4 mm as the other two (Fig. 1).

P. (D.) wagneri santaemariae is represented by a single colony that exhibits a fairly large intracolony variability in morphology of the dissepimentarium, in thickness of the median lamellae, with some tending to temporarily disappear, and in length of minor septa, only very few of which penetrate the peripheral tabularium whereas most are restricted to the dissepimentarium (de Groot, 1963, pl. 21, figs. 1a-c; Pl. 35, fig. 1 herein). Almost all morphological characteristics of *P. (D.) wagneri santaemariae*, except for shortened minor septa, occur either in *P. (D.) wagneri wagneri* or *P. (D.) wagneri intermedia*, or both.

P. (D.) perapertuensis is perhaps closely related to the *P. (D.) wagneri* group of subspecies being especially closely comparable in its n:d ratio with *P. (D.) wagneri wagneri*. Frequency peaks of both correspond to each other clearly. Its underdeveloped dissepimentarium, different microarchitecture of the external wall, and some differences in the hystero-ontogeny (see descriptions for details) prove a distinct taxonomic status. Two latter characters of *P. (D.) perapertuensis* closely resemble those in *P. (D.) cantabrica* from which it differs first of all by much smaller number of septa at comparable diameter (Fig. 1) and by an interrupted median lamella.

Only *Petalaxis (Degrootia)* sp. is comparable to *P. (D.) cantabrica* in the total number of septa and in n:d ratio (Fig. 1). This single specimen was originally included by de Groot (1963) in "*Hillia*" *cantabrica*. Monoseptal, temporary reduced median lamella in the specimen RGM 112755 versus constant and complex median lamella in the holotype and remaining paratypes of *P. (D.) cantabrica* form adequate differences for its distinction.

The above detailed discussion replaces comparisons between individual species and subspecies of *Degrootia* nom. nov., described in this paper.

***Petalaxis (Degrootia) cantabrica* (de Groot, 1963)**

Pl. 24, figs. 3-6; Pls. 25-28; Fig. 1.

e.p. 1963 *Lithostrotionella (Hillia) cantabrica* de Groot, p. 92, pl. 22, figs. 1-2, 4 [pl. 22, fig. 3 = *Petalaxis (Degrootia)* sp.]

? 1985 *Petalaxis cantabricus* (de Groot): Boll: p. 44, pl. 6, fig. 1.

Material — Five fragments of colonies. Internal structure altered diagenetically, but remnants of original microstructure recognisable (de Groot, 1963, p. 93) (except for the colony RGM 112755 = *P. (Degrootia)* sp.).

Emended diagnosis — *Degrootia* with maximum n:d ratio 28:6.8 mm; minor septa penetrate peripheral tabularium; thick median lamella permanently united with cardinal septum, incorporates few septal lamellae; lonsdaleoid dissepiments uncommon; inner wall almost exclusively septal, commonly thick.

Additional description — Intercorallite walls comprise three layers of crystals with the 0.1-0.3 mm thick middle layer sinuous when septa in adjacent corallites anastomose and almost straight when they are sitting opposite to one another (Pl. 24, figs. 4-5). Bases of septa thin abruptly inwards when transmitted into septal blades (Pl. 24, figs. 4-6). Most septa are continuous. Only some are interrupted by small to moderately long lonsdaleoid dissepiments that only exceptionally interrupt 3-4 major septa and

intervening minor septa (Pl. 28, figs. 1, 2). Only minor septa are interrupted by small lonsdaleoid dissepiments in some instances. Bases of septa may bear short strips of septal blades when interrupted (Pl. 24, fig. 5). Moderately thin major septa approach a median lamella in some corallites, but may leave an obvious distance between themselves and median lamella or their own lamellae incorporated in the latter (Pl. 28, figs. 1-2). Minor septa penetrate peripheral tabularium for up to 1.2 mm. Sections of peripheral parts of tabulae, spanned between many of them and lateral sides of adjacent major septa, prove a biformity of the tabularium. Both major and minor septa are the thickest in the thickened inner wall (Pl. 24, fig. 6).

The median lamella was invariably derived from the inner end of the elongated cardinal septum, but may form a part of the axial septum early in the hystero-ontogeny (Pl. 27, figs. 1-5). Domination of the cardinal septum is accentuated by its axial thickening and by its further growth (Pl. 27, figs. 6-8). Lack of the axial septum early in the hystero-ontogeny (Pl. 28, figs. 4-6) is unique and is here considered pathologic. The median lamella remains almost permanently united with the cardinal septum (Pl. 25, fig. 3), but not necessarily as its simple continuation. In several cases observed, the cardinal septum either curved strongly prior to reaching a median lamella (Pl. 25, fig. 2), is attached to its lateral side (Pl. 25, figs. 1) or is for a short distance isolated from it (Pl. 25, fig. 4). Also, the morphology of the median lamella varies greatly. It is simple early in the hystero-ontogeny (Pl. 27, figs. 2-6; Pl. 28, fig. 7), but incorporated septal lamellae in the neanic stage, i.e., prior to the appearance of first dissepiments (Pl. 27, fig. 8; Pl. 28, fig. 9). The median lamella is rarely monoseptal in mature corallites (Pl. 25, fig. 1) and it remains uncertain whether such a morphology is temporary or permanent. In most cases observed it incorporates one to seven septal lamellae (Pl. 25, figs. 2-4). The size of septal lamellae may vary from hardly distinguishable in the microstructure of the median lamella (Pl. 25, fig. 3, lower) through intermediate in length (Pl. 25, fig. 2) up to long (Pl. 25, fig. 4). Such long septal lamellae and sections of axial parts of tabulae produce an image of an axial column (Pl. 25, fig. 4). The true axial column does not occur in the longitudinal section (Pl. 28, fig. 3).

The tabularium is comparatively deeply concave. Thus, its biformity is better accentuated by the arrangement of sections of peripheral parts of tabulae in the transverse sections (Pl. 28, figs. 1-2) than in the longitudinal section (Pl. 28, fig. 3). It may only be predicted that lesser declined tabulae correspond to Position II and the more steeply declined ones represent Position I (Pl. 28, fig. 3, right side, middle and lower, respectively).

Hystero-ontogeny — A process of offsetting takes place in the peripheral dissepimentarium and does not disturb morphology of the inner part of the offset corallites (Pl. 28, figs. 1-2, middle). Also, in contrast to the statement by de Groot (1963, p. 92), it does not involve an appearance of lonsdaleoid dissepiments. On the contrary, such dissepiments are absent from the offset area at the beginning of the process (Pl. 27, figs. 1-2), although lonsdaleoid dissepiments may afterwards appear next to it. Most commonly, an offset inherited peripheral parts of the septa of the parent and transferred one of those into its own cardinal septum (Pl. 27, figs. 1-2). This septum dominates from the beginning of the blastogeny (Pl. 27, figs. 1-8). It may happen, however, that septa located in the middle of a neotheca and opposite to it at a atavotheca are

alar septa (Pl. 28, figs. 4-7, upper left and lower right). Those two septa dominate slightly in such a case whereas the cardinal and counter septa may be strongly underdeveloped early in the hystero-ontogeny (Pl. 28, figs. 4-6, upper right and lower left) and began to dominate when several major septa are already present (Pl. 28, fig. 7). As mentioned above, this unique morphology is considered pathologic.

Irrespective of the earliest morphology, the cardinal septum became the longest septum already in the hystero-neanic stage, i.e., when it formed a monoseptal median lamella that became rhopaloidally thickened (Pl. 27, figs. 2-7; Pl. 28, fig. 7). The counter septum was commonly inherited from a parent's corallite as an inner part of the same septum from which the cardinal septum of an offset was derived. It met the cardinal septum at the beginning of the process to form an axial septum, but this was the cardinal septum that dominates and is thickened in its axial part (Pl. 27, figs. 1-5). The counter septum is, in its further growth, commonly shorter than counter-lateral septa (Pl. 27, figs. 6-8). In contrast to offsets developed as described above, the counter septum is longer than counter-lateral septa in the second corallite described herein as an example of pathology or an extreme variant (Pl. 28, figs. 4-9). Being strongly underdeveloped early in the blastogeny (Pl. 28, figs. 4-6, lower left), this septum became rapidly elongated to meet the (also elongated) cardinal septum (Pl. 28, fig. 7) and was only slightly shortened afterwards (Pl. 28, figs. 8-9). Minor septa appeared first in the atavotheca in an irregular sequence. All structures at the neotheca were delayed slightly in the appearance.

The neotheca is a partition kind, but the microstructure of its primary layer is uncertain. It may be trabecular if short parallel bodies present in an oblique section are trabeculae (Pl. 26, fig. 5, upper). Indisputable proof for its trabecular or fibro-normal microstructure cannot be found. In most cases investigated a neotheca grew both sides towards an atavotheca without being completely united with the latter until the late hystero-neanic stage or early maturity (Pl. 27, figs. 2-7). In rare instances (Pl. 28, figs. 4-9) the neotheca became complete at an early growth stage. A long lasting incompleteness of a neotheca is interpreted as effectively enabling connections between entherons of an offset and its parent along ditches formed between the neo- and the atavotheca. The neotheca is solid in most offsets, but may split in some (Pl. 26, fig. 6) with a tabula-like body produced between its two forks.

Microstructure — Diagenetic alterations of all structural elements made identification of their original microstructure difficult. The remnant of the trabecular microstructure of septa is more easily distinguishable in the longitudinal sections (Pl. 26, figs. 1, 4, right) where rudiments of fine trabeculae or recrystallized bodies derived from them intersect several growth layers. Longitudinal sections across a median lamella (Pl. 26, fig. 3) and the intercorallite wall (Pl. 26, fig. 4, left) display a similarity in lacking any trace of middle lines. Weaker density of fibrils in the wall than in the median lamella is interpreted as caused by stronger diagenetic alterations.

Septal bases were almost certainly fibrous. This is best demonstrated by strongly sinuous walls (Pl. 26, fig. 2), but is well seen in other instances as well (Pl. 24, figs. 4-6). Fibrils in those peripheral parts of septa are arranged in more or less narrow fans depending of width of those structures. An abrupt change of the microstructure from fibrous to more or less altered trabeculae (Pl. 24, figs. 4-6) document the differential

advance of diagenesis. The rapid transfer from wide and fibrous to narrow and most probably trabecular parts of septa perhaps resulted from a fairly rapid narrowing of septal pockets. An outline of thickened peripheral parts of septa is commonly smooth (Pl. 24, fig. 6), but may be sharp (Pl. 24, figs. 4-5). It cannot be concluded whether a saw-back-like outline with shades of fibrils in some (Pl. 26, fig. 2) and sharp edges in other bases of septa (Pl. 24, fig. 5), both established in the holotype colony, are indicative for more complex microstructure of some intercorallite walls or reflect diagenetic alterations. The latter almost certainly dominate in some other colonies (e.g., Pl. 24, fig. 4).

Remarks — Two statements of de Groot (1963), i.e., an occurrence of clinotabellae and comparison of *P. (D.) cantabrica* to *Ipciphyllum*, require discussion. As in other species of both subgenera of *Petalaxis* there are no clinotabulae developed in *P. (D.) cantabrica*. All those structures are tabulae in the Position I superimposed on the generally distinctly concave tabularium. Such a concavity made an identification of tabulae in different Positions difficult. An absence of clinotabellae made comparison to *Ipciphyllum*, a waagenophyllid genus, baseless. Being closely comparable in most characters to *P. (D.) perapertuensis*, the species discussed differs from it by possessing much more numerous septa at comparable diameters. This character distinguishes it from all other species of the subgenus, except for *P. (Degrootia) sp.*, discussed below. Other differences and similarities are pointed out in the remarks on the subgenus.

Range — Santa Maria Limestone, Perapertú Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

***Petalaxis (Degrootia) perapertuense* (de Groot, 1963)**

Pls. 29, 30; Fig. 1.

e.p. 1963 *Lithostrotionella (Hillia) perapertuensis* de Groot, p. 89, pl. 19, fig. 2 [pl. 19, fig. 1 = *P. (D.) wagneri*].
1985 *Petalaxis perapertuensis* (de Groot): Boll, p. 43, pl. 5, fig. 6.

Material — Three fragments of colonies. The original microstructure is recognizable in some specimens. Diagenetic alterations advanced to an extent precluding a hystero-ontogenetic study with peels (de Groot, 1963, p. 89).

Diagnosis — *Degrootia* with maximum n:d ratio 21:5.3 mm; partition commonly 2-4 mm wide; lonsdaleoid dissepiments sporadic.

Additional description: intracolony variation of the holotype — Thickness of partitions is generally very conspicuous, but it may be reduced by more than half in some parts of a given thin section (Pl. 30, fig. 1) and even more when different sections of the holotype are compared (de Groot, 1963, pl. 19, figs. 2a-c). Microarchitecture of partitions differ in such a case, remaining septal when moderately and strongly thickened (Pl. 29, fig. 4), but becoming septo-sclerenchymal in their thin parts (Pl. 29, fig. 5), up to mostly sclerenchymal with septa comparatively thin and distant from each other

(Pl. 29, fig. 6). Reduction in thickness of the partition does not cause either a reduction in thickness of other structures or changes in their morphology.

Major septa are invariably long, approaching a thickened median lamella that is commonly monoseptal, derived from and almost permanently connected to the cardinal septum. The median lamella is elongated so as to closely approach the counter septum that may be slightly shortened when the median lamella is especially long. In rare instances there occurs thickened septal lamellae are incorporated in the median lamella. Also, but rarely observed, there are important changes in the microarchitecture of the median lamella and its relation to the cardinal septum (Pl. 30, figs. 5-10). Not only septal lamellae were incorporated in various positions, but also the median lamella became separated temporarily from the cardinal septum (Pl. 30, figs. 6-7). Minor septa reach a half to almost three quarters length of major septa (Pl. 30, figs. 1, 5-10), penetrating the tabularium deeply and establishing a biform arrangement of peripheral parts of tabulae in transverse section (Pl. 30, fig. 3). The biform tabularium is rather poorly confirmed in the oblique longitudinal section, but is recognizable when positions of tabulae of individual parts of the same corallite are compared (Pl. 29, fig. 3, middle and lower left vs. middle right).

The dissepimentarium consists mostly of interseptal, rectangular dissepiments. Lonsdaleoid dissepiments are rare and commonly accompany offsets in various stages of their late hystero-ontogeny (Pl. 30, fig. 1). They are always small, blister-like, but break both major and minor septa. The latter may form short strips at the periphery, being continuous inwards of the zone of lonsdaleoid dissepiments. Additional septa may occasionally occur in the area of lonsdaleoid dissepiments (Pl. 30, fig. 2, lower).

Diameters of corallites that can be considered mature vary from *c.* 3.5-5.4 mm with more than half of all corallites measured occurring in the class 3-4 mm. The number of septa vary from 16-17 to 21 (a single corallite measured), with 17 and 18 occurring in most corallites measured. The mean n:d ratio and its peak are regular as they should be when large number of corallites (96 in this case) are considered (Fig. 1). Intraspecific variability has not been established because one of the three colonies originally included in this species is poorly preserved, whereas the colony RGM 112744 was transferred to *P. (D.) wagneri* (see remarks).

Microstructure and diagenetic alteration — All septa are altered diagenetically. Very narrow, darker bodies perpendicular to and intersecting few growth lines are interpreted as shades of diagenetically altered trabeculae. They were recognised in a single longitudinal section of a septum (Pl. 30, fig. 4). Bunches of fibres in peripheral, strongly thickened parts of septa (e.g., Pl. 29, fig. 5, upper row of septa) may also represent altered trabeculae. All those characters are weakly accentuated and cannot be considered conclusive.

Thick intercorallite walls are composed of laterally contiguous peripheral parts of septa best seen in the transverse section (Pl. 29, fig. 4). Septotheca-forming peripheral parts of septa of adjacent corallites may be in a direct contact (Pl. 29, fig. 5) or there occurs a colourless intercorallite structure in some intercorallite walls (Pl. 29, fig. 6) that resembles a similar layer in dividing walls. Such a layer is never long and does not separate adjacent corallites completely. Possessing no rigid data concerning the original microstructure of such a colourless layer two options are proposed:—

It is purely diagenetic and do not reflect separation of adjacent polyps.

The diagenesis followed an original 4-layers wall, i.e., adjacent polyps may have been temporarily and incompletely isolated from their neighbours. Dark colour interseptal line formed by bunches of crystals (Pl. 29, fig. 4) and characters described in the next paragraph point to the first option as more probable.

A microstructure of some parts of intercorallite walls seen in the vertical sections made through their thickness demonstrate growth cones (Pl. 29, fig. 1) closely resembling those in a similarly oriented section of a median lamella (Pl. 29, fig. 2). In both instances discussed, growth cones terminate in the chain of bunches of crystals occupying middle part of the wall and the median lamella (Pl. 29, figs. 1-2). Only an upwards-growing intercorallite wall, secreted in an ectodermal fold common for adjacent corallites, may have produced such a microstructure. Thus, the wall is considered a three-layered partition.

Remarks — Morphology of corallites in the colony RGM 112744 (Pl. 31, fig. 2), transferred herein to *P. (D.) wagneri*, differs greatly from the holotype of *P. (D.) perapertuensis* in corallites reaching maximum 18 major septa and 4.2 mm corallite diameter, in possessing partitions mostly of the septo-sclerenchymal kind, median lamellae thin, locally interrupted, i.e., absent from some sections or replaced by the slightly elongated cardinal septa, and the dissepimentarium generally narrow and/or absent from some parts of corallites. All these characters match the diagnosis of *P.(D.) wagneri* precisely. It should be pointed out, however, that measurements of corallites in the colony discussed can be located within the minimum values of the holotype of *P. (D.) perapertuensis* (Fig. 1). On the other hand, those values are almost identical with those of the paratype, RGM 112738, of *P. (D.) wagneri* and closely agree with its holotype. In such a situation I consider morphological characters decisive. A taxonomic position of that specimen is further discussed with *P. (D.) wagneri* together with other remarks concerning a distinction and content of the latter species.

A small fragment of a colony illustrated by Boll (1985, pl. 5, fig. 6) closely resembles the holotype of *P. (D.) perapertuensis* in morphology and number of septa. Thus, its identification was accepted although diameters of corallites remain uncertain. This uncertainty resulted from width of the longitudinal section. Boll (1985, p. 90) claimed it was less enlarged than the transverse section, but it is wider in the picture than the largest diameter of transversally-sectioned corallites.

Range — Perapertú Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Petalaxis (Degrootia) radians (de Groot, 1963)

Fig. 1.

1963 *Hillia radians* de Groot, p. 89, pl. 20, fig. 1.

Material — Two fragments of colonies; only the holotype was thin sectioned and illustrated by de Groot (1963, p. 90, pl. 20, fig. 1).

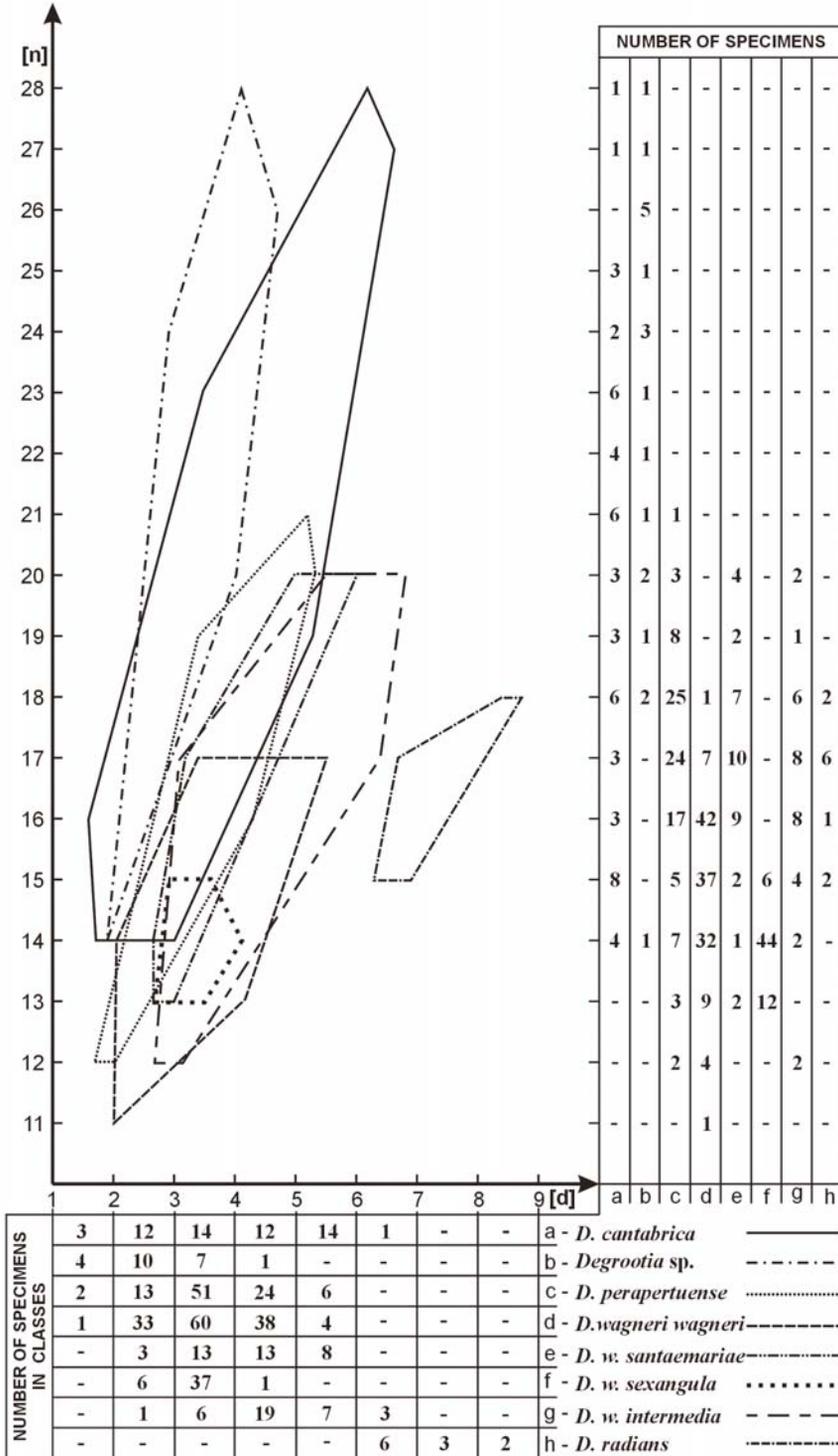


Fig. 1. Number of septa (n) to diameter of corallites (d in mm) ratio in species and subspecies included in *Degrootia* nom. nov. Numbers in right table correspond to number of corallites possessing given number of septa, whereas numbers in the lower table show number of corallites present in a given class of diameters. Individual columns in both tables correspond to taxa listed with letters "a" to "h" in the lower right corner.

Emended diagnosis — *Petalaxis (Degrootia)* with maximum n:d ratio 18:8.8 mm; partition exclusively septal; major septa closely approach thin, interrupted median lamella that may incorporate 1-3 short septal lamellae; minor septa may penetrate tabularium; dissepimentarium occupies a third to a half corallite radius; lonsdaleoid dissepiments very rare.

Additional description — Thin partitions are composed of peripherally thickened, laterally contiguous parts of septa that either alternate in neighbouring corallites or are located opposite to one another. Microstructure of innermore parts of septa is diagenetically altered, but its remnants are closely comparable to those of the type species of the subgenus. Biformity of the tabularium is not clear. It is accentuated by differentiation in a number of sections of peripheral parts of tabellae in some loculi (de Groot, 1963, pl. 20, fig. 1a), but is hardly recognizable in the others. Longitudinal sections available for the restudy are either very oblique or eccentric (de Groot, 1963, pl. 20, figs. 1b, 1c, respectively), providing no data for a proper description of that character. It may only be stated that the tabularium is generally concave, but possesses some short tabellae elevated towards the median lamella.

Remarks — The different n:d ratio, pointed out already by de Groot (1963, p. 90), forms the others of the main distinguishing character of this species when compared to others of the subgenus. It bears close morphological resemblance to *P. (D.) wagneri intermedia* and especially to the holotype of that subspecies, some corallites of which possess fairly long major septa and wide dissepimentarium. Both those features are less developed than in *P. (D.) radians*, however, whereas lonsdaleoid dissepiments are more frequent in the former.

Range — Perapertú Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

***Petalaxis (Degrootia) wagneri wagneri* (de Groot, 1963)**

Pls. 31-33; Text-fig.1.

e.p. 1963 *Lithostrotionella (Hillia) wagneri* de Groot, p. 88, pl. 18, figs. 1, 3. [Pl. 18, fig. 2 = *Petalaxis (P.) donbassicus* Fomichev, 1953].

e.p. 1963 *Lithostrotionella (Hillia) perapertuensis* de Groot, p. 89, pl. 19, fig. 1. [pl. 19, fig. 2 = *P. (D.) perapertuensis* de Groot, 1963].

non 1984 *Hillia wagneri*: Rodriguez, p. 358, text-figs. 192-195, pl. 20, figs. 2-6 [= *Petalaxis (P.) donbassicus* Fomichev, 1953].

Material — Nine fragments of colonies. Internal structures diagenetically altered to an extent allowing reconstruction of some primary characters (de Groot, 1963, p. 88).

Emended diagnosis — *Petalaxis (Degrootia)* with maximum n:d ratio 17:5.4 mm, most commonly 15-16: 3.5-4.5 mm; median lamella monoseptal and/or incorporating 1-3 septal lamellae, may be interrupted, variously thickened, mostly slightly, only elongated cardinal septum in some; dissepimentarium commonly interseptal;

development of lonsdaleoid dissepiments commonly sparse; partitions septal and septo-sclerenchymal.

Additional description: intracolony variation of the holotype — The n:d ratio is regular if the distribution of a large number of corallites is plotted (Fig. 1), but an analysis of individual classes in diameters and number of septa allows the demonstration of a moderately large variability in both those characters. This resulted from increases in septa. Although it generally is faster than an increase in a corallite diameter and may remain almost constant in mature corallites, there are corallites growing an opposite way, i.e., reaching mature diameters, but not number of septa typical for mature growth stage. As a result the field of distribution (Fig. 1) is comparatively wide.

The median lamella is never very thick, but in most corallites it is thickened and easily distinguishable (Pl. 31, fig. 1), whereas in some corallites it may be no more than an elongated inner margin of the cardinal septum that in extreme variants is reduced to the length of adjacent major septa (Pl. 32, fig. 3). A comparison of several successive transverse sections shows, however, that such a reduction is temporary. Also, the cardinal septum may be strongly elongated, but separated from a lens-like, monoseptal median lamella that in such a case resembles a true columella (Pl. 32, fig. 4, long cardinal septum right).

The dissepimentarium was developed comparatively late in the hystero-ontogeny. It is mostly interseptal and invariably incomplete in the neanic stage (Pl. 32, fig. 2; Pl. 33, figs. 6-8), but may remain incomplete in mature growth stages of rare corallites. It commonly consists of 1-2 rows of dissepiments, supplemented by additional dissepiments near some corallite corners (Pl. 31, fig. 1). Lonsdaleoid dissepiments developed most commonly in a comparatively wide dissepimentarium, but are rather rare and never form a complete ring.

All changes of individual structures are temporary. Particular variants (e.g., the cardinal septum reduced in length versus elongated to form median lamella, or continuous septa versus broken by lonsdaleoid dissepiments) replace each other in the course of growth of individual corallites. Also, there are transverse sections through a part of the holotype colony exposing more or less uniformly designed corallites. For instance, they may possess continuous major septa almost invariably, median lamellae united with cardinal septa and dissepimentaria complete or sections in which lonsdaleoid dissepiments occur in nearly all corallites. Sections like the former one closely resemble the paratype RGM 112744 of *P. (D.) perapertuensis* transferred herein to *P. (D.) wagneri wagneri* (Pl. 31, fig. 2), whereas the second resembles the holotype of *P. (D.) sexangula*. Series of peels prepared for the purpose of this paper demonstrated the variation discussed above, allowing the reidentification of some species.

Intraspecific variation — This section combines data derived from the paratypes originally included in this species and the specimen RGM 112744 that was included by de Groot (1963, p. 89) in "*Hillia*" *perapertuensis*. The latter specimen closely resembles some sections of the holotype colony of *P. (D.) wagneri* in morphology of corallites (Pl. 31, figs. 1-2), whereas its measurements are more similar to some paratypes. Differences in corallite morphology between all specimens included here in *P. (D.) wagneri wagneri* (e.g., Pl. 31, figs. 1-3) follow more or less exactly those observed within the holotype and will not be described in detail.

Microstructure and diagenetic alterations — The microstructure of septa was altered the same way as described or mentioned earlier in the present paper. Its original finely trabecular nature is demonstrated in longitudinal sections (Pl. 31, figs. 4-5). Shades of individual trabeculae are densely packed units, *c.* 0.02 mm in diameter, *i.e.*, typical for the genus. Remnants of trabeculae in the transverse sections are rare and uncertain (Pl. 32, fig. 5).

Individual parts of septa underwent different diagenetic alterations. Their thin, inner parts pass abruptly into strongly thickened, outermost parts incorporated in the partition (Pl. 31, fig. 7). Some of those thickest parts remain half-moon in shape whereas the others are elongated inwards towards the corallite lumen. Their altered microstructure is uniformly fibrous in both cases with individual crystalline fibrils very thin and not always arranged in a clear order. An absence of bunches of crystals in these parts of septa may either have resulted from more advanced diagenesis or from their nontrabecular microstructure. The second option seems more probable and was accepted in this paper.

The partition is mostly septo-sclerenchymal (Pl. 31, fig. 7). A light line dividing some sectors of the partition (Pl. 31, fig. 6) extends along comparatively short parts of it, being both ends replaced by bunches of crystals common for neighbouring corallites. Presence of a light line is mostly unrecognizable in vertical sections (Pl. 31, figs. 4-5, both left). Thus, such microstructure is perhaps short-lived. Middle parts of most vertically sectioned walls comprise bunches of crystals the nature of which is uncertain (Pl. 31, figs. 4-5, both left). They are most probably the same in origin as those present in the transverse sections of the outermost parts of septa incorporated in the partition.

Hystero-ontogeny — The process of offsetting was investigated in a dozen or so offsets of the holotype colony. It involves two major and one or two minor septa of a parent corallite. In contrast to those species of *Petalaxis* (*Degrootia*), which possess a wide dissepimentarium, inner parts of septa in the offsetting area of *P. (D.) wagneri wagneri* may undergo some morphological alterations. The beginning of an offsetting may also resemble formation of a lonsdaleoid dissepiment because septa became divided into peripheral and inner parts without earlier increase in thickness. The oblique longitudinal section (Pl. 32, fig. 7) demonstrates a role of dissepiments of a parent's corallite as a basis for the neotheca. This is better demonstrated in the longitudinal section of *P. (D.) santaemariae* (Pl. 34, figs. 3-4) and is described in more detail with the latter. The neotheca differs from the dissepiment by larger thickness and by possessing a middle line or bunches of crystalline fibrils that confirm its septal microstructure (Pl. 32, fig. 6). The initial intercorallite wall is never complete, but it may be short, leaving wide channels between its ends and the atavotheca or it almost reaches the atavotheca on both sides of the offsetting sector (Pl. 33, figs. 1-5). Irrespective of length of the neotheca, the communication between an offset and a parent is easily available above the initial neotheca, that plays mostly role of a supporting structural element.

Some offset septa are invariably inherited from a parent. They are always located at the atavotheca, most commonly constituting the counter septum and counter-lateral septa of an offset. The cardinal septum of an offset is almost always formed at the neotheca either as a rudiment of an inner part of the same septum from which the

counter septum is formed (Pl. 33, figs. 1-3) or, most commonly, as a neo-septum appeared at the neotheca opposite to the counter septum. Irrespective of its insertion, the cardinal septum appears as the first septum of cardinal quadrants. Only in a single observed offset was the cardinal septum inserted at the atavotheca. This leads to a very irregular insertion of remaining septa, making their sequence unrecognizable.

An insertion of septa in counter quadrants prevails over that in the cardinal quadrants (Pl. 33, figs. 3-7). This may be in part artificial, resulting from orientation of sections, more oblique in peripheral part of an offset. In contrast to at least some delay in the development of septa in cardinal quadrants, the cardinal septum developed well and soon became a dominant septum (Pl. 33, figs. 3-8, upper left). A median lamella that is formed from the inner margin of the cardinal septum is invariably monoseptal during the hystero-neanic stage (Pl. 33, figs. 7-8), but may be more or less thickened. Septal lamellae appear within the median lamellae only in a fully mature growth stage of an offset. This appearance may be strongly depleted or the median lamella remained monoseptal.

Alar septa are often the second longest septa (Pl. 33, figs. 5-7), whereas length of the counter septum varies, but it mostly equals the counter-lateral septa (Pl. 33, figs. 6-8). First minor septa appear in the loculi between the counter septum and counter lateral septa whereas first dissepiments, invariably interseptal, were secreted with some delay (Pl. 33, figs. 6-8).

Remarks — Reasons for considering some formerly independent species as subspecies of *P. (D.) wagneri*, and the distinction between this species *s.l.* and remaining taxa included in the subgenus, are discussed above. It should only be pointed out that the position of *P. (D.) santaemariae* within *P. (D.) wagneri* is especially uncertain due to the small number of measured corallites. Restricted data are distributed in two classes leaving some doubts about the prevailing n:d ratio. A very close similarity between *P. (D.) wagneri* and *P. (D.) intermedia* in all morphological characters indicates in turn a close relationship or a synonymy of those taxa. This is further proven by an almost complete inclusion of the frequency field of *P. (D.) wagneri* in that of *P. (D.) intermedia* (Fig. 1). A larger maximum number of septa and a frequency peak which appeared in the larger class form the main distinguishing characters of *P. (D.) intermedia*, adequate for no more than a subspecific distinction.

Range — Perapertú Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

***Petalaxis (Degrootia) wagneri intermedia* (de Groot, 1963)**

Fig. 1.

1963 *Lithostrotionella (Hillia) intermedia* de Groot, p. 90, pl. 20, figs. 2-3.

? 1985 *Petalaxis intermedius* (de Groot): Boll, p. 43, pl. 5, fig. 7.

Material — Three fragments of colonies, but only the holotype thin sectioned. Internal structure only slightly altered diagenetically (de Groot, 1963, p. 91).

Emended diagnosis — *P. (D.) wagneri* with maximum n:d ratio 20:6.8; 17-18:4-5 prevail; median lamella weak, interrupted, with 1-2 septal lamellae incorporated rarely; dissepimentarium complete, lonsdaleoid dissepiments frequent; partition exclusively septal.

Remarks — A close similarity of *P. (D.) intermedia* to *P. (D.) wagneri wagneri* is pointed out above. Nevertheless, it is separated on the subspecies level for the time being. More material investigated may either confirm or reject that arbitrary decision.

A fragmentary colony inadequately described and poorly illustrated by Boll (1985) may not belong to this species. It is difficult to judge, however, whether a very weak or absent median lamella and prevailing lonsdaleoid dissepimentarium are typical for the colony or were incidently exposed by the thin section of few corallites illustrated. Also, the concave tabularium shown in the longitudinal section may illustrate only the Position I but not the complete morphology.

Range and occurrence — As for the nominative subspecies.

Petalaxis (Degrootia) wagneri santaemariae (de Groot, 1963)

Pl. 34; Pl. 35, figs. 1-2; Fig. 1.

1963 *Lithostrotionella (Hillia) santaemariae* de Groot, p. 91, pl. 21, fig. 1.

Material — A single fragment of a colony, diagenetic alterations moderate (de Groot, 1963, p. 91).

Emended diagnosis — *P. (D.) wagneri* with maximum n:d ratio 20:6.0 mm; 16-17: 3.5-5.0 prevails; median lamella monoseptal or with 1-3 short lamellae incorporated, very weak (interrupted?) in some; dissepimentarium incomplete; lonsdaleoid dissepiments infrequent; most minor septa do not enter tabularium when dissepimentarium developed.

Additional description: intracolony variation — The subspecies is represented by a single colony. Thus, intraspecific variation cannot be established. De Groot (1963, p. 91) pointed out an incompleteness of the dissepimentarium, but this character differs from section to section of mature corallites, whereas it is common mainly in the immature ones. A median lamella derived from and permanently united with a cardinal septum is the only axial structure. In most corallites observed it is monoseptal, but may incorporate 1-3 short, inconspicuous septal lamellae in fully mature corallites (Pl. 35, fig. 1). An interruption of a median lamella has not been established, but its strong thinning in some corallites may indicate such a possibility. Variation in length of counter septa is not conspicuous, but they may be equal to adjacent septa, slightly shortened or elongated so as to reach a median lamella.

The tabularium is concave in both positions (Pl. 35, fig. 2), making recognition of its biformity difficult except for some particular instances (e.g., Pl. 34, fig. 1) where the Position I (lower) and its transfer into Position II (middle and upper in the picture) is excavated by an incidental longitudinal section. Thus, clinotabellae postulated by de Groot (1963, p. 91) do not occur in the species discussed.

Microstructure and diagenetic alteration — The primary microstructure of septa and intercorallite walls was diagenetically altered in all thin sections examined. Those alterations, closely comparable to other taxa, are not described in detail. Some rudiments allow consideration of the microstructure of septa and columella trabecular. Parallel bodies, *c.* 0.02 mm wide and intersecting several incremental lines (Pl. 34, fig. 2), are diagenetically altered trabeculae. The trabecular microstructure is better accentuated in the longitudinal section of a median lamella, cut slightly oblique along its middle part (Pl. 34, fig. 8). Remnants of trabeculae intersecting several growth lines are best seen in the lower part of the picture.

The transverse section of the intercorallite wall (Pl. 34, fig. 5) shows little more than its sinuous shape and some crystalline fibrils arranged more or less perpendicular to the middle line. Longitudinal sections made perpendicular to the wall thickness expose bunches of crystalline fibrils identical to those in the median lamella (Pl. 34, figs. 6, 7, respectively). The microstructure similar to that is exposed in all better preserved sections studied (e.g., Pl. 34, figs. 3, upper, 4, left). This may suggest a trabecular microstructure of the intercorallite wall, but in contrast to the median lamella (Pl. 34, fig. 8) trabeculae were not discovered in the longitudinal section made along the middle part of the wall. Nevertheless, its identification as a partition seems undoubted.

Hystero-ontogeny — Not investigated in detail because quality of peel impressions appeared very poor. However, longitudinal thin sections of two offsets (pl. 34, figs. 3-4) allow some general considerations. In the first instance (Pl. 34, fig. 3) the neotheca looks almost entirely independent from any former structural element of the parent. Protrusions of the neo- and atavotheca (lower right) are in touch, but their crystalline fibrils grew in opposite directions. I interpret the section as exposing a channel, commonly present between the neotheca and atavotheca. The microstructure of the earliest part of the neotheca looks fibro-normal. Bunches of crystalline fibrils appeared only in its upper, i.e., ontogenetically more advanced, part.

Bunches of crystalline fibrils are not recognizable in the neotheca of the second offset (Pl. 34, fig. 4). It obviously set on the dissepiment (compare less magnified Pl. 35, fig. 2, upper left). Its middle dark line was constituted from two dark lines that form a regular triangle on the surface of the dissepiment. Such an image was possible to achieve in a following sequence; the polyp's basal disc was disconnected from the formerly secreted dissepiment and formed a triangular septal pocket. Reduced thickness of the dissepiment at the base of the triangle, increased both sides of it, confirms such an interpretation. The calcium carbonate was secreted by both walls of that pocket and continued upwards to form a solid wall common for both corallites, i.e., the partition.

Two kinds of constitution of the neotheca partition described above can be treated as a checkpoint for almost all instances described in this paper and, more widely, in many instances of formation of a partition neotheca. In many processes of offsetting investigated by me so far in detail there occur no more than variants of those two examples.

Range — Santa Maria Limestone, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Petalaxis (Degrootia) wagneri sexangula (de Groot, 1963)

Pl. 35, figs. 3-8; Fig. 1.

1963 *Lithostrotionella sexangula* de Groot, p. 84, pl. 16, figs. 3-4.non 1978 *Lithostrotionella sexangula*: Fan, p. 182, pl. 67, fig. 2.

Material — Four fragments of colonies. Internal structure diagenetically altered, making the original microstructure hardly distinguishable in most instances (de Groot, 1963, p. 85).

Emended diagnosis — *Petalaxis (Degrootia) wagneri* with maximum n:d ratio 15:3.7; 14:3.0-3.7 greatly prevail; median lamella monoseptal, rarely interrupted; dissepimentarium incomplete; lonsdaleoid dissepiments sporadic.

Additional description — De Groot (1963, p. 84), describing tabulae, wrote "...may then have either upturned or downturned peripheral edges." This description indicates recognition of the biform tabularium without putting a name on that structure. Indeed it is clearly recognizable in each longitudinally sectioned loculum suitable for such an observation. The tabula sectioned in the area of its strongest curve (Pl. 35, fig. 5, middle left) illustrates a true shape of any tabula in Position I. Tabulae in that position are most commonly cut by a given longitudinal section into two or three separate fragments. Such a situation with a peripheral fragment of the tabula in Position II, transparent through the sectioned septum, is seen immediately below in the same picture whereas its upper part illustrated tabulae in Position II (Pl. 35, fig. 5, left).

Corallites in the paratype colony (de Groot, 1963, pl. 16, fig. 4) differ from the holotype corallites in possessing rare lonsdaleoid dissepiments in the strongly underdeveloped dissepimentarium. Also, major septa and columellae in the paratype corallites are thinner. Dimensions and morphology of the tabularium in corallites of both holotype and paratype colonies are closely comparable (de Groot, 1963, pl. 16, figs. 3a, 4a and Pl. 35, fig. 3; Fig. 1 herein), allowing those differences to be accepted as intraspecific. The number of septa and corallite diameters in the subspecies discussed expose a strikingly reduced individual variation, forming its important distinguishing character. 44 out of 62 measured corallites possess 14 major septa and diameters ranging from 3.0 to 3.6 mm. Only a single corallite reached 4.1 mm in the diameter. This constant character forms the main difference of *P. (D.) sexangula* when compared to *P. (D.) wagneri* and the main reason for its recognition here as a subspecies of the latter despite the fact that its field of n:d ratio is almost completely included in that of the nominative subspecies (Fig. 1).

Microstructure and diagenetic alteration — The microstructure of septa is poorly preserved and inadequately exposed in the longitudinal section. Thus, it was not illustrated. It seems to be finely trabecular with individual trabeculae not exceeding 0.02 mm in diameter. Their size and arrangement are similar to those illustrated for *P. (D.) santaemariae* (Pl. 34, figs. 2, 8). Like in that species the size of trabeculae seen in septa and median lamella seems to differ. Trabecular microstructure of the median lamella was observed in the longitudinal section oriented perpendicular to its length (Pl. 35,

fig. 6). Individual trabeculae reach almost 0.25 mm in the diameter. Such a discrepancy is considered secondary and diagenetic.

Vertical sections of the median lamellae (Pl. 35, fig. 6) and the wall (Pl. 35, fig. 7) are strikingly similar. The latter looks like diagenetically more altered trabecular wall, but trabeculae were not recognized either in the transverse (Pl. 35, fig. 8) or longitudinal section of intercorallite walls. Nevertheless, the microstructure of the wall discussed suggests the partition.

The partition can be either trabecular or fibro-normal in the microstructure. In the case of trabecular wall the size, area of development and direction of growth of trabeculae may differ. Stolarski (1995) and Roniewicz & Stolarski (1999) discussed several instances of trabecular and non-trabecular external walls in the primitive Scleractinia. Neither of these or similar examples were found in the material studied herein. Thus, the idea of trabecular intercorallite walls in *P. (D.) w. sexangula* is unsupported.

Remarks — De Groot (1963, p. 84) referred in her remarks to the idea of genomorphs writing in the last sentence "... the coralla contain also corallites of the *Hillia*-type." She obviously observed a close similarity of "*Lithostrotionella*" *sexangula* to "*Hillia*" and "*H.*" *wagneri* in particular. Differences pointed out in her remarks are not substantial, except for slightly longer minor septa and slightly better developed dissepimentarium in the holotype of "*Hillia*" *wagneri* and much better developed lonsdaleoid dissepiments in the holotype of "*L.*" *sexangula*. That strict similarity resulted in considering "*L.*" *sexangula* a subspecies of "*H.*" *wagneri*.

The identification by Fan (1978) of one of the Chinese petalaxids as *Lithostrotionella sexangula* and placing it in the subfamily Thysanophyllinae, together with other "lithostrotionellas," is not supported herein. Corallites in the Chinese specimen are much larger than those in the Spanish types, reaching up to 6 mm whereas they possess similar number of major septa with 18 prevailing. These made their n:d ratio different. Also, their lonsdaleoid dissepimentarium is better developed and their minor septa are much longer, penetrating the tabularium distinctly. The microstructure of septa and intercorallite walls and morphology of the tabularium (biform or regular) in the Chinese specimen are unknown. Judging from Fan's (1978, pl. 67, fig. 2a) illustration, an occurrence of three layers or even septal walls in the Chinese specimen is probable. Thus, their position within *Degrootia* subgen. nov. is likely, but this does not apply to *P. (D.) w. sexangula*.

Range — Westphalian D (Upper Moscovian).

Occurrence — Northern Palencia, Spain.

Petalaxis (Degrootia) sp.

Pls. 36, 37; Fig. 1.

e.p. 1963 *Lithostrotionella (Hillia) cantabrica* de Groot, p. 92, pl. 22, fig. 3.

Material — A single colony, RGM 112755. Diagenetic alterations of internal structures moderately advanced (de Groot, 1963, p. 93).

Description — Partitions thick, almost exclusively septal (Pl. 36, figs. 5-6). The partition forming peripheral parts of major and minor septa almost equally thickened. Dividing area of the partition either artificially expressed or camouflaged by diagenesis (Pl. 36, figs. 5, 6, respectively).

Thinning of septa outside partitions is abrupt, smooth (Pl. 36, fig. 5) or with carinae-like bodies (Pl. 36, fig. 6) discussed in more detail below. Some swellings may also occur in dissepimental parts of septa (Pl. 37, figs. 5-6). Tabular parts of major septa thin, differentiated in length from reaching a median lamella to approaching less than half tabularium width. Many of them join axially. Such a grouping together does not reflect quadrants in most cases (Pl. 37, fig. 1). The protosepta vary in length, sometimes greatly within individual corallites sectioned. This variety does not necessarily reflect intercorallite variability, but rather changes occurring in the course of growth of individual corallites. The cardinal septum in early hystero-ontogeny is invariably elongated to form a median lamella that may remain connected with the cardinal septum (Pl. 37, fig. 1). The disconnection exposed in some sections rarely resulted in shortening of the cardinal septum and slight elongation of the counter septum (Pl. 37, fig. 3, right and left respectively) or, more commonly, the cardinal septum remains long (Pl. 37, figs. 5-6). In rare instances and probably temporarily, the median lamella is reduced (Pl. 37, fig. 4). Minor septa invariably penetrate the peripheral tabularium (Pl. 37, figs. 5-6). Dissepimentarium rarely consists of more than three rows of regular dissepiments, occupying approximately one fifth to one third of the shortest corallite radius. It may remain underdeveloped up to early maturity (Pl. 37, fig. 6, left). Additional dissepiments occur in corallite corners.

In the longitudinal section (Pl. 37, fig. 2) dissepiments are small, regular, globose, arranged in vertical rows. Tabularium is biform as confirmed by the arrangement and number of sections of peripheral parts of tabulae in individual septal loculae (Pl. 37, fig. 5-6). The biform arrangement is also well seen in the longitudinal section (Pl. 37, fig. 2, middle and lower right) where tabulae in Position I form a row of dissepiment-like bodies. Long, deeply depressed tabulae in the same section (Pl. 37, fig. 6, middle left) correspond to Position I, whereas much lesser declined tabulae adjacent to them, lower and upper in the section, are interpreted as arranged in Position II.

Microstructure and diagenetic alterations — The microstructure of septa and median lamella is finely trabecular with the diameter of individual trabeculae varying between 0.05-0.10 mm. Trabeculae in septa (Pl. 36, fig. 4) may be either truly narrower than those in the median lamellae (Pl. 36, fig. 2) or that enlargement resulted from a diagenetic thickening. First option is considered more probable because remnants seen in the transverse section (Pl. 36, fig. 1) are comparatively large. Besides, a differentiation in size of trabeculae, or their diagenetic replacement in median lamella and septa, was observed in other species (see above). Length of individual trabeculae in the median lamella is very large, with the longest measured exceeding 10 mm.

The microstructure of septa observed in transverse sections exhibits strong differences in the arrangement of crystalline fibrils within wide septal basis and their narrow blades. The fan-shaped arrangement of calcite fibrils in septal bases (Pl. 36, fig. 5) is interpreted as reflecting the less advanced non-trabecular, originally fan-shaped microstructure. In the case of more advanced diagenesis (Pl. 36, fig. 6) there are only

few remnants of the fan-shaped arrangement of crystalline fibrils, whereas most of them are disordered. Also, the carinae-like bodies, present in some septa at the border between their thin and thick parts (Pl. 36, fig. 6), may be diagenetic in nature.

The longitudinal section of the partition, made perpendicular to its thickness (Pl. 36, fig. 3), exposes bodies in its middle part closely comparable to trabeculae. A trabecular partition is here considered probable, but not confirmed. A precisely oriented section along a partition was not available for the present study. This problem is more widely discussed with remarks on *P. (D.) wagneri sexangula*.

Remarks — Corallites of the colony discussed differ greatly from those in the holotype colony of "*Lithostrotionella*" ("*Hillia*") *cantabrica* de Groot, 1963, in the microstructure and morphology of its median lamella. The latter structure is invariably monoseptal, commonly thin, elongated and interrupted in *Petalaxis (Degrootia)* sp. Also, partitions in the latter are thinner, major septa joining to form groups and tabulae more deeply sagging in the longitudinal section. Paratypes of *P. (D.) cantabrica*, including that derived from the same locality as *P. (Degrootia)* sp. and morphologically most similar on the first glance (de Groot, 1963, pl. 22, fig. 2), differ in possessing fairly well developed lonsdaleoid dissepiments, major septa separated from each other and median lamellae thick, rather short and incorporating septal lamellae in some corallites. This paratype may in fact belong to a separate species or subspecies.

Range — Perapertu Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia, Spain.

Subclass Dividocorallia Fedorowski, 1991
Order Calyxcorallia Fedorowski, 1991
Family Heterostrotionidae Poty & Xu, 1996

Synonym — Stylostrotionidae Fedorowski, 1991.

Genera included — *Arctocorallium* gen. nov., *Donophyllum* Fomichev, 1939; *Dematophyllum* Wu & Jiang in Wu *et al.*, 1981; *Heterostrotion* Poty & Xu, 1996 (if not a younger synonym of *Donophyllum*); *Scruttonia* Cherepnina, 1974. (Berkowski (2002) has proven the synonymy of *Sudetiphyllia* Fedorowski, 1991, with *Scruttonia* Cherepnina, 1974. Following Poty & Xu (1996, p. 104) who included *Sudetiphyllia* in the Heterostrotioninae, I do the same with *Scruttonia*.)

Emended diagnosis — Fasciculate, subcerioid, thamnasterioid or aphroid dissepimental corals; major septa arranged in Heterocorallia-like pattern, sometimes withdrawn from corallite axis or form an aulos; lonsdaleoid dissepiments may occur (partly after Poty & Xu, 1996, p. 104).

Remarks — The introduction of the subclass Dividocorallia and the order Calyxcorallia (Fedorowski, 1991, 1993) was criticized by Wrzołek (1993), Poty & Xu (1996, 1997)

and Berkowski (1997). Criticisms concern, firstly, the distinction between the Rugosa and the Calyxcorallia. Indeed, morphology of those two groups is very similar in several characters whereas the hystero-ontogeny showing totally different models of increase in septa was either not considered or underestimated by the critics. Secondly, the close relationship of the Heterocorallia and the Calyxcorallia postulated by Fedorowski (1991, 1993) and exemplified in placing both suborders in the subclass Dividocorallia looked too strange. Indeed, the calice lacking, non-dissepimental taxa were placed together with caliculate and dissepimental ones. Why, however, was this argument not extended to the Rugosa, in which the Heterocorallia are traditionally included? Moreover, why was the increase in septa in the Heterocorallia and their pattern, totally different from the Rugosa and closely comparable to the Calyxcorallia, either omitted from the consideration or underestimated? The difference in the insertion of septa and their pattern is generally accepted as decisive for the distinction between the Scleractinia and the Rugosa in every palaeontological textbook. Why not for the Dividocorallia and the Rugosa? Lack of answers to those questions as well as new data published in this paper (see hystero-ontogeny sections below) and collected from several Devonian taxa restudied, but not yet published, strengthened my original opinion about the distinction between the Rugosa and the Dividocorallia.

The Heterocorallia-like pattern of major septa and their potential to disintegrate in corallite axes, was fully accepted by Poty & Xu (1996, 1997) as diagnostic. In contrast to Fedorowski (1991, 1993), however, Poty & Xu (1996) dedicated a low (subfamily) rank to those characters and included such corals in the family Lithostrotionidae of the Rugosa. The occurrence of minor septa and dissepimentarium are additional arguments of those authors against separating the Heterocorallia-like corals from the Rugosa. I do not agree with this position and keep considering the heterocoralloid arrangement of septa and a peculiar hystero-ontogeny (not examined by Poty & Xu, 1996, 1997) adequate for excluding their bearers not only from the family Lithostrotionidae, but also from the Rugosa. Also, the short radial plates in Calyxcorallia are analogous, but not homologous, to minor septa in the Rugosa because their origin and role are totally different (see hystero-ontogeny below). The dissepimentarium is a minor problem in taxa possessing a convex tabularium composed of tabellae. There is almost no difference from the morphogenetic point of view in secretion of a tabula and a dissepiment. Also, the relationship between dissepimental and non-dissepimental corals can easily find its counterparts in the Rugosa. For example, the dissepimental *Prosmilia* Koker, 1924, or *Adamanophyllum* Vassilyuk, 1960, are unanimously placed among the otherwise non-dissepimental Plerophyllina. Maintaining my original opinion (Fedorowski, 1991, 1993), I am aware of phylogenetic uncertainties within the Calyxcorallia, and particularly the gap between the latter and the Heterocorallia in the arrangement of their polyps and skeletons, but I consider these questions as a problem to be solved rather than a wall impossible to break down.

Strengthening of my position is due to the courtesy of Professor Edouard Poty who allowed me to examine the protocorallite illustrated by Poty & Xu (1996, pl. 8, fig. 4, letter "P"). During our discussion in Liège (1998) I pointed out the typically heterocoralloid morphology of this protocorallite. It could not have been distinguished from *Hexaphyllia* Stuckenbergh, 1904, or *Mariaephyllia* Fedorowski, 1991, if found disconnected from the colony of *Heterostrotion* cf. *minus*. Thus, there is an

alternative; to consider it the oldest known *Hexaphyllia*, the youngest known *Mariaephyllia* or to accept its original recognition as the protocorallite of *Heterostrotion* cf. *minus*. An attachment to a corallite inside the colony and its unique presence speak in favour of the last option. Although all three options are not rigid and the corallite was exposed by an incidental transverse section and not traced in other thin sections of the colony, its supposed role as a sexually produced individual supports the idea of the distinction of Calyxcorallia from the Rugosa. There is not a single rugose coral, solitary or colonial, that possesses the Heterocorallia-like pattern in its early ontogeny.

New data published elsewhere and unpublished pieces of information gathered since the introduction of the order Calyxcorallia (Fedorowski, 1991), allowed a change of mind about some lower rank questions. This concerns first of all my identification of fasciculate colonies from the uppermost Famennian strata of the Sudetes as a new species of *Stylostrotion* Chi, 1935 (Fedorowski, 1991). The new family Stylostrotionidae, created on the basis of this genus, was only a consequence of such recognition. The reference to a weakly known Chinese genus, instead of creation of a new genus based on well-established species from the Sudetes, was an obvious mistake resulting in the synonymy of Stylostrotionidae with Heterostrotionidae. Further remarks are included in the genus *Donophyllum*, below.

The familial diagnosis proposed by Poty & Xu (1996, p. 104) was simplified a little with the phrase "typically pinnately connected" omitted as little supplementing the information about the Heterocorallia-like pattern. A possibility to develop an aulos was tentatively accepted although more data than those published by Poty & Xu (1997, pl. 1) are needed to prove its common and diagnostic occurrence in particular lower rank taxa of the Heterostrotionidae. The occurrence of lonsdaleoid dissepiments was mentioned in the emended diagnosis in order to accept *Dematophyllum* Wu & Jiang in Wu *et al.*, 1981, a member of Heterostrotionidae as postulated by Poty & Xu (1996, 1997). In contrast to my earlier opinion (Fedorowski, 1991), I now accept an independent status of that genus. *Cionodendron* of Ivanovsky (1967), considered earlier a possible younger synonym of *Stylostrotion* (Fedorowski, 1991, p. 70), is now omitted from the list because my doubts concerning its morphology increased. It is impossible to prove the Heterocorallia-like pattern of septa in that species and its quadri-lateral symmetry early in the hystero-ontogeny until detailed study are made.

Genus *Donophyllum* Fomichev, 1939

Type species — *Donophyllum diphyphyllodeum* Fomichev, 1939, designated by Lang *et al.* (1940, p. 54); Upper Bashkirian-Lower Moscovian (Limestones K8-L5) of the Donets Basin, Ukraine.

Synonymy — Potential synonyms include: —

- e.p. 1933 *Diphyphyllum* Lonsdale, Yu, p. 82.
- 1939 *Diphyphyllum* (*Donophyllum*) Fomichev, p. 59.
- 1940 *Donophyllum* Lang *et al.*, p. 54.
- e.p. 1953 *Diphyphyllum* (*Donophyllum*) Fomichev, p. 440.
- 1962 *Diphyphyllum* (*Donophyllum*) Soshkina & Dobrolyubova, p. 338.

- e.p. 1963 *Lithostrotion* de Groot, p. 47.
 e.p. 1977 *Lithostrotion* Jia *et al.*, p. 192.
 e.p. 1977 *Diphyphyllum* (*Donophyllum*) Jia *et al.*, p. 197.
 1983 *Donophyllum* Yu *et al.*, p. 112.
 1984 *Diphyphyllum* (*Donophyllum*) Khoa, p.13.
 1984 ?*Lithostrotion* Rodriguez, p. 223.
 1987 *Diphyphyllum* (*Donophyllum*) Tan *et al.*, p. 143.
 e.p. 1989 *Donophyllum* Wu & Zhao, p. 125.
 1991 *Stylostrotion* Fedorowski, p. 70.
 1996 *Heterostrotion* Poty & Xu, p. 104.
 1997 *Heterostrotion* Poty & Xu, p. 100.
 1997 *Stylostrotion* Berkowski, p. 155.

The above list contains all citations of fasciculate species possessing the Heterocorallia-like pattern of major septa known to me. Their common generic status requires a rigid proof of *Heterostrotion* to be a younger synonym of *Donophyllum*. Such a proof was impossible to demonstrate on the basis of the material studied up to date by authors (see discussion below). It seems useful to demonstrate, however, that the Heterocorallia-like septal pattern is fairly common and widespread amongst the uppermost Devonian and Carboniferous fasciculate Anthozoa.

Emended diagnosis — Fasciculate colonies; increase lateral; major septa may shorten and lose their Heterocorallia-like arrangement in individual corallites within colonies; minor-like septa and dissepimentarium well developed; tabularium convex, more or less clearly tripartite; carinae may occur; microstructure of septa trabecular.

Remarks — In spite of *Donophyllum* Fomichev, 1939, being accepted herein to include "*Lithostrotion*" *reticulatum* (Fomichev) of de Groot (1963), the taxonomic position of the genus *Stylostrotion* Chi, 1935, is discussed first. Its introduction four years earlier than *Donophyllum* would have resulted in its priority over the latter if synonymy of those two are proven. My original reference to *Stylostrotion* (Fedorowski, 1991, 1993) was based on the heterocoralloid pattern of major septa recognizable in at least some illustrations by Chi (1935, pl. 1, figs. 1a [left], 1d) and on a lack of knowledge about preservation of the type specimen of *Stylostrotion intermedium* Chi, 1935.

Poty & Xu (1996, 1997) did not question the heterocoralloid arrangement of septa in *Stylostrotion intermedium* Chi, 1935, but postulated an occurrence in that species of a columella (i.e., median lamella in the here accepted nomenclature). Their position is based partly on the statement by Chi (1935) concluding the development of "palicolumella," partly on his illustrations, and partly on the single corallite of the holotype of *S. intermedium* Chi, 1935. The reinvestigation of that corallite was not pointed out by Poty & Xu (1996), but was mentioned by Xu (1996, p. 153) in his unpublished Ph.D. thesis. Unfortunately, the specimen was not reillustrated in either of the last two papers mentioned. My recent search for the holotype, kindly helped by Dr. Xiangdong Wang from the Institute of Geology and Palaeontology, Academia Sinica in Nanjing, ended with the following information transmitted by Dr. Wang in August 27, 2003: "We checked the number of *Stylostrotion intermedium* Chi 1935... in the record, among 6 types (5991a-f), only 2 (5991b, 5991f) were housed and other 4 were not submitted.

The 5991b is neanic stage, and 5991f is longitudinal section." The information cited shows clearly that the basis for identification of the morphology, including its intracolony and intraspecific variability, the hystero-ontogeny and other substantial characteristics of *Stylostroton intermedium* Chi, 1935, cannot be observed as does not the basis for the identification of the genus. Also, topotypes have not been collected (Xu, 1996, p. 153). To officially suppress that generic name by ICZN commission will perhaps be the best solution.

Thus, I do not identify as *Stylostroton* any fasciculate rugose coral colony with corallites possessing major septa arranged in the Heterocorallia-like pattern because they cannot be compared to the type. I do not discuss herein the new meaning of the genus *Stylostroton* introduced by Xu (1996), but only point out that Xu allocated his Early Viséan corals to Weiningian (Upper Carboniferous) species, ignoring the very severe extinctions experienced by the Rugosa in the early Bashkirian. He did not document any reason for such an extraordinary approach. Therefore, it was no more than his subjective decision to implant characteristics of his corals to the practically unknown *Stylostroton intermedium*. Such a procedure does not fulfil an acceptable scientific standards and cannot be followed. Besides, that concept was introduced in the unpublished Ph.D. thesis and cannot be treated equally with published data or position. Nevertheless, Poty & Xu (1996, 1997) omitted all those problems from their papers and considered the new concept of *Stylostroton intermedium* proven.

Corals with a morphology similar to that described from Spain by de Groot (1963) and Rodriguez (1984), and redescribed below, were first described from South China by Yu (1933) as *Diphyphyllum? vesicotabulatum*. They were redescribed by Smith & Yu (1943) who pointed out their distinction from aulate corals and similarity to cerioid species identified by Yu (1933, 1937) as *Prismatophyllum*. This question is discussed below with remarks on *Arctocorallium* gen. nov.

Fomichev (1939) was the next author after Yu (1933) who dealt with corals of the Heterocorallia-like pattern of major septa. He described and illustrated *Donophyllum reticulatum* as a new species of a new subgenus of the genus *Diphyphyllum* Lonsdale, 1845, and illustrated another new species, *D. diphyphyллоideum*. Unfortunately, he failed in that paper to indicate the type species for his new subgenus. Publication of his basic monograph, yielding the formal introduction of *D. reticulatum* as the type species (Fomichev, 1953, p. 442), was delayed for 14 years for political and other reasons. Many taxa introduced by him in that excellent study and placed in the synonymy with other taxa afterwards, would have had priority otherwise. The same would have been true for *D. reticulatum*. Unfortunately, Lang *et al.* (1940, p. 54) selected the originally undescribed *D. diphyphyллоideum* Fomichev (cited by them as *diphyphyллоidium*) the type species of *Donophyllum* and placed that subgenus in the synonymy with *Diphyphyllum* Lonsdale, 1845. Their very unfortunate selection of the type species resulted in either rejection of that genus (Poty & Xu, 1996, 1997) or in the misunderstanding of its morphology and taxonomy (de Groot, 1963, p. 49; Hill, 1981, p. F394).

Fomichev (1953, p. 442) was aware of the close relationship between the Chinese and the Donets Basin corals because he wrote "It should be mentioned that corals typical for the subgenus *Donophyllum* subgen. nov., described by Yu (1933, pp. 87-88, pl. 14, fig. 5a-d; pl. 15, fig. 5a-b) as *Diphyphyllum? vesicotabulatum* sp. nov., were found already in the *Yuanophyllum*-zone (Upper Viséan - Namurian?) of China" [translated

herein from Russian]. Thus, the type species of the genus *Heterostrotion*, chosen by Poty & Xu (1996), was a few decades earlier considered informally a member of *Donophyllum*.

Donophyllum Fomichev, 1939, was not acknowledged by Poty & Xu (1996, 1997) as potentially including fasciculate colonies with corallites possessing the Heterocorallia-like pattern of major septa. This is clearly documented in the synonymy to their new genus *Heterostrotion* and was to some extent based (Poty & Xu, 1996, p. 105) on photographs taken from two thin sections of the holotype of *D. diphyphyllloideum* published by Fedorowski (1991, pl. 9, figs. 2a, b) as exposing an extremely simplified morphology.

There are no doubts that *Donophyllum diphyphyllloideum* represents a morphology different from *Heterostrotion* in most corallites, but it is equally true that few long septal corallites and rudiments of the Heterocorallia-like pattern of major septa occur in the holotype of *D. diphyphyllloideum* (Pl. 38, figs. 1-3). Those few corallites, exposed by poor acetate peels taken from small fragment of the dolomitized holotype, do not form a rigid basis for the final conclusion, whereas it was impossible to investigate the hystero-ontogeny. They form a good indication, however, for a close relationship between *D. diphyphyllloideum*, *D. intermedium* and *D. reticulatum*, mentioned already by Fomichev (1939, p. 59). Moreover, diphyphylloid corallites are common in *D. intermedium* whereas their occurrence in *D. reticulatum* is less frequent. Thus, a sequence from most to less advanced reduction in length of major septa exists and should not be underestimated. It is also worth mentioning that those three species occur together, sometimes in the same beds, and possess very similar diameters and number of septa of corallites. All those characters are supportive for their very close relationship. Differences in the hystero-ontogeny related to the reduction in length of major septa, observed within the same colony (see description of *D. reticulatum*, below), may speak in favour of the reduced value of that shortening.

A sort of stratigraphic sequence in increase of the axial disconnection of major septa should also be mentioned. "*Stylostrotion*" *sudeticum*, stratigraphically the oldest fasciculate species known so far (latest Famennian *Quasiendothyra cobeitusana* Zone), exposes a permanent axial connection of major septa (Fedorowski, 1991, pls. 3-7). Weak disconnection occurs in the Upper Tournaisian *Heterostrotion* cf. *minus* (Zuo, 1977) of Poty & Xu (1996, pl. 8, fig. 4) and Early Viséan *Diphyphyllum?* *vesicotabulatum* (Yu, 1933, pl. 15, fig. 5a). Unfortunately, there is a gap in the occurrence of *Donophyllum*-like or *Heterostrotion*-like corals spanning at least the Serpukhovian and Lower Bashkirian. This may explain a very advanced axial disintegration of major septa in the youngest known taxa, but may also be interpreted as the phylogenetic disconnection between the Upper Bashkirian and the Viséan taxa. Nevertheless, a close morphological similarity of *Donophyllum reticulatum* to *Diphyphyllum?* *vesicotabulatum* Yu, 1933, cannot be questioned. Following Fomichev's (1959) opinion and in spite of the gap mentioned, I consider these two taxa related.

The discussion in the preceded paragraphs cannot be considered decisive for the synonymy of *Heterostrotion* with *Donophyllum*. It does show a presence of sequential changes in morphology, an axial disconnection of major septa in particular. Thus, it may only be a matter of a subjective attitude where to place the boundary between these genera. Does, for instance, the corallite published herein in Plate 41 belong to *Heterostrotion* because all its morphological attributes fits the diagnosis of that genus

perfectly, whereas its neighbour from the same colony, illustrated in Plates 43, 44, does not because its morphology fits exactly that of *Donophyllum diphyphyloideum*?

Assuming a close relationship, perhaps synonymy, of *Donophyllum* or at least *D. reticulatum* and *Heterostroton* very probable, the origin of the latter genus should be briefly discussed. Poty & Xu (1996, p. 105), following Poty (1984), suggested a close relationship between *Solenodendron* Sando, 1976, and *Heterostroton*. Their recognition is based on the formation of an aulos in both genera and on "lack of cardinal fossula, protosepta which usually are not recognizable, presence of minor septa, similar interseptal dissepiments." The last two characters listed have restricted taxonomic value on a level higher than species. Very similar minor septa and interseptal dissepiments occur in *Siphonodendron*, *Lithostroton*, *Nemistium* and many other genera, including so distant ones as solitary *Haplolasma*. Thus, those characters are omitted from the discussion.

The first two characters are ambiguous as well. Unrecognizable protosepta and lack of a cardinal fossula are not unique in mature corallites of the Rugosa. Not only *Solenodendron*, but also *Opiphyllum*, *Tschussovskenia* and some other genera among dissepimental Carboniferous and Permian corals, and such phylogenetically distant Rugosa as, for instance, *Amplexus* and *Metrioplexus*, may be pointed out as examples. Thus, those characters are useful in the Rugosa only as additional features to plot with a set of diagnostically more important ones.

It should also be pointed out that the Rugose coral kind of protosepta and the cardinal fossula are absent from the Calyxcorallia. This problem was widely discussed and illustrated by Fedorowski (1991, 1993), who recognized an occurrence of the so-called "fossae" reflecting particular arrangement of major septa. Fossae are not combined with depressions of tabulae, i.e., are not analogous or homologous to true fossulae appearing in the Rugosa. Fossae, but not fossulae, occur in *Heterostroton*. Thus, an absence of distinguishable protosepta and fossulae, superimposed on the heterocoralloid pattern of septa, stressed a non-rugosan affinity of that genus.

Development of the aulos was considered by Poty & Xu (1996, 1997) the most important argument proving the relationship between *Solenodendron* and *Heterostroton*. Indeed, that structure was in several instances applied in the Rugosa as the first rank character to distinguish between genera. I am aware of that because I separated on this basis the generally accepted genus *Communia* from *Pentaphyllum*. Also, nobody questions the occurrence of the aulos in *Solenodendron*. One picture of that structure in *Heterostroton* (Poty & Xu, 1997, pl. 1, fig. 3) looks convincing whereas the other two are not. This problem is immaterial, however, and I omit from the discussion the question whether the structure developed in *Heterostroton* fulfils the diagnosis by Hill (1981, p. F32) or not. It appears unimportant when the timing of the appearance of individual taxa is taken into the consideration. *Solenodendron* appeared only in the Upper Tournaisian whereas "*Stylostroton*" *sudeticum*, unquestionably included in the synonymy with *Heterostroton* by Poty & Xu (1996, 1997), was documented to occur in the latest Famennian *Quasiendothyra cobeitusana* Zone. Thus, "*Stylostroton*" *sudeticum* must be considered either unrelated to younger *Heterostroton* species, or to be an ancestor of *Solenodendron* from which those taxa were derived, or the phylogenetic line of *Solenodendron* has nothing in common with the lineage of *Heterostroton*-like corals. Only the third solution looks rational to me. A predicted argument that such corallites as those illustrated by Fedorowski (1991, pl.

4, figs. 2a [lower], 2c [upper]) have the potential to form an aulos can easily be rejected by indicating a similar arrangement of septa in the calice-lacking *Mariaephyllia* (Fedorowski, 1991, pl. 2, fig. 5) and *Oligophylloides* (Chwieduk, 2001, text-fig. 14Ga; pl. 1, figs. 5, 6c, e; pl. 3, figs. 4a, b).

The discussion by de Groot (1963, p. 49), supporting the idea of the identification of the Donets Basin and Spanish donophylla as either belonging in *Diphyphyllum* [*D. diphyphyllodeum*] or *Lithostrotion* [*D. reticulatum*] appears baseless due to different order identification. It should also be mentioned that Rodriguez (1984, p. 227) has priority in considering Spanish specimens with Heterocorallia-like pattern of septa similar to both *Stylostrotion* and *Donophyllum*. An uncertain taxonomic status of both those genera led to him questionably and temporarily including *Donophyllum reticulatum* Fomichev in *Lithostrotion*.

The following general remarks are necessary to mention for making the hystero-ontogeny in Calyxcorallia better understood:—

Corals belonging in this order offset peripherally, i.e., an offset is formed within a calice on the top of dissepiments or on the top of peripheral tabulae when the dissepimentarium is reduced from the offsetting area. Such a position of an offset creates a close analogy to the peripherally offsetting Rugosa.

Calice floors in Calyxcorallia (i.e., tabulae alone and/or supplied with tabellae) are more or less convex whereas major septa are elevated only slightly above their surfaces and are amplexoid.

Every transverse section exposes a combination of structures secreted in slightly different growth stages. This results from direction of growth of an external skeleton; always inwards of external walls in a calice, but not necessarily axial-wards. An axial elevation of a calice resulted in growth of structural elements developed in that area both upwards and towards a periphery.

A section cut below a tabula commonly exposes a disconnection of some inner margins of major septa resulted from their amplexoid nature.

A neotheca grew only upwards whereas the peripheral part of an offset grew both upwards and towards the periphery. Thus, serial sections oriented perpendicular to the former, as is traditional, expose ontogenetically differentiated parts of an offset with the peripheral part being more advanced in the development. Besides, septa sectioned in that part are artificially elongated by an obliqueness of a given section at the periphery.

An insertion of septa by splitting may be camouflaged by some factors listed above, but is obvious from several sections. There are rare examples, however, in which given septa, especially minor-like septa, are inserted without an obvious connection to any adjacent septum.

***Donophyllum reticulatum* Fomichev, 1939**

Pl. 39, figs. 2-3; Pls. 40-45.

1939 *Donophyllum reticulatum* Fomichev, p. 59, pl. 9, fig. 2.

1953 *Donophyllum reticulatum*: Fomichev, p. 443, pl. 29, fig. 9.

1963 *Lithostrotion reticulatum* (Fomichev): de Groot, p. 48, pl. 5, figs. 1-2.

1984 *Lithostrotion(?) reticulatum* (Fomichev): Rodriguez, p. 224, pl. 6, figs. 7-9, text-figs. 96-97.

Material — Ten fragments of colonies included in that species by de Groot (1963, p. 49) were reinvestigated. All of them exhibit similar intracolony variability and only colony RGM 112598 was investigated in detail, including hystero-ontogeny. Also, a small fragment of the holotype colony of *D. reticulatum* Fomichev, 1939, was available for study.

Emended diagnosis — *Donophyllum* with maximum n:d ratio of corallites 18:5.0 mm; 13-14:3.0-3.5 mm prevails; heterocoralloid pattern of thin major septa inconstant; most minor-like septa enter peripheral tabularium deeply, some reduced; one, rarely two incomplete rows of regular dissepiments; tabularium uniform, domed.

Additional description; morphology — External wall c. 0.2 mm thick, without waviness indicative of presence of septal furrows. Septa thin, dip with their triangular, slightly thickened bases into inner part of the wall. Major septa vary in length and arrangement during growth of individual corallites (e.g., Pl. 39, figs. 3a-c; Pl. 42, figs. 1-4). An arrangement typical for regularly arranged septa in *Heterophyllia* (e.g., Schindewolf, 1941, pl. 15, figs. 1-7) or *Mariaephyllia* (Fedorowski, 1991, pl. 1, figs. 1-2, 4, 9-11) was not found in the colony investigated in detail, but there are corallites in each transverse section that exhibit a heterocoralloid pattern (Pl. 40, fig. 1; Pl. 41, figs. 1, 4).

Comparison of septal pattern within individual corallites during the course of their growth was not studied up to now in any species included in *Donophyllum* or *Heterostrotion*. Forty corallites investigated herein have shown that the arrangement may change considerably within a few tens of mm of their growth. Three transverse sections of a corallite are illustrated herein as an example (Pl. 39, figs. 3a-c). Individual septal pattern replaced each other for few times during c. 10 mm growth of the specimen, with the typical Heterocorallia-like pattern being less common. In most corallites there remain some major septa free axially.

Detailed investigation of 40 or so corallites of the colony RGM 112598 indicate that particular morphotypes may prevail during the course of growth of individual corallites. Several corallites investigated do not develop a Heterocorallia-like pattern after more than 10 mm of growth, whereas a more or less complete pattern of that kind prevails in only few other ones. The intermediate corallites, i.e., those with “diphyphyloid” and more or less obvious Heterocorallia-like pattern replacing each other for few times are most common. The prevailing arrangement of major septa in given mature corallites is commonly reflected in their hystero-ontogeny that may differ in details to a considerable extent when such morphologically different corallites are studied (see below).

Corallites possessing all major septa arranged in the Heterocorallia-like pattern are rare in Spanish colonies and such an arrangement may last for only a short distance of growth. A small fragment of the holotype colony of *D. reticulatum* (Pl. 39, figs. 2a-d) confirms observations made on the Spanish colony.

Some major septa in transverse sections may resemble cardinal septa of the Rugosa. This is only a short lasting impression resulted from a peculiar and always temporary pattern of major septa sectioned beneath tabulae (e.g., Pl. 39, figs. 3b, c, right). Thus, an occurrence of protosepta postulated by de Groot (1963, p. 48) was not confirmed.

Minor-like septa vary greatly in length, a character already pointed out by de Groot (1963, p. 49). In mature corallites most of them are free. There are growth fragments when they join systems of major septa, becoming indistinguishable from them (Pl. 39, fig. 3a, lower and lower left versus fig. 3b). Like the arrangement of major septa such an arrangement of minor-like septa is always temporary (see blastogeny below). Morphology in the longitudinal section (Pl. 39, figs. 2c, d; Pl. 40, figs. 2-3) changes in accordance with the variation in pattern of major septa. The dissepimentarium consists of a single, rarely interrupted row of globose dissepiments. Two rows may occasionally, and for a short distance of growth, be developed. Tabulae corresponding to the "diphyphylloid" pattern of septa are commonly domed, but are often divided into axial and peripheral parts by sections of inner parts of major septa. Such a pattern closely resembles an aulos when supplemented by flat axial tabellae (Pl. 40, fig. 2, middle). Neither deflected nor rhopaloidally thickened inner margins of major septa prevent recognition of such a morphology as an aulos. In fragments with a heterocoralloid pattern the tabularium became more convex with short flat tabellae declined towards individual sections of septa (Pl. 39, fig. 2d; Pl. 40, fig. 2, upper). Peripheral tabellae occur irregularly.

Microstructure and diagenetic alterations — For the purpose of this paper the microstructure of septa was investigated in the holotype of *D. reticulatum* (Pl. 40, fig. 6) and in Spanish specimens included in this species. Unfortunately, diagenetic alterations are advanced in both. Some rudiments seen in the obliquely longitudinal section of a septum in the holotype (Pl. 40, fig. 6) suggest trabecular microstructure. If the altered bodies present in this septum are trabeculae, their diameters would have been almost two times smaller than described in "*Stylostroton*" *sudeticum* (Fedorowski, 1991, pl. 6, figs. 1, 2a). Transverse sections of the holotype and Spanish specimens do not exhibit remnants of trabeculae and are not illustrated.

Hystero-ontogeny — The process of offsetting varies in detail and depends to some extent on the prevailing morphology of a given offsetting corallite. Also, characters constant for the Calyxcorallia, but different from the Rugosa, can be established only when the insertion of septa in particular quadrants are analysed in detail. Some corallites characterised by an advanced shortening of major septa (Pls. 43-45) offset in a way hardly comparable to that of corallites with long and mainly united major septa (Pl. 41). There are others, however, that are intermediate in character (Pl. 42). Thus, three series of offsetting were described separately with the common and most important characters summarised at the end. I decided to introduce such a long description in order to make my conclusions acceptable.

1. *The most advanced Heterocorallia-like pattern of septa* (Pl. 41, figs. 1-11) — A single corallite among all those investigated in detail exposed that mode of offsetting. Thus, such a mode should be treated as a very important variant, but not as fundamental for the species and genus. Both the Heterocorallia-like arrangement of major septa and the occurrence of the oblique septum in the parent's corallite are fairly easily distinguishable (Pl. 41, figs. 1, 4). Thus, it is possible to determine as the second generation (Fedorowski, 1991, nomenclature) the major septum located in the middle of the offsetting

area and leading in the process of the septogenesis of the offset. The process of offsetting was fast in the case discussed, being completed within 1.5 mm of growth, starting from its earliest phenomena (Pl. 41, fig. 1) and ending with completion of the permanent offset's wall (Pl. 41, fig. 11). Numbers in left corners, corresponding to distances in mm between individual sections, illustrate rapid morphological changes. Some bias towards an earlier development of left quadrants, observed during earliest growth stages of the offset (Pl. 41, figs. 1-5) disappeared in its further growth (Pl. 41, figs. 6-11).

Three major and two minor-like septa were involved in the process that began with a peripheral split of two parent's major septa (Pl. 41, fig. 1, lower middle and left). The parent's minor-like septum located between those two major septa either split as well or became divided into a free, grain-like body situated next to the left major septum and a curved structure to the right of the former, extending to the external wall. The grain-like body either disappeared from the common parent/offset area within 0.1 mm of further growth or was transmitted into the partition. The peripheral rudiment was retained between the thick right fork of the left major septum and thin left fork of the middle major septum. Its inner margin is slightly curved towards the latter (Pl. 41, fig. 2). In the next sections the rudiment became elongated and attached to the left fork of the parent's middle major septum (Pl. 41, figs. 3-4), i.e., the future symmetry septum (a new term, explained in the terminology). Thus, the major septum adjacent to the symmetry septum from the left is the transformed minor-like septum of the parent corallite. The major septum neighbouring the symmetry septum to the right arose from the right fork of the parent's middle major septum. Thus, all three first septa of the offset are atavosepta, but only the first two were derived from the parent's middle major septum and played a particular role in the septogenesis (see the second following paragraph).

The remaining septa of the left peripheral offset quadrant are all more or less clearly connected to the left parent's major septum and its forks. Both peripheral forks of that septum (Pl. 41, fig. 1, left) were at the very beginning thickened and extended scissors-like towards the periphery, but became parallel to each other within only 0.1 mm of further growth (Pl. 41, fig. 2, left). The thin, inner part of the parent's major septum remained attached to both its forks at almost right angle. Forking of the major septum discussed became more regular within the next 0.2 mm of growth, i.e., when the partition was extended up to there (Pl. 41, fig. 3, middle left). At the level of growth now under discussion, the left parent's major septum lost a direct connection with its right fork that became shortened and transmitted into the minor-like septum (Pl. 41, fig. 3, lower left). The left fork of the parent's left major septum (Pl. 41, fig. 3 left) became disconnected from it within only 0.1 mm of further growth (Pl. 41, fig. 4) and was transformed into the offset's major septum, extending with its inner margin rightwards up to meeting the older offset's major septa near the partition (Pl. 41, figs. 5, 6). Its inner margin was then united with the preceding major septum near the offset's axis (Pl. 41, fig. 7). The position of this major septum became stabilized between eight and nine o'clock by comparison to a clock's face (Pl. 41, fig. 7-11). It constituted the boundary of the left peripheral quadrant of the offset's septa. All major septa of that quadrant, except for those developed last and next to the symmetry septum, were atavosepta.

The only major neoseptum in this quadrant was inserted early in the hystero-

ontogeny by a peripheral split (Pl. 41, figs. 3, 4, lower) of the septum transmitted from the peripheral part of the minor-like septum (see description above). This neoseptum and the neoseptum inserted on the opposite side of the symmetry septum (Pl. 41, fig. 5) played a role of minor-like septa first (Pl. 41, figs. 5-8), but were afterwards transformed into major septa (Pl. 41, figs. 9-11).

The leading role of the parent's middle major septum and its two forks mentioned above become best understood when discussed together with the formation of inner (i.e., located at the neotheca) quadrants of the offset's septa. The beginning of formation of those quadrants should not be correlated with the earliest stage of the partition, because both forks of the middle parent's major septum continued directly to the atavotheca and constituted first offset's atavosepta (Pl. 41, fig. 2). The earliest septogenesis at the neotheca corresponded to the union of inner margins of the first offset's atavosepta and the connection of those united margins with the thick right fork of the parent's middle major septum (Pl. 41, fig. 3, middle right), best documented in the next section (Pl. 41, fig. 4). That thick fork and its left counterpart that became free axially for a short period of growth (Pl. 41, figs. 3, 4, respectively) constituted the first two offset's septa at the neotheca. Thus, these septa should be considered the atavosepta directly related by their origin to two first peripheral atavosepta of the offset. Such a close relationship, and the ephemeral formation of the oblique septum, is best demonstrated in the next section (Pl. 41, fig. 5).

Both inner quadrants of the offset's septa were accelerated in an increase, making its step-by-step deciphering difficult. This process is, in fact, possible to decipher only in the left inner quadrant. The early stage of formation of that quadrant followed the transformation of the inner parts of forks of the parent's middle major septum into the first offsets major septa at the neotheca. Next offset's major septum appeared at the partition left of those first two septa (Pl. 41, fig. 3, middle left). The inner end of that septum was attached to the inner part of the septum described above as being transformed from the minor-like septum (Pl. 41, fig. 3), but it was forked from the parent's left major septum. This is proven by the next section (Pl. 41, figs. 4) exposing its obvious connection to that fork and a neighbourhood to the left atavoseptum of the first two, free in this section. Presumed in this level of growth, but confirmed clearly in the following section, the next septum was inserted in the left offset's corner (Pl. 41, fig. 4). It is almost parallel to the neotheca and perpendicular to the peripheral part of the left parent's major septum, but its inner margin extends to the preceding major septum. This is well exposed in the following section (Pl. 41, fig. 5, left corner) that also documents an increase of the two next septa, probably derived by a split of the peripheral part of the left parent's major septum (compare Pl. 41, fig. 4 vs. fig. 5, left corner). As documented by further growth (Pl. 41, figs. 6-11), these two major septa inserted last, completing the number of major septa in the left inner quadrant.

The development of the right two quadrants of the offset's septa began with a transformation of the right parent's minor-like septum included in the offsetting sector. Being regular and simple at the beginning (Pl. 41, fig. 1, right), this septum became divided into the peripheral part remaining at the external wall and the inner part attached to the middle major septum to form a peripheral fragment of the partition (Pl. 41, fig. 2, right) in the manner observed in some offsets of *Arctocorallium trimorphum* (see description of that species below). The inner part of this septum, long and

resembling a major septum during some period of the corallite growth (Pl. 41, figs. 3-5), became shortened to the size of regular minor-like septa and occupied a position of the latter on the parent's side of the partition (Pl. 41, figs. 6-9). The peripheral rudiment of that minor-like septum became elongated (Pl. 41, fig. 3) and constituted the future second major septum of the right peripheral quadrant (Pl. 41, figs. 4-7). Simultaneously with that elongation of the peripheral part of the former minor-like septum, a new short septum appeared in an unknown manner leftwards to it (Pl. 41, fig. 3, lower right). This new septum is the first minor-like septum of the right peripheral quadrant.

It is not quite clear how the last septa of the right peripheral quadrant were inserted and how they are related to major septa of the right inner quadrant. This is mainly due to the shortening of septa on the right side of the offset in two sections (Pl. 41, figs. 6, 8). Comparison of the intervening and last long septal sections (Pl. 41, figs. 7, 9-11) suggest that the last septa in the right peripheral quadrant were inserted by peripheral split (Pl. 41, figs. 7, 9, 10, right). It remains uncertain, however, whether all three of them are major septa or one (two?) will eventually be transferred into minor-like septa. All of them were united by inner margins first, but the last one in the series became free without being shortened (Pl. 41, fig. 11, right). Whatever the interpretation, these were the last septa inserted in the right peripheral quadrant, thus confirming a rightwards increase in septa in that quadrant.

An insertion of septa in the right inner quadrant looks chaotic due to the appearance of additional septal bodies and horn-like elongations of septal forks in some sections (Pl. 41, figs. 7-9). All those bodies were either ephemeric or connected to forks of the parent's middle major septum that did not lose its central position. Thus, the insertion of all septa in the inner right quadrant took place right of those forks and most probably successively towards the right from the symmetry septum. This is the only quadrant of the offset described and the direction in the increase in septa was not established with adequate confidence.

The development of two major neosepta located next to the symmetry septum seems to contradict the mode of increase accepted typical for the Calyxcorallia and points towards the Rugosa. In my opinion this does not. At first those two septa were transformed into major septa from short septa inserted early in the septogenesis (at least one of it by peripheral split) and acting as minor-like septa during the early blastogeny. A transformation of the minor into the major septa late in the ontogeny or hysterio-ontogeny does not occur in the Rugosa and contradicts the rule of the insertion of septa in that subclass either in the sense of Kunth (1869) or Weyer (1972a). It should be pointed out that according to the latter author there were short major septa, but not minor septa, inserted as the last septa in individual quadrants of the Rugosa. Alternating furrows of major and minor septa (e.g., Fedorowski, 1987, pl. 3, figs. 8a, 10a) support Kunth's (1869) model, but Weyer's (1972a) model may perhaps be an alternative in some cases. Irrespective of the model, however, the last septa inserted in quadrants do not last short in the Rugosa when subsequent septa are inserted.

All major septa, other than the two discussed in the preceding paragraph, were inserted in four directions starting from the symmetry septum and ending at the periphery of each quadrant. It was proven that two of those major septa were transformed from the parent's minor-like septa, a case never observed in the Rugosa.

The potentially creative septa (Fedorowski, 1991) in the Heterocorallia may have got activated in almost any part of a corallite growth and in any part of a quadrant (Fedorowski, 1991; Chwieduk, 2001). Thus, the case discussed may well demonstrate the same phenomenon, i.e., an elongation of some septa after a period of resting and imitating minor septa.

Thus, four characters are most important for the offsetting of the corallite, as described in detail above: permanently long peripheral parts of septa inherited by the offset (Pl. 41, figs. 1-3); an increase of most septa by splitting (Pl. 41, figs. 2-9); four directions of an increase in septa in most parts of the septogenesis; and transformation of some minor-like septa of the parent corallite into the major septa of the offset. Despite its rarity in the colonies restudied herein, the mode of offsetting described above best exposes the characters typical for the Calyxcorallia.

2. *The moderate reduction of Heterocorallia-like arrangement of septa* — Two series of peel replicas were included in this category and one was described in detail (Pl. 42, figs. 1-8). The series described exposes more similarities to the offsetting of corallites showing advanced heterocoralloid morphology than to the 'diphyphylloid' one described below. Similarly to the hetero-ontogeny in the corallite showing the advanced Heterocorallia-like pattern of septa, three major and two minor-like septa were perhaps involved in the process of the offsetting now under study, but the latter septa were not distinguished with certainty. Peripheral parts of the parent's septa, i.e., atavosepta of the offset, are continuous at the early stage of the hystero-ontogeny (Pl. 42, figs. 1-4) like in the first variant. Here, however, the left parent's major septum split to form the parent's minor-like septum from its left fork and the peripheral part of the partition from the right one (Pl. 42, figs. 1-3, left). The inner, long fragment of this left parent's major septum remained attached to the partition from the parent's side, undergoing little modification (Pl. 42, figs. 3-6) and becoming eventually transferred back to the parent's external wall (Pl. 42, fig. 8, left). At the beginning of the process, the parent's right major septum underwent similar modifications. Its thickened peripheral part formed a fragment of the partition (Pl. 42, figs. 2-3, right). Its further modifications were more complex, however, and are described below. It eventually joined the parent's external wall (Pl. 42, figs. 7-8, right). Thus, only the parent's middle major septum remained in the common parent/offset area till the end of the hystero-ontogeny. Like in the case of the hystero-ontogeny of the corallite possessing a Heterocorallia-like of well developed pattern septa, this middle parent's major septum was the leading septum in the septogenesis of the offset, being the founder of the symmetry septum (Pl. 42, figs. 2-4, 7-8).

The instability in the development of the inner part of the symmetry septum, its reduction to a thin strip (Pl. 42, figs. 4, 6) and an almost total disappearance for a short period of growth (Pl. 42, fig. 5), when it is manifested only as a small knob on the neotheca, may suggest an increase in septa at the neotheca directed inwards from the periphery. The close analysis of the early growth (Pl. 42, figs. 2-4, middle) allows rejection of such a suggestion. Permanent position of the left fork of the parent's middle major septum at the neotheca may serve as a key point. It was continuous and reached the atavotheca at the very beginning of the hystero-ontogeny (Pl. 42, 1-2, middle), being reduced to a thick knob (Pl. 42, figs. 3-4), but occupies the same position irrespective

of changes of the symmetry of the septum. This first septum of the inner left offset's quadrant may be temporarily elongated so as to meet the inner margin of the peripheral part of the symmetry septum (Pl. 42, fig. 5). Thus, the septum that was inserted at the neotheca to the left of that constant offset's septum and was connected to it with its inner margin (Pl. 42, fig. 4, left corner) must be considered the second septum of the quadrant of septa mentioned.

The constitution of the remaining part of this quadrant of septa is peculiar in the sense that the partition-kind neotheca is indistinguishable from a septum and seems to be its substitution for some part of growth (Pl. 42, figs. 5-7, thick peripheral body left of the second inserted septum). A true nature of that body is documented when two last sections illustrated are compared (Pl. 42, figs. 7-8, left); there remain only two septa inserted one by one in the quadrant discussed (Pl. 42, figs. 4-5, 7), whereas that thickened body disappeared.

One more question concerning the inner left quadrant should be clarified. The parent's part of the left fork of the parent's major septum was undoubtedly transmitted into the parent's minor-like septum. Its permanent position between the middle and left parent's major septa proved that well (Pl. 42, figs. 3-8, middle left). The undoubtedly major septum role of the offset's part of the left fork of the parent's middle major septum at the beginning of the hystero-ontogeny was documented above. The role of this septum in the further offset's growth remains uncertain because the series of peels started from that level and was continued down to the earliest stage. The position of that septum opposite the parent's minor-like septum and the length reduced by comparison to adjacent septa (Pl. 42, figs. 6-8) may suggest its transformation into the minor-like septum.

The right fork of the middle parent's major septum, extended to the atavotheca and constituted of the symmetry septum of the offset, is comparable to the rugose coral axial septum in the sense that it crossed the entire offset's calice at the earliest growth stage (Pl. 42, figs. 1-3). The isolated position of this septum is well accentuated by positions of remaining septa (Pl. 42, figs. 3-8). Its asymmetrical growth resulted in the underdevelopment of the left inner quadrant early in the hystero-ontogeny (Pl. 42, figs. 3-5). Also, the inner part of that septum was reduced to a form of knob, as mentioned above. The permanent position of the peripheral fragment and the redevelopment of the inner fragment in a close connection to the parent's middle major septum prove the symmetry septum status of those two fragments (Pl. 42, figs. 6-8).

Septa of the left peripheral quadrant were inserted early in septogenesis with connection to the left fork of the parent's middle major septum (Pl. 42, figs. 1-3). It is uncertain whether the thin septum attached obliquely to that fork (Pl. 42, figs. 1-2, middle left) was the elongated minor-like septum or split from that fork. However, irrespective of its origin, this was the permanent atavoseptum attached to the atavotheca. The next septum in the quadrant discussed appeared close to the atavotheca (Pl. 42, fig. 3, left), but it was rearranged to constitute the marginal septum of the left peripheral quadrant. This septum may join inner margins of septa of the inner left quadrant to build a temporary heterocoralloid arrangement (Pl. 42, figs. 5-8). Nevertheless, an increase in septa peripheral-wards is undoubted in both left quadrants.

Development of the partition, temporarily incorporating thickened and strongly curved parts of the parent's right major septum, made a sequence in increase of septa in the right inner quadrant doubtful. At the beginning of the blastogeny the major septum discussed curved strongly with its peripheral part towards the offset and was supplemented with a thin septum at the offset's side (Pl. 42, figs. 1-2). This thin septum may either be a peripheral fork of the major septum or, more probably, the minor-like septum. It disappeared from the offset soon after (Pl. 42, fig. 4). The parent's right major septum played a double role in further development; it joined the atavotheca to form the marginal fragment of the partition and reached the adjacent parent's septum with its inner, thickened part, curved strongly rightwards (Pl. 42, fig. 3, right). It is uncertain whether the fragment of the right major septum, included previously in the partition, either became transformed into the thick septum spanned between the neotheca and the atavotheca (Pl. 42, fig. 4, middle right) or it disappeared from the atavotheca. Considering the first option more probable, two septa were derived from that long, thick septum by its middle thinning or a temporary disconnection; one at the atavo- and one at the neotheca (Pl. 42, figs. 5-6). The periaxial connection of those septa in further growth (Pl. 42, figs. 5-8) suggests their recognition as the second generation septa in the calyxcoralloid sense, whereas subsequent septa, inserted towards the right corner of the offset, would have appeared inside the frame of those two forks in the next generation. Such an explanation does not contradict the calyxcoralloid pattern because it has happened in the Heterocorallia.

Septa in the right peripheral quadrant were inserted one by one starting from the symmetry septum to the right (Pl. 42, figs. 2-7) with the first septum appearing very early in the blastogeny and without an obvious connection to any earlier existing septum (Pl. 42, figs. 2-3, middle right). All three septa inserted in that quadrant during the growth studied (Pl. 42, figs. 4-8) are perhaps major septa.

To sum up the above description, the following main characteristics of this type of the blastogeny are:—

The beginning of the offsetting closely resembles that in the corallite exposing Heterocorallia-like pattern of septa. This is best accentuated by elongation of first septa from the atavotheca to the neotheca.

In further growth the inner margins of major septa did not form a complete heterocoralloid pattern, but connections of inner margins of several septa commonly occur next to the free axial area.

Except for the earliest growth stage, the symmetry septum is divided into the inner and outer fragment with the former being temporarily reduced in length. This did not preclude an increase of septa in most quadrants towards their periphery.

A different direction established in the inner right quadrant is non-rugosan, but can be compared to the Heterocorallia. It should be considered calyxcoralloid.

3. *The extreme reduction of the Heterocorallia-like arrangement of major septa* (Pls. 43-45) — The corallite described in this section was selected for two reasons.

To illustrate the irregularity in the insertion of the septa. Such an irregularity resulted from two factors; the development of the inner fragment of the symmetry septum of the offset from the right, but not the middle, parent's major septum and

from deformation of the offset during its early growth, caused by an adjacent corallite.

To describe the hystero-ontogeny of the corallite possessing its axial area empty from inner margins of major septa along the entire growth investigated, i.e., along *c.* 5 mm.

Individual groups of major septa in the offsetting corallite were only occasionally united by their inner margins in the dividocoralloid manner (e.g., Pl. 43, figs. 1, 4; Pl. 44, fig. 10). Major and minor septa in the offsetting sector underwent several modifications prior to the process of offsetting (Pl. 43, figs. 1-4). One major septum, i.e., the future parent's middle major septum in the offsetting area, and two minor septa adjacent to it on both sides became twisted, making their identification impossible (Pl. 43, fig. 2). Thus, it may only be presumed by comparison to the earlier growth (Pl. 43, fig. 1) that three major septa and two intervening minor-like septa were involved in the hystero-ontogeny.

Further growth (Pl. 43, figs. 3-4) exposed another peculiarity of the offsetting discussed; the parent's middle major septum was reduced from the periphery in two steps, documented by its short and thin strips attached to the external wall first (Pl. 43, fig. 3, lower middle), and to the dissepiment subsequently (Pl. 43, fig. 4). Two thickened septa at the periphery of the future offset are parent minor-like septa. This is documented by adjacent, obviously major septa. The right of those minor-like septa became united with the inner fragment of the parent's middle major septum and the left one remains free (Pl. 43, fig. 4, lower). Such an arrangement closely resembles a peripheral split, but cannot be equated with that phenomenon. Thus, the beginning of the hystero-ontogeny is in this case different from that in the earlier described two examples.

A temporary reduction of peripheral fragments of middle parent's septa involved in the blastogeny (Pl. 43, fig. 5) constituted the next important difference of the offsetting now under discussion. This peripherally aseptal period of growth lasted for only 0.2 mm and was compensated by morphological changes in the common parent/offset area, but its occurrence is important for two reasons; all septa at the atavotheca should be considered neosepta despite their origin and the thickened minor-like septa present in the preceded growth may have been deleted. Thus, two thick forks that appeared in the common parent/offset area may have originated by a split from the parent's middle major septum (Pl. 43, fig. 5, middle). A fairly constant position of those forks, lasting for at least 0.7 mm of the offset's growth (Pl. 43, figs. 5-8; Pl. 44, figs. 9-10), their direct connection to the parent's middle major septum and similar forking of remaining two parent's major septa involved in the hystero-ontogeny support such a thesis. One of those forks initiated perhaps a neoseptum in the offset's side of the partition (Pl. 44, fig. 9, middle left). Minor-like septa were absent from the partition neotheca of the parent's side in this and a slightly higher level (Pl. 44, figs. 12-14).

From three septa inserted at the atavotheca at the end of the aseptal stage (Pl. 43, fig. 6), only the middle one intersected the offset's lumen and is considered the outer fragment of the symmetry septum (Pl. 43, fig. 6, middle). This short lasting morphology resembles the comparative growth stages of the other two offsets, described above in detail although the remaining two septa at the atavotheca are short. Both of them point towards the left and right parent's major septa and most probably correspond to those septa. The aseptal stage preceding an appearance of those three offsets' first septa precluded their identification as atavosepta.

The insertion of neosepta differs considerably in the future offset's quadrants, being simplest between three first offset's major septa at the atavotheca. Two lateral septa border both peripheral quadrants divided by the peripheral fragment of the symmetry septum. The first major neoseptum was inserted right of the symmetry septum (Pl. 44, figs. 12-13) and is followed by the insertion of two minor-like septa both sides (Pl. 44, figs. 13-15). Such an increase may suggest the rugosan pattern according to Weyer (1972) with the last septum inserted being the major septum.

The quadrant on the opposite side of the symmetry septum lacks septa for a period of growth slightly longer than that described above. Also, its bordering septum may temporarily disappear (Pl. 44, fig. 9). Two septa were inserted contemporaneously in this quadrant, both connected by tabulae to the left bordering septum (Pl. 44, figs. 12-13). The length of these two major septa increased quickly and two minor-like septa were inserted between them. The minor-like septum next to the symmetry septum appeared with some delay (Pl. 44, figs. 14-15). None of major and minor-like septa described so far was inserted by peripheral split of a preceding septum.

Development of the right inner quadrant began with further modifications of the right parent's major septum that constituted a fragment of the partition in the earlier growth (Pl. 43, fig. 6, right). It became divided into two fragments; an inner, attached to the partition of the parent's side, and a thickened outer fragment (Pl. 43, fig. 7, right). The latter thins peripheral-wards and split (Pl. 43, figs. 7-8, right). A thick body that appeared right to that forking part was most probably a fragment of the partition (compare Pl. 44, figs. 9-13, right corner). Two thin forks of the parent's right septum were retained at the atavotheca as first septa inserted in the quadrant discussed, but the thickened part of that septum was temporarily isolated from them, and reduced first to the right fork of the parent's right major septum (Pl. 44, fig. 9, right) and to a part of the partition subsequently (Pl. 44, figs. 11-13). Only a very short-lasting elongation of that septum, intervening between the above two morphologies and its union with peripheral forks (Pl. 44, fig. 10, right), proves its permanent although suppressed occurrence.

The inner fragment of the symmetry septum remains variable in thickness, length and shape almost till the end of the blastogeny. It was attached to the partition (Pl. 44, figs. 4, 15; Pl. 45, figs. 16-18) until the dividing wall invaded the common parent/offset area. It was then attached to the right side of that wall (Pl. 45, figs. 19-20). The origin of the inner part of the symmetry septum from the right parent's major septum resulted in the asymmetry of quadrants; the right quadrants are more restricted in volume and there is one major septum more in the peripheral left quadrant (Pl. 45, figs. 20-21).

It is uncertain at first glance which septa eventually became the major septa in the inner right quadrant. Two septa inserted in that quadrant by a split of the peripheral part of the right parent's major septum (Pl. 43, figs. 7-8) played a role of the offset's major septa in the sense that the next two septa were inserted between them. First, one with a connection to the inner margin of the symmetry septum as its possible split (Pl. 44, fig. 10, right), the second as a split of the peripheral septum in the quadrant (Pl. 44, figs. 11-13, lower right). The latter septum split again to complete the total number of major and minor-like septa in the quadrant discussed (Pl. 44, fig. 14). The further growth of all those five septa suggests, however, that first septa, i.e., those derived as peripheral forks of the symmetry septum (Pl. 43, figs. 7-8), eventually became minor-like septa. The right one was adjacent to the inner fragment of the symmetry septum

and the left one bordered the quadrant after producing its adjacent right major septum by split (Pl. 44, figs. 14-15). Thus, all septa in the quadrant discussed were inserted by peripheral split in the area bordered by first septa derived from the symmetry septum and transformed into minor-like septa. Also, all those septa appeared in sequence from the symmetry septum outwards.

It is uncertain whether the first septum in the left inner quadrant was derived from the parent's middle or left major septum. A small knob that appeared first (Pl. 44, fig. 9, middle left) and some fragments of further growth (Pl. 44, figs. 13-15) suggest the second option. Thus, the middle parent's major septum may have not participated in the formation of the offset's septal apparatus, except for a possible insertion of a peripheral fragment of the symmetry septum. The second major neoseptum in the quadrant discussed was either derived from the left parent's major septum (Pl. 44, fig. 13) or formed at least its temporary elongation (Pl. 44, fig. 15). Like in the case of other septa derived from a parent's septa, its position differs from section to section (Pl. 44, figs. 13-15; Pl. 45, figs. 16-17), but it was eventually stabilized next to the left peripheral quadrant (Pl. 45, figs. 18-21), being divided from it by the minor-like septum that was inserted almost simultaneously (Pl. 44, fig. 13).

Summing up the hystero-ontogeny described above, the following characters should be emphasized:—

Preconditions mentioned at the beginning of this section resulted in leaving the offset's side of the neotheca almost empty from septa along most of the process (Pl. 43, figs. 7-8; Pl. 44, figs. 9-12).

Nearly all septa were inserted at the atavotheca and all should be considered neosepta because the short-lasting aseptal stage occurred early in the hystero-ontogeny.

Peripheral quadrants were bordered by two septa inserted first and contemporaneously with the peripheral part of the symmetry septum. An increase of septa within those frames was too fast to establish their sequence with adequate certainty, but their insertion towards the symmetry septum is possible.

An insertion of septa in the inner quadrants was in sequence towards septa bordering outer quadrants, i.e. outwards from the symmetry septum.

Changes in the notification of septa from minor-like to major and the insertion of major septa by peripheral split of minor-like septa or *vice versa* have a fundamental diagnostic value. It allows to question a distinction between septa in the traditional, rugosan manner, i.e., major and minor.

Most major septa of the offset were free from their beginning. This concerns those inserted by split as well as those that appeared independently. Only the rare elongation of them on surfaces of tabulae (Pl. 45, figs. 17, 19-20) may have resulted in temporary Heterocorallia-like connection of two or three of them.

The insertion of septa described is far from that considered classic for the Calyxcorallia. However, it does not follow the rugose corals pattern as summarized in the preceding paragraph. Thus, I consider it an extreme variant of the Calyxcoralloid pattern. It resulted from a shortening of major septa of the parent corallite, bias in the insertion of the inner fragment of the symmetry septum and deformation of the offset by the adjacent corallite. Corallites from the same colony offsetting in a conventional manner support that interpretation.

Summary — Despite substantial differences in details, the process of offsetting in *D. reticulatum* is fairly constant in its fundamental characters. Four-directional increase prevails. It varies in detail because some septa may have forked not in sequence, some delayed in forking or were inserted so quickly one after the other that the sequence cannot be established despite very close peeling (see also Fedorowski, 1991, 1993).

An increase in the number of septa commonly took place due to a peripheral split of earlier inserted septa. They may either be replaced by an insertion of some septa in a form of isolated bodies or a connection of those bodies with preceding septa was not established. Parallel to the advancement in reduction of the Heterocorallia-like pattern of major septa, the insertion by split may perhaps be partly replaced by an independent insertion of some septa, best accentuated in the third example of the hystero-ontogeny (Pls. 43-45). A classic Heterocorallia-like arrangement of septa was achieved by rare offsets and only when parent corallites exposed this character fairly constantly.

Although most of the shorter septa, called here the minor-like septa, were perhaps analogous in their function to minor septa in the Rugosa, they cannot be considered homologous to the latter. Most of them were inserted by a split of major septa, whereas some gave rise to the latter either by split or due to increasing their length and meeting the major septa. Such elongated minor-like septa either became included in the Heterocorallia-like pattern of remaining major septa or remained free, but became indistinguishable from the latter by length and position because new minor-like septa were inserted in their adjacent loculae.

Partitions appeared early in the hystero-ontogeny. Those structures did not isolate the parent's and offset's polyps (Pl. 40, figs. 4-5), but acted as supporting structures for septa in the common parent/offset area. Parent's septa were involved in formation of the partition with their thickened peripheral fragments constituting individual parts of that structure. Variability in function of peripheral parts of parent's major septa is considerable, as described in detail above.

Remarks — In the description of septa the nomenclature introduced by Fedorowski (1991) for Dividocorallia was not applied. A rugosan nomenclature was considered more proper because individual generations of septa are unrecognizable when a 'diphyphylloid' pattern occurs.

Diameters and number of septa in corallites vary slightly between individual Spanish colonies described by de Groot (1963) and Rodriguez (1984), being very similar within a given colony. In general, they are closely comparable in that character to the holotype colony. The same is true for an arrangement of major septa (e.g., Pl. 39, figs. 2a, b). The prevailing 'diphyphylloid' morphology in the colonies revised herein may point towards *D. intermedium* rather than *D. reticulatum*, whereas specimens illustrated by Rodriguez (1984, pl. 6, figs. 7-9) expose an opposite trend; major septa are axially united in almost all corallites. The holotype of *D. intermedium*, briefly revised for the purpose of the present paper, shows most corallites to be very short-septal and the Heterocorallia-like pattern to be rare and incomplete (e.g., Pl. 39, figs. 1a, b). Those characters made that colony much closer to the holotype of *D. diphyphyllodeum* (e.g., Pl. 38, figs. 1-3) than to *D. reticulatum*; I consider *D. reticulatum* and *D. intermedium* to be conspecific. A wide variability is shown by the holotype of *D. reticulatum*, but the number of corallites with the Heterocorallia-like pattern of septa prevails (Fomichev,

1953, pl. 29, fig. 9b; Pl. 39, figs. 2a-d herein). Thus, the variability exposed by both Donets Basin and Spanish specimens, overlapping greatly with each other, supports their synonymy.

Range — Perapertu Formation, limestones K8-L5; Upper Bashkirian-Lower Moscovian.

Occurrence — Donets Basin (Ukraine), Northern Palencia (Spain).

Genus *Arctocorallium* gen. nov.

e.p. 1963 *Lithostrotion* de Groot, p. 47 (*non* Fleming, 1828, p. 508).

e.p. 1989 *Petalaxis* Wu & Zhao, p. 131 (*non* Milne-Edwards & Haime, 1852, p. 204).

Type species — *Lithostrotion trimorphum* de Groot, 1963, p. 50. The only species known.

Derivation of name — Latin *artus* = dense, compact, *corallium* = a coral. Named after the cerioid growth form.

Diagnosis — Colony cerioid; offsetting lateral; Heterocorallia-like pattern of septa inconstant; microstructure of septa finely trabecular; dissepimentarium of interseptal and lonsdaleoid dissepiments; tabularium convex.

Remarks — Some Devonian cerioid and aphroid colonies expose a calyxcoralloid morphology and were included in the subclass Dividocorallia (Fedorowski, 2001). Berkowski (2002) restudied the Famennian *Scruttonia*, named *Sudetiphyllia* by Fedorowski (1991), and continued to identify it as a phillipsastraeoid rugosan. These Devonian genera are omitted from the following discussion, although I do not accept the position of Berkowski (2002).

Carboniferous cerioid colonies exposing a calyxcoralloid morphology are rare. They were either distinguished as separate taxa or assigned to existing genera and/or species. The first of them were two species introduced by Yu (1933) as *Prismatophyllum carbonicum* and *P. spongiophylloides* from the Viséan of South China. Both of them were inadequately studied and poorly illustrated. Jia *et al.* (1977) reprinted Yu's (1933) illustrations, transferred *P. spongiophylloides* to the genus *Aphrophyllum* Smith, 1920, and introduced a new species *A. tholusitabulatum* Xu and a new subspecies *A. naliokini luzhaiense* Kuang. A more or less obvious Heterocorallia-like pattern of septa seen in some corallites indicates that both of those species may be Calyxcorallia. The same is true for *Arachnastraea minor* Wu (Jia *et al.*, 1977, pl. 78, fig. 3). This thamnasterioid coral seems to exhibit a Heterocorallia-like pattern of septa and an absence of median lamella. *Aulina puerilis* Smith & Yu of Wu & Zhao (1974, p. 267, pl. 135, figs. 10-11) may form another example of a calyxcoral with thamnasterioid colony. Unfortunately, the existing illustrations and descriptions are insufficient to decide the calyxcoralloid affinity of all these species.

Yu's (1933) original illustrations of *Prismatophyllum carbonicum* were repeated by Wang (1978, pl. 39, figs. 2a, b) under the name *Donophyllum (Polygonaria) carbonica* and

were supplemented by a new oblique longitudinal section and a well oriented transverse section showing some mature and immature corallites that expose a simplified Heterocorallia-like pattern of major septa (Wang, 1978, pl. 39, figs. 1a, b). Wang's (1978) specimen resembles "*Prismatophyllum*" sp. listed by Yu (1937, p. 56) and illustrated by Smith & Yu (1943, p. 55, pl. 9, figs. 16-17). The latter authors pointed out its similarity to Chinese Carboniferous species of "*Prismatophyllum*" and questioned an identification of all those Carboniferous species as *Prismatophyllum* proper, i.e., a Devonian coral genus unrelated to those Carboniferous colonies.

An idealized drawing of the longitudinal section of "*Prismatophyllum*" sp. Yu, 1937 (Smith & Yu, 1943, pl. 9, fig. 16), apparently proving an occurrence of the aulos in that corallite, cannot be accepted as real. A comparison with the transverse section of the same colony and especially with the longitudinal section of "*P.*" *carbonicum* (Yu, 1933, pl. 14, fig. 2b) shows that the interpretation by Smith & Yu (1943, pl. 9, fig. 16) was false. The picture exhibits not an aulos, but axial parts of tabulae or tabellae, subhorizontally arranged and spanned between sections of inner margins of septa. Also, a further mistake cannot be excluded when comparing the drawing discussed to the middle part of Yu's (1933, pl. 14, fig. 2b) picture. The drawing may be either an idealized version of part of the photograph or exposes a striking similarity to it. Thus, an occurrence of an aulos in the Chinese Carboniferous "*Prismatophyllum*" is not accepted.

?*Thysanophyllum* sp. of Yu (1937, p. 51, fig. 6a, b) is another potential member of cerioid Calyxcorallia described by that author. A single corallite illustrated in the transverse section does not supply an adequate basis for discussion, except for pointing out that its septal pattern is Heterocorallia-like.

The colony of *Lithostrotion maccoyanum* Milne-Edwards & Haime illustrated by Smith & Yu (1943, pl. 8, fig. 3) from the "*Dibunophyllum* Zone," i.e., Asbian or Brigantian of Oswestry, Shropshire, England, exposes some resemblance to the Calyxcorallia and to *Arctocorallium* gen. nov. In the figure caption (*ibid.*, p. 59) those authors mention the columella as "much reduced and even absent." A reinvestigation of this colony, with special attention to the hystero-ontogeny, may prove its position within the Calyxcorallia.

Colonies distinguished by Pickett (1966) as a new Australian Viséan genus, *Aphrophyllloides*, and included by him in the family Lonsdaleiidae Chapman, 1893, exhibit some similarity to the Calyxcorallia in transverse and, especially, oblique longitudinal sections. The axial split observed in those sections cannot be conclusive, however, and a detailed study on the hystero-ontogeny and the microstructure of this genus is required before its relationship to Calyxcorallia is proven. The Australian Lower Carboniferous coral fauna was considered endemic (Hill, 1973). Its very distinct character, camouflaged by the use of European generic and family names, was emphasized by Fedorowski (1981, p. 121). However, some Euro-Asiatic genera, including *Heterophyllia*, that possess a special value in the context of this discussion, occur in Australia.

The genus *Aphrophyllloides* was considered (Lin *et al.*, 1995) to be a senior synonym of *Donophyllum* (*Polygonaria*) Fan, 1978. Such a position can neither be fully accepted nor rejected because of lack of basic data, the hystero-ontogeny in particular. Fan (1978) introduced three new species, with *Donophyllum* (*Polygonaria*) *regularis* as the type species of the subgenus. In none of the illustrations of that author (Fan, 1978, pl. 64, figs. 1-3) are early growth stages shown. Thus, a weak but easily recognizable Hetero-

corallia-like pattern of septa in transverse sections of those corals cannot be considered conclusive for their calyxcoralloid affinity.

The above discussion shows that two generic names are potentially available for cerioid Carboniferous corals exposing a Heterocorallia-like pattern of septa, *Aphrophylloides* and *Polygonaria*. Despite this and the rarity of the Spanish material, only a fragment of the colony being available, a new generic name was introduced for that specimen. Reasons for this were:—

An inadequate knowledge of most important diagnostic characters of existing genera. This will make my identification of the Spanish specimen suspicious whichever of those names is accepted.

My experience with accepting the poorly known genus *Stylostrotion*. The situation discussed above with remarks on *Donophyllum* are likely to be repeated in the case here under discussion.

A possibility to prove the calyxcoralloid offsetting in *A. trimorphum*. This character, valid for the type species of the new genus, could be questioned as such if "*Lithostrotion*" *trimorphum* is included in any of those two incompletely known genera. The taxonomic value of the blastogeny, established in *A. trimorphum*, cannot be overestimated for the distinction between the Rugosa and the Calyxcorallia.

Polygonaria may or may not be a junior synonym of *Aphrophylloides*. This problem, important in the context of an identification of the Spanish colony, cannot be solved on the basis of the existing data.

Taking all those reasons into account, I prefer to temporarily consider *Arctocorallium* gen. nov. a well studied potential synonym of a theoretically existing, but suspicious, genus than to include the Spanish specimen in any of the inadequately investigated and poorly known genera. Due to the uncertainties mentioned, the synonymy of *Arctocorallium* gen. nov. was limited to the type species and its potential synonym. Its taxonomic content was restricted to the type species, with the potential members indicated in the discussion above. Also, its morphological similarities, distinctions and suspected affinities to potentially related genera *Aphrophylloides* and *Polygonaria* were not discussed in detail.

The colony included by Wu & Zhao (1989) in *Petalaxis trimorphum* (de Groot) is morphologically so similar to the Spanish specimen that I decided to include it in the synonymy with *Arctocorallium* gen. nov., although I do not consider the Spanish and Chinese colonies conspecific. Nevertheless, an occurrence of such a specimen in China indirectly proves the potential of the specimens discussed above to truly belong in Dividocorallia.

***Arctocorallium trimorphum* (de Groot, 1963)**

Pls. 46-54.

1963 *Lithostrotion trimorphum* de Groot, p. 50, pl. 6, fig. 1.

Material — One fragment of a cerioid colony, RGM 112599, from which were prepared several thin sections and a series of 69 acetate peel impressions, exposing several offsetting corallites.

Diagnosis — *Arctocorallium* with 13-15 major septa and 3.5-5.0 mm corallite diameters; Heterocorallia-like pattern of septa, with commonly 3, rarely 4 generations of major septa, anastomosing with pseudoradial pattern; minor-like septa interrupted, commonly restricted to dissepimentarium that consists of 1-2 rows of interseptal and lonsdaleoid dissepiments.

Description — Colony cerioid. Mature corallites bordered by dividing walls that either zig-zag towards bases of septa (Pl. 46, fig. 4) or are almost straight. Despite diagenetic alterations, two-directional growth of crystals is recognizable in longitudinal sections made perpendicular to the thickness of walls (Pl. 46, fig. 6). Partitions, developed early in the hystero-ontogeny, remain incomplete until the insertion and development of *c.* 10-12 major septa. A process of transformation of partitions into dividing walls was not established in detail (see hystero-ontogeny, below).

The Heterocorallia-like pattern of major septal insertion is inconstant, and varies both between corallites and in the course of growth of particular individuals. In order to prove this, more than 20 corallites were studied along 7.5 mm growth of the colony with acetate peel impressions taken from 69 ground and polished surfaces. Two corallites, one possessing a well-developed lonsdaleoid dissepimentarium (Pl. 48, figs. 1-8) and the other almost lacking that character (Pl. 47, figs. 1-12), were illustrated as their most distinct variants.

Investigation of corallite II began where its Heterocorallia-like pattern is obvious although the oblique septum is suspected rather than recognized (Pl. 48, fig. 1). Quadrants are unequal and fossae are absent, but four septa of the first generation are easily recognizable near the corallite axis (Pl. 48, figs. 1, 5). The upper quadrant is best developed and consists of four generations of recognizable septa. The left quadrant, consisting of three generations of septa, is also regular, but the arrangement of major septa in the two remaining quadrants is camouflaged by the disconnection of the inner margins of some septa.

Comparison of the pattern described above to those of the next four pictures, distant from each other by 0.7 to 2.2 mm (Pl. 48, figs. 2-5), indicates a high variability in mutual relationships of individual major septa and, consequently, in the recognition of individual generations. Septa of the first generation remain recognizable in all those pictures, but others either became temporarily free axially or unite with the inner margins of their neighbouring septa. Such freedom in the connection of inner margins of major septa makes the content of individual quadrants inconstant and differentiated, depending on counterparts of the second generation major septa. In some cases (Pl. 48, fig. 4) a bilateral symmetry appears due to the domination of two first generation major septa that form an almost straight line. Such a pattern of septa is better demonstrated in corallite I (e.g., Pl. 47, figs. 1, 4).

Three last pictures of the series of the corallite I (Pl. 48, figs. 6-8) were selected to illustrate both the pseudoradial pattern of septa and changes in that pattern depend on the section; just beneath (Pl. 48, figs. 6, 8) versus just above the surface of a tabula (Pl. 48, fig. 7). In the first case most major septa of the first two to three generations became free. Oblique, i.e., artificially widened and thickened sections of the tabula connect inner margins of several septa (Pl. 48, figs. 6, 8). Septa of some generations are recognizable in individual sections, whereas others are not. Also, comparison of the

individual pictures (Pl. 48, figs. 1-8) demonstrates an inconstant character of the lonsdaleoid dissepimentarium that prevails in rare sections (e.g., Pl. 48, fig. 4), occurs in several (Pl. 48, figs. 1-6) and is almost absent from others (Pl. 48, fig. 8).

The corallite I (Pl. 47, figs. 1-12) demonstrated the following patterns of major septa; the Heterocorallia-like pattern (Pl. 47, figs. 3, 10-11), the pseudoradial pattern (Pl. 47, fig. 5, 12), the bilateral pattern emphasized by a formation of a kind of an "axial septum" (Pl. 47, figs. 1-2, 4) and an "axial structure" (Pl. 47, figs. 6-9). Comparisons of septal patterns demonstrated in individual pictures plotted against distances in growth of the corallite have shown that some morphological changes may be rather quick. The Heterocorallia-like pattern (Pl. 47, fig. 3) was replaced by the bilateral one (Pl. 47, fig. 4) within 0.7 mm and was followed by the pseudoradial one (Pl. 47, fig. 5) within the next 1.7 mm of growth. In the case of morphology just beneath and just above a tabula, c. 0.3 mm of corallite growth was enough to change from a "diphys-trotonid" morphology with an open axial area to the appearance of an "axial structure" (Pl. 47, figs. 5-6). In contrast to corallite II and despite a very large morphological variation in the septal pattern, corallite I remains almost constant in size and with an underdevelopment of lonsdaleoid dissepiments.

By studying all corallites in individual peels along 7.5 mm growth of the colony, it was possible to recognize a given pattern of major septa that may prevail in the course of growth of particular corallites, an irregular Heterocorallia-like and pseudoradial pattern prevails among all corallites studied, and, in some transverse sections, a given pattern is more common than the other listed above. Patterns of major septa resulted most probably from the commonly flat tabulae (Pl. 46, fig. 2) and from two main characters of those septa; an amplexoid nature and an advanced reduction of the oblique septum. An amplexoid character of major septa resulted in formation of a pseudoradial pattern of axially free major septa sectioned below tabulae (Pl. 47, figs. 2, 5, 12; Pl. 48, figs. 6, 8). The regular "axial structure" is seen in sections made just above tabulae (Pl. 47, figs. 6, 8) whereas disconnected "septal lamellae" (Pl. 47, figs. 7, 9) or irregular "axial structure" (Pl. 48, fig. 7) appeared in sections partly above, partly beneath tabulae. The bilateral symmetry (e.g., Pl. 47, fig. 4) and a cross of four major septa of the first generation occurring occasionally in a corallite axis (Pl. 48, fig. 5) resulted from the reduction of the oblique septum.

A bilateral symmetry (Pl. 47, fig. 4) occurs when only two septa of first generation, i.e., the symmetry septum, dominate whereas an oblique septum is totally reduced. Two other septa of the first generation may be reduced in length, being temporarily unrecognizable from those of remaining generations. A cross of major septa (Pl. 48, fig. 5) appears when septa of the first generation are equal in length, meet at the corallite axis and the symmetry septum is temporarily unrecognizable. A typical Heterocorallia-like pattern is recognizable only when a rudiment of an oblique septum is long enough to obviously separate four major septa of the first generation and expose their split. In corallites studied in detail such a classic arrangement did not appear, but some are similar (Pl. 47, fig. 3; Pl. 48, fig. 1). Three generations were recognized in most sections exposing the Heterocorallia-like pattern, but perhaps no more than four generations occur.

Minor-like septa vary greatly in their development, but occur in almost all loculae of mature corallites. Continuous minor-like septa, penetrating the tabularium, were

recognized in very rare instances as temporary structures present for less than 1 mm growth of a corallite and in number not exceeding 2-4 septa in a given mature corallite. In most corallites they form only short strips on a dividing wall (Pl. 47, figs. 1-12; Pl. 48, figs. 1-8). Some minor-like septa are hardly recognizable or marked only as protrusions of a wall. Short strips of minor-like septa may also be recognized on dissepiments (Pl. 47, fig. 9, lower; Pl. 48, figs. 2-3, left). An insertion of minor-like septa is described below with the hystero-ontogeny.

The microstructure of septa is trabecular, but length, width and shape of individual trabeculae were not established. The only longitudinal section exposing the microstructure cuts peripheral part of the septum as documented by shades of dissepiments (Pl. 46, fig. 5). Nevertheless, the darker bodies intersecting few growth lamellae cannot be anything else but trabeculae.

The dissepimentarium occupies one third to one quarter of the corallite radius and consists mostly of interseptal dissepiments arranged in the pseudo-herringbone pattern of 3-6 anastomosing dissepiments. Small, globose, lonsdaleoid dissepiments vary in number from none to few in individual sections. They most commonly interrupt one, or rarely two, major septa near the dividing wall. A complete ring of lonsdaleoid dissepiments has not been observed. Also, their occurrence changes in the course of growth of individual sections of corallites (Pl. 47, figs. 1-12; Pl. 48, figs. 1-8). One, two or rarely three rows of slightly convex dissepiments, arranged in almost vertical rows, were observed in longitudinal sections (Pl. 46, fig. 2).

Morphology of the tabularium varies slightly depending on the pattern of major septa. In fragments corresponding to the pseudoradial pattern, tabulae are almost flat and complete or the tabularium consists of long, flat, anastomosing tabellae. The axial part of the tabularium is slightly convex, flat or sagging (Pl. 46, fig. 2, lower and middle). In fragments corresponding to axially united major septa the tabularium became more convex, consisting of obliquely inclined tabulae and anastomosing tabellae, some of which may be bulbous in the corallite axis (Pl. 46, fig. 2, upper). These may correspond to the "axial structures."

Hystero-ontogeny — Three series of closely spaced acetate peel impressions were described and illustrated in detail, and few other series were studied in detail for comparison. Main characters distinguished in those three examples of offsetting are separately described below in order to expose the principal variants established within a single colony. The process of offsetting invariably began with a strong thickening of peripheral parts of some major and minor-like septa (Pl. 49, figs. 1-2; Pl. 51, figs. 1-2; Pl. 52, fig. 1). Those septa were either continuous or interrupted by lonsdaleoid dissepiments prior to becoming involved in the process of offsetting. All septa involved in the offsetting, irrespective of their earlier morphology, became attached to a parent's corallite wall at the beginning of the hystero-ontogeny.

A division of the thickened parts of parent's septa into peripheral and inner segments, i.e., formation of the offset's tabularium, differs slightly in details, but it generally is a step-by-step process involving particular septa one by one, with the middle major septum of the thickened parent's septa being divided first (Pl. 49, fig. 3; Pl. 51, figs. 3-4; Pl. 52, fig. 2). Peripheral segments of divided septa, i.e., atavosepta of an offset, thin quickly, whereas the inner segments remain thick. The latter constituted

the main skeletal supporting structures in the common parent/offset area, being in this respect closely comparable to septal pinnacles in the Rugosa, reconstructed by Fedorowski & Jull (1976, text-fig. 1). Also, they are important constituents of a partition (Pl. 49, figs. 4-8; Pl. 50, figs. 9-12; Pl. 51, figs. 4-9; Pl. 52, figs. 10-15; Pl. 53, figs. 6-12; Pl. 54, figs. 13-15). In two offsets investigated, these inner segments became united with their adjacent septa (Pl. 51, fig. 3; Pl. 52, figs. 3-4) making an impression of a split of the latter towards the parent corallite. The attached septa began the partition in both instances observed, but one of them (Pl. 53, figs. 5-6) split towards the offset, leaving one fork as a part of the partition and forming the first neoseptum of an offset.

In an early stage of offsetting the number of septa at the atavotheca of an offset corresponds in most instances to the number of inner thickened segments of parent's septa. Thus, all such corresponding septa are considered atavosepta. Such a direct relationship is well demonstrated in the early growth of the corallite "A" (Pl. 49, figs. 3-4, 6-7), but in few instances an insertion of a given septum in an offset is uncertain. In the corallite "B" (Pl. 51, figs. 2-4, left) one septum in the offset seems to represent an additional septum formed in the offsetting area of the parent corallite and inherited by the offset. This ephemeral septum points towards its former left neighbour septum during 0.1 mm growth (Pl. 51, fig. 5, left) and to its right neighbour afterwards (Pl. 51, figs. 6-9; Pl. 52, figs. 10-12). Such an inconstant position of a septum is not unique and not restricted to the septum in question. It was mentioned here to illustrate a situation when the insertion of new septa and/or their connection to the existing ones is uncertain.

The inconstant position of some major septa and the amplexoid character of all of them make it almost impossible to recognise generations of septa in the blastogeny of the Calyxcorallia, postulated by Fedorowski (1991) on the basis of Heterocorallia. It is possible, however, to establish the sequence in the insertion of septa, crucial for understanding and accepting the difference between the Rugosa and the Calyxcorallia. In offsets of the species discussed, the symmetry septum is almost invariably constituted from two segments. It was formed from one of the earliest atavosepta at the atavotheca and from the first neoseptum inserted at the neotheca opposite to the former.

Corallite "A" — The earliest stages of the hystero-ontogeny, i.e., the thickening of peripheral parts of four septa, documented an incorporation of two minor-like septa in that process. Also, it shows how the left minor-like septum, separated from the wall by lonsdaleoid dissepiments, became attached back to it (Pl. 49, figs. 1-2). Almost simultaneously with the process of attachment of the left minor-like septum, the middle parent's major septum and soon after the left minor-like septum divided to form an initial offset's calice (Pl. 49, figs. 3-4). These inherited peripheral segments of two parent's septa, i.e., first two atavosepta of the offset, are permanent and constant in their positions at the atavotheca as additionally documented by comparison of their position against the wall of two adjacent corallites (Pl. 49, figs. 4, 6-9, lower). Sections of tabulae (Pl. 49, fig. 5, middle) may disturb that clear picture in some peels. The data mentioned allowed it to be established that not the peripheral segment of the major septum, but that of the left minor-like septum, became the peripheral segment of the symmetry septum (Pl. 49, figs. 7-8; Pl. 50, figs. 9-16).

There appeared some ephemeral structures in the early hystero-ontogeny that camouflage the true sequence in the insertion of septa and/or recognition of some septa as major or minor-like. These are:—

The short strip, septal in the microstructure, that was inserted at the base of the right thickened minor septum (Pl. 49, fig. 1, right) and persisted in that position for *c.* 0.5 mm of a corallite growth (Pl. 49, figs. 2-4, right).

Sections of tabulae imitating the Heterocorallia-like pattern of septa (Pl. 49, figs. 5-6).

Sections of tabulae imitating ephemeral septa at the atavotheca (Pl. 49, fig. 5).

The variable status of the right thickened major septum in the offsetting area and the thickened minor-like septum to its left require special attention. The long septum attached to large lonsdaleoid dissepiment is the major septum. This is proven by the position of its short strip left at the corallite wall inside the dissepiment (Pl. 49, fig. 1, right). Thus, the thickened septum to the left to it must be the minor-like septum. However, the innermost part of the major septum discussed was shifted step-by-step leftwards (Pl. 49, figs. 2-7, right) up to a position opposite the parent's segment of the former right minor-like septum (Pl. 49, fig. 8, right) and eventually becoming united with it (Pl. 50, figs. 9-14, right). Thus, the septum that appeared in the right peripheral quadrant of the offset's septa as a peripheral strip of that former minor-like septum (Pl. 49, figs. 5-8) may be considered as derived either from the major or from the minor-like parent's septum. Appearances described in this paragraph were considered important to mention because they document an inconstant status of major and minor-like septa, and their potential to replace one another, a character common for the Heterocorallia and the Calyxcorallia, but unknown in the Rugosa.

The right peripheral quadrant of major septa in the offset "A" was constituted early in the blastogeny, together with the insertion of the third septum derived from the peripheral part of the right parent's minor-like septum (Pl. 49, figs. 5-7, right). Thus, both major septa in this quadrant were the atavosepta, but one of them originated from the parent's major septum and the second one from the parent's minor-like septum. The insertion of minor-like septa in this quadrant was delayed (Pl. 50, figs. 9-12). They were most probably inserted simultaneously and by a peripheral split of two major septa bordering the quadrant, i.e., the symmetry septum by its rightwards split and by the last inserted major septum leftwards (Pl. 50, fig. 13). Such an interpretation, although most likely, was not confirmed by the microstructure and available peels. Thus, an optional interpretation, i.e., an insertion of the minor-like septa in a form of independent knobs on the offset's wall, cannot be rejected. Although preferring the first option, especially in the case of the right minor-like septum which appeared as a strong body connected obliquely to its suspected parental septum (Pl. 50, figs. 13-14, right), I cannot reject the second, supported by a further independent position of minor-like septal knobs (Pl. 50, figs. 15-16, right).

An insertion of septa in the remaining quadrants is less obvious. A short thick strip, attached to the atavotheca and derived from the left parent's major septum (Pl. 49, fig. 6, left), was ephemeral and disappeared from the offset within a further 0.3 mm corallite growth, i.e., on the level when the left parent's major septum reached the atavotheca again (Pl. 49, fig. 7) to form a fragment of the partition. Few tabulae were attached to the atavotheca in the future left peripheral quadrant, but it was aseptal for *c.* 0.8 mm growth (Pl. 49, figs. 7-8). Two major septa of that quadrant appeared in sequence from the symmetry septum to the left (Pl. 50, fig. 9). Their insertion was so quick one after the other that it looks almost simultaneous. Also, they appeared without

an obvious connection to any preceding septa, and are interpreted as inserted independently and not by a peripheral split. The insertion of minor-like septa was delayed for almost 3 mm growth (Pl. 50, figs. 9-14). The first appeared next to the symmetry septum and independent from major septa (Pl. 50, figs. 15-16). All septa in this quadrant, major and minor-like, are neosepta.

The insertion of septa in the inner quadrants was rapid with some acceleration in the left quadrant. Two septa were inserted at the neotheca first; the inner segment of the symmetry septum in the middle and first septum of the left inner quadrant (Pl. 49, fig. 8, middle left). Inner margins of those first major septa were either united or, more probably, connected by a section of a tabula. Both of them derived from thickened margins of parent's major septa, included in the partition; the symmetry septum from the parent's middle major septum and the other offset's major septum from the right fork of the left parent's major septum. The left fork of that major septum gave rise to the second offset's major septum in that quadrant (Pl. 50, fig. 9). Its third and last major septum derived most probably from the parent's minor-like septum, attached to the peripheral left part of the neotheca (Pl. 50, figs. 9-11). This septum was afterwards transmitted onto the atavotheca (Pl. 50, figs. 11-13). All major septa in this quadrant were inserted by derivation from the parent's major septa and should be considered the atavosepta. Minor-like septa, like those in the preceding quadrant, were inserted independently, in a form of knobs on the neotheca, beginning with the loculum next to the inner segment of the symmetry septum (Pl. 50, figs. 12-16). Thus, they are neosepta.

Insertion of major septa in the right inner quadrant was directly connected to the right parent's major septum, transformed from its right minor-like septum (see above). The first septum in that quadrant derived from the left fork of the parent's right major septum (Pl. 50, fig. 9, right). The insertion of the next two is difficult to recognize. Left of them was obviously connected to the right fork of the right parent's major septum (Pl. 50, figs. 10-12, upper right), but the right and last septum in the quadrant may have been transformed from the peripheral right part of the partition (Pl. 50, figs. 10-12, right). Whatever the interpretation would be those two septa are either united with their inner margins from the very beginning (Pl. 50, fig. 10) or were united soon after and lasted in such a union for at least 2 mm of growth (Pl. 50, figs. 11-14). At least two first major septa in this quadrant are atavosepta. Minor-like septa were inserted in the same way as in the preceding quadrant.

Summing up this part of the description, it is right to point out that an insertion of septa occurred in four directions. Thus, septa that were inserted last in individual quadrants occur together in pairs. Most major septa of the offset are atavosepta, but few are neosepta. All minor-like septa are neosepta. Most or perhaps all of them were inserted independently from preceding septa. Their appearance both sides of both parts of the symmetry septum first (Pl. 50, figs. 13-16), and step by step appearance in the following loculae left and right of the former, forms the next proof for the two-directional insertion of septa in the specimens discussed.

The axial and inner part of the offset was perhaps altered diagenetically. Thus, shortening of its septa early in the blastogeny may be apparent. An outline of periaxial sections of tabulae (Pl. 49, figs. 6-8; Pl. 50, figs. 9-11) bordering large areas empty from the coral skeleton, but occupied by very large calcite crystals, a step-by-step disap-

pearance of that empty area in the course of grinding and a sudden elongation of both segments of the symmetry septum (Pl. 50, fig. 12) up to their union (Pl. 50, fig. 13), makes such an option likely. The heterocoralloid pattern best seen in the last section cited, taken just above the surface of an axial tabula, disappeared and reappeared in further growth (Pl. 50, figs. 14-16) depending on the orientation of the given section against the tabula, i.e., in a way characteristic for the amplexoid septa.

The reconstruction of the parent's septal apparatus was in part described above when shifting of the inner segment of the right parent's major septum and its union with the inner margin of the minor-like septum was mentioned. The left parent's major septum underwent a less dramatic transformation. Its middle, thickened segment (Pl. 49, fig. 8) pointed towards and eventually became united with its innermost part and attached to the dividing wall (Pl. 50, figs. 9-16, upper left). Minor-like septa on the parent's side of that wall appeared after some delay and most probably independently (Pl. 50, figs. 13-16, upper).

Corallite B (Pl. 51, figs. 1-9; Pl. 52, figs. 10-15) — This corallite exemplifies a short-septal kind of an offset and some peculiarities in the increase in septa. The most important of the latter are unique insertion of the offset's septa in the left peripheral quadrant (see below) and transformation of two parent's septa near the common parent/offset area at the right corner of the future offset (Pl. 51, figs. 1-2, lower right).

The parent's major septum, bordering the offsetting area from the right, splits peripherally to form the minor-like septum to its right (Pl. 51, fig. 1, right). The minor-like septum status of that fork is best documented in the next section (Pl. 51, fig. 2, right). It shows the continuous parent major septum composed of the left thickened fork and the thin, long inner blade. The thickened right fork, free in this picture, is bordered by the parent major septum rightwards. Thus, its minor-like septum position is the only one possible. The next section (Pl. 51, fig. 3) exhibits reunion of two forks discussed that continued for *c.* 0.7 mm of growth (Pl. 51, figs. 2-7). The status of those forks changed, however. The right fork, short at the beginning and occupying the minor-like septum position, became elongated and united with the thin, innermost segment of the parent's major septum to constitute its continuous major septum, whereas the originally long left fork, i.e., the parent's major septum, became step-by-step shortened to eventually become the parent's minor-like septum (Pl. 51, figs. 7-9; Pl. 52, figs. 10-15).

The second transformation concerns the thickened parent septum to the left of the formerly discussed septum (Pl. 51, figs. 1-2, middle right). It was the major septum prior to the beginning of the offsetting (not illustrated), but its peripheral part became thickened and separated from the thin innermost part. A remnant of that inner part was attached to the section of the tabula (Pl. 51, figs. 1-3, middle). Shortening of this septum and the neighbourhood of the major septum to the right suggests its minor-like septum status for some period of the offsetting (Pl. 51, figs. 1-4). However, the thin inner part of the parent major septum, previously attached to the tabula, was shifted to the right (Pl. 51, figs. 4-6, middle), up to becoming united back to the apparent minor-like septum in question (Pl. 51, fig. 7), that again became the parent middle major septum in the offsetting area (Pl. 52, figs. 10-15).

The apparently minor-like and truly the parent middle major septum disintegrated

first, starting the process of formation of the offset's calice (Pl. 51, fig. 3). Its peripheral segment remained long early in the hystero-ontogeny and played the role of the peripheral part of the symmetry septum (Pl. 51, figs. 4-7). The length of that part varied greatly in further growth. It was very long at the beginning (Pl. 51, figs. 3-7) and rapidly shortened afterwards when becoming integrated with a tabula (Pl. 51, figs. 8-9; Pl. 52, figs. 10-12, peripheral right corner). Its strip extended slightly from the atavotheca to the tabula below the latter (Pl. 51, fig. 9; Pl. 52, figs. 10-11) and elongated along its surface or just above it (Pl. 52, figs. 12, 13, respectively). The peripheral segment of the symmetry septum was afterwards equalized in length to remaining offset's major septa (Pl. 52, fig. 15).

Composition of the left peripheral quadrant, mentioned above as the peculiarity of the offset "B," began with the septum that either derived from the left parent's minor septum or was inserted independently. A large part of the attachment of that strip to the atavotheca, by comparison with the earlier attachment of the parent septum (Pl. 51, figs. 2-3, lower left), supports the second option, whereas an inconstant position of that parent septum (Pl. 51, figs. 1-2) and the parent/offset symmetry, favours the first option, accepted herein. Irrespective of the interpretation, this was the second septum inserted at the offset's atavotheca and first septum in its left peripheral quadrant (Pl. 51, figs. 2-3, left). The second septum was inserted by splitting of the parent's major septum at the very left periphery of the offset (Pl. 51, fig. 1, left). This septum remained as a thin strip or protuberance of the atavotheca (Pl. 51, figs. 2-3, left, respectively) until the separation of the parent thickened septum from the atavotheca (Pl. 51, figs. 4-5, left). Its position as the second septum in the left quadrant was fixed since. It is uncertain whether or not the third major septum in the quadrant discussed derived from peripheral part of the left parent's major septum as suggested by short, inconstant strips at the atavotheca (Pl. 51, figs. 6-9; Pl. 52, figs. 10-13, left) or independently. The second option, less well supported, is not accepted. The insertion of minor-like septa in this, as well as in the remaining, quadrants was delayed and they most probably were inserted in a form of independent protrusions of the offset's walls (Pl. 52, figs. 13-15).

Insertion of septa in the peripheral right quadrant was similar to that in the left quadrant in the sense that its second septum was inserted by a split of the parent septum before being incorporated in the offset (Pl. 51, fig. 4, right). Also, it may only be suspected that the first major septum in that quadrant was inserted independently and slightly prior to or simultaneously with the separation from the atavotheca of the parent forking septum (Pl. 51, fig. 5, middle and right). The length of these two offset major septa varies, but their positions remain constant (Pl. 51, figs. 7-9; Pl. 52, figs. 10-15).

Despite the short strip being temporarily present at the left side of the neotheca (Pl. 51, fig. 2), only the insertion of two constant neosepta in its middle part (Pl. 51, fig. 7) was considered to be the beginning of the septogenesis at that part of the offset. Both those septa were derived from widely opened forks of the parent middle major septum that were earlier involved in the partition (Pl. 51, figs. 5-6). The loop-like structure attached to the middle part of the partition (Pl. 51, figs. 5-6) was a sectioned tabula. The insertion of the next septa at the neotheca was quick, when they appeared left and right of the inner part of the symmetry septum and towards the periphery (Pl. 52, figs. 10-15).

The Heterocorallia-like arrangement of septa was not observed in the part of the

offset investigated although inner margins of some septa were temporarily united. The ontogenetically more advanced part of that offset was destroyed and the study could not have been continued. It may only be pointed out that an arrangement of septa in its parent corallite is Heterocorallia-like.

Both corallites (A and B) documented the so-called wandering of septa, i.e., their inconstant position. First established by Schindewolf (1941) in the Heterocorallia and supported afterwards by studies of RóŹkowska (1969), Fedorowski (1991) and Chwieduk (2001), this character should therefore be considered universal for the Dividocorallia. Moreover, the transformation from minor-like into major septa and *vice versa*, occurring in the Calyxcorallia, precludes consideration of the shorter septa in the Calyxcorallia as the rugosan minor septa.

Corallite C — This corallite exhibits best the Heterocorallia-like pattern of major septa and the development of the symmetry septum. The initial phase of offsetting, which occurred in a very narrow area, resulted in some uncertainty concerning an appearance of two atavo-septa adjacent to the symmetry septum. Only an insertion of the latter, derived by the division of the thickened, parent middle major septum, is obvious (Pl. 52, figs. 1-4). Left of these uncertain septa may have derived by a split of the peripheral segment of the symmetry septum. This is to some extent proven by its forking in the inner margin (Pl. 52, fig. 2, lower right) prior to becoming divided in its peripheral part (Pl. 52, figs. 3-4, lower right). Almost simultaneously with this suspected split of the symmetry septum, another short and thin septum appeared at the atavotheca (Pl. 52, fig. 3, lower middle). This septum may have been inserted independently, but it may have resulted from a further split of septa mentioned above. The latter option is more probable as shown by the next section (Pl. 52, fig. 4) where that third septum meets the inner margin of the septum adjacent to and perhaps derived from the symmetry septum. An early separation of those two septa is apparent, resulting from both the amplexoid character of major septa that may be united mainly or only on surfaces of tabulae and the position of the section against the tabula, on (Pl. 52, fig. 4) and beneath its surface (Pl. 52, fig. 3). Irrespective of the interpretation, however, the sequence of an increase in septa in this part of the offset is from the symmetry septum to the left, towards the future neotheca. Such a sequence is further documented by an insertion of the next septum in this area (Pl. 53, fig. 5, lower left).

The septum at the atavotheca, located to the right of the symmetry septum and mentioned above as uncertain in the origin, either corresponds to the right thickened parent septum or was inserted independently at its base (Pl. 52, fig. 4, upper). This septum changes its position in further growth, being shifted towards the symmetry septum (Pl. 53, figs. 5-6, upper) where its position as the major septum adjacent to the symmetry septum was stabilized (Pl. 53, figs. 7-12; Pl. 54, figs. 13-20). The insertion of the next septum towards the future neotheca, by a peripheral split of the former, is in this part of an offset well documented (Pl. 53, figs. 6-9, upper). Thus, the sequence and direction of the insertion of major septa at the atavotheca is unquestionable although formation of some of those septa by a peripheral split may be disputed.

The first septum at the neotheca, i.e., the inner part of the symmetry septum, is inserted early by either split or extension of the middle thickened parent septum (Pl. 53, fig. 5). The status of this parent septum was unknown at the beginning of the offset-

ting (Pl. 52, figs. 1-2) and uncertain in slightly higher growth where a thin, fragmented septum of the parent corallite was attached to the section of a tabula between two thickened septa (Pl. 52, figs. 3-4; Pl. 53, fig. 5). However, connection of this thin fragment to the middle thickened septum became obvious after only 0.2 mm of further growth (Pl. 53, fig. 6). Two thickened septa adjacent to the former one must therefore be considered equivalents to the minor-like septa.

Reconstruction of the septal apparatus of the parent corallite (Pl. 53, figs. 7, 9, 11) demonstrated peripheral forking of individual pairs of its major septa (i.e., reestablishment of generations of septa) and a direct connection of those reconstructed septa of the parent corallite with individual thickened septal bodies located at the parent/offset border. The symmetry septum formed a temporary axis for the arrangement of the parent and the offset septa (Pl. 53, figs. 10-12; Pl. 54, figs. 13-15).

Two thickened septa, adjacent to the symmetry septum at the neotheca, played an important role as supporting structural elements in the common parent/offset area, but their role in the formation of the offset's septal apparatus is uncertain. Their elongation into the offset cavity may be interpreted as formation of its septa, especially where their ends thin (Pl. 53, figs. 7-11). This character is inconstant, however, and an insertion by elongation or split of a parent septum is documented only for the inner fragment of the symmetry septum. It may be predicted only that one of these thickened parent septa was shifted to the lower corner of an offset (Pl. 53, figs. 9-12) and constituted a basis for the permanent major septum present near this corner in the hystero-neanic growth (Pl. 54, figs. 13-20, lower left). The thickened septum located on the opposite side of the symmetry septum and the fourth thickened parent septum that bordered the offset on the right side in the hystero-brephic growth (Pl. 53, figs. 5-10, upper) may have been transformed into two major neosepta of an offset (Pl. 53, figs. 11-12; Pl. 54, figs. 13-14). Despite a very close peeling, only a position of neosepta at the neotheca in that corner and their temporary axial junction (Pl. 54, fig. 15) comparable to that observed 0.2 mm lower (Pl. 54, fig. 14) supports such a prediction.

The number of septa close to that of the mature corallites is achieved already in the late hystero-brephic/early hystero-neanic stage (Pl. 54, figs. 13-16) where constant positions of major septa is also established. An insertion of the last constant septum, observed in the series discussed, resulted from a peripheral split (Pl. 53, figs. 10-12, lower middle and left). This septum elongated slowly, giving the impression of being the minor-like septum (Pl. 54, figs. 13-14). Its elongation and the axial connection to the left neighbouring major septum coincided with an appearance of two minor-like septa on its sides (Pl. 54, fig. 15). An insertion of first minor-like septa both sides of the last inserted major septum, but not both sides of the symmetry septum, differs from that in other offsets. Also, an insertion of other minor-like septa looks incidental rather than sequential (Pl. 54, figs. 16-20), although the first minor-like septum at the neotheca was inserted next to the symmetry septum (Pl. 54, fig. 15, upper left).

The bilateral arrangement of major septa, with the symmetry septum forming the symmetry axis, lasted perhaps for as long as the partition neotheca existed. The way of transformation of the latter into the predicted dividing wall (cf. Pl. 54, figs. 16, 17) was not established because the state of preservation did not allow observation of the microstructure in peels. The longitudinal thin section of the offset/parent area (Pl. 46, fig. 3) did not solve the problem. The solid middle line, that appeared in the level of

growth mentioned and persisted till the end of the series of peels (Pl. 54, figs. 17-20), an union of that line with similar lines of adjacent corallites and observations in thin sections (Pl. 46, figs. 4, 6), suggesting the occurrence of the dividing wall as mentioned in the general description of the species.

The neanic growth (Pl. 54, figs. 17-20) demonstrates almost all variants of septal pattern described above on the basis of serial sections of two corallites (Pls. 47-48) except for the total disconnection of inner margins of septa. Such variability, observed early in hystero-ontogeny, proves that neither the 'classic' Heterocorallia-like pattern with a suspected oblique septum (Pl. 54, fig. 18) nor a disordered one (Pl. 54, fig. 19) can be considered typical for the species and genus. Also, temporary disconnection of axial and peripheral parts of major septa (Pl. 54, figs. 17, 20) did not make the rugosan septal lamellae of the former.

Remarks — Comparison of *A. trimorphum* to potential members of the genus cannot be made without a thorough revision of the latter. The potential for such a taxonomic comparison is mentioned above with remarks on the genus.

Range — Perapertu Formation, Upper Bashkirian to Lower Moscovian-Vereian.

Occurrence — Northern Palencia (Spain).

Discussion

The present paper is mostly devoted to the supplementary description of the morphology of most species from the original collection of de Groot (1963). Special attention has been paid to the hystero-ontogeny, and to the microstructure and diagenetic alterations of septa in all growth forms and intercorallite walls in massive colonial corals. Both those topics are poorly known in the Rugosa, whereas their role as tools for the taxonomy and phylogeny cannot be overestimated. A comprehensive solution of these topics will require additional investigations on material other than that available for this paper. Thus, the remarks that follow should be treated as introductory.

Microstructure and diagenesis — Skeletons of the Rugosa are almost univocally considered calcitic and well preserved, contrasting in this respect with aragonitic and mostly diagenetically damaged skeletons of Scleractinia. Rare researchers (e.g., Oekentorp, 1980; Wendt, 1990) considered some rugose coral skeletons aragonitic, but data supporting such an idea appeared inadequate. Nevertheless, Oekentorp (1980) was perhaps the first who questioned the perfect preservation and an absence of diagenetic alterations in the Middle and Upper Permian corals from Timor. Several students of corals (e.g., Sorauf, 1984; Fedorowski, 1986a) disagreed with such a position more or less clearly, but Oekentorp's (1980, 2001) general idea, i.e., diagenetic origin of several microstructural items, such as the zig-zag microstructure of external corallite walls and secondary sheets of septa (e.g., Pl. 5, fig. 8) or strongly curved "middle lines" of septa (e.g., Pl. 5, fig. 7), considered originally biogenic by some authors, is supported in the present paper.

The idea of the "microlamellar" microstructure introduced by Lafuste (1970), developed in his further papers (Lafuste *et al.*, 1993) and followed by several authors (e.g., Semenoff-Tian-Chansky, 1974; Rodriguez, 1989; Rodriguez *et al.*, 2002), was applied to both the tabulate and the rugose corals. I agree with the conclusion by Oekentorp (2001, p. 194), who considered this microstructure probably diagenetic. Sorauf (1996) also mentioned such a probability.

Oekentorp (2001) kept considering the so-called "Stirnzonen" diagenetic and applied his earlier idea (Oekentorp & Brühl, 1999) of cyanobacterial influence on the origin of some structures considered by him secondary. I do not exclude some diagenetic alterations in the formation of "Stirnzonen," but data supplied by the material here under study support my earlier idea (Fedorowski, 1974a), timing the occurrence of "Stirnzonen" with the direction of growth of trabeculae versus orientation of a transverse section. It was postulated (Fedorowski, 1974a, text-fig. 2) that "Stirnzonen" reflect the obliquely sectioned trabeculae. This simple statement is in full agreement with the well-documented and generally accepted idea that septal trabeculae grow towards an inner margin of a septum when arranged in a single row. It is equally well known that an outline of any septum reflects its growth. Reducing all possible variants of the outline to the most common case, i.e., more or less widely rounded in the upper part and nearly vertical in a lower inner margin, positioning trabeculae perpendicular to the margin and sectioning them in a way we normally do, i.e., perpendicular to a corallite, not to a septum, a differentiated picture is achieved. A section made more or less perpendicular to trabeculae, i.e., mostly at the periphery of a septum best exposes their real shape and separated position. "Stirnzonen" appeared in the part of a septum corresponding to its curvature, i.e., to the oblique sections of individual trabeculae, and the "dark middle line" occurs in the inner part of a septum where trabeculae are longitudinally sectioned. A fairly long section of a septum is required to show all those "variants" in a large magnification, but some elements are illustrated herein (Pl. 4, figs. 1, 5; Pl. 8, fig. 2).

Only exclusively large trabeculae may be traced along most sectioned septa. Characterophylloid trabeculae known from some Devonian Rugosa may serve as the best examples. In the case of fine trabeculae, characteristic for the great majority of Carboniferous and Permian Rugosa, only their fragments are exposed in given longitudinal sections. Nevertheless, changes in direction of their growth depending on the outline of a septum (Pl. 16, fig. 7) or direction of growth of a median lamella (Pl. 36, fig. 2) can be established.

Almost all species investigated for the purpose of this paper originally possessed the trabecular microstructure of most parts of their septa, except perhaps for peripheral-most parts in some. The apparently non-trabecular peripheral parts of septa, best exemplified by *Petalaxis (Degrootia) cantabrica* in its septothecal walls (Pl. 24, figs. 4-6; Pl. 26, fig. 2), do not demonstrate the fibro-normal microstructure of Kato (1963) because there occur no middle line dividing individual crystal rows. Thus, the original fibro-normal microstructure of peripheral parts of such septa seems very unlikely. (Note added in proof: In this paper I do not consider the idea of Stolarski (2003) to reject the occurrence of trabeculae.)

Three kinds of peripheral segments of septa, all present in the holotype colony of *P. (D.) cantabrica*, can be distinguished.

1. Wide, laterally contiguous and uniform peripheral segments, transformed abruptly, but smoothly, into thin segments exposing rudiments of trabecular microstructure (Pl. 24, fig. 6).

2. An intermediate morphology. The peripheral-most parts of septal segments are built as in (1), but thin, trabecular inner segments of septa either are isolated from them or not centred (Pl. 24, fig. 5, right and left, respectively). Also, inner margins of peripheral segments of this type form horn-like protuberances.

3. Wide, laterally contiguous segments, following sinuous curvature of middle line, with inner margins toothed and with inner, trabecular parts of septa either separated from those peripheral segments or attached to them with kind of a boundary (Pl. 26, fig. 2, lower).

All septa are secreted in septal pockets. Step by step secretion in septal pockets, that were wide to an extent precluding formation of trabeculae, can perhaps be accepted as an explanation for the appearance of laterally contiguous parts in all three kinds distinguished above. Fast-narrowing of those predicted wide septal pockets, allowing secretion of trabeculae, is most probable for (1), but not (2) and (3). The isolated or eccentrically attached inner segments of septa (2) were most probably secreted in secondary septal pockets based on lonsdaleoid dissepiments. Thus, the wide peripheral septal pockets may have been acting temporarily, i.e., until the formation of wide peripheral septal segments. The toothed margin and some remnants of crystalline fibrils arranged in semi-separate units (Pl. 26, fig. 2) may suggest an original development of trabeculae that were recrystallized afterwards. The suspected trabeculae may have been developed in the innermost parts of the second kind of peripheral segments of septa distinguished above, being restricted to horn-like protuberance, but may have been present in most (all?) of the thickness of peripheral segments of septa in (3). Unfortunately, crystalline fibrils were altered diagenetically to an extent precluding a rigid documentation. Nevertheless, it may be suspected that septothecal walls in at least some representatives of *Petalaxis* (*Degrootia*) subgen. nov. may have been multi-trabecular.

An idea of "mésoplasme," introduced by Semenoff-Tian-Chansky (1974) in order to explain differences in the microarchitecture of inner and outer parts of septa in some Carboniferous rugose corals, is only briefly discussed in these considerations. Although the term "mésoplasme" was introduced mainly in order to point out a position of particularly arranged crystals within a septum, it also intended to replace such terms as "Primärstreif" or "Urseptum." This was perhaps because the author believed in a single secretion act of septa when writing (Semenoff-Tian-Chansky, 1974, p. 39), "Les septes peuvent être secretés en une seule phase: mésoplasme et stéréoplasme sont alors confondus..." I do not follow this interpretation, but agree with morphogenetic reconstructions by Schouppé & Stacul (1955, 1959, 1966), and an idea of secretion of a primary (mostly or exclusively trabecular) septum first and its fibrous or fibro-lamellar sclerenchymal sheets afterwards.

The idea of lateral growth of septa in a single phase contradicts the sketch of a septum provided by Semenoff-Tian-Chansky (1974, text-fig. 13), showing a distinct boundary between "mésoplasme" and "stéréoplasme," documented by different directions of lines exemplifying crystalline fibrils. Such a dramatic difference in the

orientation of fibrils could not have happened without change of secreting conditions, i.e., without two phases being involved.

The question of a single *vs.* two phases in secretion of septa would have been nearly semantic if a microstructure sketched in Semenoff-Tian-Chansky (1974, text-fig. 13) and observed in some septa studied for the purpose of the present paper (e.g., Pl. 4, fig. 2; Pl. 8, fig. 2, middle) could have been secreted in a way generally accepted for septa, i.e., in septal pockets with individual fibrils growing perpendicular to the epidermis in the case of the fibro-normal microstructure of Kato (1963) and with individual trabeculae growing towards the inner margin of a septum. Such a growth cannot be achieved by a *mésoplasme* sketched by Semenoff-Tian-Chansky (1974, text-fig. 13), but is easily understood when diagenetic alterations and recrystallization of trabeculae is accepted. Widened segments of "*mésoplasme*" correspond to altered middle parts of trabeculae, its narrowings representing inter-trabecular areas and some assymetry, common in that structure, resulted from the internal pressure during the recrystallization. An involvement of stereoplastic sheets of septa in an advanced recrystallization would have resulted in a "single phase of secretion" and an apparent absence of a boundary between the "*mésoplasme et stéréoplasme*" postulated by Semenoff-Tian-Chansky (1974, p. 39). An occurrence of trabeculae within the "*mésoplasme*" in the same septum (Pl. 8, fig. 2) forms an additional argument for that structure being diagenetically caused in most cases described in this paper and elsewhere.

Rodriguez (1984, text-fig. 238), in his early paper, accepted the possibility of an occurrence of trabeculae in the *mésoplasme*. Such a position contradicts the main part of the Semenoff-Tian-Chansky (1974) idea, exemplified by his drawing mentioned in the preceding paragraph. Critically reading the present paper, Professor S. Rodriguez drew my attention to two fragments from Semenoff-Tian-Chansky (1974, p. 269), omitted by me from the discussion. Trabeculae were mentioned in these fragments as occurring in the *mésoplasme*. Although thankful to Professor Rodriguez for his reminder and comments, I do not change my mind concerning the idea of *mésoplasme* expressed above. Trabeculae present in the *mésoplasme* of a septum thickened by stereoplastic sheets prove its secretion in two steps, as postulated by Schouppé & Stacul (1955, 1959, 1966), thus making the *mésoplasme* idea unsupported. Some parts of septa, closely comparable to *mésoplasme* with trabeculae adjacent to fans of crystals (e.g., Pl. figs. 3, 5, 7; Pl. 8, fig. 2; Pl. 9, figs. 1-2), may only mean that there were remnants from the original trabecular microstructure present next to the diagenetically more altered ones. Such a picture does not demonstrate a single act of secretion of the *mésoplasme*, as it does not show two kinds of microstructures occurring in the single septum, as postulated by Rodriguez *et al.* (2001).

The "transition from the trabecular microstructure (left) to water-jet microstructure (right)" and "fan structure of trabeculae in the dissepimentarium" (Rodriguez *et al.*, 2001, figs. 4d and 3d, respectively) demonstrate most probably carinae misinterpreted as individual trabeculae in the dissepimentarium of the corallite described by those authors and the diagenetically altered inner (tabularial?) part of the septum. The comparison with the detailed study by Oliver & Sorauf (2002) of *Heliophyllum* shows a close similarity between fans of carinae in the longitudinal sections of the latter species (Oliver & Sorauf, 2002, pl. 4, fig. 1; pl. 5, fig. 3; pl. 7, figs. 1-3) to fans illustrated by Rodriguez *et al.* (2001, fig. 3d). The similarity between the Figures 3e and 4d of the

latter authors to several transverse sections illustrated by Oliver & Sorauf (2001, pl. 3, figs. 3, 10; pl. 5, fig. 2; pl. 8, fig. 3) can be reduced to the size and inner structure of bodies discussed; carinae in *Heliophyllum* are long and complex whereas those in *Aulocoinckophyllum carinatum* are simple and very short when sectioned transversally. The "dark line" between individual "trabeculae" (Rodriguez *et al.*, 2001, fig. 3e, 4d) confirms such an interpretation. There is not a single example in the literature of the Rugosa and Scleractinia showing individual trabeculae widely spaced and separated by "dark lines," whereas such a picture is typical for carinae. The three-dimensional reconstruction by Hill (1981, fig. 9:1) demonstrates this well.

The "water-jet" microstructure cannot be accepted primarily for a simple reason; all crystalline fibrils in sclerenchymal sheets of septa, the fibro-normal microstructure (in the sense of Kato, 1963) and basal skeleons of the Anthozoa, such as dissepiments and tabulae, grow perpendicular to the ectodermal layer, whereas crystals in the "water-jet" are oriented obliquely to the surface. This is proof of their pattern of secondary and diagenetic origin. Thus, I cannot accept the occurrence of different microstructure within a single septum as postulated by Rodriguez *et al.* (2001).

Peculiar differences, observed in transverse sections of septa versus longitudinal sections made along their middle lines, may suggest incorrect reconstruction and interpretation of the microstructure of septa as originally trabecular. A different involvement of diagenesis in the transverse and longitudinal section, but not apparently different results of that process, exposed by differently oriented sections, appears logical and acceptable to the present author. A transversally sectioned trabecula remains recognizable for as long as the centripetal direction of its crystalline fibrils can be established. The further process of recrystallization led to the disappearance of individual fibrils, but rounded shades of trabeculae with diagenetic crystals replacing the organic crystalline fibrils may remain (e.g., Pl. 2, fig. 4; Pl. 23, fig. 2). Such an artefact is distinguishable in the same way as an original trabecula; diagenetic crystals remain radially arranged in the transverse section. In still more advanced diagenesis (e.g., Pl. 5, figs. 1, 4, 8) a seemingly solid "middle dark line" appeared. A close analysis of such a "dark line" allows establishment of its sometimes unequal thickness and darkness. It is suggested here that the darkest dots correspond to the crystalline centres or axes of trabeculae, i.e., areas where crystalline fibrils were narrowest, most densely packed and thus transmitting the least amount of light. The above explanation bears strong signs of subjectivity because the darkest dots do not necessarily follow a regular order of trabeculae, some may disappear and others may be hardly recognizable as illustrated in the pictures cited. All those differences and uncertainties resulted most probably from the diagenesis and depend on the advancement of that process. Besides, the longitudinal section of a single trabecula may produce a similar image. In the latter instance, however, the dark line should not include darker and lighter dots.

The increase of density towards trabeculae centres, not always recognizable in transverse sections, is doubled in its effect in longitudinal sections as explained below. Besides, in contrast to the transverse section that expose best a small axial point of a trabecula, the longitudinal section exposes its long axis or at least a part of it when obliquely oriented. The well-known microarchitecture of a trabecula with individual fibrils growing radially off its axis may be partly or totally replaced by secondary

crystals that appeared during a process of recrystallization. It has been commonly observed, however, that such crystals follow the original arrangement of crystalline fibrils that form a kind of matrice to their growth. Thus, the original microstructure may disappear, secondary crystals may be much larger than original fibrils, but they kept centering towards the former axis of a trabecula. Also, their C-axes follow the pattern of C-axes of crystalline fibrils. The longitudinal section of such a diagenetically altered trabecula, like the original one, will show the following; crystals oriented perpendicular to the section are cut perpendicular to their C-axes and absorb most of the transparent light whereas those oriented with their C-axes parallel to the section transmit most light. The latter crystals of an original or recrystallized trabecula are directed to adjacent trabeculae and form the most transparent parts of a longitudinally sectioned septum, contrasting with its least transparent parts, corresponding to axes of either original trabeculae or their diagenetic artefacts. Isolated dark rods, included in lighter background produced that way, are much easier and better recognizable than less diversified dots in transverse sections. Also, recognition of the centred arrangement of crystals is unnecessary for the recognition of trabecula in the longitudinal section. Individual crystalline fibrils or secondary crystals may not be recognized in such dark rods, but their arrangement and position within the middle parts of septa support the interpretation. Thus, the primary trabecular microstructure of septa may be recognized even though the crystalline fibrils disappear. My recognition of the trabecular microstructure of septa discussed herein is reduced to the recognition of such diagenetic artefacts because I was not able to see and describe original crystalline fibrils.

Hystero-ontogeny — Hystero-ontogenetic studies by means of acetate peels remain rare despite their obvious cognitive value. Such a situation resulted in part from an inadequate preservation of the material, as in the case of some species revised in this paper, but other reasons remain mysterious. In this brief summary only the difference between the Rugosa and the Calyxcorallia in the insertion of septa is discussed. Morphogenetic reconstructions of some events need additional investigations and were omitted. It should only be pointed out that several items, taxonomically important at first glance, may find their easy explanation precluding such a value.

The disconnection of major septa, leading towards diphyphyloid morphology in fasciculate colonies and “diphystrotonid” morphology in the massive ones, is perhaps the most easily recognizable character seemingly speaking in favour of the rugosan relationship of their bearers. In several instances observed, such morphology is inconstant, being a simple consequence of the amplexoid nature of septa and their very limited protrusions above surfaces of tabulae. In other instances, best exemplified so far by *Donophyllum diphyphyloideum* Fomichev, 1939, the disintegration of inner margins of septa forms a prevailing character. As in the rugose corals, however, such a character cannot be over-evaluated in the Calyxcorallia. Nobody would synonymize the Carboniferous *Diphyphyllum* with the Devonian *Disphyllum* because both those genera display comparatively short and radially arranged septa, and nobody will find those characters adequate for distinguishing their bearers on the suborder or order level. The same is true for *Donophyllum*. The shortening of septa in that genus has limited value when compared to such substantial distinguishing characters as an

increase in septa. Remarks on *Donophyllum* have shown that disintegration of inner margins of septa in both genera of Calyxcorallia discussed in this paper cannot be evaluated higher than genus.

The sequence of septal insertion in the Rugosa was established by Kunth (1869). Attempts by further authors in modifications of "Kunth's law," as we use to say, were discussed by Fedorowski (1997) and will not be repeated. The generally accepted insertion in quadrants with an invariable trend to insert a new major septum in the closest possible neighbourhood of the cardinal septum, i.e., at the counter septum side of alar septa and next to the cardinal septum itself, is well established in solitary taxa, but remains almost unknown from the protocorallites of exclusively colonial rugose coral taxa. The reason is simple; preservation of such an early growth stage of a colony is possible only in extremely favourable conditions and due to extremely careful collection, or it is incidental. The so-called incipient colonies or earliest ontogeny of protocorallites investigated in Permian "*Heritschioides*" sp. (Fedorowski, 1978) cannot be considered representative for all colonial Rugosa. The former are no more than occasionally offsetting solitary corals whereas the latter included both solitary and colonial growth forms. Nevertheless a comparison of main characteristics of the ontogeny and the hystero-ontogeny established in such taxa and close similarity of those two processes, makes the latter a very promising and important tool. Consequently, data of the increase in septa in truly colonial taxa, based on the hystero-ontogeny, are credible.

In these abbreviated considerations, only rugose coral species investigated in detail for the purpose of this paper (Pls. 18-20, 27, 28, figs. 4-9, Pl. 33) are considered and compared to the calyxcoral species (Pls. 41-45, 49-54). Results published by Berkowski (1997, 2002) are not considered.

Description and analysis of illustrations of the hystero-ontogeny in all rugose coral species investigated so far leave no doubts that the main principles of "Kunth's law" were followed; the major septa were inserted in quadrants and in sequences directed bilaterally towards the cardinal septum within each quadrant. There occur individual variants in the material studied in this paper, such as a delay in the insertion of the counter septum or a simultaneous insertion of four neosepta (Pl. 18, figs. 5-6), an acceleration in an increase in septa in particular quadrants (Pl. 20, figs. 3-6) or delay in an elongation of the cardinal septum (Pl. 28, figs. 4-7), but none of those contradicts the rule. Also, the continuous axial septum occurs only in some of the species or specimens investigated (Pl. 27, figs. 1-5), but is absent from others. Such an omission is not unique from the earliest ontogeny of several solitary Rugosa (e.g., such families as Pentaphyllidae, Verbeekellidae and Dalniidae). Thus, its absence from early hystero-ontogeny should not be overevaluated. The hystero-ontogeny in the Rugosa, investigated in adequate detail, exhibits similar pattern and variation.

The hystero-ontogeny in several offsetting corallites of fasciculate and massive species included within the order Calyxcorallia display variability in details similar to the colonial Rugosa (see descriptions of species for details). At the same time, however, the increase in septa in the Calyxcorallia is as constant as in the Rugosa; four-directional in the former and two-directional in the latter. An insertion by a peripheral split of two first septa of a quadrant and an increase in septa within such bordered quadrant, is the second, rarely observed mode of the insertion in Calyxcorallia, but unknown from the Rugosa.

In the hystero-ontogeny of both, the Rugosa and the Calyxcorallia there almost invariably occurs a septum or (more commonly) a pair of septa, located opposite each other at the atavo- and the neotheca. These septa began the septogenesis and form the symmetry axis of a new individual. Those two septa in the Rugosa, i.e., the cardinal and the counter septum, are either derived from the axial septum by its transverse disintegration in a corallite axis or are inserted as separate blades. In the Calyxcorallia the situation is similar. Two opposite septa are most commonly the first septa in the offset. They are united axially in those parts of a corallite growth that form a Heterocorallia-like pattern, but are separated from each other where major septa lose their axial connection. This leading septum is named herein the "symmetry septum" irrespective of it being continuous or divided into two segments. It remains uncertain, however, whether the symmetry septum should be equated with the oblique septum in the Heterocorallia or should be treated as its replacement. The oblique septum is hardly if at all distinguishable within most corallites of the Calyxcorallia, but a short blade may exist between first generation septa in some transverse sections, as pointed out in the description of *Artocorallium trimorphum*.

The symmetry septum appears most commonly in two segments, being also in this respect similar to some Rugosa. Either both of those segments or only the peripheral segment is inherited from a parent corallite. I do not propose different names for those two segments irrespective of their origin, because their role in septogenesis is identical. In a single corallite investigated (Pl. 43, fig. 5), a short lasting aseptal stage occurred. Thus, all septa were considered neosepta in this case, although the first three were inserted at the atavotheca exactly opposite three major septa of the parent corallite. Such a position suggests strongly a short lasting disappearance of septal pockets and their quick reappearance, i.e., a close relationship of the parent and first offset septa as in the remaining offsets of the same colony.

The position of the symmetry septum in Calyxcorallia is identical to the axial septum in the Rugosa. Consequently, the cardinal and counter protosepta in the Rugosa can be equalized to two segments of the symmetry septum. Also, the oldest, i.e., first inserted major septa in quadrants of the Calyxcorallia are located on both sides of the symmetry septum and opposite to each other. Such an arrangement corresponds to the textbook arrangement of first septa in the Rugosa; the axial septum or the cardinal and the counter septum opposite each other, and the alar and counter-lateral septa neighbouring the protosepta on both sides. In contrast to the Rugosa, however, in which all next septa are inserted towards the cardinal septum, i.e., outwards of the counter-lateral and alar septa, all next septa in the Calyxcorallia are inserted outwards of both segments of the symmetry septum. As the result of such an increase in septa in the Calyxcorallia, the last inserted septa in quadrants are located most closely to each other, whereas they are most distant in the Rugosa. Also, neither segment of the symmetry septum can be called the cardinal septum in the rugosan sense, because new septa were not inserted towards either of them.

Four directions in an increase in septa established for the Calyxcorallia resulted in formation of four groups of septa, analogous but not homologous to the rugose coral quadrants resulted from bilateral increase in septa. Nevertheless, the name "quadrant" is borrowed from the Rugosa for such a group of septa in the Calyxcorallia. Despite different constitutions of quadrants in both subclasses and their dif-

ferent function (an absence of the cardinal fossula in the Calyxcorallia), I cannot see a need for different names.

In this place I have to cite one of Professor Edouard Poty's comments to my paper. The remarks that follow would not be understood otherwise. Professor E. Poty wrote "You do not explain why in Calyxcorallia you have: 1) Dissepiments and tabulae as in Rugosa; 2) Minor septa. These characters are fundamental in the distinction of Rugosa and you have to explain why they appear also in Calyxcorallia and not in Scleractinia, Heterocorallia or other groups of corals."

I begin my remarks with the repetition of my earlier position (Fedorowski, 1991, p. 47, text-fig. 15) pointing to the Rugosa as the ancestral group for the Calyxcorallia. Very late separation of the Calyxcorallia, in the sense of evolution of the Rugosa, resulted in derivation of many rugosan characters, the mineralogy of skeletons and its microstructure, not mentioned by Professor Poty, in the first place. This is why several morphological characteristics, common in the Rugosa and well fixed in their genetics in the sense of both possibilities to change and restriction of changes, were inherited by the Calyxcorallia when a large mutation in the pattern and increase of septa appeared.

Change of symmetry from bilateral to quadrilateral, achieved by different directions in the increase in septa (see above), was the keystone for the distinction of the new group, but not the dissepiments and tabulae that can easily be accepted as inherited from the Rugosa. Moreover, structures closely comparable to the dissepiments in the Rugosa are known in the Scleractinia, where they bear the same name and are derived the same way, i.e., as basal structures. Peripheral tabulae in Tabulata, and Syringoporida in particular, function similarly to the dissepiments in the Rugosa and their origin is identical, although they do not bear the name dissepiments. There is no need to mention that tabulae occur in all Anthozoa and play the same role, although their morphology may be very different. Thus, neither dissepiments nor tabulae can be called fundamental for the Rugosa.

Minor septa are characteristic for the Rugosa in the sense of their insertion different from the cyclic insertion of the second cycle septa in the Scleractinia. One may consider minor septa the second cycle of septa in the Scleractinia comparable in their function to minor septa in the Rugosa, when next cycles do not appear. It is also important to remember that several genera included in the Permian family Wentzelellidae produced up to four kinds of septa. Also, there are numerous rugose coral genera, belonging to various higher rank taxa, that possess minor septa that did not function, i.e., totally unrecognizable from the microstructure of external walls and from a corallite surface when the wall is externally smooth. Minor septa of that kind occur in the suborder Diffingiina Fedorowski, 1986b, where they are commonly seen only in upper parts of calices and in a form of peripheral splits of major septa (e.g., Fedorowski, 1986b, pl. 14, figs. 1-3). Thus, this character is extremely variable in the Rugosa. Nevertheless, it is true that the insertion of minor-like septa seems similar to minor septa in the Rugosa when they did not appear by split. However, it is premature at the present level of knowledge to decide whether the minor-like septa were inherited from the Rugosa and then made replaceable for major septa in the Calyxcorallia or these are new structures, analogous to the rugosan minor septa in their function, but not homologous to them in origin. I prefer the second option as being simpler and easier

to achieve in the process of evolution, but I do not consider the first option impossible. A similar origin of major and some minor-like septa and the ability of the latter to become involved in the major septa pattern or to replace major septa and *vice versa*, was discussed in detail with description of the hystero-ontogeny of *D. reticulatum* and *A. trimorphum*. Nothing like that was ever documented in the Rugosa.

Relationships of the calice-lacking Heterocorallia are a problem. This problem increases, however, when that group is included as an order of the Rugosa instead of the Dividocorallia. I do see no reason to place in the subclass Rugosa the group of corals totally different in the pattern and increase in septa, i.e., in the characters really fundamental for the distinction on the subclass level. This character was successfully applied for the distinction between Rugosa, Scleractinia, Heliolithida and Tabulata. Why not for the Dividocorallia? A distinction on the subclass level of the Heterocorallia and the Calyxcorallia, although not supported by identical patterns and similar increases in septa, is more logical to me than to include both of them as orders within the Rugosa.

Acknowledgements

I sincerely thank Dr. C.F. Winkler Prins for his permission to loan the thin sections and some samples, for fruitful scientific discussions and for very friendly hospitality during my stay in Leiden. Professors Edouard Poty from the University in Liège and Sergio Rodriguez from the Complutense University in Madrid are cordially greeted for their critical remarks. I thank Mr. Wouter Wildenberg for all sorts of help; an improvement of quality of several thin sections and arrangement of the loan, in particular. I also thank Mrs. Marta Bartkowiak for preparing all additional thin sections and most peels. My stay in Leiden and the investigation summarised in this paper was available due to the financial support of the Polish Committee for Scientific Research, grant No. 6 P04D 06720.

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Appendix

Several species described by de Groot (1963) were omitted from detailed revision for various reasons (see 'Introduction'). Some of them and several undescribed specimens were briefly restudied. Remarks included in this appendix are introduced as a brief, but perhaps useful, supplement to main revision. Species described by de Groot (1963) are listed below by names and in the order introduced by that author. Specimens not included by that author in her description follow the former and are listed by numbers.

Cyathaxonia group of species — Most taxa included by de Groot in *Cyathaxonia* were further described and discussed by Rodriguez (1984) and Rodriguez & Kullmann (1990, 1999), but there remain some formal and content related remarks that should supplement those papers.

Cyathaxonia cornu cantabrica de Groot, 1963 — Rodriguez (1984, p. 165) synonymized this subspecies with the nominative subspecies. Also, he included in that synonymy *C. archangelskyi* Fomichev, 1953, from Bashkirian deposits (Limestones G-K) and *C. tenuiseptata* Fomichev, 1953, from Gshelian deposits (Limestone O6) of the Donets Basin. Such a treatment extended the range of that species to nearly the entire Carboniferous. Rodriguez & Kullmann (1990, 1999) accepted only the synonymy of *C. cornu* and *C. cornu cantabrica*, reducing an upper limit of such understood species to Westphalian C, i.e., Lower Moscovian. Long stratigraphic range cannot be excluded for any fossil species. The problem is, however, whether we are dealing with truly related specimens occupying variegated areas and existing in different time or unrelated morphotypes which were included in the same species only because they are similar. I have no rigid answer to this question that must remain rhetoric for the time being, but the second option looks more probable to me.

The main characteristics of the holotype, RGM 112540, of *Cyathaxonia cornu cantabrica*: Columella narrow, rounded, composed of radially arranged crystalline fibrils. Inner margins of major septa crowded into the columella with a sharp boundary, i.e., do not constitute a part of the latter. Crystalline fibrils of the columella penetrate interseptal spaces. Contratingent minor septa attach the major septa at approximately three quarters length of the latter. Carinae-like protuberances of septa better developed at the periphery.

RGM 112542 displays a morphology of the columella comparable to that in the holotype. Its septa are more thickened, especially at the periphery and carinae-like protuberances have not been traced. Lack of them may be apparent, resulting from advanced diagenetic alterations.

Cyathaxonia aff. cornu — Represented by a single, incomplete specimen, RGM 112544, and one thick thin section, described by de Groot (1963, p. 26) within *C. cornu cantabrica* in the last paragraph of the "Material" section. The specimen possesses a very narrow columella of the untraceable microstructure. Major septa thin, reaching the columella. Minor septa contratingent, reaching the major septa at c. four fifths the length of the latter.

Cyathaxonia corisensis de Groot, 1963 — Holotype, RGM 112546, according to the original designation in text (de Groot, 1963, p. 28); erroneously printed as RGM

112545 in captions to plate 2 therein. The latter number corresponds in the text to *Cyathaxonia* no. 1 (de Groot, 1963, p. 27, text-fig. 17). Thin section RGM 112545 was not traced; remarks on it are omitted. Neither the drawing of the holotype of *C. corisensis* (de Groot, 1963, text-fig. 18) nor that of the paratype RGM 112548 (text-fig. 19) corresponds to illustrations published by de Groot (1963, pl. 2). Only the thin section and *ibid.* (pl. 2, fig. 4) are considered the holotype. It displays the columella comparatively wide, rounded, composed of centripetally arranged crystalline fibrils with growth lines weakly marked. Major septa thickened at the periphery and slightly rhopaloid near the columella. They crowd into the columella slightly. Minor septa contratingent, thinner than major septa, attach the latter just beneath their rhopaloid periaxial thickenings. Septotheca comparatively narrow.

Paratype, RGM 112548 (= RGM 112549, *ibid.*, pl. 2 captions) displays the morphology and thickness of the external wall similar to that of the holotype. Its columella, similar to that in the holotype in the morphology, is wider when compared to the corallite diameter. Minor septa are thinner in comparison to major septa and shorter than in the holotype. They do not reach the vicinity of the columella.

Cyathaxonia sp. 2 de Groot, 1963 (pl. 2, fig. 6) — Renamed *Cyathaxonia degroot* by Rodriguez (1984, p. 171) on the basis of his own type specimen. Rodriguez & Kullmann (1999) accepted that decision. I introduce only few remarks. None of the drawings in de Groot (1963, text-fig. 20) corresponds to the thin section RGM 112552. The thin section labelled as above and illustrated by de Groot (1963, pl. 3, fig. 6) displays the following characteristics: Major septa thick, deeply crowded into the columella or *vice versa*: the crystalline fibrils of the columella spread out deeply between inner margins of thick major septa, reaching the minor septa in the area adjacent to the slightly shortened cardinal septum. Minor septa contratingent, only slightly exceed half major septa in length, laterally contiguous with the latter in cardinal quadrants. If the strong thickening of septa is original and not diagenetic, the corallite can hardly if at all be compared to specimens illustrated by Rodriguez (1984) and Rodriguez & Kullmann (1999).

Carcinophyllum (*Axolithophyllum*) *quiringi* and *C. (A.) quiringi major* — RGM 112771, 112774, 112783-112785. Already Rodriguez (1984, pp. 416, 420, respectively) accepted an independent generic position of *Axolithophyllum* Fomichev, 1939, and synonymized the subspecies *major* (forma of de Groot, 1963) with the species. I agree with both those decisions. In contrast to observations and illustration by Rodriguez (1984, text-fig. 239), the microstructure of septa is trabecular, at least in the best preserved specimen, RGM 112783, consisting of large and densely packed trabeculae. These trabecular, primary septa are covered by thick stereoplasmic sheets of septa. Diagenetic alterations of septa, involving both the primary septa and their sheets, may have resulted in the disappearance of trabeculae.

Lonsdaleoides hispanicus de Groot, 1963 — RGM 112788-112791. Microstructure of septa difuso-trabecular. Septa pseudo-naotic at the periphery. Median lamella derived from the cardinal septum, thick and monoseptal in early stage, incorporates septal lamellae in further growth. Not a single case of an offsetting was observed. All immature corallites, small and morphologically simple in several cases, remain outside the

large ones. Also, such characters common for offsetting corallites as morphological changes in peripheral parts of septa and the dissepimentarium in mature corallites or an absence of a wall between mature and immature corallites were not found. Thus, I consider Spanish specimens to represent gregaria rather than colonial corals. The same may well be true for the type species. No offsetting corallite was illustrated by Heritsch (1936). Microstructure of septa was not investigated in the latter specimen.

Ivanovia freieslebeni (Stuckenberg) — RGM 112796, 112798, 112799, illustrated by de Groot (1963, pl. 26, figs. 2-4), display considerable differences between individual colonies in morphology of the median lamella. It is mostly (exclusively?) monoseptal in the transverse section of all colonies. In the longitudinal sections there may be a complex and well-isolated axial column in some corallites and rather simple one in the others. It remains uncertain whether those differences reflect an intracolony (intraspecific?) variability, a different orientation of individual sections (more or less centric) or should be considered diagnostic. The name *I. freieslebeni* in the sense of de Groot (1963) may cover more than one species.

There occur substantial differences between specimens described by de Groot (1963) and those included by Dobrolyubova (1935) in *Cystophora freieslebeni* (Stuckenberg). Minor septa mostly penetrate tabularium in Russian specimens, but are absent from the Spanish ones. Also, they display intercorallite walls fairly well developed, whereas the Russian ones are almost totally aphroid. Unfortunately, descriptions and illustrations by Dobrolyubova (1935) were based on new material, but not on Stuckenberg's specimens included in *Phillipsastraea freieslebeni* Fischer or *Phillipsastraea rossica* Stuckenberg, synonymized by Dobrolyubova (1935, p. 20). Thus, it may only be concluded that Spanish colonies do not belong in the species represented by specimens included in *C. freieslebeni* by Dobrolyubova (1935). Their final species identification should be suspended until revision of the Russian type or topotype specimens is completed.

Generic position of the Spanish specimens within *Ivanovia* remains uncertain as well. The type of the genus designated by Dobrolyubova (1935, p. 46, pl. 12, figs. 1-2) is represented by an aphroid colony, corallites of which possess a complex median lamella, incorporating few septal lamellae, and axial cones probably developed, whereas median lamellae in Spanish corallites are monoseptal (at least in the thin sections restudied) and axial cones are absent. The microstructure of septa remains unknown in both Russian and Spanish specimens.

Specimens not included by de Groot (1963) in the original description

RGM 299173 — *Bothrophyllum* cf. *pseudoconicum*. Specimen poorly preserved, slightly damaged by compaction. Major septa approach corallite axis. Cardinal septum shortened, in open cardinal fossula. Counter septum elongated. Minor septa restricted to dissepimentarium. Small grape-like arranged dissepiments at periphery.

RGM 299187 — Probably fasciculate colony, morphologically close to *Fomichevella schrenki* (Stuckenberg, 1895) if colonial growth form confirmed. Corallite c. 10 mm in diameter. Major septa short, with a wide free axial area. Cardinal septum slightly shortened, in shallow, open cardinal fossula. Minor septa restricted to peripheral part of narrow dissepimentarium.

RGM 299067 — *Bothrophyllum* sp. superficially similar to species included by Kossovaya (2001) in her new genus *Alekseeviella*. The correctness and need for distinction of the latter is not discussed. Major septa thin, leave comparatively wide, free axial area in cardinal quadrants. Cardinal septum shortened, in shallow, open cardinal fossula. Counter septum and few other major septa of counter quadrants reach or almost reach corallite axis. Minor septa restricted to peripheral part of moderately wide dissepimentarium, composed mostly of herringbone dissepiments.

RGM 298976 — *Spirophyllum* sp., perhaps belonging to a new species. Columella disintegrated into individual constituents, septal lamellae in particular. Resembles *S. perditum* Fedorowski, 1970. Some septal lamellae remain laterally contiguous and connected with rudiments of median lamella.

RGM 299037 — *Monophyllum* sp. morphologically similar to *M. sokolovi* Fomichev, 1953, and probably belonging to that species. Cardinal septum shortened, located in narrow, triangular cardinal fossula. Counter septum strongly rhopaloidally thickened in corallite axis. Microstructure of septa probably finely trabecular.

RGM 299041 and RGM 299042 — *Fomichevella* sp. resembling "*Campophyllum*" *orientalis* Stuckenberg, 1895. Median lamella absent from both early hystero-neanic and mature growth. Major septa thin. Cardinal septum shortened, in open cardinal fossula. Counter septum equal to other major septa. Minor septa cross entire dissepimentarium that occupies about one third of the corallite radius.

Plate 1

Transverse thin sections.

Fig. 1. *Actinophrentis* sp., RGM 112574. (a, b) Juvenile (peels). (c, d) Mature growth stage (c = peel).

Figs. 2-4. *Roptiphyllum exile* de Groot, 1963.

Fig. 2. RGM 112501, holotype, immature growth stage.

Fig. 3. RGM 112502, mature growth stage.

Fig. 4a,b. RGM 112512, juvenile growth stage.

Fig. 5. *Bradyphyllum? oppositum* Fomichev, 1953, RGM 112515, mature growth stage.

Fig. 6. Gen. et sp. indet., RGM 112515, mature growth stage, $\times 5$.

All figures $\times 8$ unless stated otherwise.

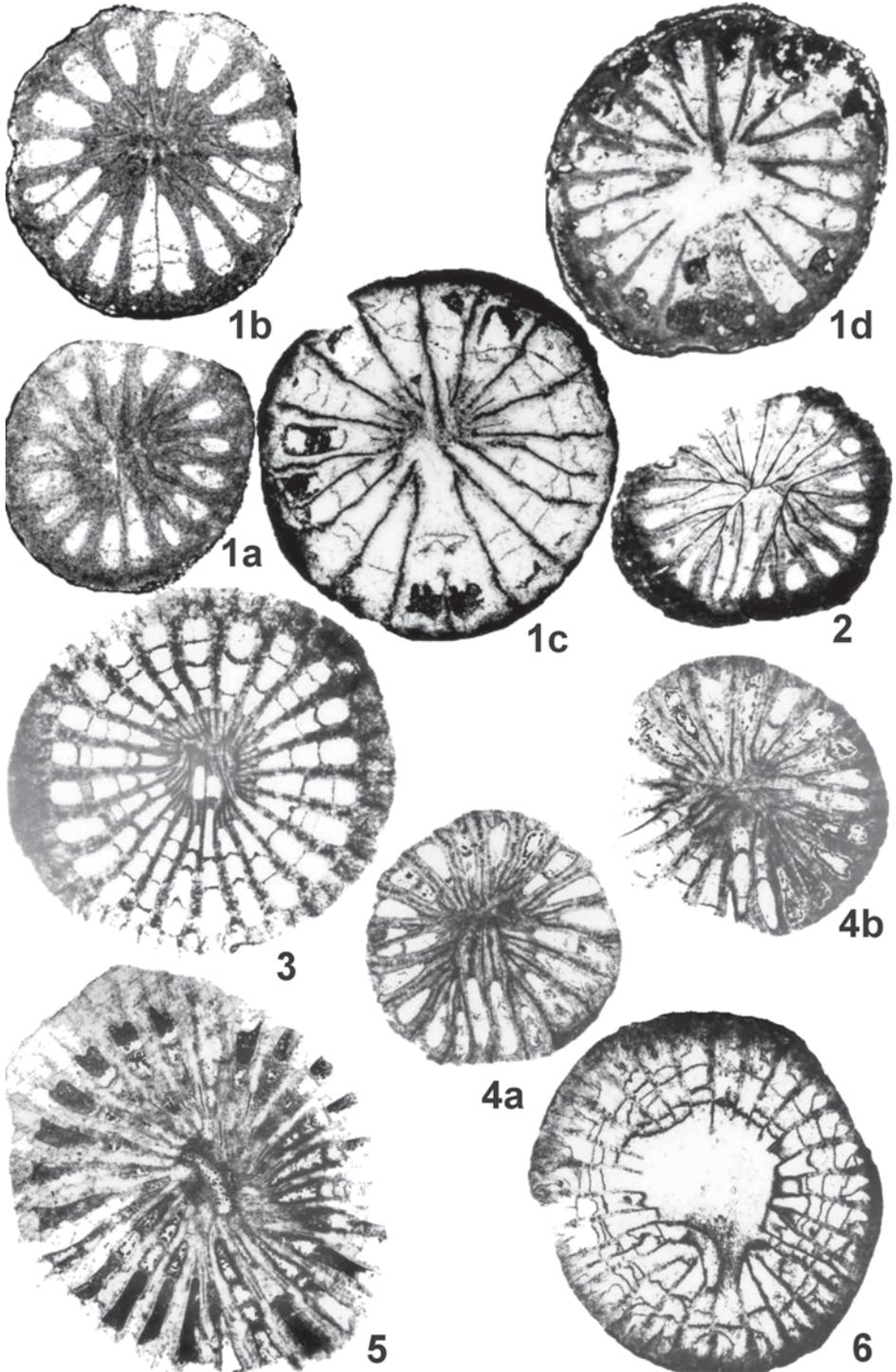


Plate 2

Transverse thin sections.

Figs. 1-3. *Actinophrentis* sp., RGM 112574. Microstructure and diagenetic alterations of septa.

Figs. 4-7. *Bradyphyllum? oppositum* Fomichev, 1953, RGM 112514. Microstructure and diagenetic alterations of septa.

All figures $\times 50$.

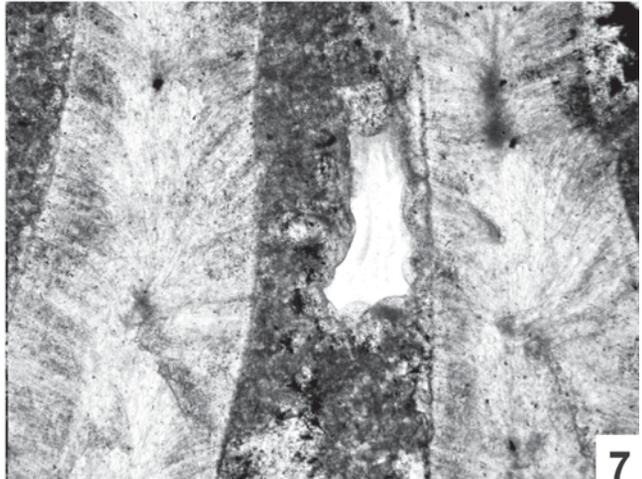
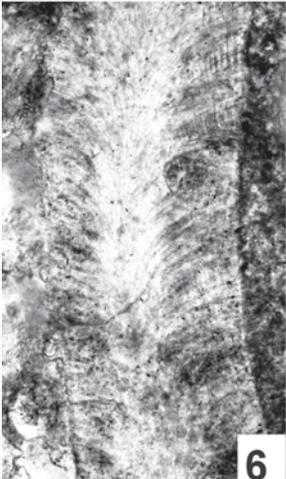
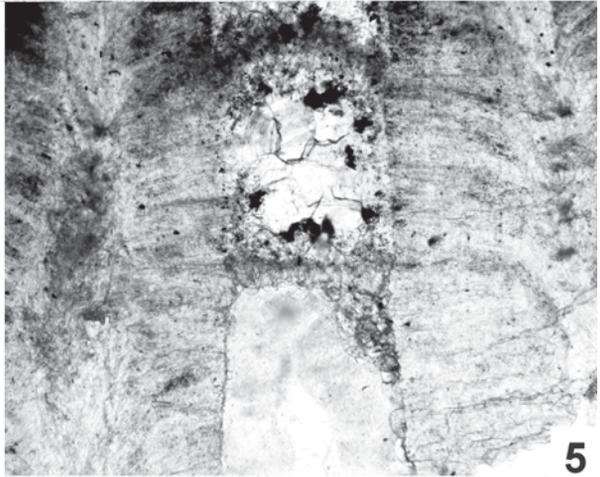
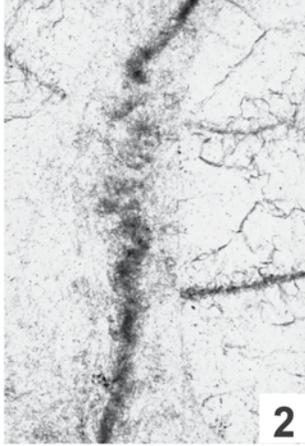
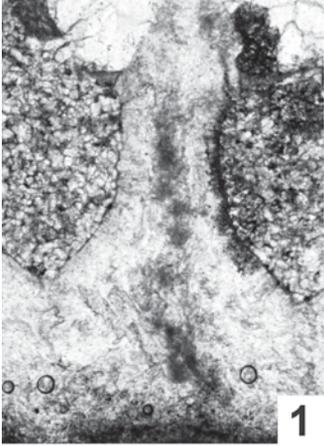


Plate 3

Transverse thin sections.

Figs. 1-4. *Rotiphyllum paralleloides* (de Groot, 1963).

Fig. 1. RGM 112572. (a, b) Mature growth stage. (c) Just above calice floor at periphery (peel). (d) Middle of calice (peel).

Fig. 2. RGM 112580, above calice floor.

Fig. 3. RGM 112576, early mature growth stage.

Fig. 4. RGM 112571, late mature growth stage; partly above calice floor at periphery.

Figs. 5-6. *Ufimia alternans* de Groot, 1963.

Fig. 5. RGM 112539.

Fig. 6. RGM 112538.

All figures $\times 5$.

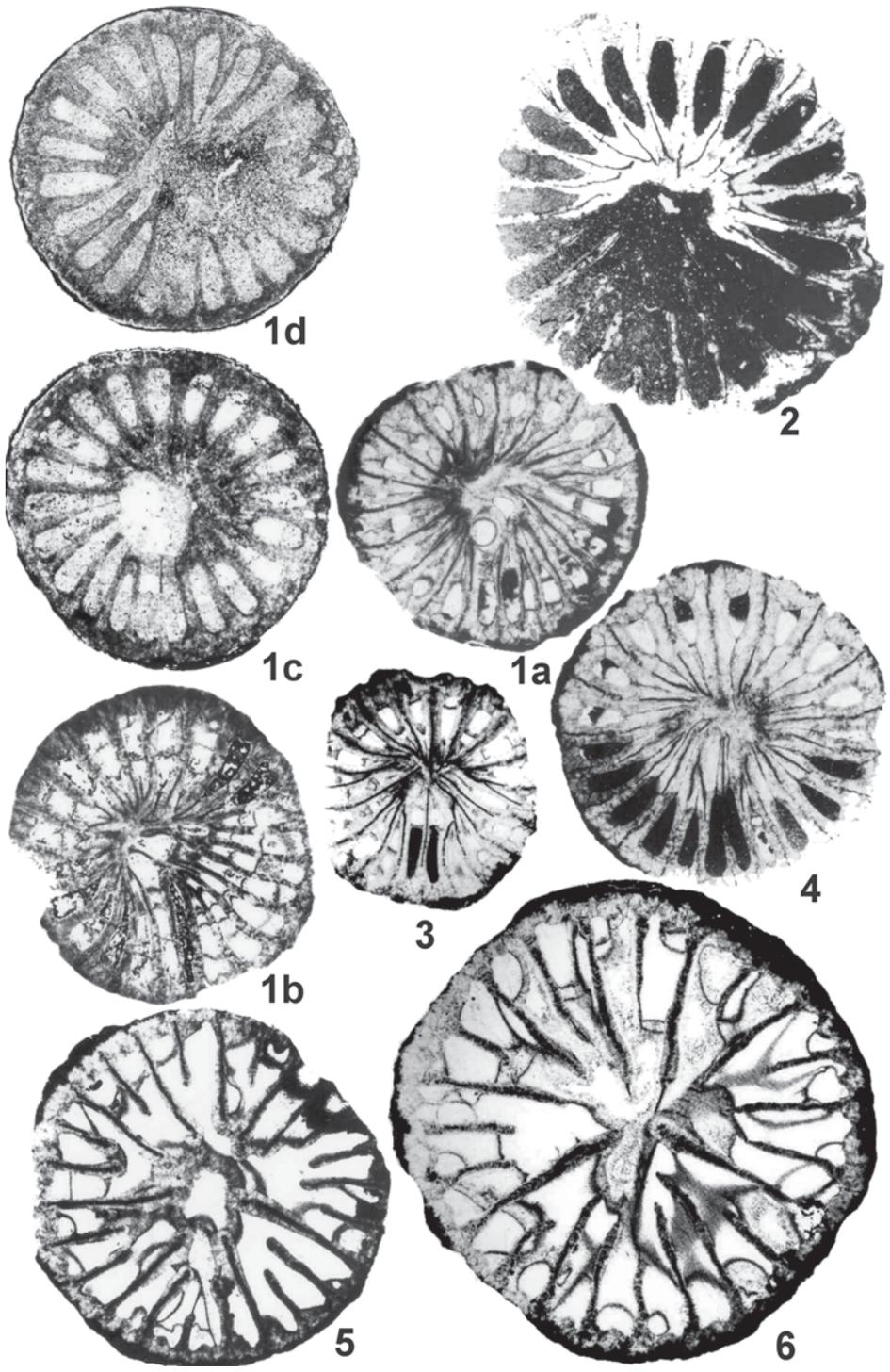


Plate 4

Transverse thin sections.

Figs. 1-4. *Rotiphyllum exile* de Groot, 1963. Microstructure and diagenetic alterations of septa.

Fig. 1. RGM 112504.

Fig. 2. RGM 112512.

Fig. 3. RGM112502.

Fig. 4. RGM 112501, holotype.

Figs. 5-8. *Rotiphyllum paralleloides* (de Groot, 1963). Microstructure and diagenetic alterations of septa.

Figs. 5, 7. RGM 112571.

Fig. 6. RGM 112580.

Fig. 8. RGM 112 577.

All figures $\times 50$.

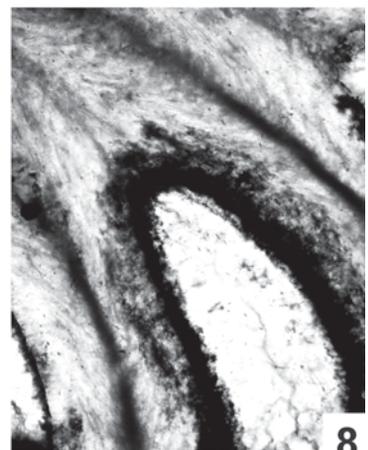
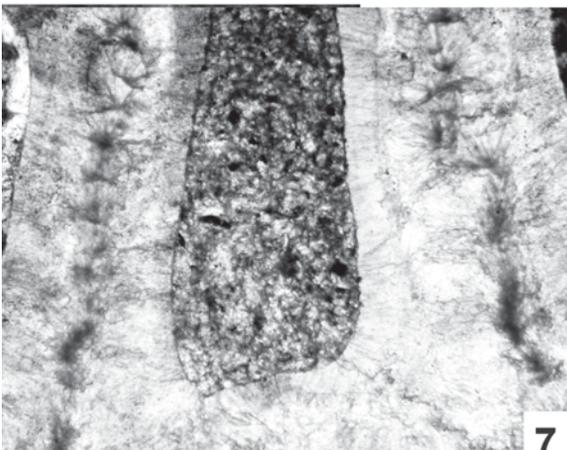
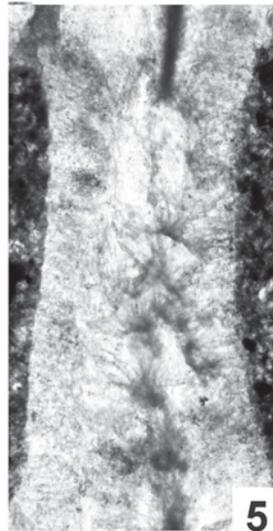
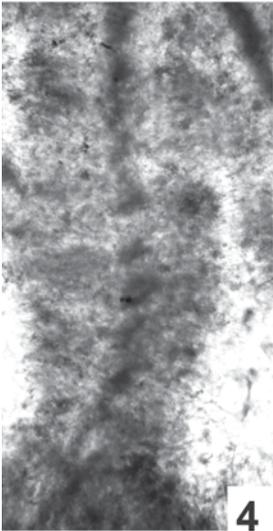
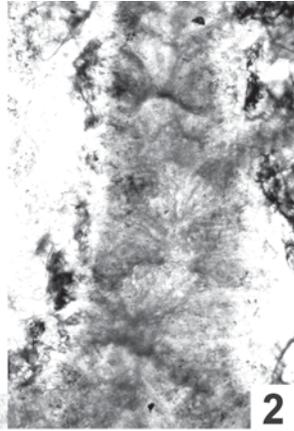
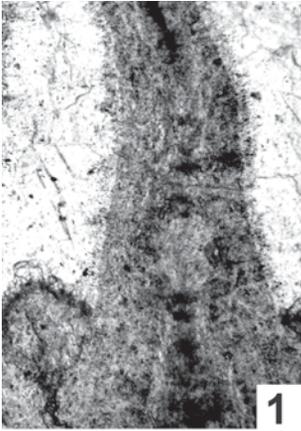


Plate 5

Transverse thin sections.

Figs. 1-4. *Soshkineophyllum corisense* de Groot, 1963.

Figs. 1, 3-4. RGM 112534, diagenetic alteration from advanced (with no trabeculae) to less advanced (retaining rudiments of trabeculae).

Fig. 2. RGM 112533, very advanced diagenetic alteration.

Figs. 5-8. *Ufimia alternans* de Groot, 1963.

Figs. 5, 7. RGM 112535, holotype. (5) Rudiments of trabeculae and (7) primary septa curved diagenetically up to become broken (upper).

Fig. 6. RGM 112538, rudiments of trabeculae and beginning of formation of "Stirnzonen."

Fig. 8. RGM 112536, strongly altered septa with zig-zag pattern in their stereoplasmic sheets.

All figures $\times 50$.

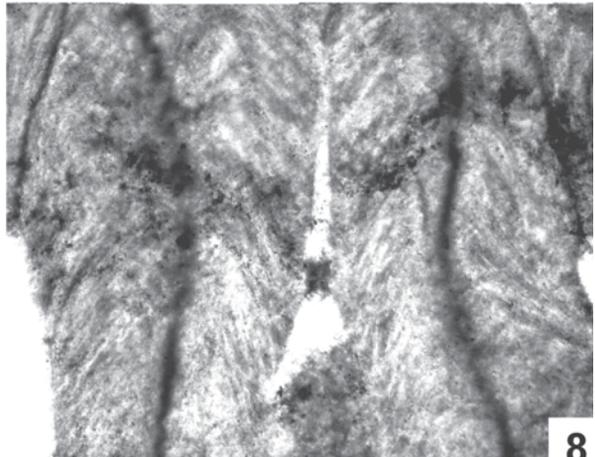
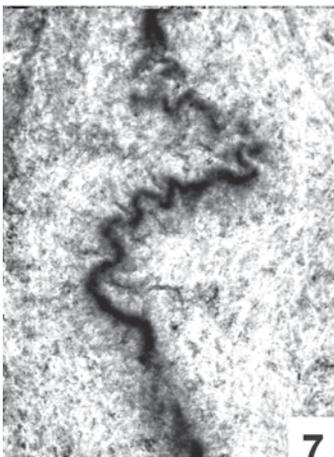
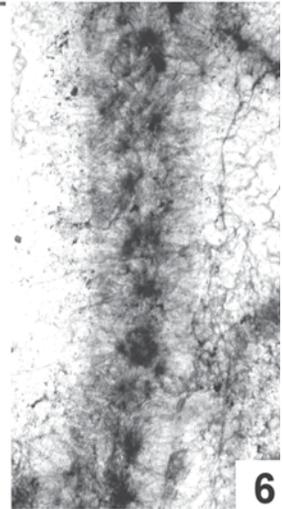
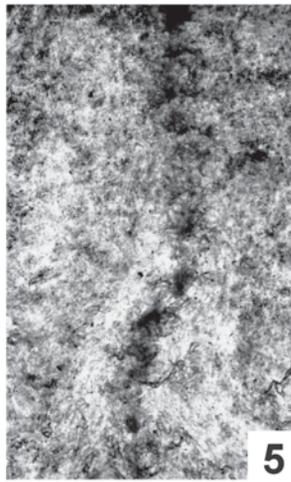
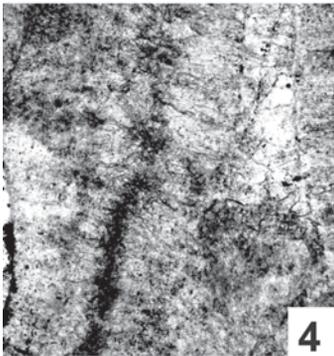


Plate 6

Transverse thin sections.

Figs. 1-3. *Ufimia alternans* de Groot, 1963.

Fig. 1. RGM 112536, diagenetically broken row of fairly well-preserved trabeculae.

Fig. 2. RGM 112535, holotype. Thin axial extension of rhopaloid major septum.

Fig. 3. RGM 112538, thin axial extension of rhopaloid major septum with recognizable trabeculae.

Figs. 4-5. *Lophophyllidium (Lophophyllidium) minus* de Groot, 1963, RGM 112568.

Fig. 4. Inner margin of columella showing two septal lamellae incorporated.

Fig. 5. Trabecular microstructure of primary septa.

Fig. 6. *Lophophyllidium (Lophophyllidium) breimeri* de Groot, 1963, RGM 112569. Compact columella extending from counter septum and bifurcated reduction of minor septa. $\times 15$.

All figures $\times 50$ unless stated otherwise.

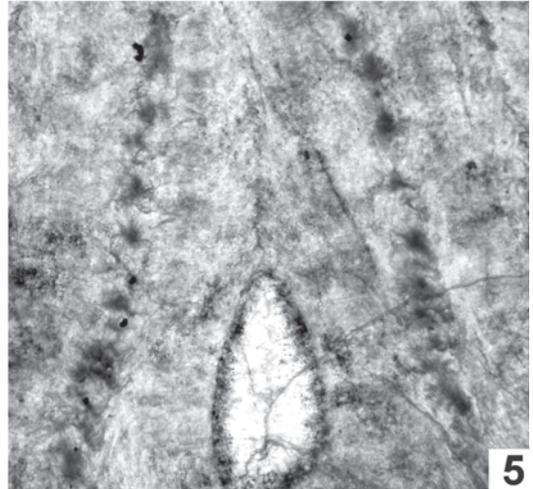
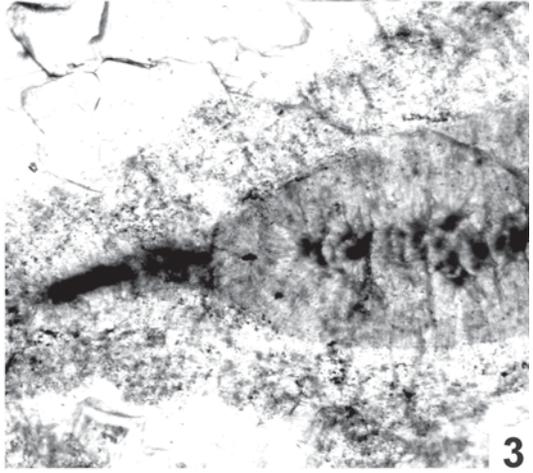
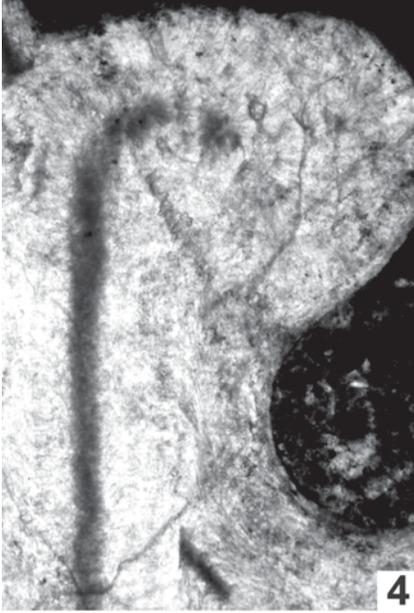
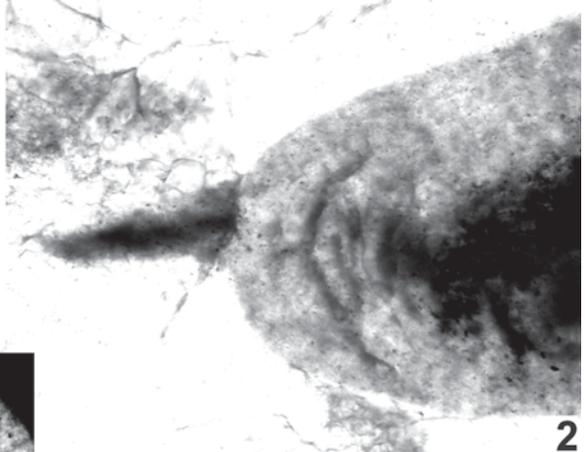
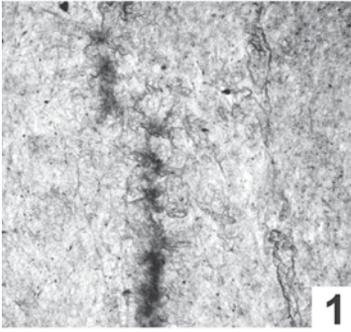


Plate 7

Transverse thin sections.

Figs. 1-4. *Lophophyllidium* (*Lophbillidium*) *breimeri* de Groot, 1963.

Fig. 1. RGM 112553, holotype. (a) Neanic growth stage. $\times 8$. (b) Mature growth stage. $\times 6$.

Fig. 2. RGM 112569, early mature growth stage. $\times 6$.

Fig. 3. RGM 112557, mature growth stage. $\times 6$.

Fig. 4. RGM 112558, mature growth stage. $\times 6$.

Fig. 5. *Lophophyllidium* (*Lophophyllidium*) *minus* de Groot, 1963, RGM 112568. (a) Neanic growth stage.

(b) Mature growth stage. (c) Above calice floor. All $\times 8$.

Fig. 6. *Ufimia alternans* de Groot, 1963, RGM 112535, holotype. (a) Neanic growth stage. (b) Mature growth stage. Both $\times 5$.

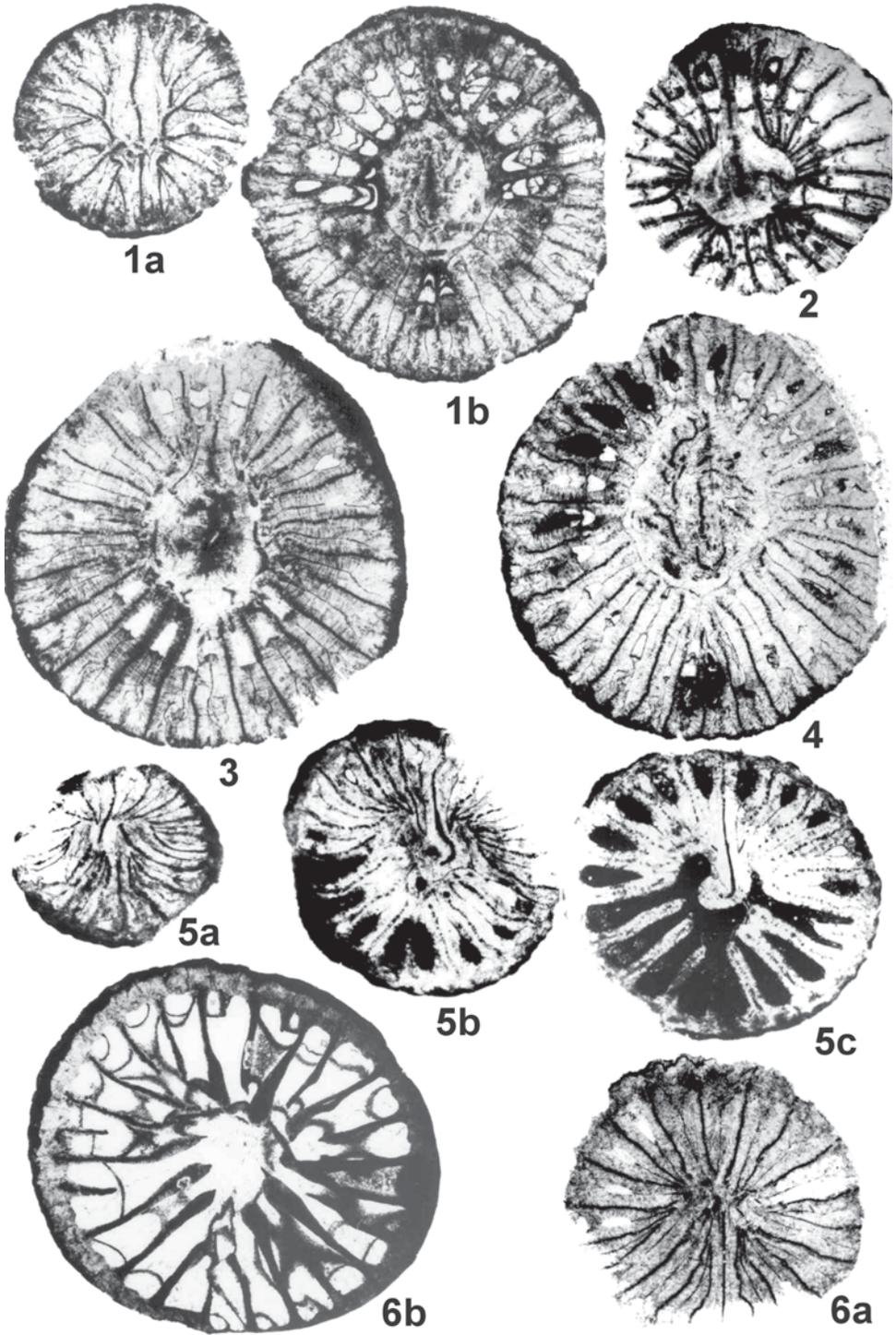


Plate 8

Transverse thin sections.

Figs. 1-7. *Lophophyllidium* (*Lophbillidium*) *breimeri* de Groot, 1963.

Figs. 1-2, 5-6. RGM 112553, holotype.

Fig. 1. Microstructure of inner part of complex columella.

Fig. 2. Cardinal septum with trabeculae at periphery, strong diagenetic alterations in the middle and "dark line" in the inner part.

Fig. 5. Trabecular microstructure of primary septum diagenetically altered in part.

Fig. 6. Biform reduction of minor septa. $\times 10$.

Figs. 3-4. RGM 112558.

Fig. 3. Inner part of complex columella. $\times 10$.

Fig. 4. Trabecular microstructure of septum strongly diagenetically altered in left part.

Fig. 7. RGM 112557, biform reduction of minor septa next to counter septum. Sections of tabulae proof biform tabularium. $\times 10$.

All figures $\times 50$ unless stated otherwise.

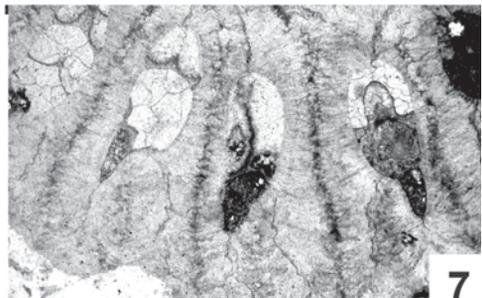
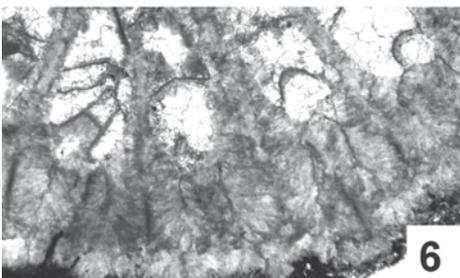
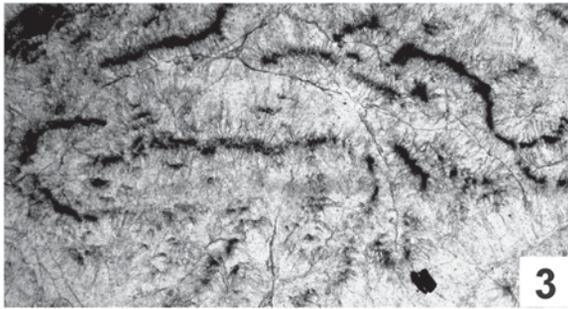
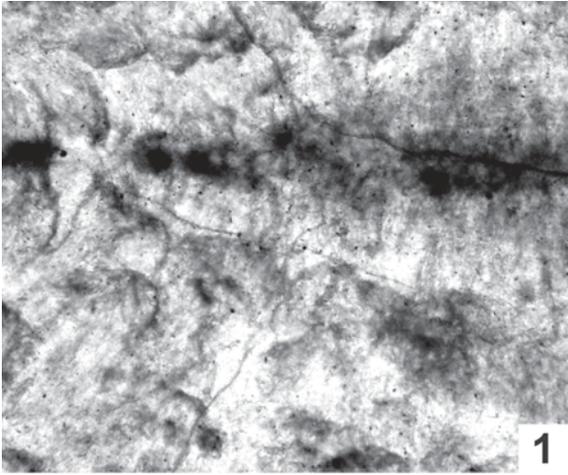


Plate 9

Figs. 1-3. Gen. et sp. indet., RGM 112515, transverse sections.

Figs. 1-2. Diagenetic alterations of originally trabecular microstructure of major septa. $\times 50$.

Fig. 3. Peripheral part of corallite showing biform morphology of tabularium and septothecal external wall. $\times 10$.

Figs. 4-6. *Mirka histiophylloides* (de Groot, 1963), RGM 112652, holotype.

Fig. 4. Transverse section showing duplicated major septa. $\times 20$.

Fig. 5. Transverse section showing diagenetic alterations of microstructure in major septum. $\times 50$.

Fig. 6. Longitudinal section, rudiments of finely trabecular microstructure. $\times 50$.

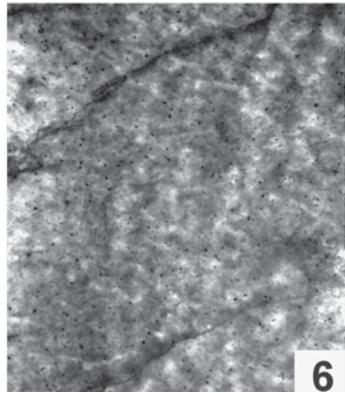
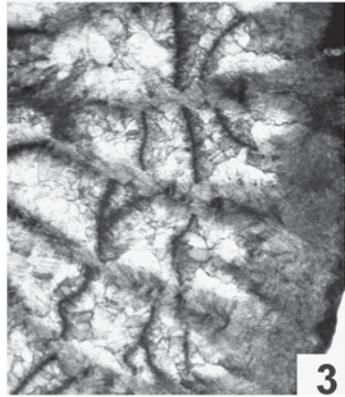
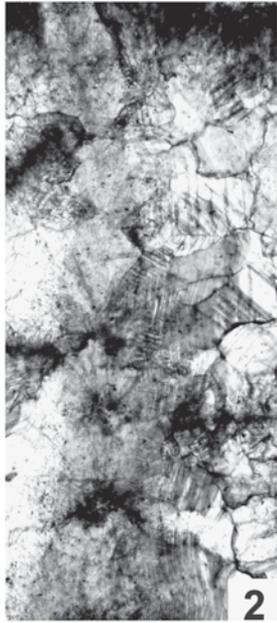
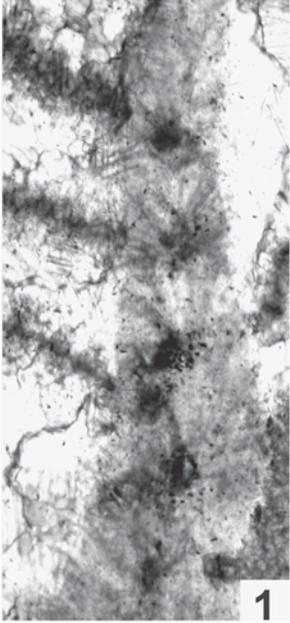


Plate 10

Figs. 1-6. *Mirka histiophylloides* (de Groot, 1963).

Figs. 1-5. RGM 112652, holotype. Transverse sections.

Fig. 1. Fragmented part of major septum. $\times 50$.

Fig. 2. Longitudinally split part of major septum. $\times 50$.

Figs. 3-4. Disintegrated major septa (4) with and (3) without carinae. Both $\times 15$.

Fig. 5. Transverse section of mature growth stage. $\times 2$.

Fig. 6. RGM 112653, eccentric longitudinal section. $\times 2$.

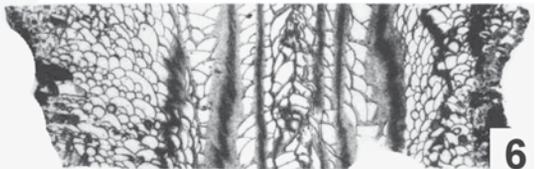
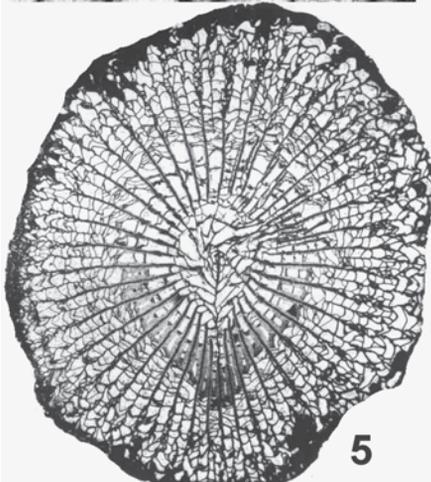
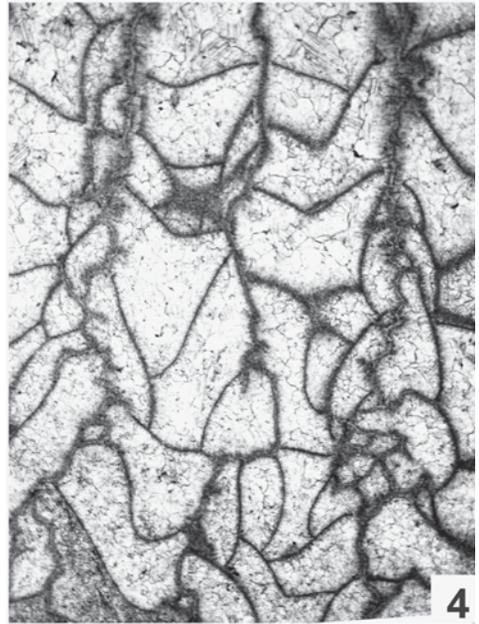
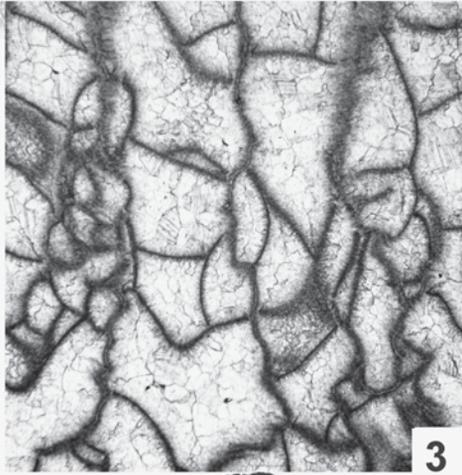
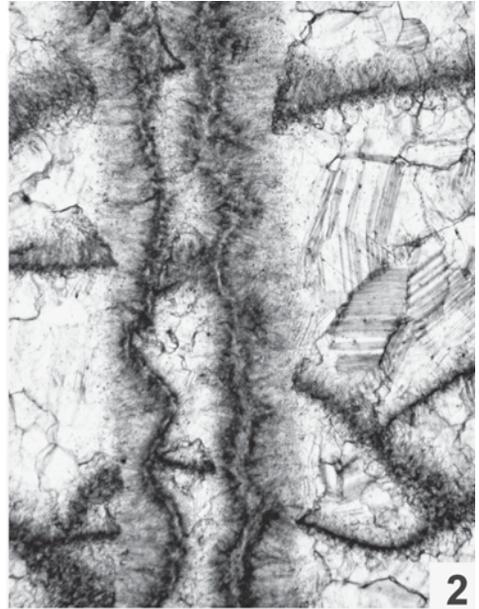


Plate 11

Figs. 1-6. *Nervophyllum* sp., RGM 112622.

Fig. 1. Transverse section; microstructure of septum strongly altered diagenetically. $\times 50$.

Fig. 2. Oblique longitudinal section showing rudiments of fine trabeculae. $\times 50$.

Fig. 3. Oblique longitudinal section. $\times 3$.

Fig. 4. Transverse section just above rejuvenation. $\times 3$.

Figs. 5-6. Axial structure (5) prior to and (6) after rejuvenation. Both $\times 15$.

Fig. 7. *Asturiphyllum semenoffi* Rodriguez, 1984, RGM 112621. Biform tabularium in transverse section. $\times 15$.

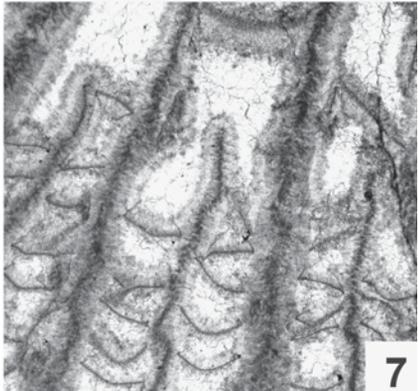
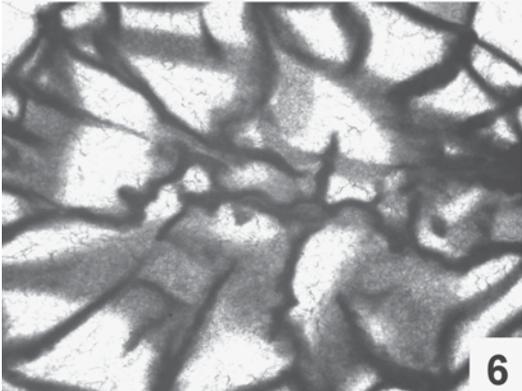
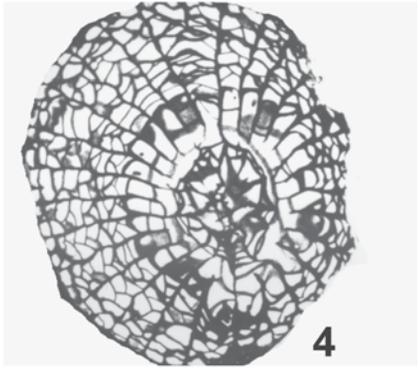
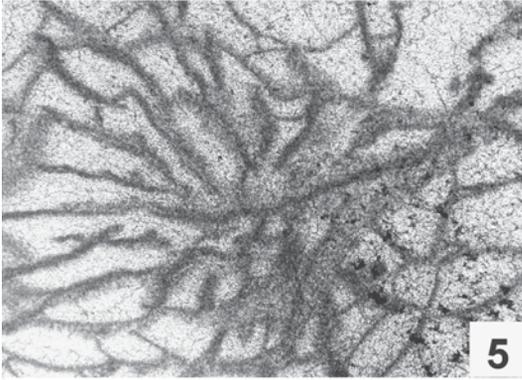
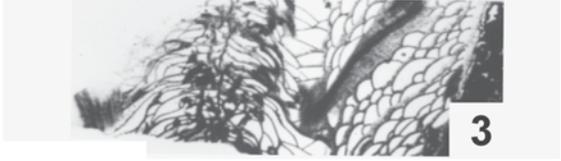
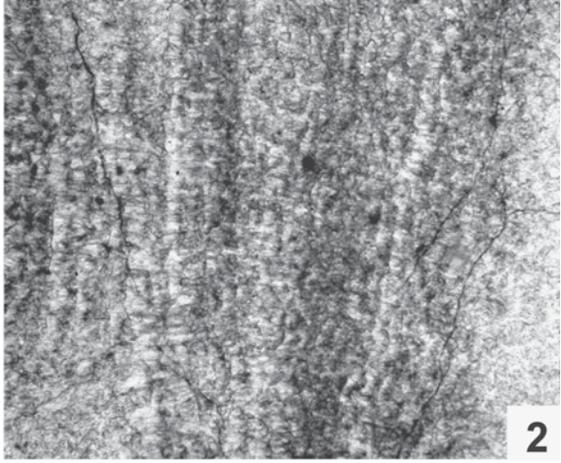


Plate 12

Figs. 1-7. *Asturiphyllum semenoffi* Rodriguez, 1984, RGM 112621.

Figs. 1, 2, 6. Transverse sections.

Figs. 1, 2. Fragments of axial structure with extra septal lamellae (2) and median lamella prolonging into cardinal septum. Both $\times 20$.

Fig. 6. Mature growth stage. $\times 2.5$.

Figs. 3-5, 7. Longitudinal sections.

Figs. 3, 4. Biform tabularium with dissepiment-like and curved tabulae (3, left) and clinotabellae-like tabulae in Position I transparent through stereoplasmic sheet of septum (4, right). Both $\times 20$.

Fig. 5. Mature growth (oblique). $\times 3.5$.

Fig. 7. Remnants of trabeculae. $\times 100$.

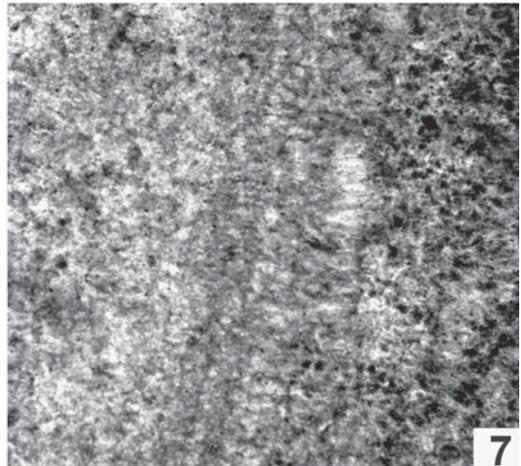
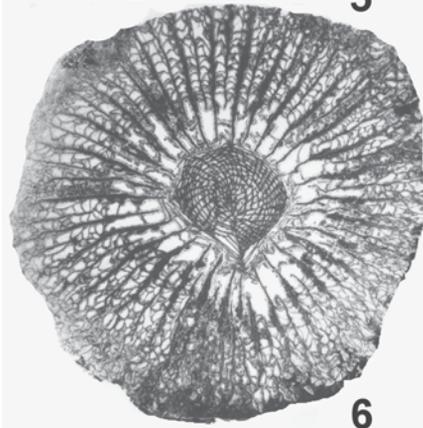
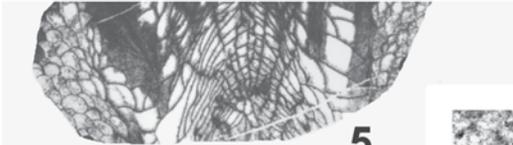
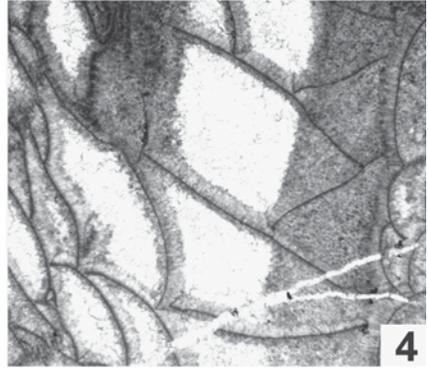
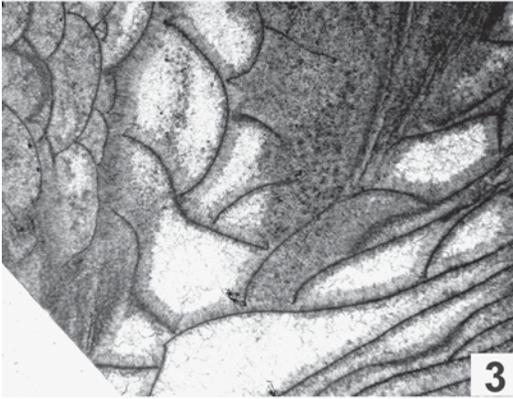
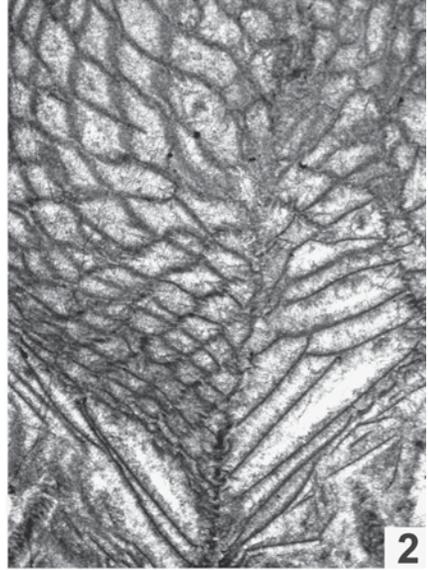


Plate 13

Figs. 1-7. *Dibunophyllum(?) gentisae* (de Groot, 1963), RGM 112643.

Figs. 1, 3-6. Transverse sections.

Fig. 1. Mature growth stage. $\times 2$.

Figs. 3-4. Various diagenetic alterations of major septa. $\times 50$.

Figs. 5, 6. Axial structure; immature (5) and mature (6). $\times 100$

Fig. 2. Longitudinal section. $\times 2$.

Fig. 7. Rudiments of trabeculae intersecting few strong growth lines in longitudinal section. $\times 50$.

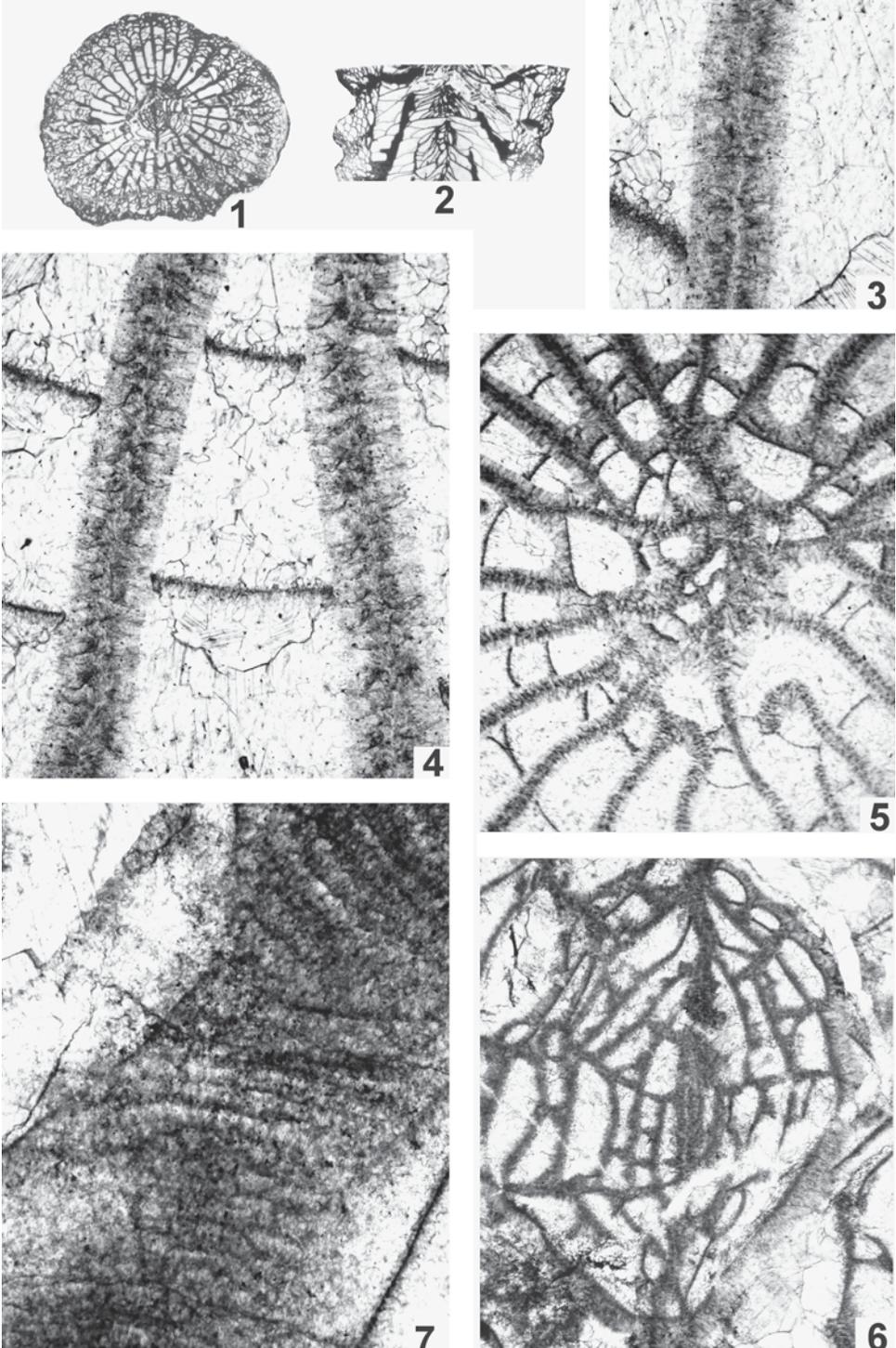


Plate 14

Figs. 1-6. *Corwenia cantabrica* de Groot, 1963. Transverse sections.

Figs. 1-3. RGM 112678, holotype.

Fig. 1. Axial structure. $\times 50$.

Fig. 2. Offsetting corallite. $\times 15$.

Fig. 3. Microstructure of incomplete neotheca. Enlarged from and positioned in the picture perpendicular to the former. $\times 50$.

Figs. 4-6. RGM 112658.

Fig. 4. Axial structure. $\times 50$.

Fig. 5. Immature corallite. Axial structure and connection to the parent corallite (down). $\times 15$.

Fig. 6. Mature corallite. Arrangement of tabulae indicating bifiform tabularium. $\times 15$.

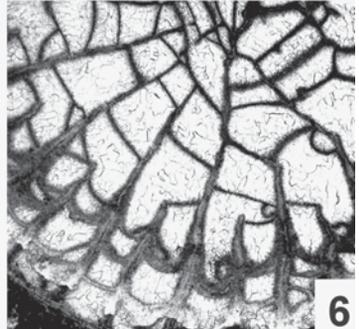
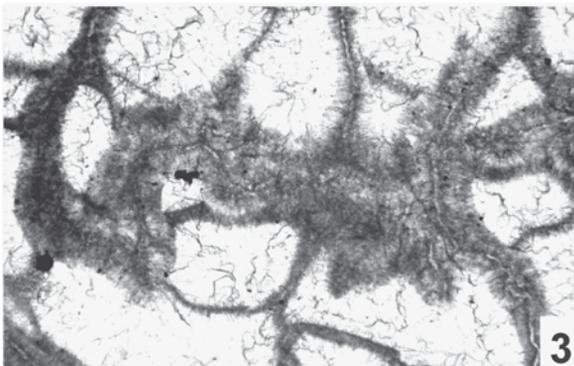
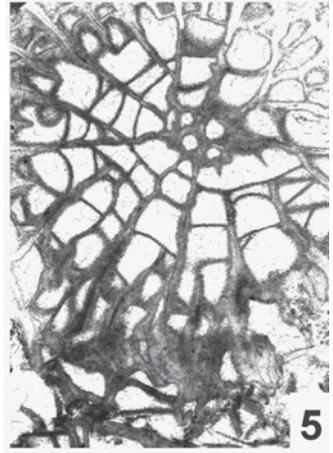
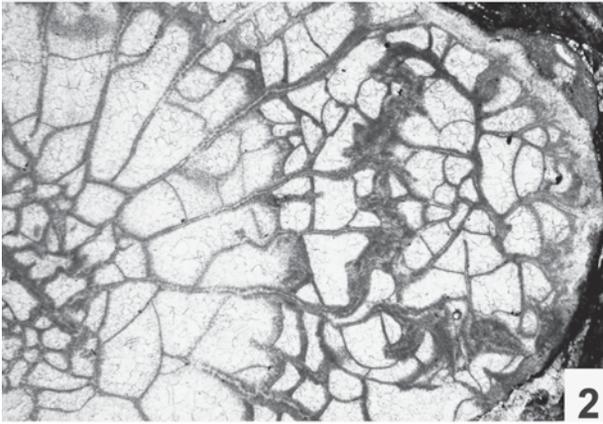
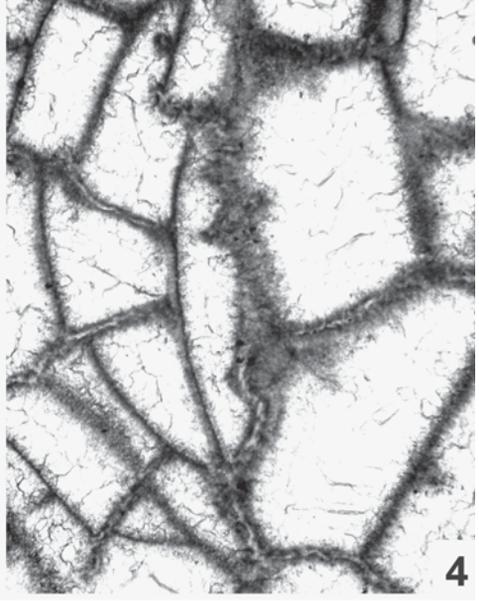
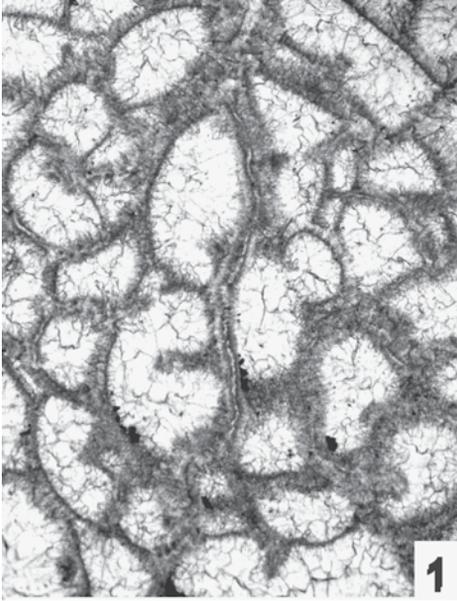


Plate 15

Figs. 1-8. *Corwenia cantabrica* de Groot, 1963.

Figs. 1-3, 8. RGM 112678, holotype.

Fig. 1. Transverse section of fragment of colony. $\times 5$.

Fig. 2. Longitudinal section. $\times 5$.

Fig. 3. Transverse section. Prolonged connection of corallites mature in morphology. $\times 15$.

Fig. 8. Remnants of trabeculae in longitudinal section. $\times 50$.

Figs. 4-7. RGM 112667.

Fig. 4. Longitudinal section. $\times 4$,

Figs. 5-6. Transverse sections showing successive growth stages. $\times 4$.

Figs. 7. Remnants of trabeculae in longitudinal section. $\times 50$.

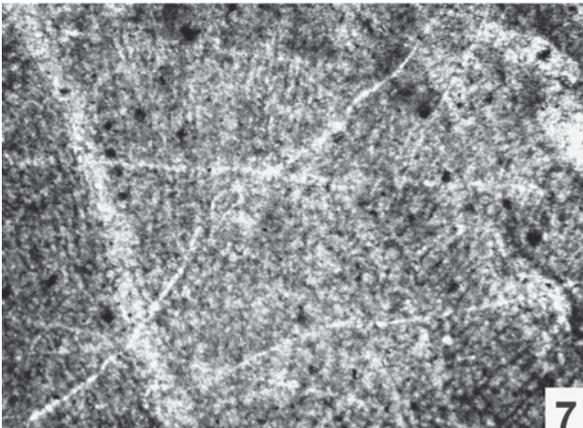
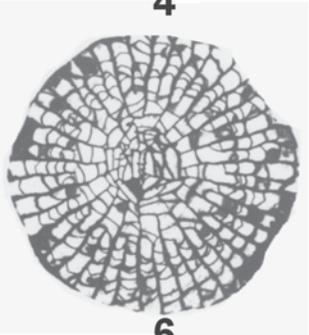
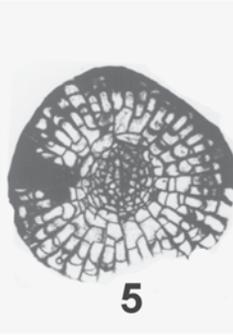
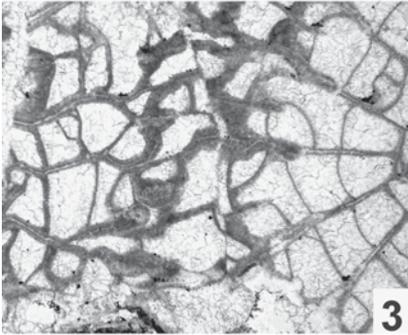
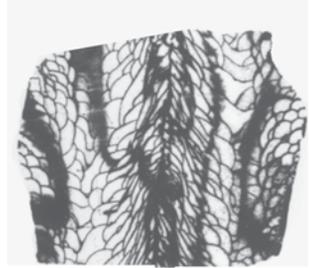
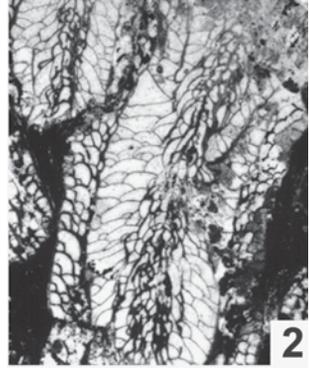
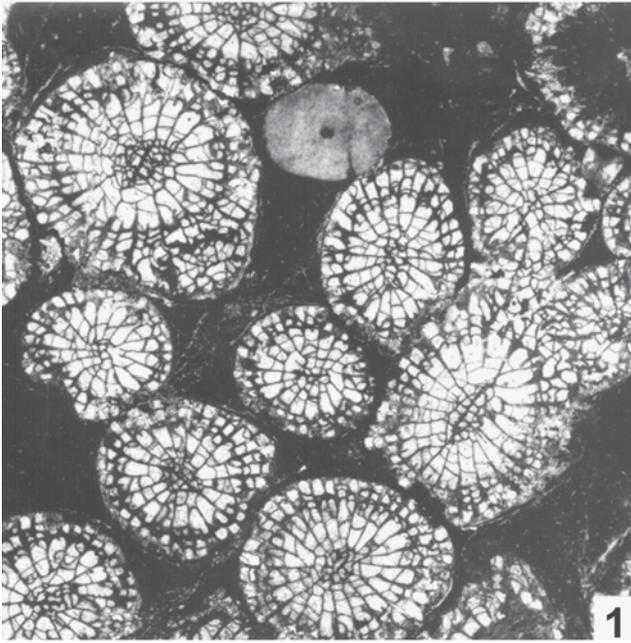


Plate 16

Figs. 1-3. *Spirophyllum multilamellatum* (de Groot, 1963), RGM 112630. Transverse sections showing microstructure of septa and its diagenetic alterations. All $\times 50$.

Figs. 4-6. *Thysanophyllum grootae* sp. nov., RGM 112600, holotype. Longitudinal sections.

Fig. 4 Diagenetic alterations in corallite wall. $\times 50$.

Figs. 5-6. Beginning of formation of neotheca. $\times 40$.

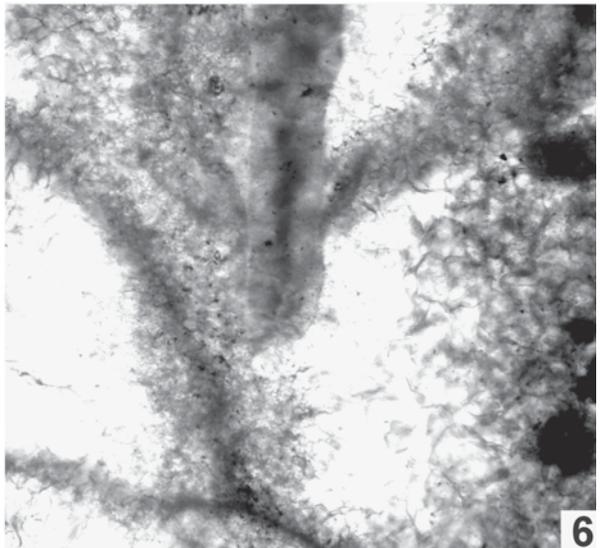
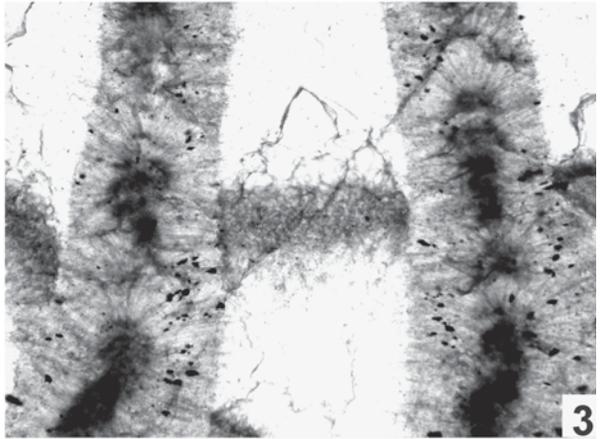
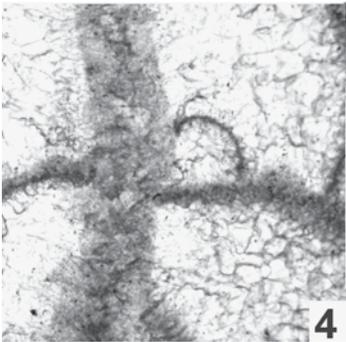
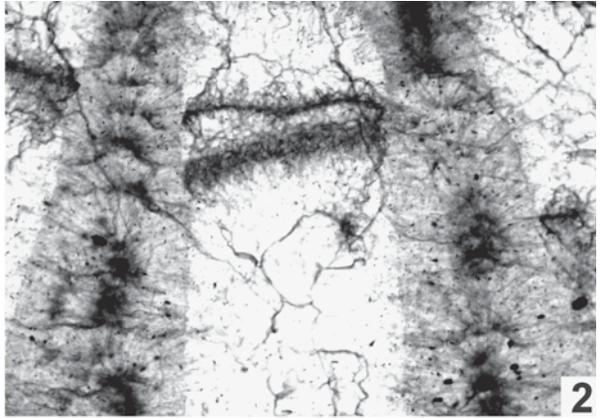


Plate 17

Figs. 1-6. *Thysanophyllum grootae* sp. nov., RGM 112600, holotype. All transverse sections except Fig. 2.

Fig. 1. Fragment of colony. $\times 5$.

Fig. 2. Longitudinal section, offsetting corallite. $\times 5$.

Fig. 3. Mature corallite with elongated counter septum. $\times 10$.

Figs. 4-5. Formation of neotheca based on septa and dissepiments. $\times 30$.

Fig. 6. Microstructure of intercorallite wall and positions of septa. $\times 50$.

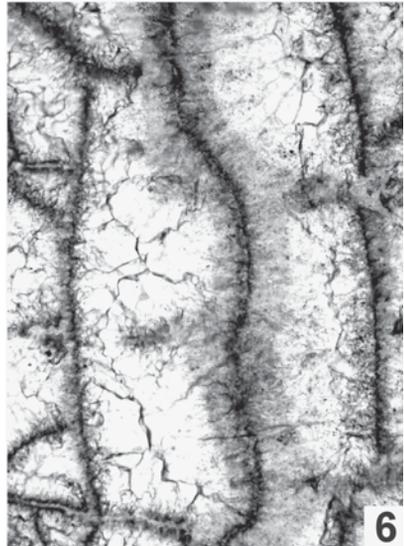
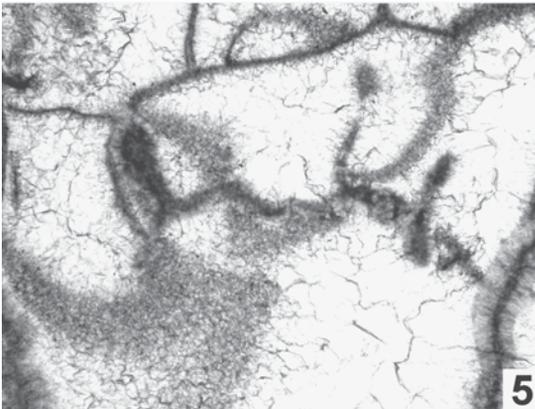
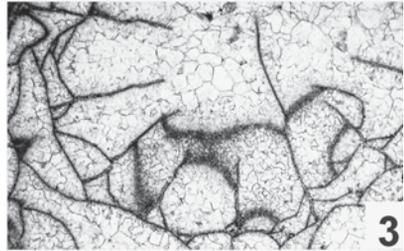
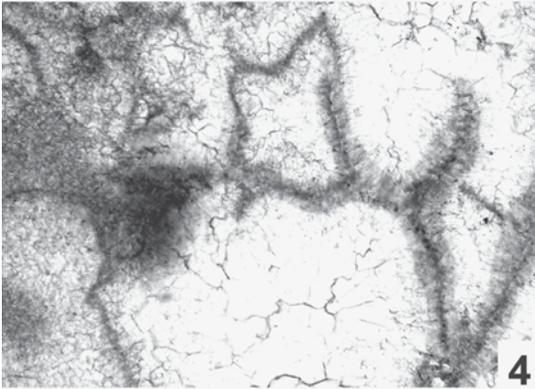
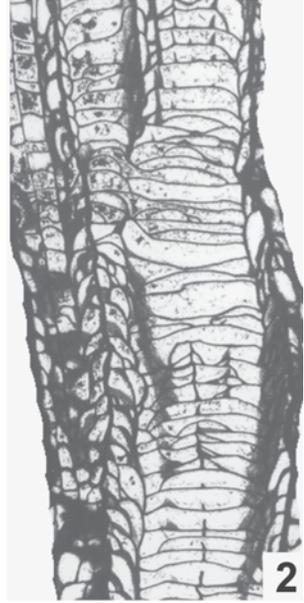
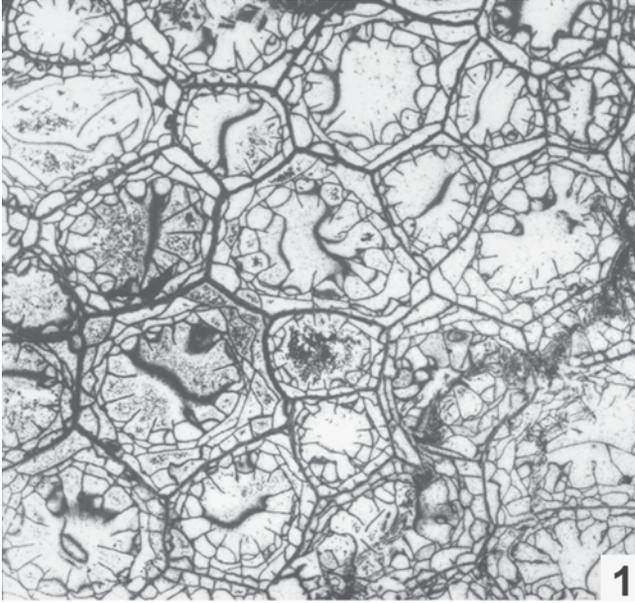


Plate 18

Figs. 1-6. *Thysanophyllum grootae* sp. nov., RGM 112600. Corallite "a". Serial transverse acetate peels through hysterobrephic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm). All $\times 15$.

Continued on Plate 19.

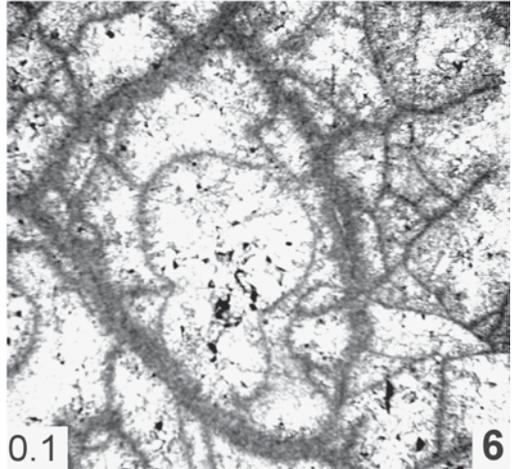
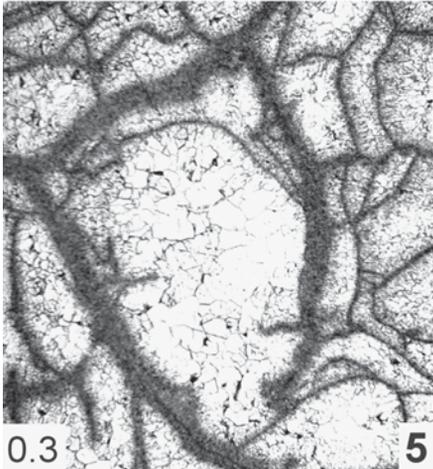
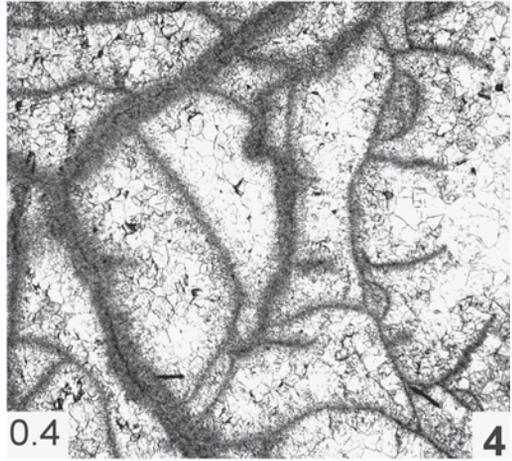
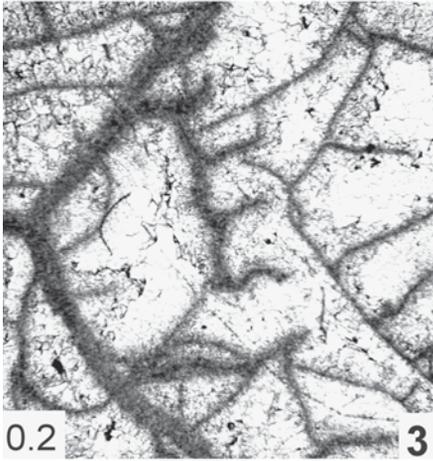
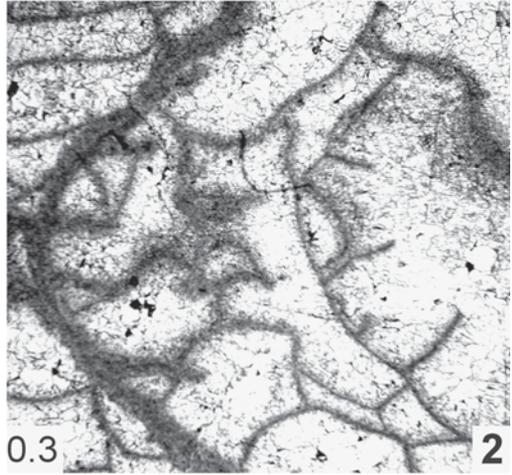
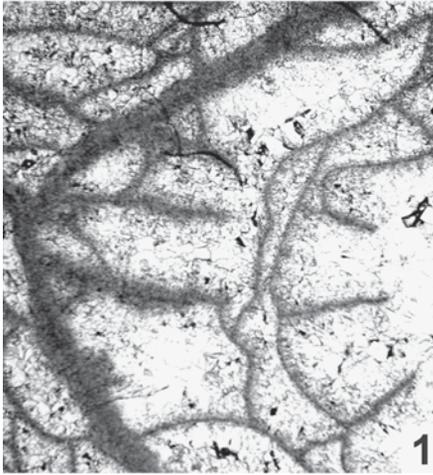


Plate 19

Thysanophyllum grootae sp. nov., RGM 112600.

Figs. 7-10 (continued from Plate 18). Corallite "a". Serial transverse acetate peels through hystero-neanic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm).

Figs. 1-2. Corallite "b". Serial transverse acetate peels through hystero-brephic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 15$. Continued on Plate 20.

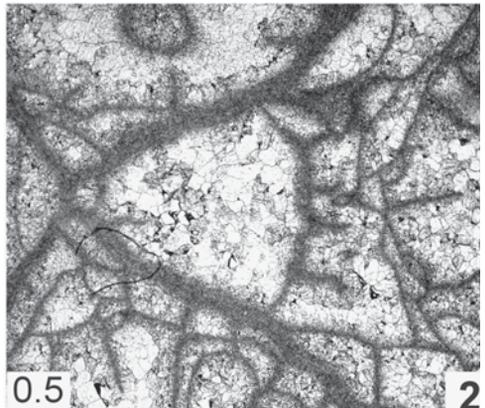
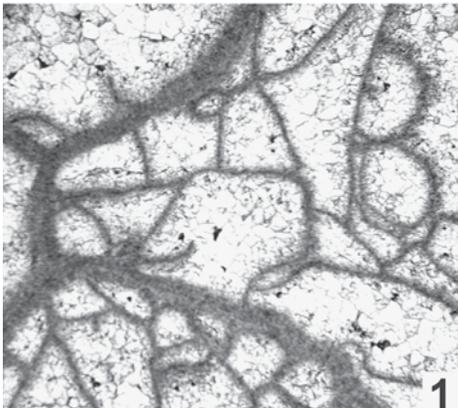
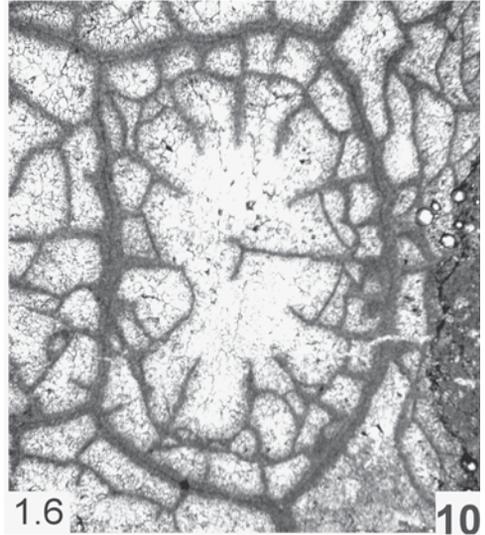
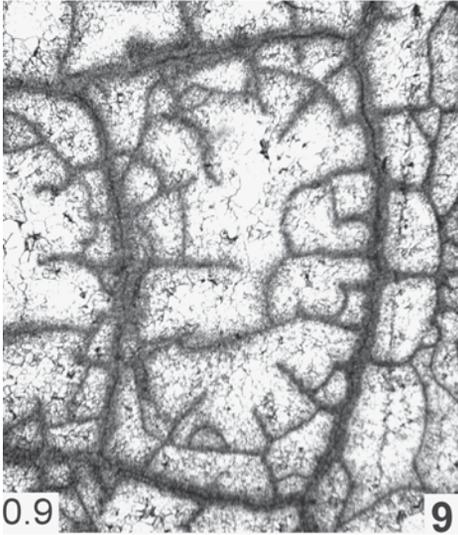
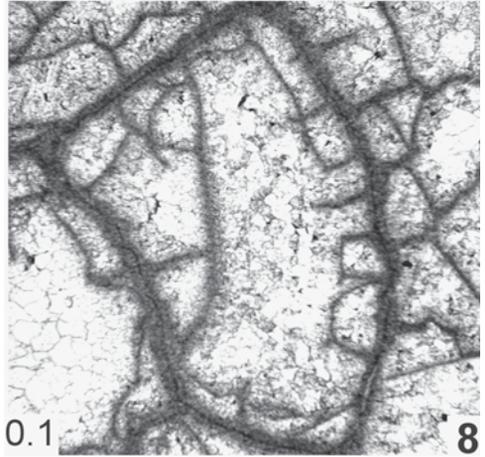
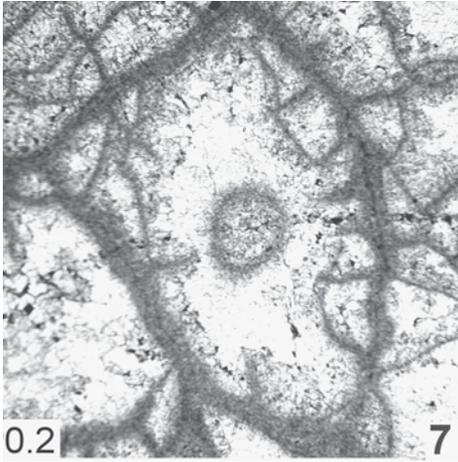


Plate 20

Figs. 3-8. *Thysanophyllum grootae* sp. nov., RGM 112600.

Figs. 1-5. Corallite "b". Serial transverse acetate peels through late hystero-brephic and hystero-neanic stages. Fig. 6. Corallite "c". Hystero-neanic stage. Numbers in lower left corners show distances between adjacent pictures (in mm). All turned 90° left by comparison to Plate 16, figs. 1-2.

All figures $\times 15$.

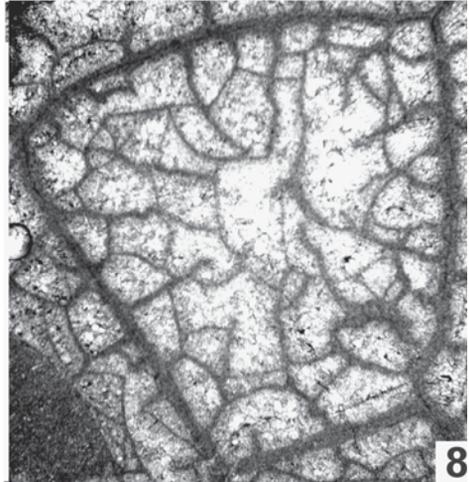
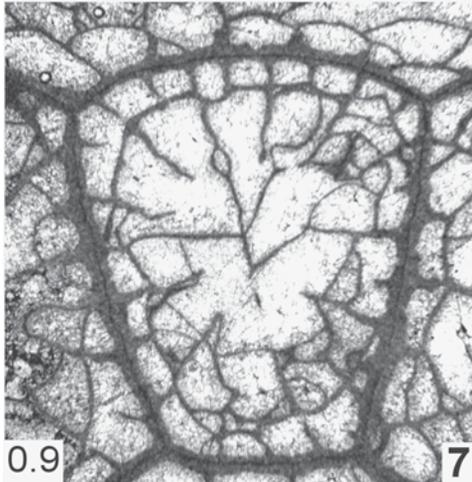
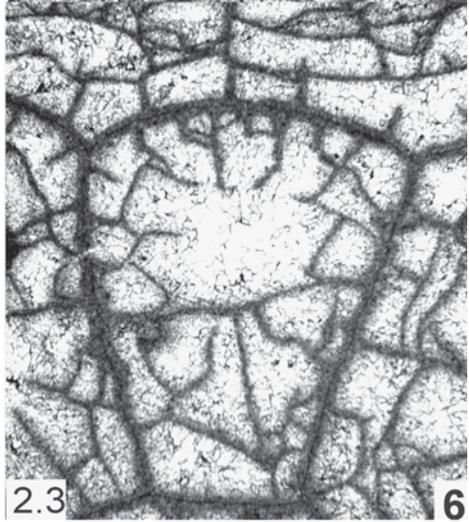
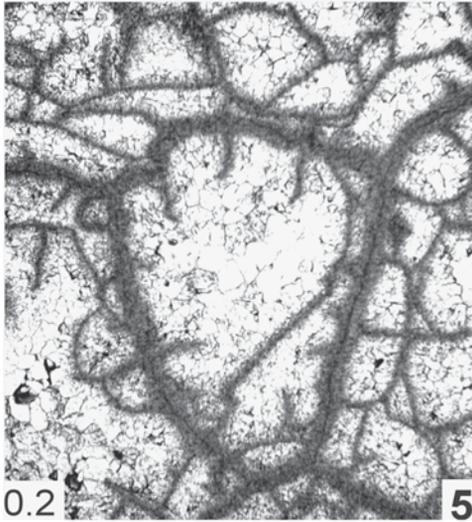
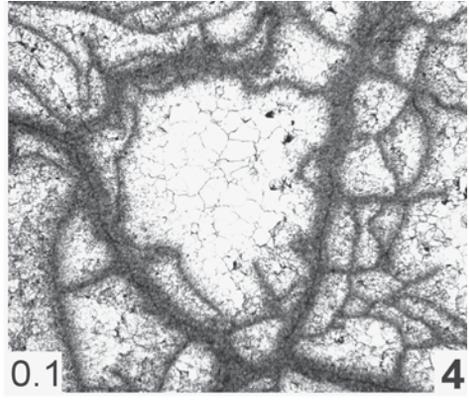
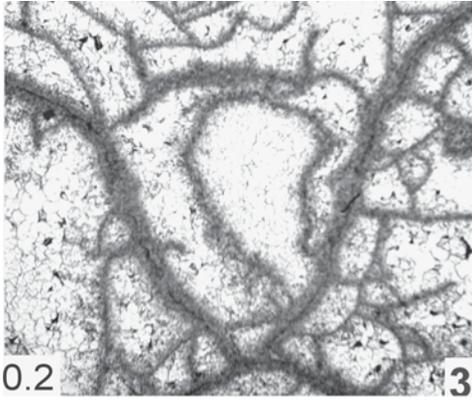


Plate 21

Figs. 1-3. *Cystolonsdaleia densiconus* (de Groot, 1963), RGM 112719, holotype.

Fig. 1. Transverse section. $\times 5$.

Fig. 2. Longitudinal section. $\times 5$.

Fig. 3. Remnants of trabecular microstructure of septum in longitudinal section. $\times 50$.

Figs. 4-7. *Petalaxis (Petalaxis) maccoyanus* (Milne Edwards & Haime, 1851), RGM 112721.

Fig. 4. Longitudinal section showing remnants of trabecular microstructure of septum. $\times 50$.

Fig. 5. Longitudinal section perpendicular to thickest part of columella with rudiments of trabeculae. $\times 50$.

Fig. 6. Mature corallite (eccentric longitudinal section). $\times 5$.

Fig. 7. Transverse section. $\times 5$.

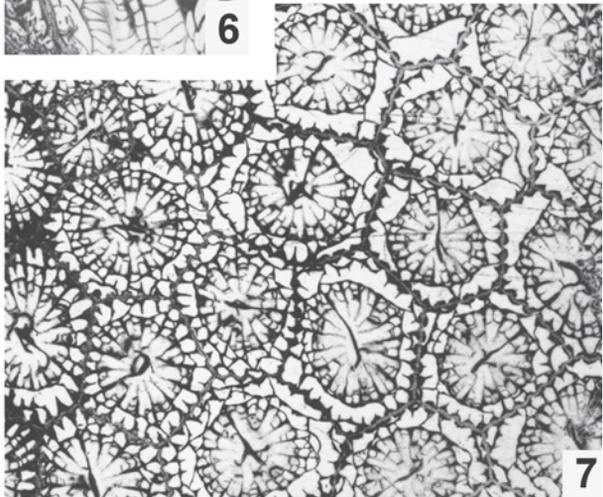
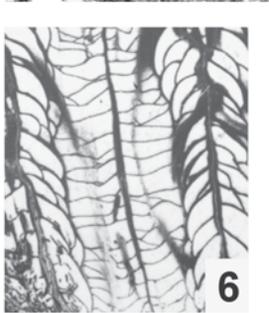
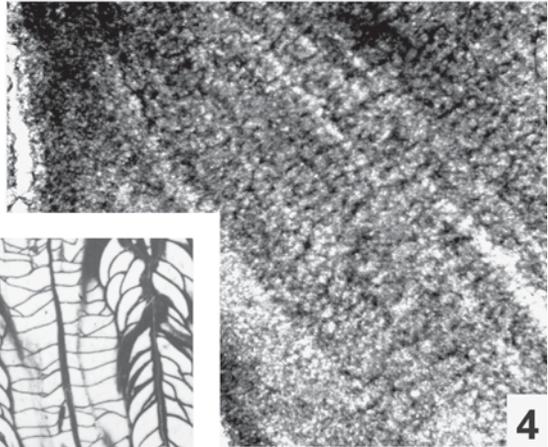
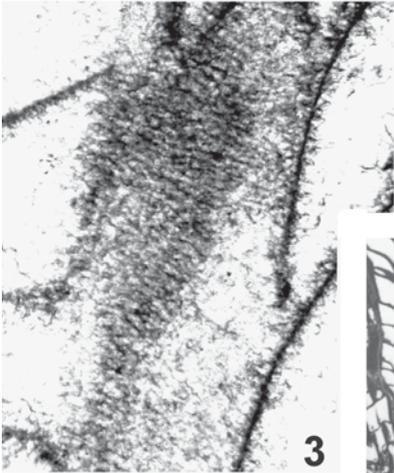
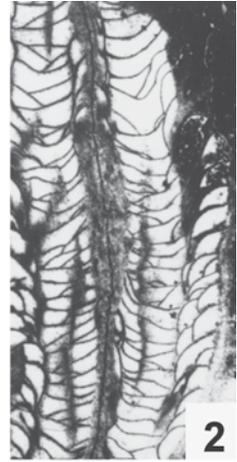
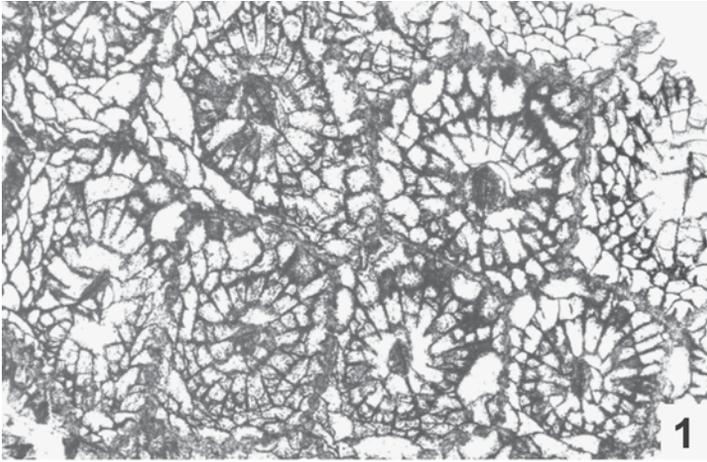


Plate 22

Figs. 1-8. *Petalaxis (Petalaxis) orboensis* (de Groot, 1963), RGM 112732, holotype. Transverse sections except where stated.

Fig. 1. Fragment of colony. $\times 4$.

Fig. 2. Longitudinal section. Morphology of tabularium altered by incorporation of strange object $\times 4$.

Fig. 3. Longitudinal section. Biform tabularium. Transmission from Position II (lower) to Position I (upper left) right and left from septum.

Fig. 4. Two neosepta and part of neotheca with remnants of probable trabecular microstructure. $\times 50$.

Fig. 5. Four layers dividing wall. $\times 50$.

Fig. 6. Shortened counter septum (left) and biform tabularium demonstrated by different number of sections of tabulae in neighbouring septal loculi.

Fig. 7. Monoseptal median lamella intersects entire axial area.

Fig. 8. Corallite with axial area free. Slightly elongated cardinal septum middle down.

All figures $\times 10$ unless stated otherwise.

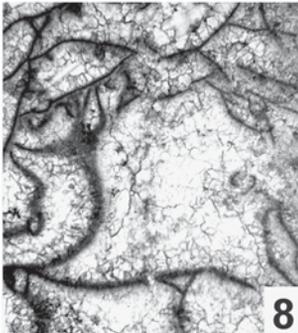
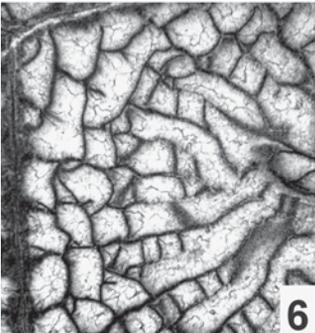
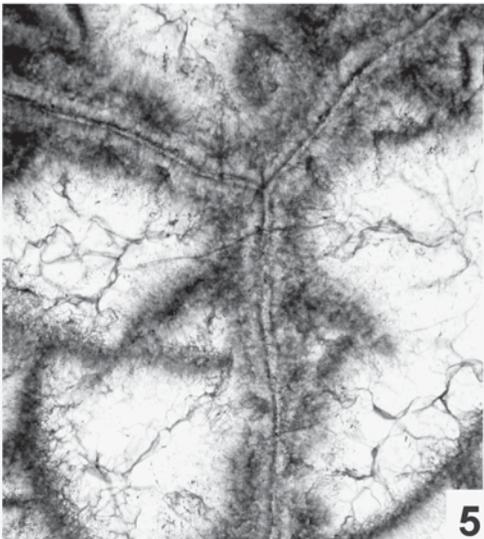
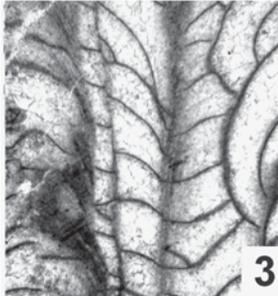
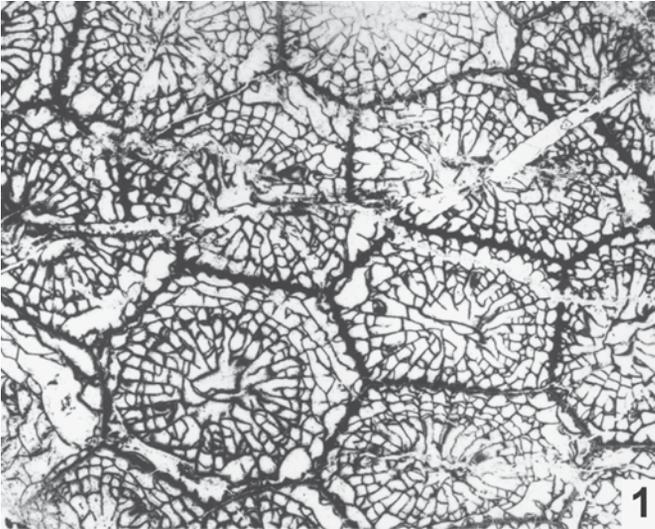


Plate 23

Figs. 1-7. ?*Petalaxis monocyclicus* (de Groot, 1963), RGM 112731, holotype. Transverse sections.

Fig. 1. Fragment of colony. $\times 4$.

Fig. 2. Rudiments of trabeculae in median lamella. $\times 50$.

Fig. 3. Wall morphology of mature (upper and right) and immature corallites.

Fig. 4. Channel through walls of adjacent corallites.

Figs. 5-7. Various developments of median lamellae; cardinal septum down.

Fig. 5. United with cardinal and counter septum.

Fig. 6. Disconnected. Both protosepta remain long.

Fig. 7. Disconnected cardinal septum surrounds columella right side; counter septum equal to major septa.

All figures $\times 15$ unless stated otherwise.

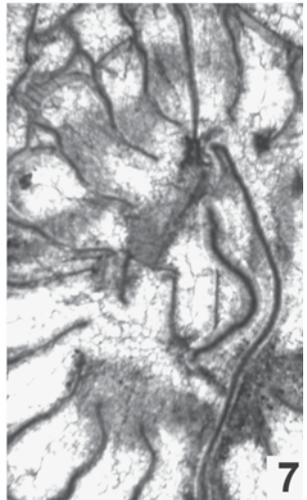
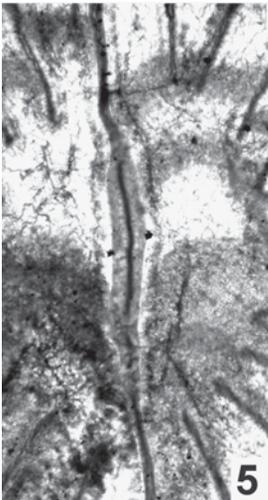
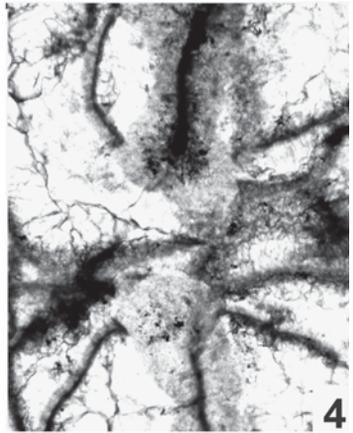
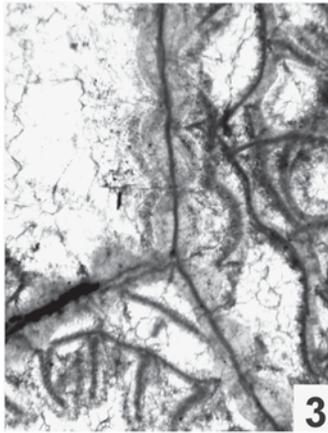
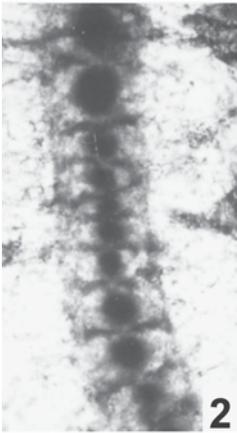
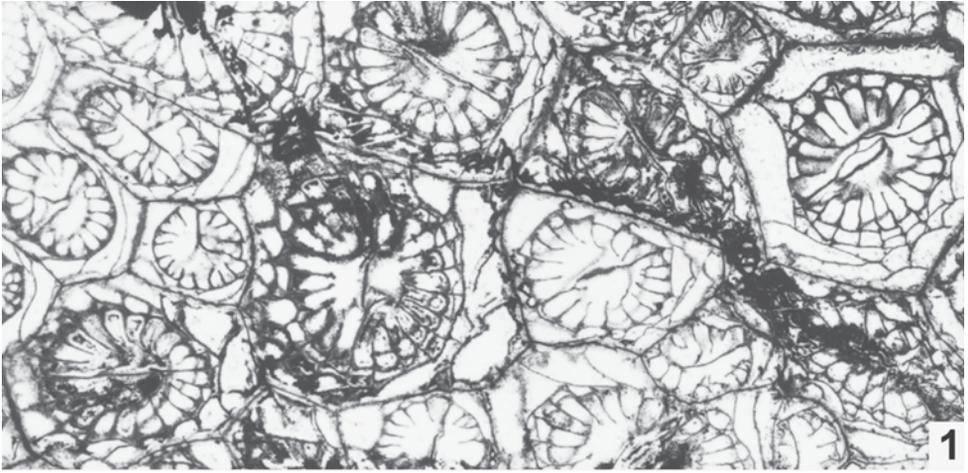


Plate 24

Figs. 1-3. *Wentzellophyllum* sp., VP 10-3. Pho Bang area, Vietnam, Upper Permian. Transverse sections of densely and weakly packed septotheca.

Figs. 4-6. *Petalaxis (Degrootia) cantabrica* (de Groot, 1963). Transverse sections.

Fig. 4. RGM 112754. Partition with peripheral parts of septa almost in lateral contiguity. Part of partition common for adjacent corallites altered diagenetically (light). $\times 35$.

Figs. 5-6. RGM 112752, holotype. Septotheca with peripheral parts of septa in lateral contiguity. (5) $\times 35$.

All figures $\times 50$ unless stated otherwise.

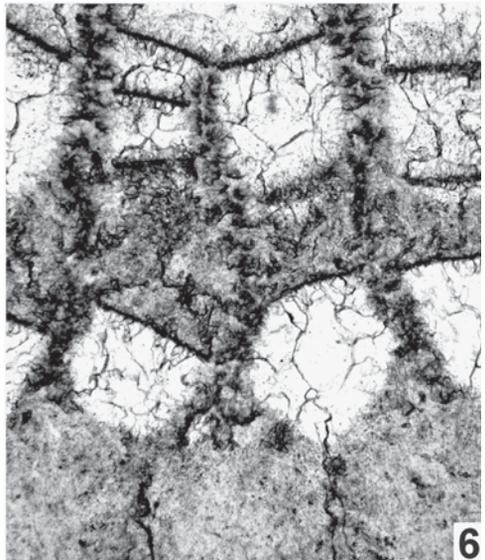
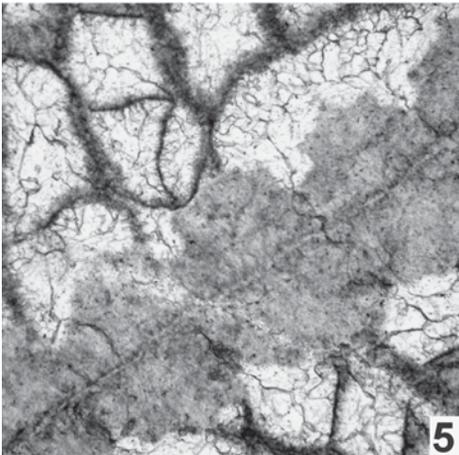
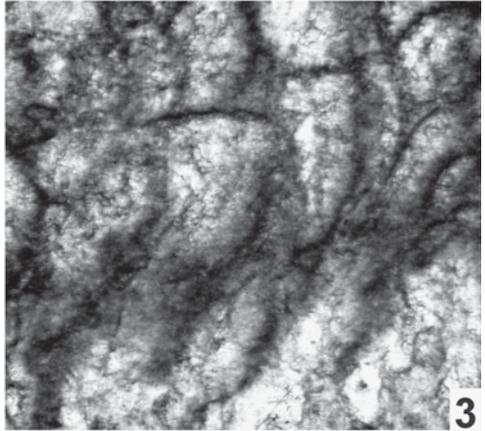
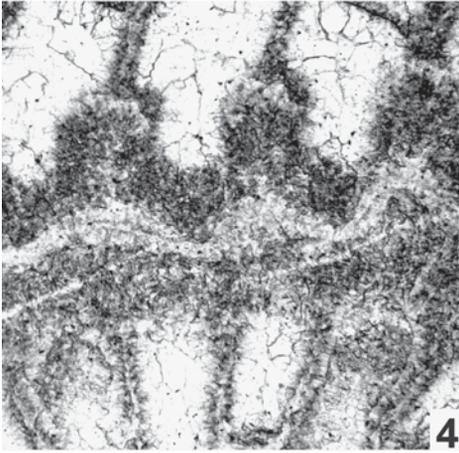
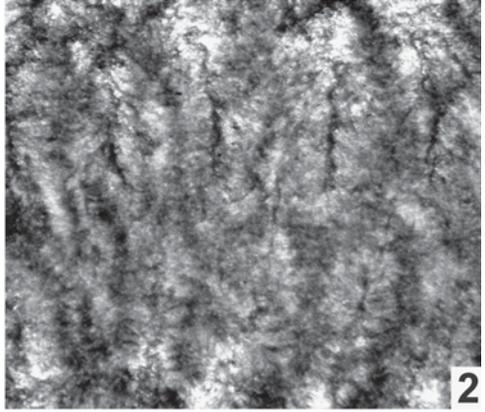


Plate 25

Figs. 1-4. *Petalaxis (Degrootia) cantabrica* (de Groot, 1963). Transverse sections showing different morphologies of median lamellae.

Figs. 1-2. RGM 112754.

Figs. 3-4. RGM 112752, holotype.

All figures $\times 40$.

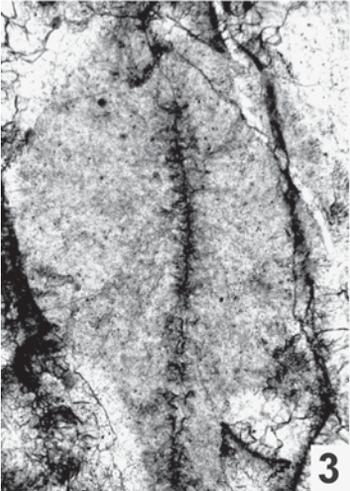
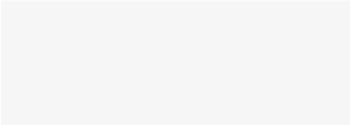
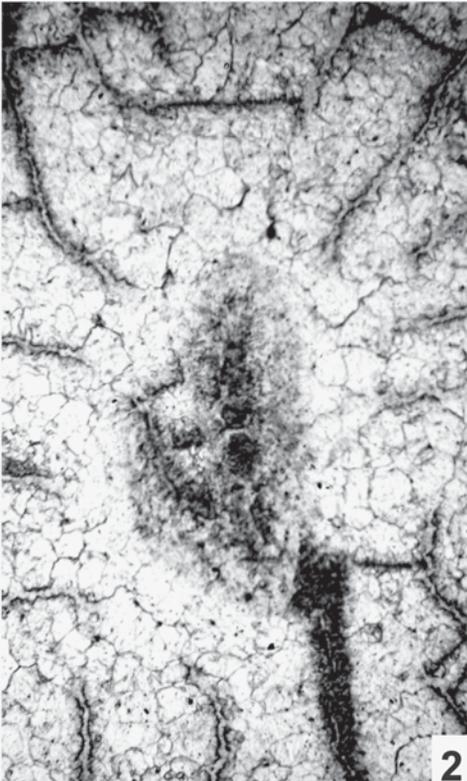


Plate 26

Figs. 1-6. *Petalaxis (Degrootia) cantabrica* (de Groot, 1963).

Fig. 1. RGM 112754. Remnants of trabecular microstructure in longitudinal section.

Figs. 2-6. RGM 112752, holotype.

Fig. 2. Transverse section. Half-moon bases of septa in sinuous septotheca. $\times 35$.

Fig. 3. Longitudinal section perpendicular to thickness of columella.

Fig. 4. Longitudinal section perpendicular to thickness of partition (left) and along middle of septum (right) showing remnants of trabeculae.

Fig. 5. Median lamella (lower) and neotheca of offset.

Fig. 6. Splitted neotheca of offset (middle in picture).

All figures $\times 50$ unless stated otherwise.

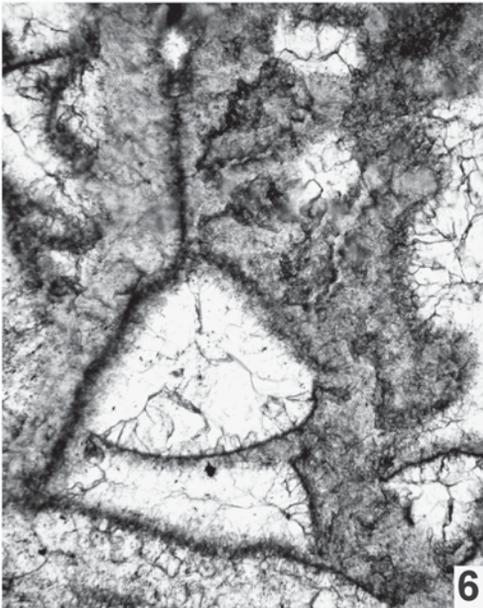
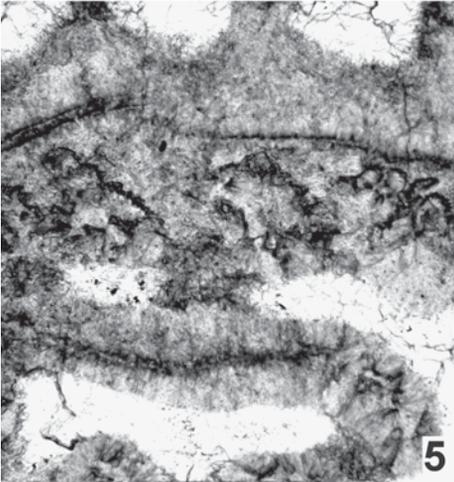
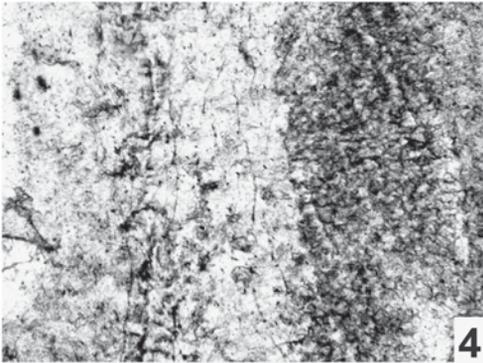
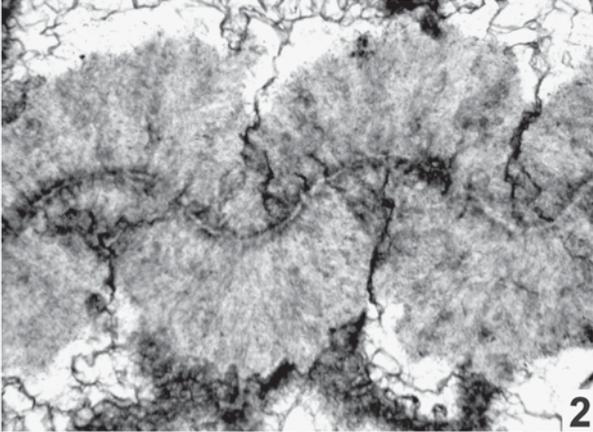
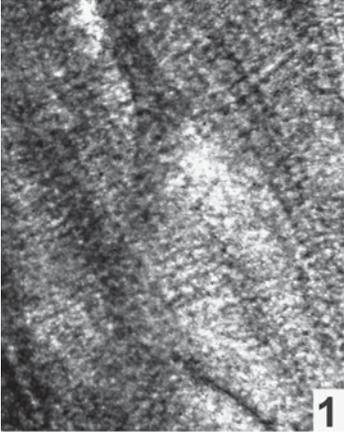


Plate 27

Figs. 1-8. *Petalaxis (Degrootia) cantabrica* (de Groot, 1963), RGM 112752, holotype. Serial transverse acetate peels through hystero-brephic (1-5) and hystero-neanic (6-8) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 12$.

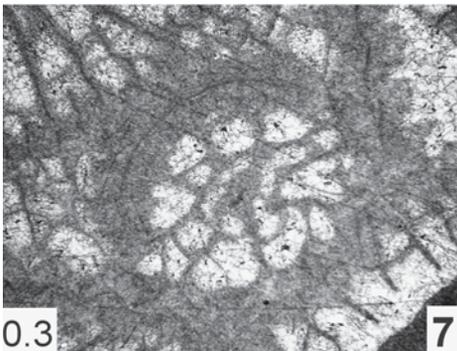
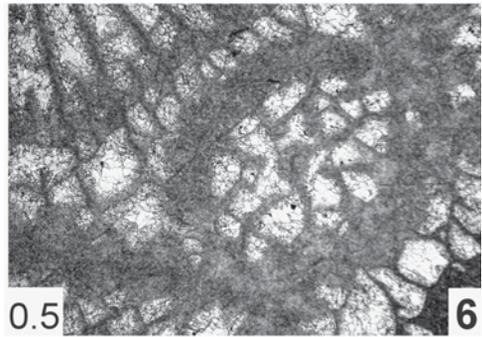
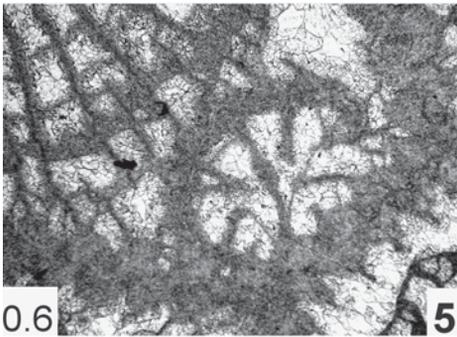
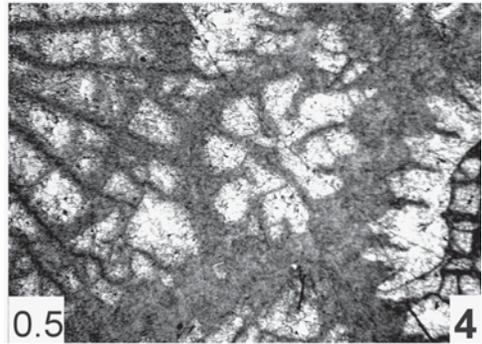
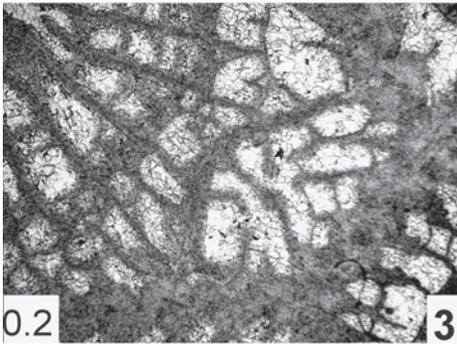
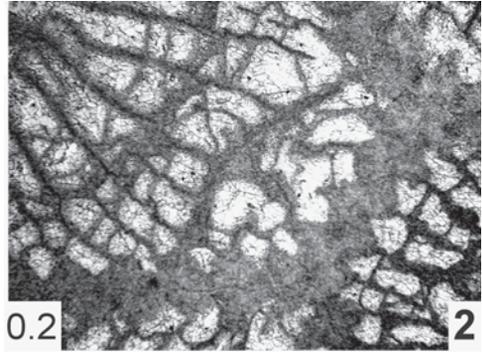
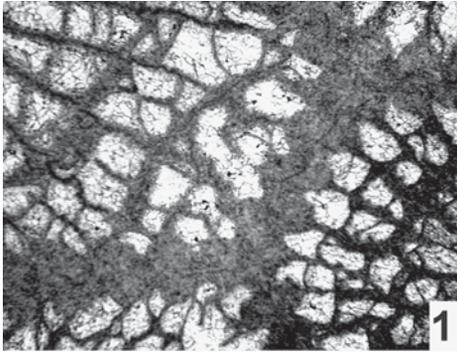


Plate 28

Figs. 1-9. *Petalaxis (Degrootia) cantabrica* (de Groot, 1963), RGM 112752, holotype. Transverse sections except where stated.

Figs. 1-2. Fragments of colony. $\times 4$.

Fig. 3. Slightly oblique longitudinal section. $\times 4$.

Figs. 4-9. Hystero-brephic (4-6) and hystero-neanic (7-9) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm). All $\times 12$.

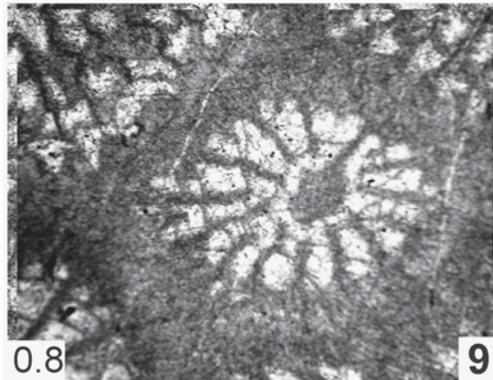
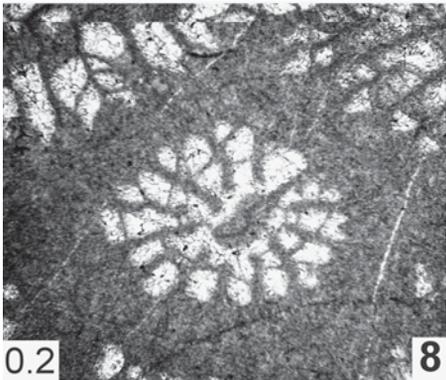
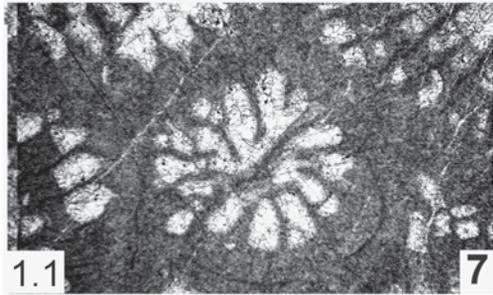
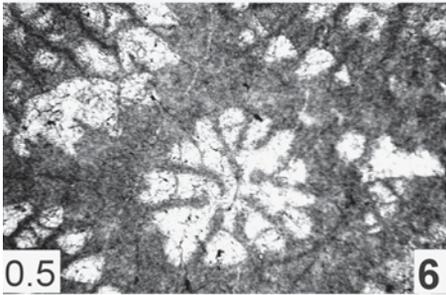
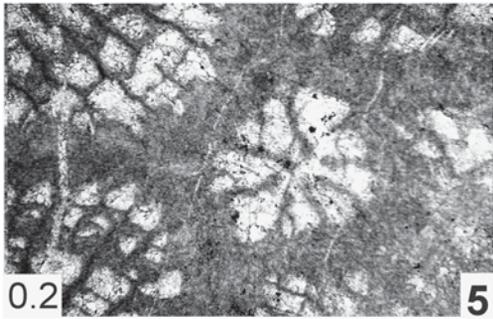
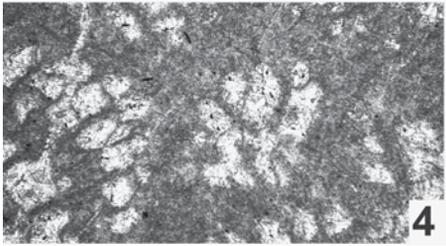
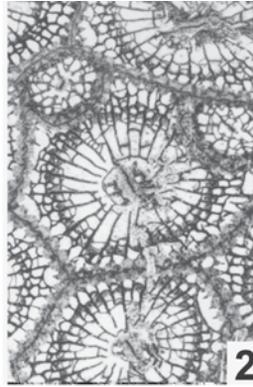
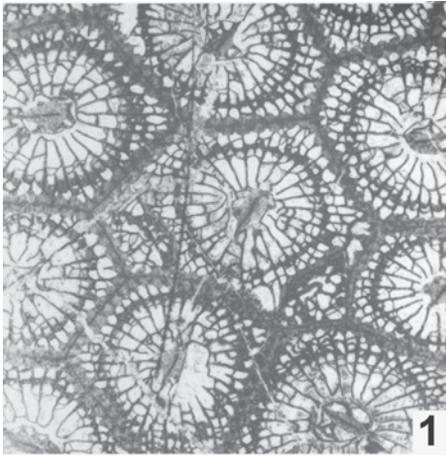


Plate 29

Figs. 1-6. *Petalaxis (Degrootia) perapertuensis* (de Groot, 1963), RGM 112743, holotype.

Figs. 1-2. Longitudinal sections perpendicular to thickness of partition (1) and median lamella (2). Both expose essentially the same microstructure. Slightly eccentric section of septum (1, right) shows rudiments of trabeculae. Both $\times 50$.

Fig. 3. Longitudinal section. Tabulae in Position I (lower left) and Position II elsewhere. $\times 6$.

Figs. 4-6. Transverse sections. Microstructure of partition from septal (4) through partly (5) to mostly sclerenchymal (6). All $\times 30$.

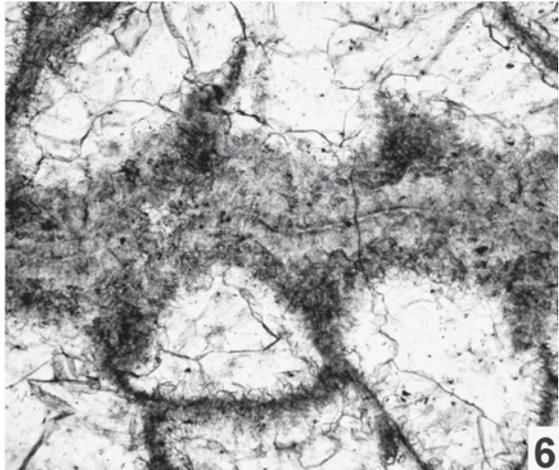
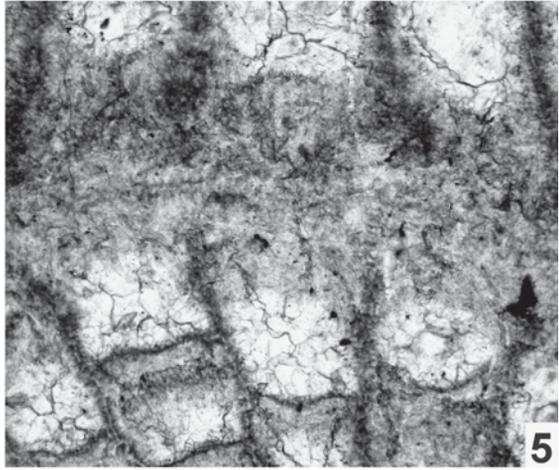
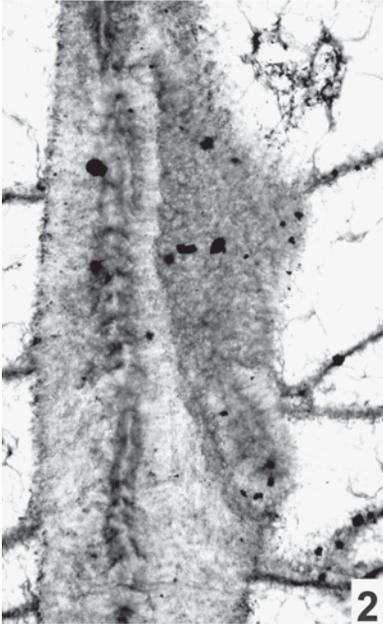
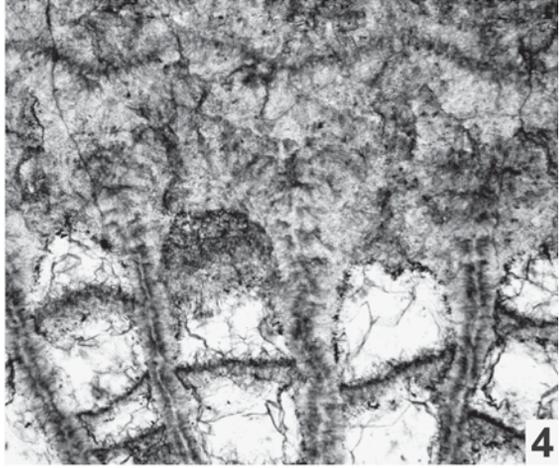
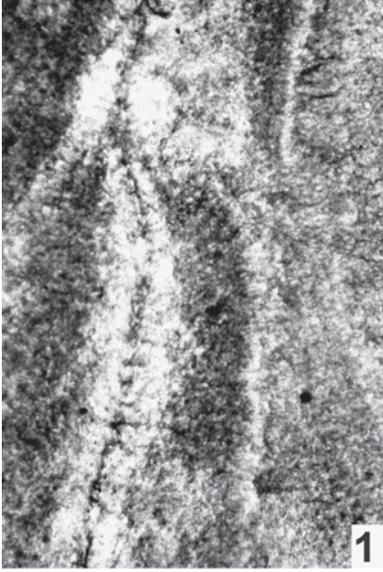


Plate 30

Figs. 1-10. *Petalaxis (Degrootia) perapertuensis* (de Groot, 1963), RGM 112743, holotype. Transverse sections except for (4).

Fig. 1. Part of colony. $\times 4$.

Fig. 2. Formation of lonsdaleoid dissepiments. $\times 20$.

Fig. 3. Biform tabularium next to counter septum. Counter-lateral minor septa very long. $\times 20$.

Fig. 4. Longitudinal section. Rudiments of very fine trabeculae. $\times 50$.

Figs. 5-10. Changes in morphology of columella in course of growth of corallite "A" (5-8) and "B" (9-10). All $\times 10$.

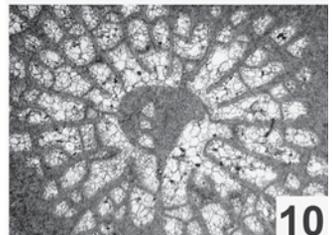
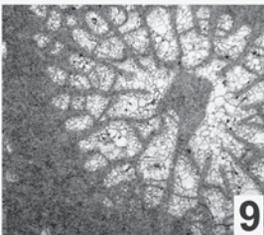
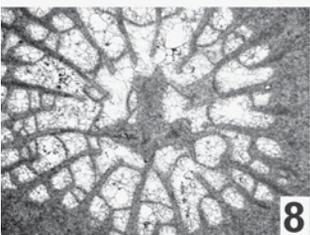
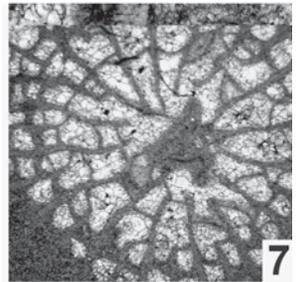
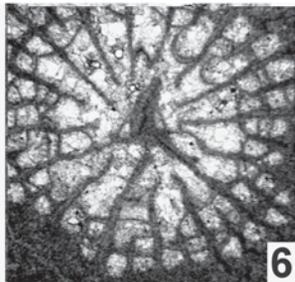
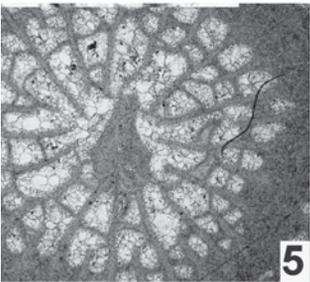
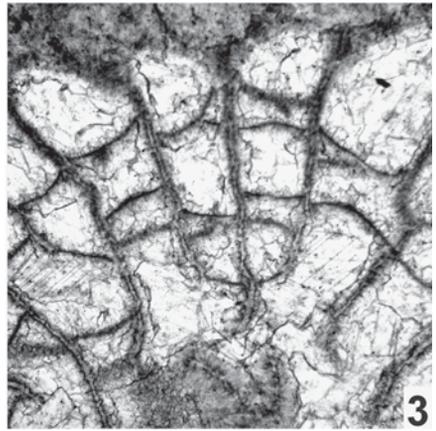
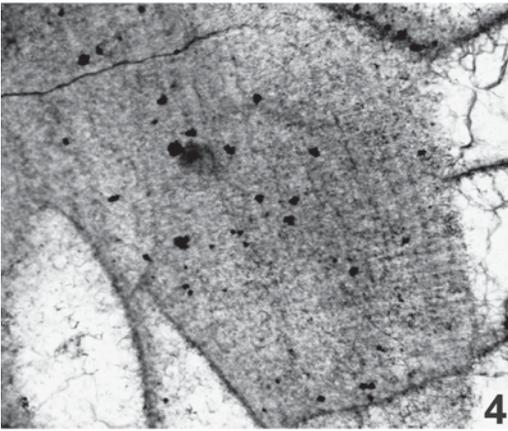
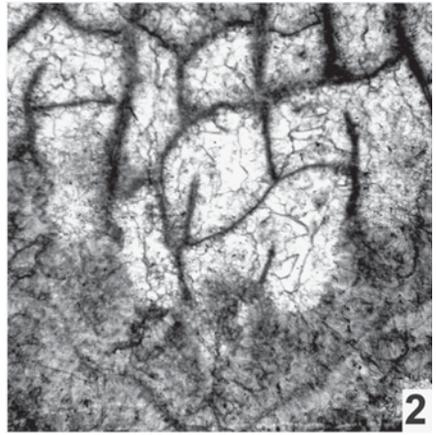
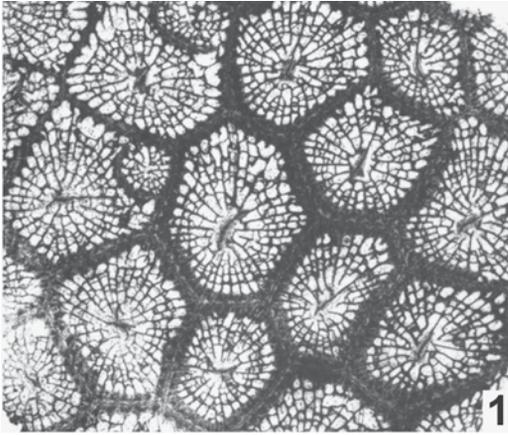


Plate 31

Figs. 1-7. *Petalaxis (Degrootia) wagneri wagneri* (de Groot, 1963). Transverse sections except (4-5).

Figs. 1, 4-7. RGM 112734, holotype.

Fig. 1. Part of colony. $\times 4$.

Figs. 4-5. Longitudinal sections. Diagenetically altered microstructure of partitions (left) and septa (right). $\times 50$.

Figs. 6-7. Diagenetically altered microstructure of partitions. $\times 50$.

Fig. 2. RGM 112744, part of colony. $\times 4$.

Fig. 3. RGM 112744, part of colony. $\times 4$.

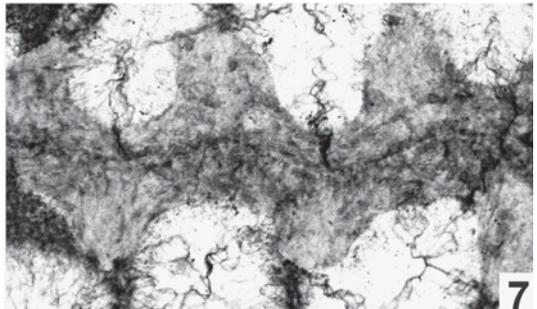
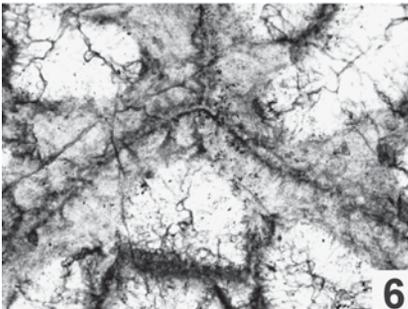
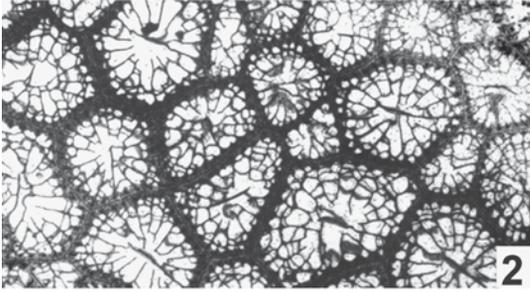
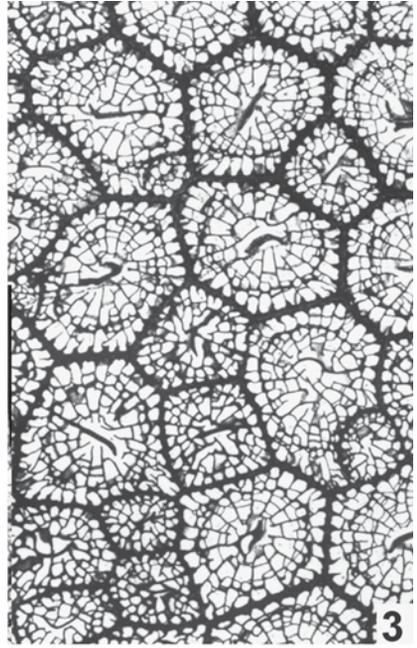
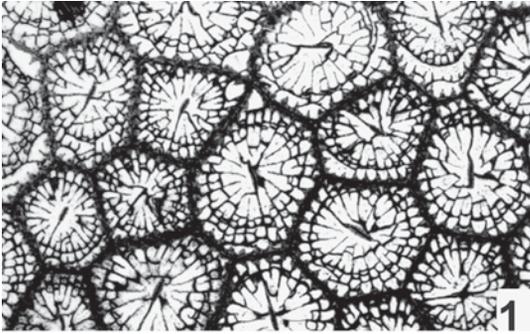


Plate 32

Figs. 1-7. *Petalaxis (Degrootia) wagneri wagneri* (de Groot, 1963), RGM 112734, holotype. Transverse sections except (7).

Fig. 1. Biform arrangement of peripheral tabulae next to cardinal septum. $\times 15$.

Fig. 2. Neanic corallite with incomplete dissepimentarium. $\times 8$.

Fig. 3. Corallite lacking median lamella. $\times 25$.

Fig. 4. Corallite with free, simple median lamella. Long cardinal septum right. $\times 25$.

Fig. 5. Diagenetically altered microstructure of septum. $\times 50$.

Fig. 6. Incomplete (left) and complete (right) partition of neighbouring offsets. $\times 50$.

Fig. 7. Eccentric longitudinal section of offset and partition (right). $\times 15$.

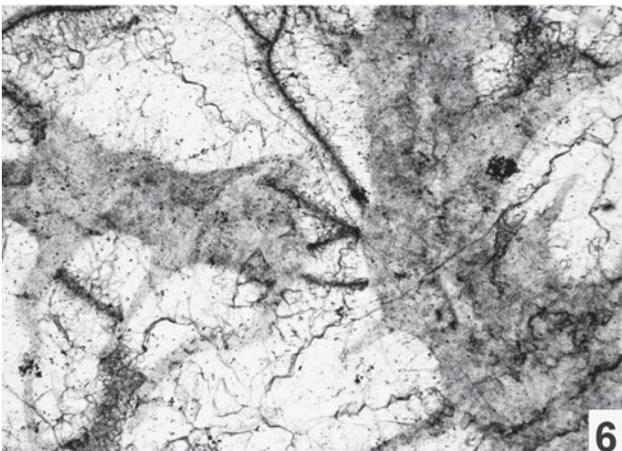
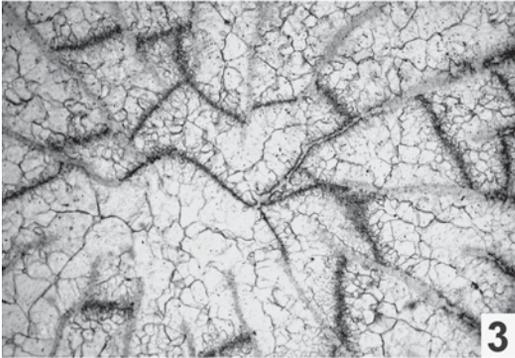
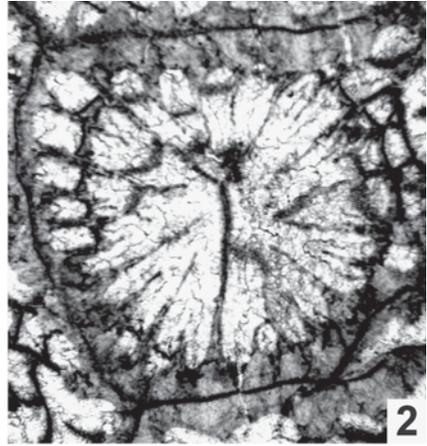


Plate 33

Figs. 1-8. *Petalaxis (Degrootia) wagneri wagneri* (de Groot, 1963), RGM 112734, holotype. Serial transverse acetate peels through hystero-brephic (1-4) and hystero-neanic (5-8) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm). All $\times 15$.

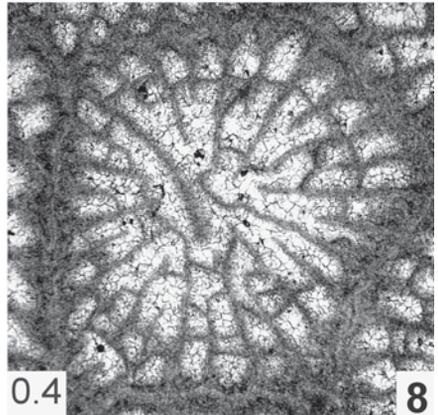
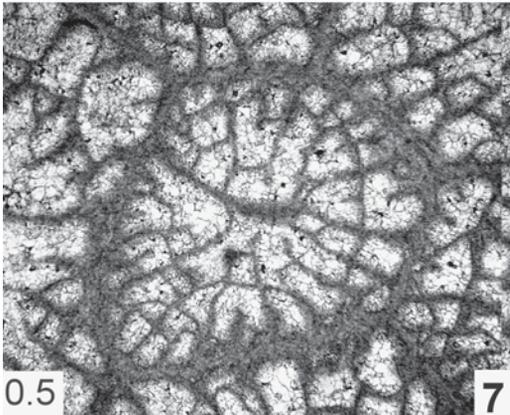
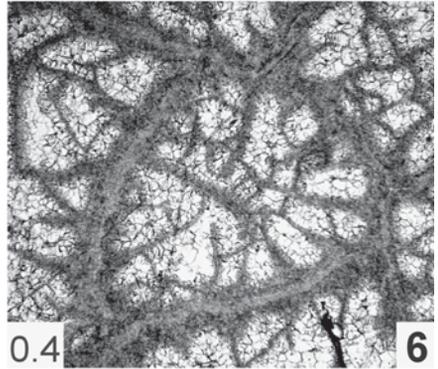
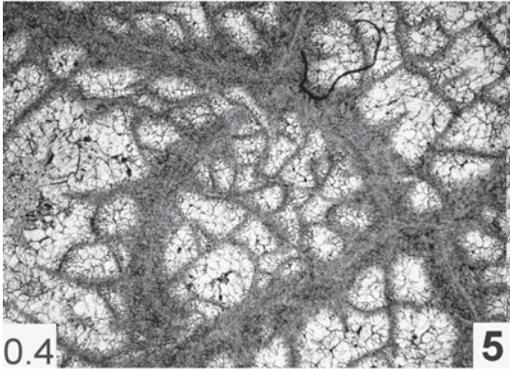
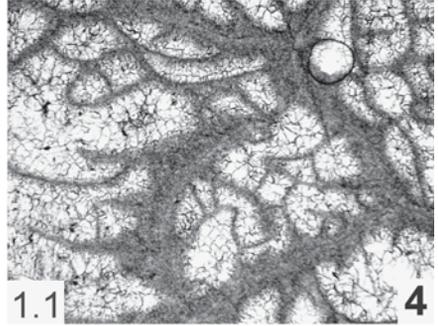
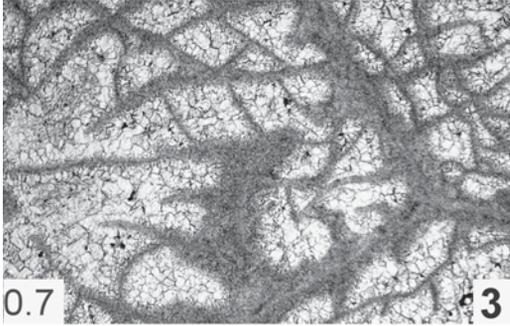
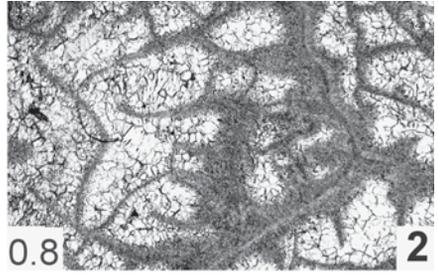
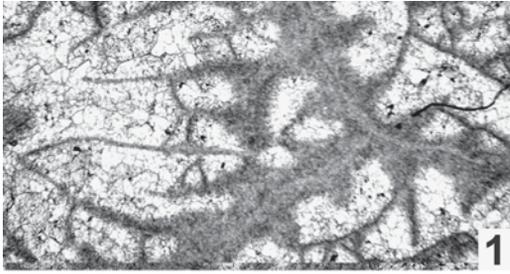


Plate 34

Figs. 1-8. *Petalaxis (Degrootia) wagneri santaemariae* (de Groot, 1963), RGM 112751, holotype. Longitudinal sections except where stated.

Fig. 1. Biform tabularium. Tabulae in Positions I and II (lower and middle) transmitted into Position II (upper). $\times 10$.

Fig. 2. Remnants of finely trabecular microstructure of septum.

Figs. 3, 4. Formation of new partition in connection to dissepiment (4) and free (3). Both $\times 30$.

Fig. 5. Transverse section of partition.

Fig. 6. Partition sectioned perpendicular to its thickness. Trabeculae-like bodies in the middle.

Fig. 7. Median lamella sectioned perpendicular to its thickness.

Fig. 8. Oblique section of median lamella. Remnants of trabeculae intersect strong, arching growth lines.

All figures $\times 50$ unless stated otherwise.

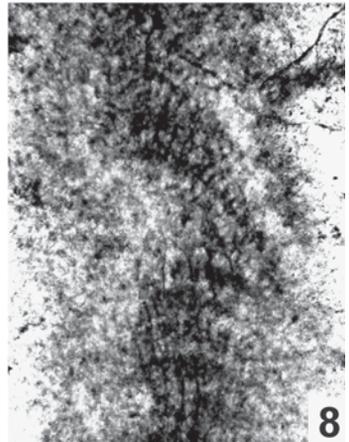
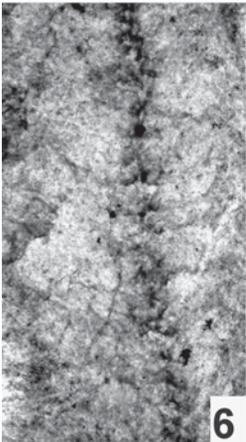
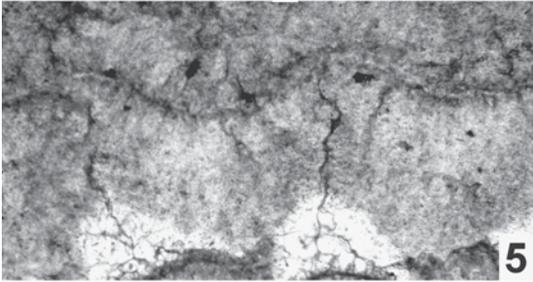
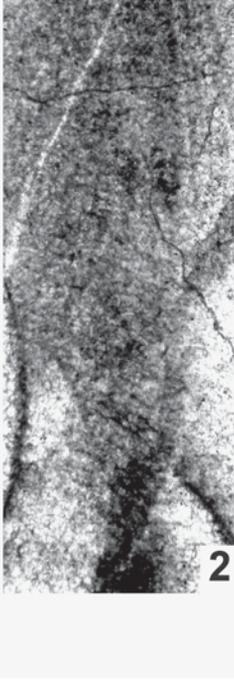
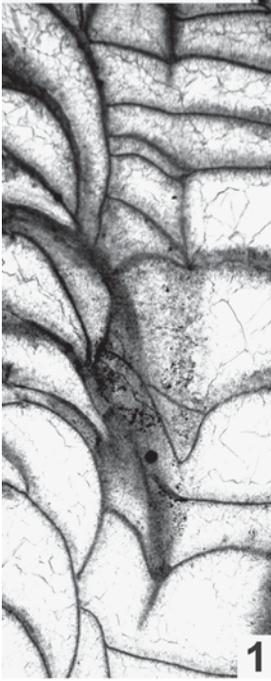


Plate 35

Figs. 1-2. *Petalaxis (Degrootia) wagneri santaemariae* (de Groot, 1963), RGM 112751, holotype.

Fig. 1. Transverse section. $\times 4$.

Fig. 2. Longitudinal section. $\times 4$.

Figs. 3-8. *Petalaxis (Degrootia) wagneri sexangula* (de Groot, 1963), RGM 112727, holotype.

Longitudinal sections unless stated otherwise.

Fig. 3. Fragment of colony. $\times 4$.

Fig. 4. Transverse section. Fragment of colony. $\times 4$.

Fig. 5. Enlarged fragment showing transition from Position I (middle left) to Position II (upper left) of biform tabularium. $\times 10$.

Fig. 6. Median lamella sectioned perpendicular to its thickness. Remnants of trabeculae. $\times 50$.

Fig. 7. Partition sectioned perpendicular to its thickness. Trabeculae-like bodies in the middle. $\times 50$.

Fig. 8. Transverse section of partition. $\times 50$.

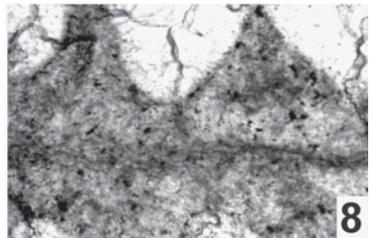
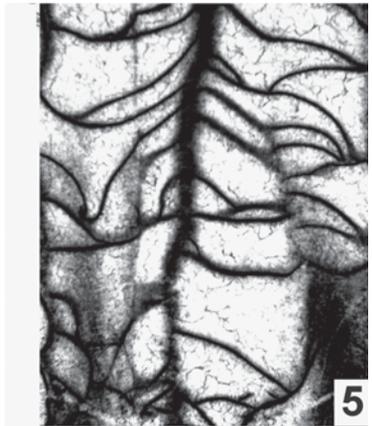
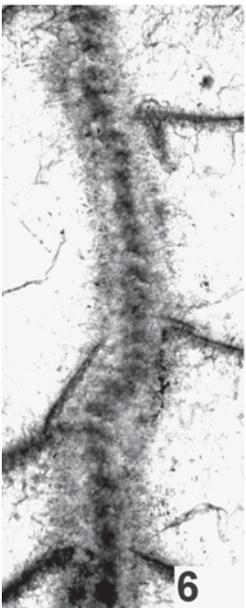
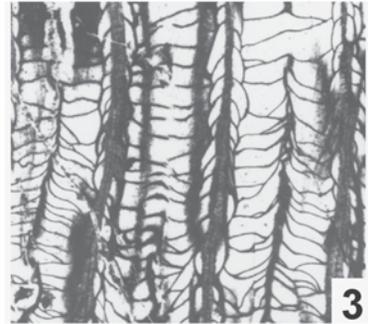
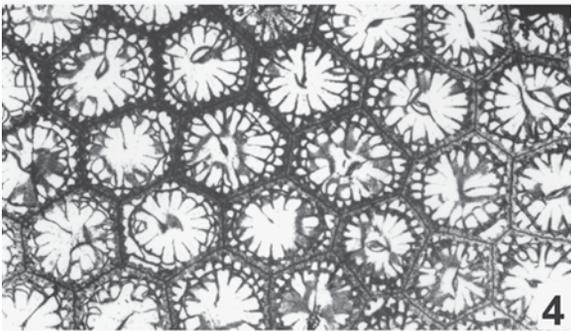
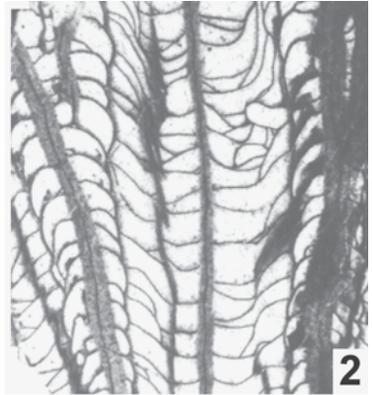
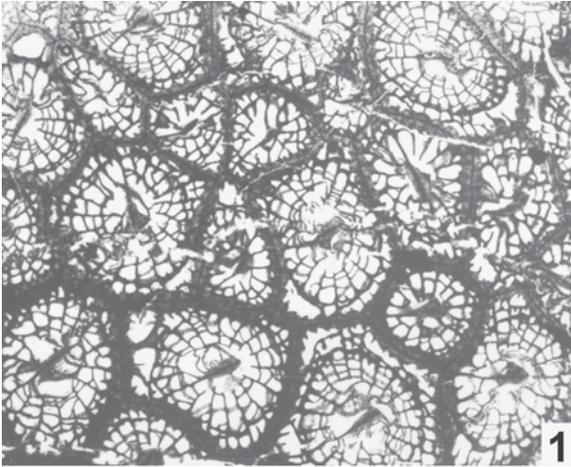


Plate 36

Figs. 1-6. *Petalaxis (Degrootia)* sp., RGM 112755.

Fig. 1. Transverse section. Median lamella with remnants of trabeculae.

Fig. 2. Longitudinal section of median lamella. Long remnants of trabeculae intersect strong growth lines.

Fig. 3. Longitudinal section. Partition sectioned perpendicular to its thickness with trabeculae-like bodies.

Fig. 4. Remnants of trabeculae in longitudinal section of septum.

Figs. 5-6. Transverse sections. Different diagenetic alterations of septal partitions.

All figures $\times 50$.

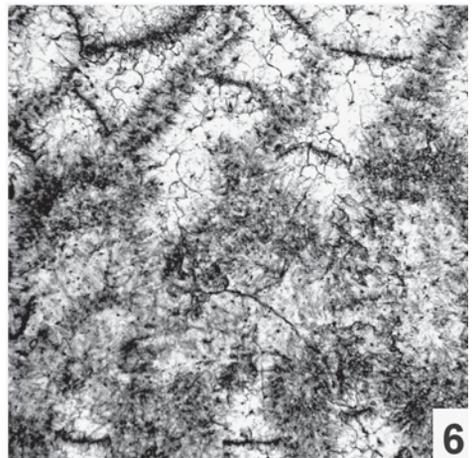
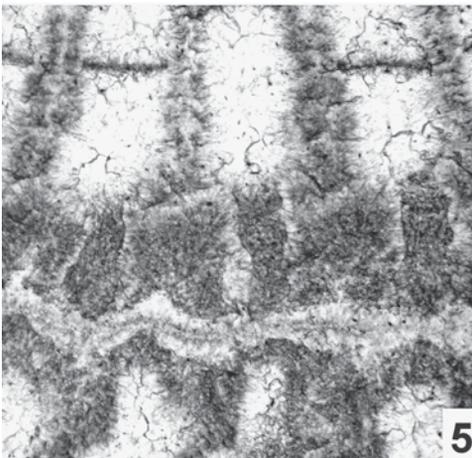
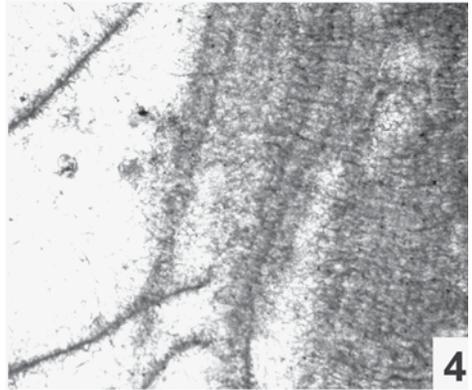
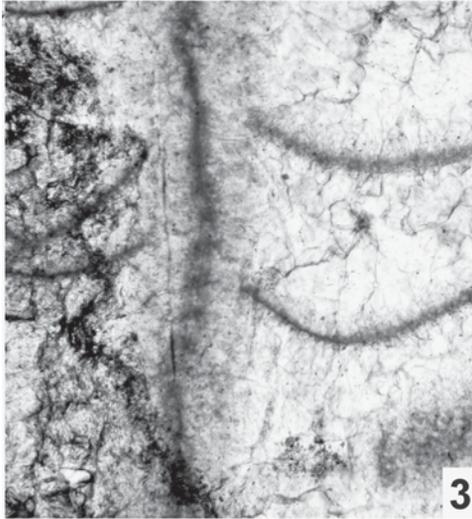
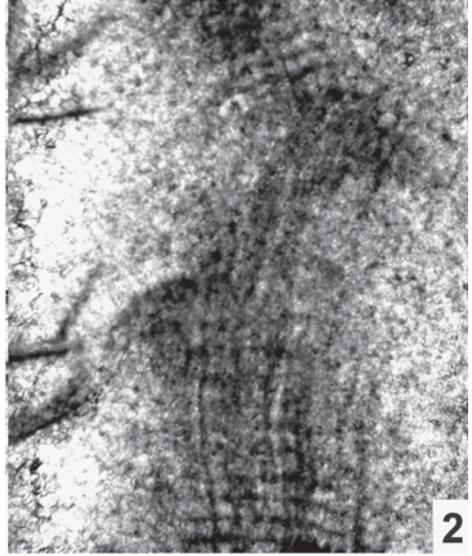
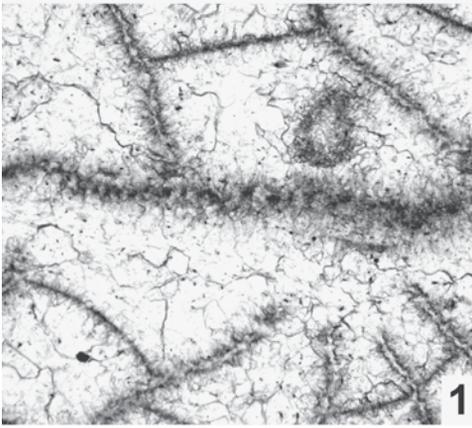


Plate 37

Figs. 1-6. *Petalaxis (Degrootia)* sp., RGM 112755. Transverse sections unless stated otherwise.

Fig. 1. Part of colony. $\times 6$.

Fig. 2. Longitudinal section. $\times 6$.

Fig. 3. Thin, free median lamella, elongated counter septum (left) and shortened cardinal septum (right). $\times 20$.

Fig. 4. Median lamella temporarily reduced. $\times 20$.

Figs. 5-6. Thick (5) and moderate (6), free median lamellae, elongated cardinal septa and biform arrangement of sections of tabulae in most septal loculi. $\times 15$.

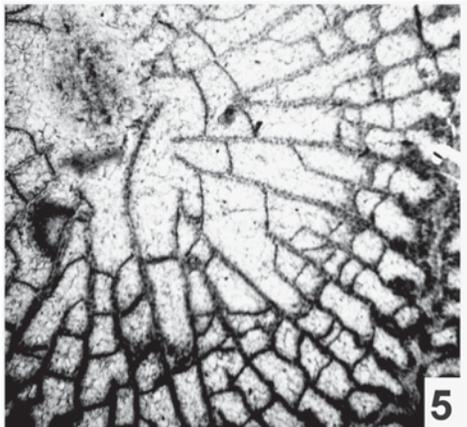
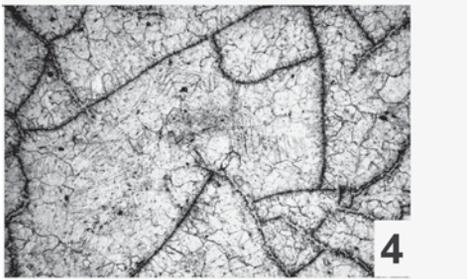
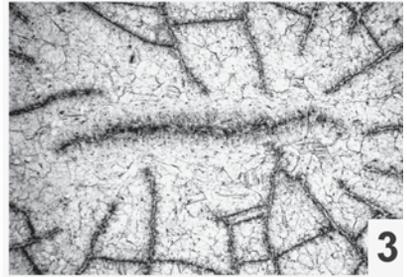
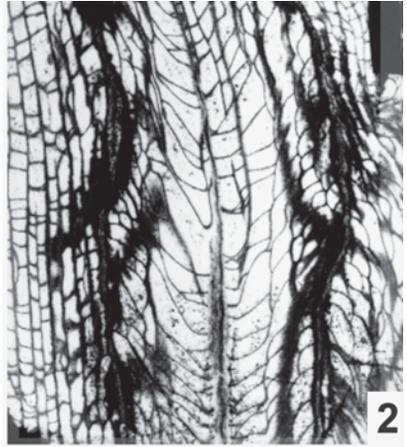
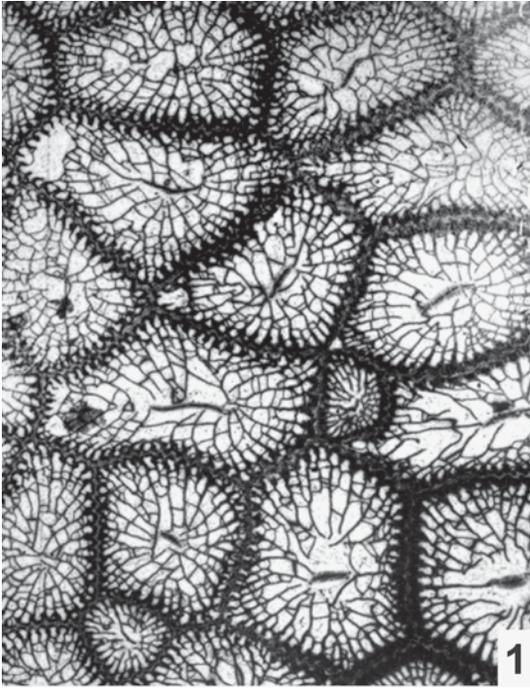


Plate 38

Figs. 1-3. *Donophyllum diphyphyloideum* Fomichev, 1939, specimen no. 99, holotype. Donets Basin. Limestone K8, Melekevskiy Stage, Upper Bashkirian. Transverse sections with peels of selected corallites showing major septa elongated and rudiments of Heterocorallia-like pattern in their arrangement.

Figs. 1a-3a. Photographs.

Figs. 1b-3b. Drawings on digital photographs.

All figures $\times 15$.

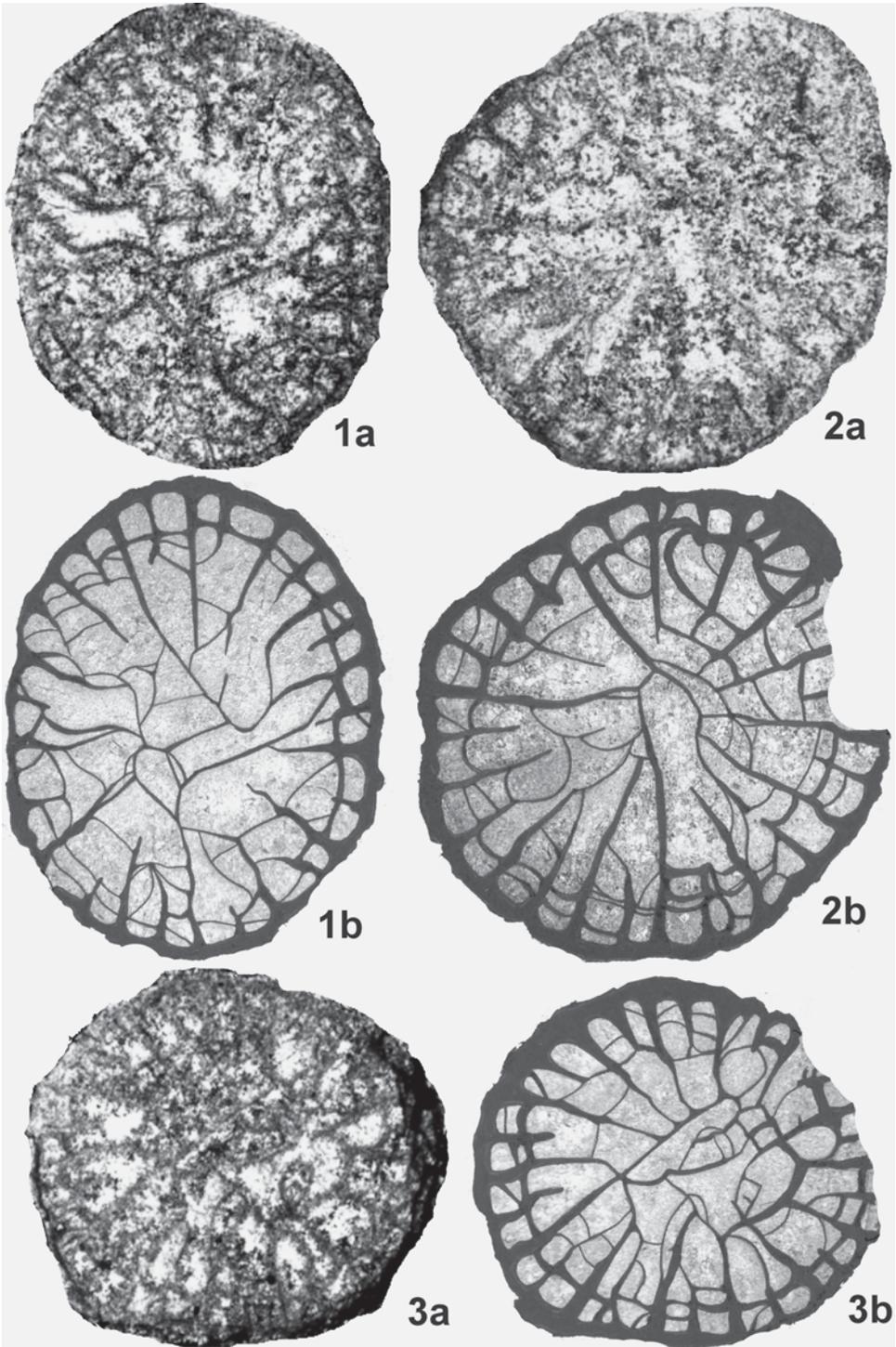


Plate 39

Fig. 1a, b. *Donophyllum intermedium* Fomichev, 1953, specimen no. 91, holotype. Donets Basin. Limestone K8, Melekevskiy Stage, Upper Bashkirian. Transverse sections (peels) of selected corallites showing "diphyphylloid" morphology (1a, left) and major septa elongated to form rudiments of Heterocorallia-like pattern.

Figs. 2. *Donophyllum reticulatum* Fomichev, 1939, specimen No. 81, holotype. Donets Basin. Limestone K8, Melekevskiy Stage, Upper Bashkirian.

Figs. 2a, b. Transverse sections (peels). Major septa meet in corallite axes to form more or less obvious Heterophyllia-like pattern. (b) $\times 15$.

Figs. 2c, d. Longitudinal sections (peels).

Figs. 3a-c. RGM 112598. Vañes formation, Westphalian C(?), Northern Palencia, Spain. Successive transverse sections (peels) showing a transmission from Heterocorallia-like to "diphyphylloid" morphology in 1.1 mm growth of a specimen. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 10$ unless stated otherwise.

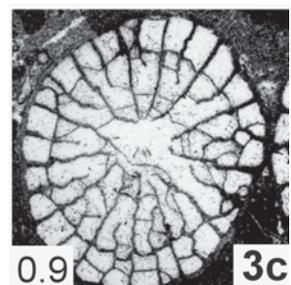
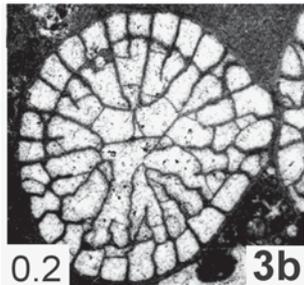
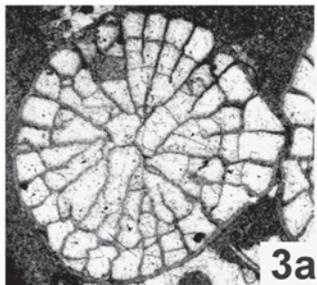
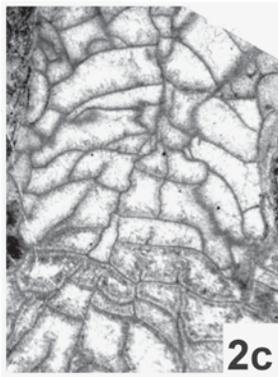
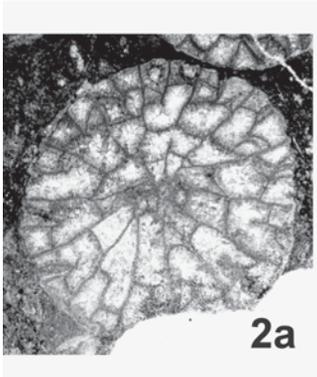
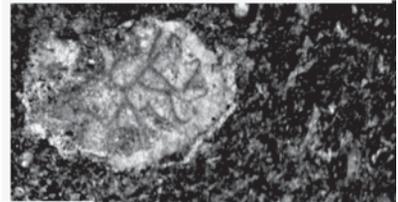
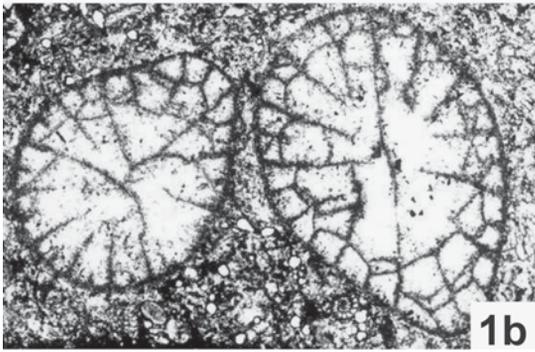
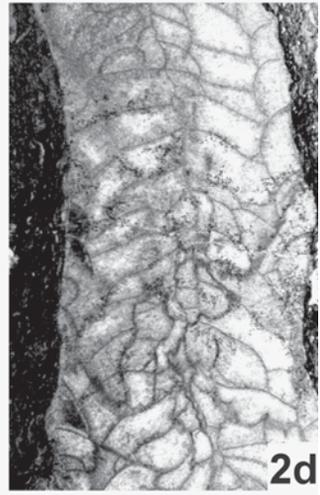
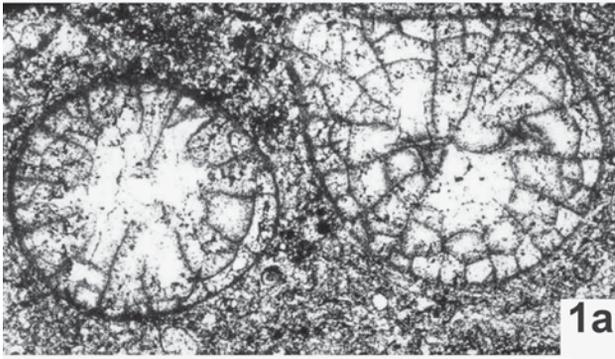


Plate 40

Figs. 1-6. *Donophyllum reticulatum* Fomichev, 1939.

Figs. 1-5. RGM 112598.

Fig. 1. Transverse section of fragment of colony. $\times 6$.

Fig. 2. Slightly excentric longitudinal section. $\times 6$.

Fig. 3. Axial split of major septa. $\times 25$.

Fig. 4. Oblique longitudinal section of offsetting corallite with neotheca in the middle and split of first septum in offset (left). $\times 25$.

Fig. 5. Oblique longitudinal section of offsetting corallite. Independent(?) insertion of three first septa. $\times 15$.

Fig. 6. Specimen 81, holotype. Longitudinal section. Remnants of trabeculae, $\times 50$.

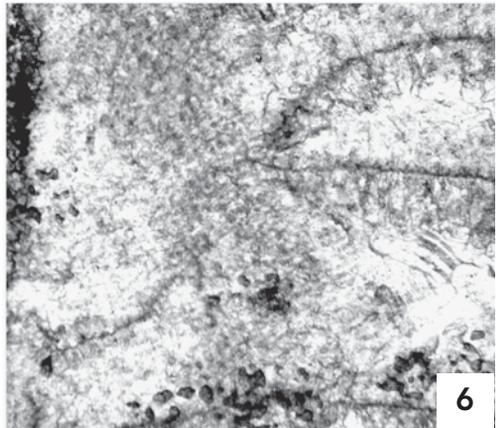
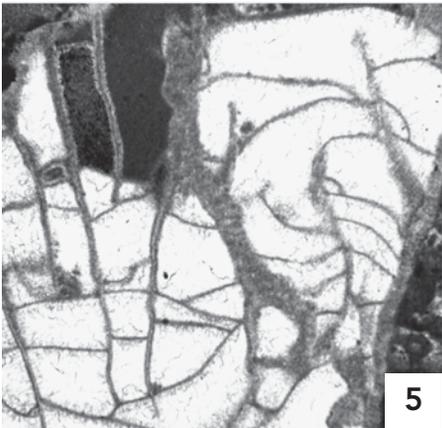
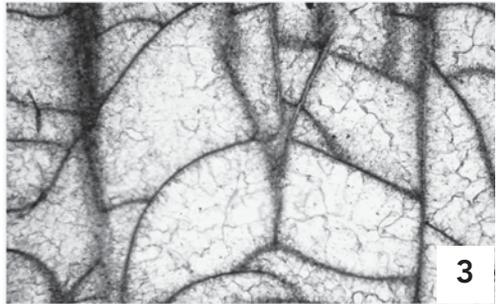
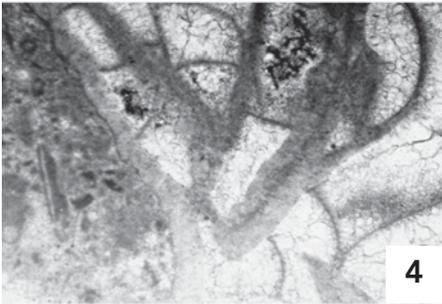
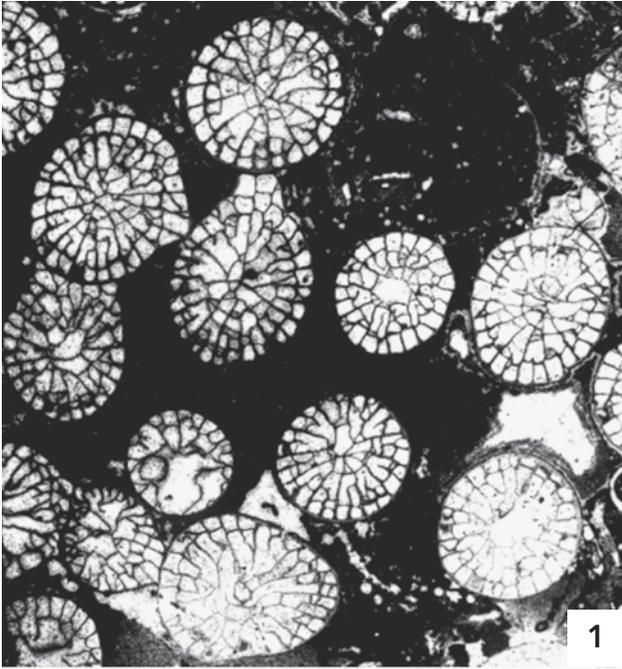


Plate 41

Figs. 1-11. *Donophyllum reticulatum* Fomichev, 1939, RGM 112598. Serial transverse acetate peels through hystero-brephic (1-9) and hystero-neanic (10-11) growth stages. Parent and offset corallite show almost persistent Heterocorallia-like pattern of major septa. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 20$.

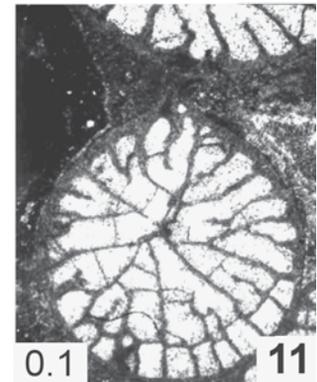
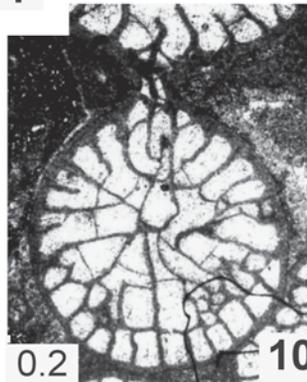
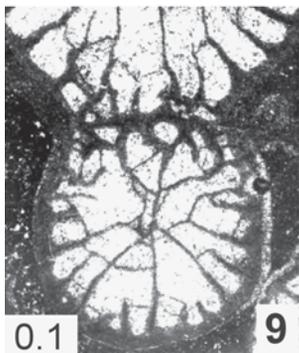
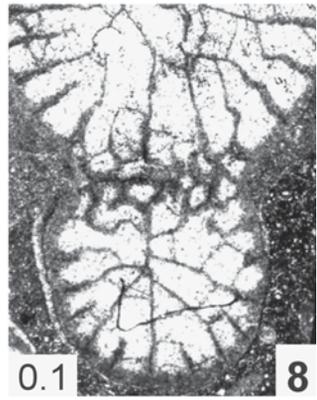
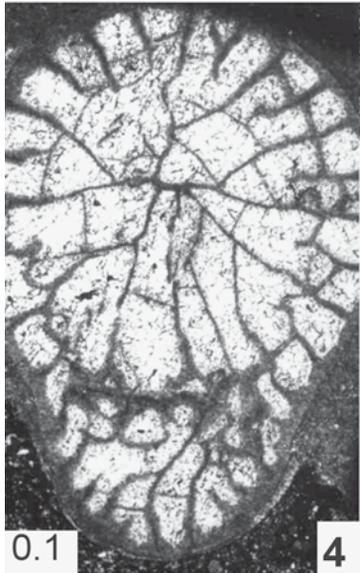
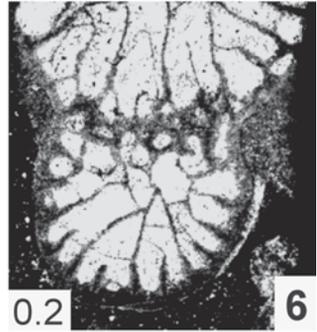
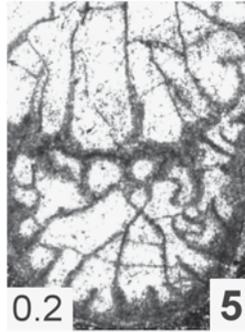
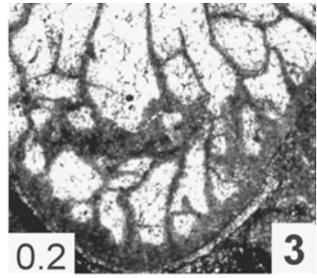
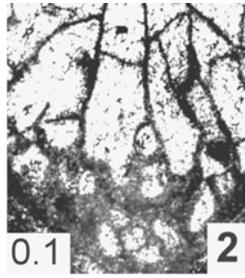
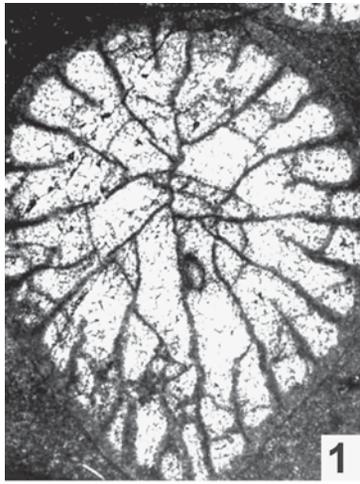


Plate 42

Figs. 1-8. *Donophyllum reticulatum* Fomichev, 1939, RGM 112598. Serial transverse acetate peels through hystero-brephic (1-5) and early hystero-neanic (6-8) growth stages. Parent and offset corallite show Heterocorallia-like pattern of major septa weakly expressed and inconstant. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 20$.

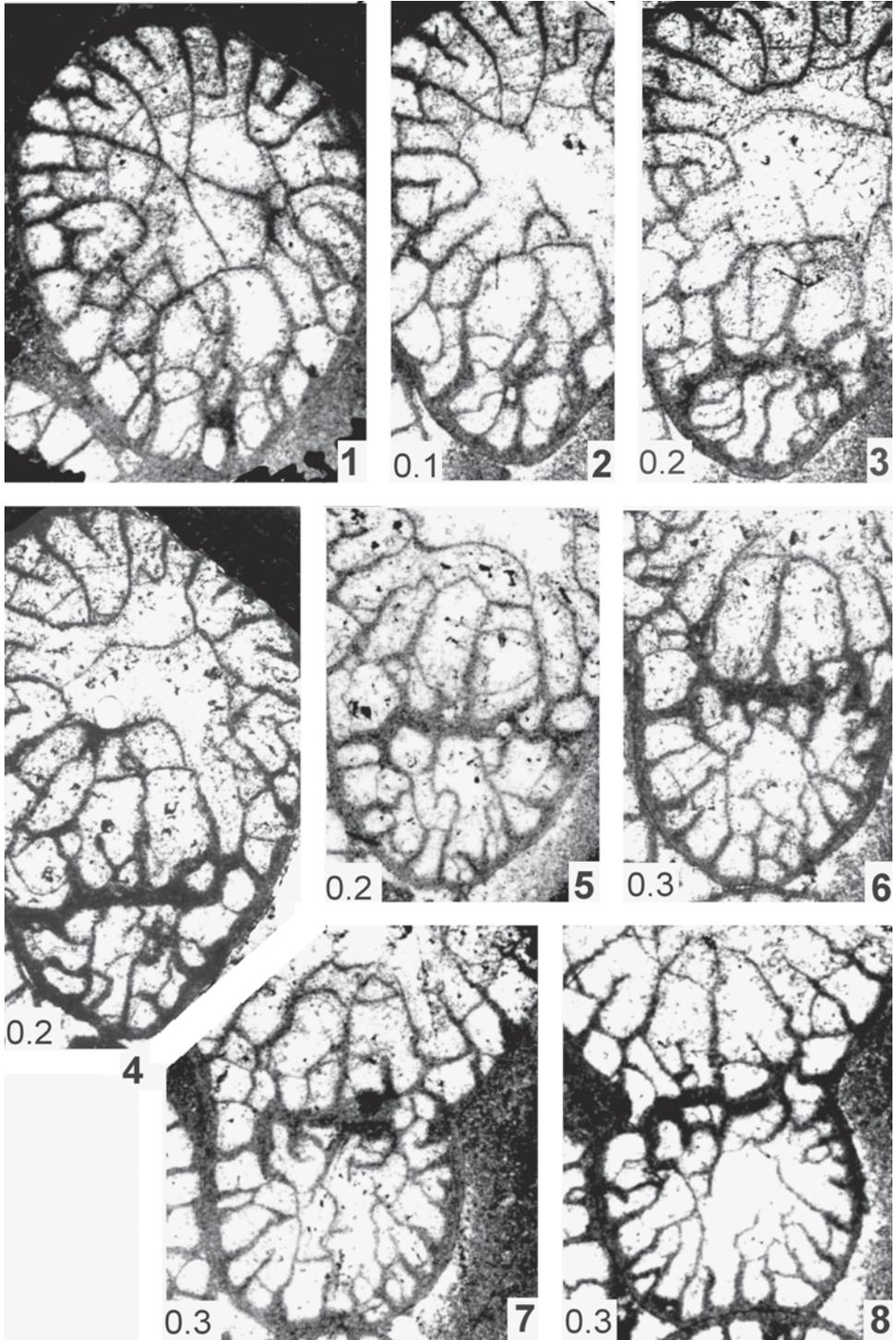


Plate 43

Figs. 1-8. *Donophyllum reticulatum* Fomichev, 1939, RGM 112598. Serial transverse acetate peels.

Figs. 1-2. Morphological changes preceding formation of offset.

Figs. 3-8. Hystero-brephic stage. Parent and offset corallites "diphyphylloid". Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Plate 44).

All figures $\times 20$.

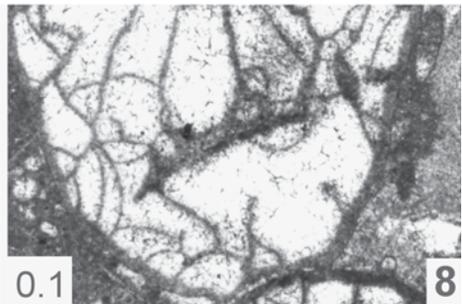
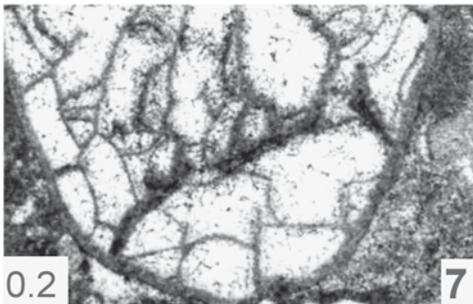
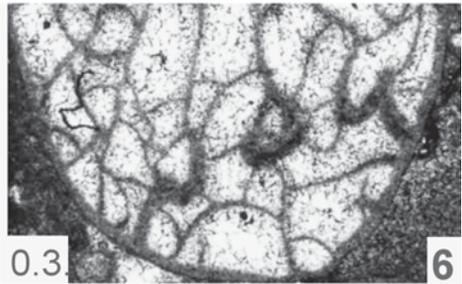
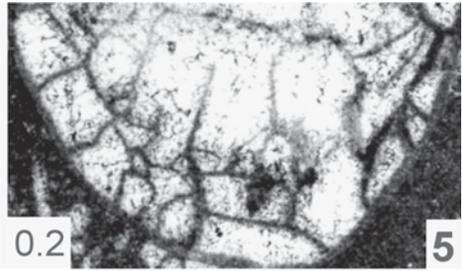
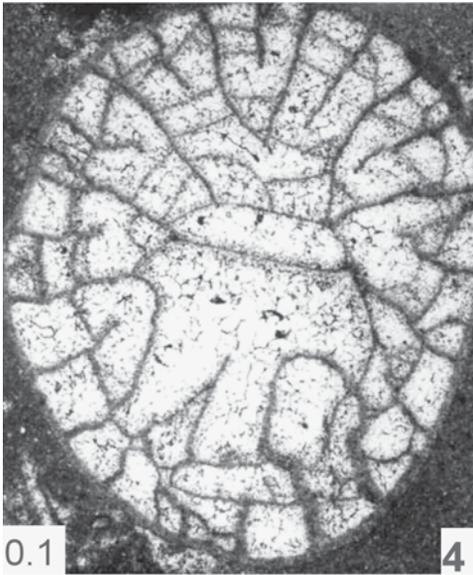
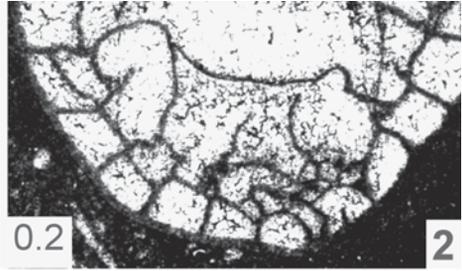
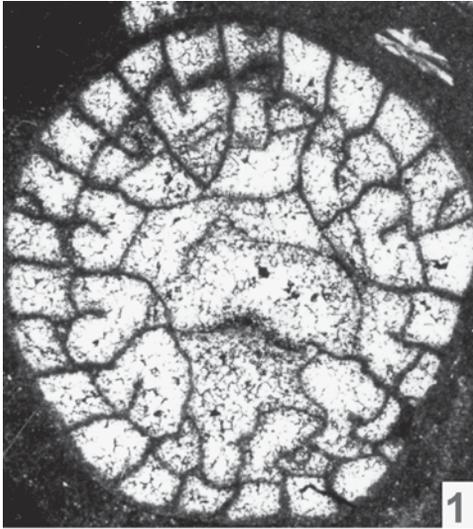


Plate 44

Figs. 8-15. Continued from Plate 43. Late hystero-brephic (9-13) and early hystero-neanic (14, 15) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Pl. 45).

All figures $\times 20$.

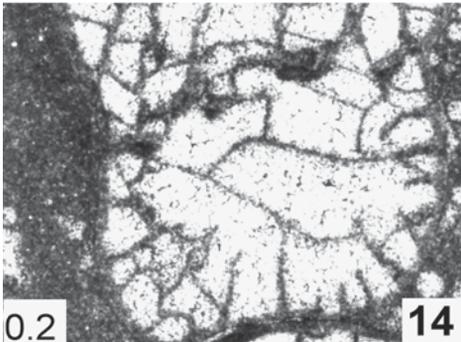
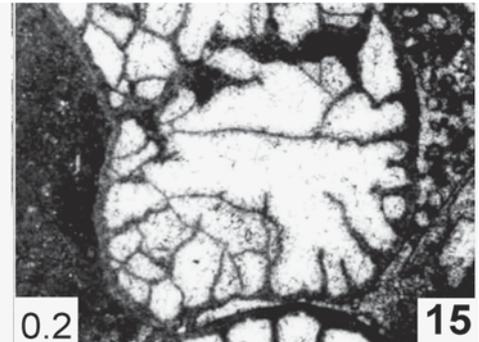
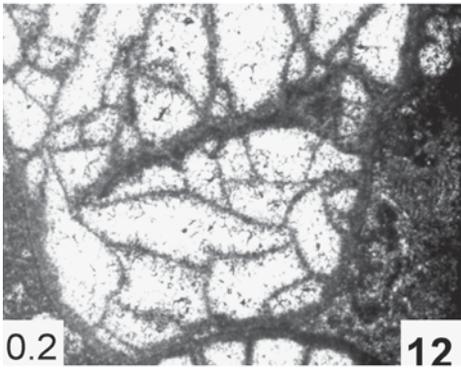
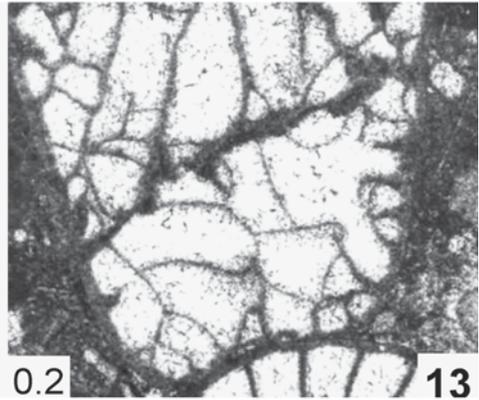
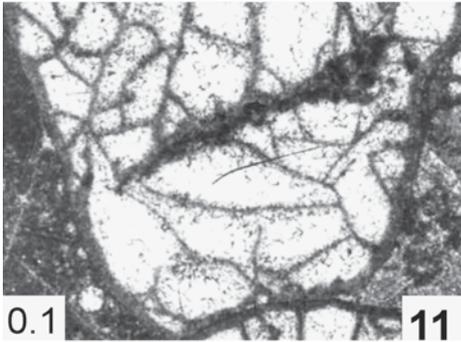
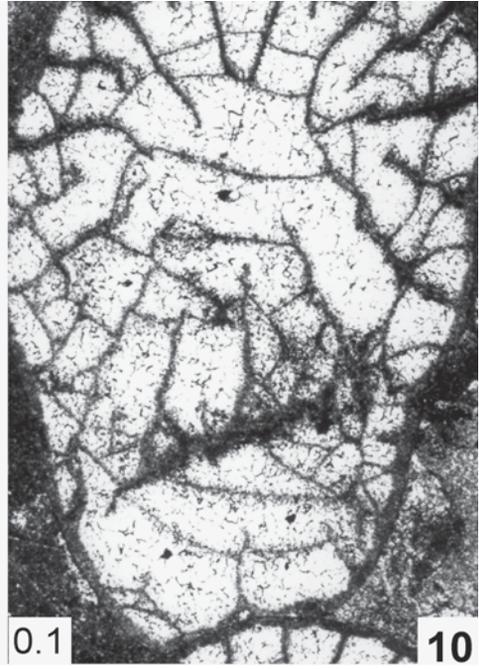
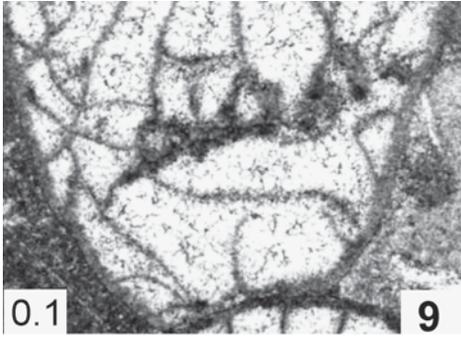


Plate 45

Figs. 16-21. Continued from Plate 44. Early hystero-neanic (16-19) and hystero-neanic (20-21) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 15$.

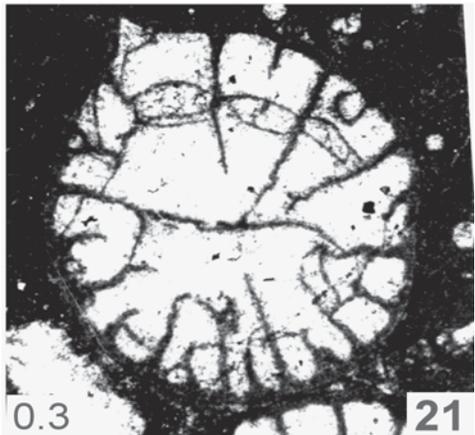
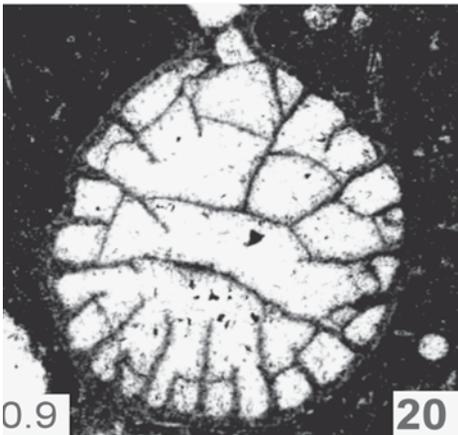
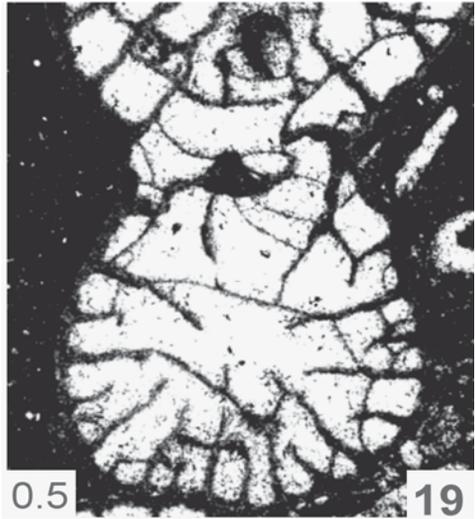
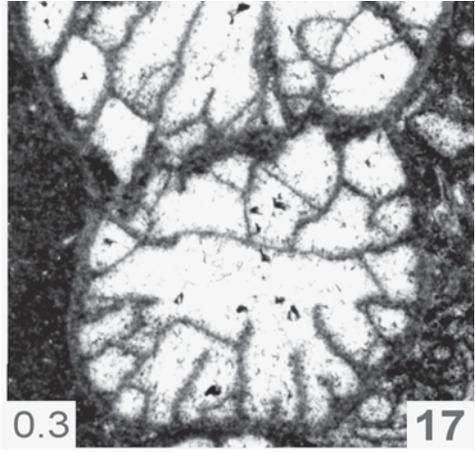
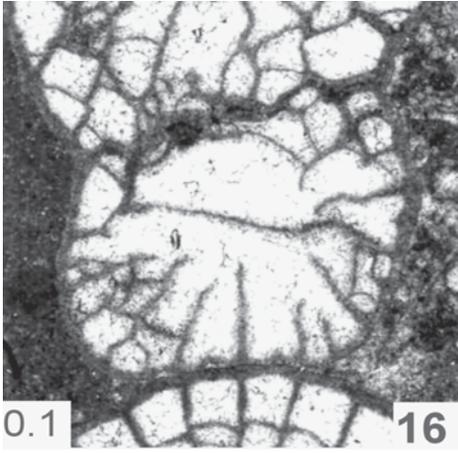


Plate 46

Figs. 1-6. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype.

Fig. 1. Transverse section of part of colony. $\times 4$.

Fig. 2. Longitudinal section. $\times 4$.

Fig. 3. Longitudinal section of offsetting corallite. Neotheca based on dissepiment. $\times 15$.

Fig. 4. Transverse section of zig-zaging intercorallite wall. $\times 75$.

Fig. 5. Longitudinal section. Remnants of trabeculae in peripheral part of septum. $\times 50$.

Fig. 6. Longitudinal section of intercorallite wall, perpendicular to its thickness. $\times 50$.

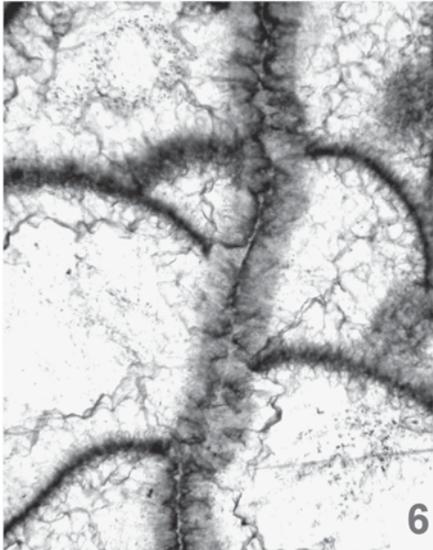
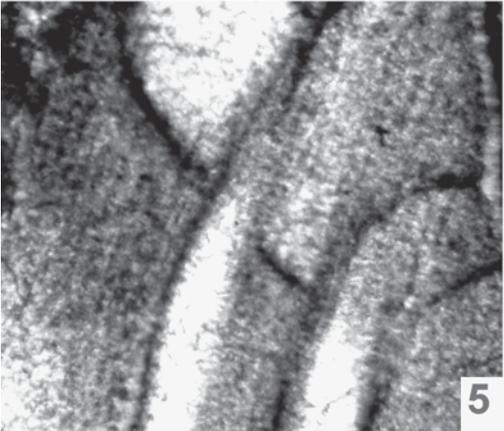
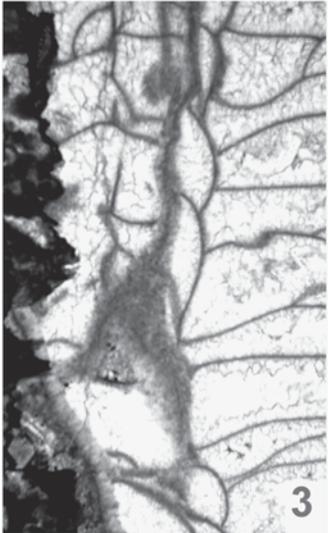
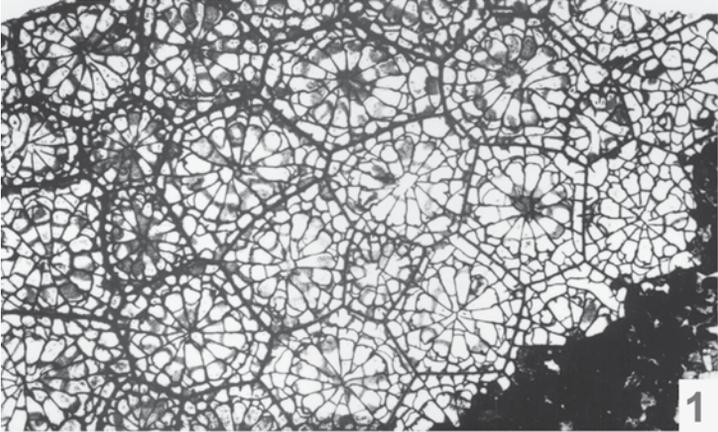


Plate 47

Figs. 1-12. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype. Serial transverse acetate peels through 7.3 mm growth of corallite I showing changes in its morphology. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 10$.

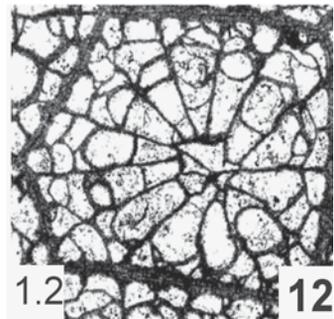
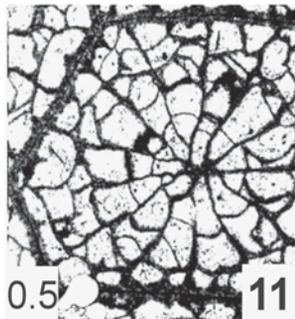
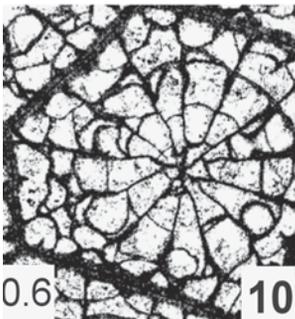
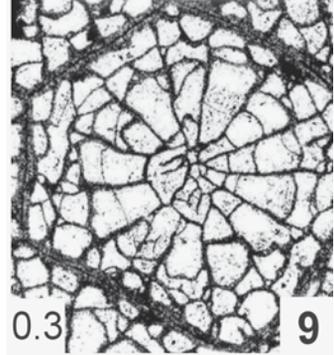
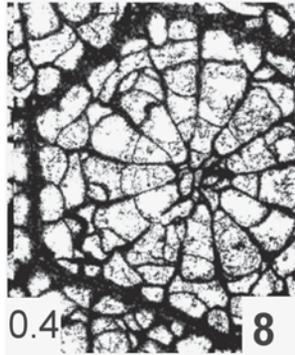
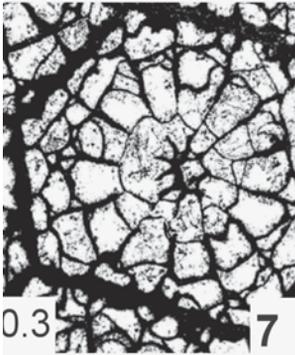
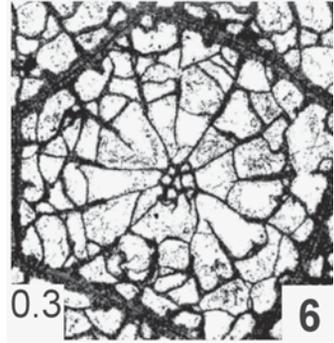
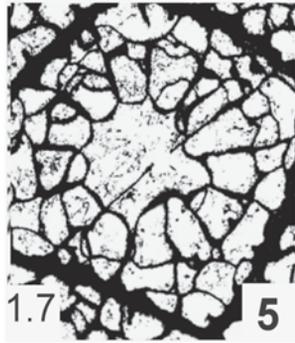
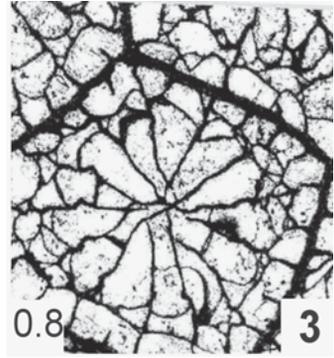
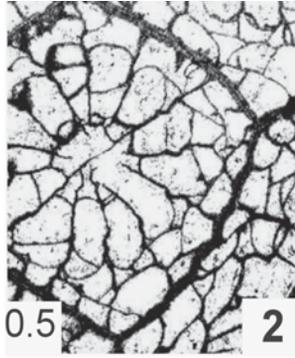
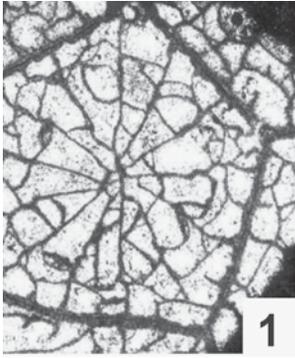


Plate 48

Figs. 1-8. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype. Serial transverse acetate peels through 7.9 mm growth of the corallite II showing changes in its morphology. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 10$.

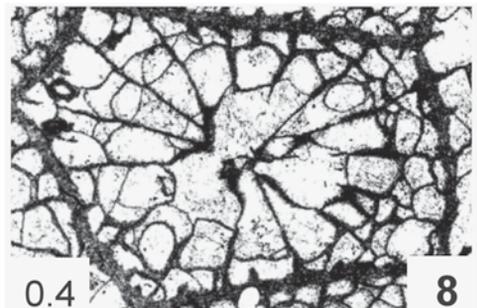
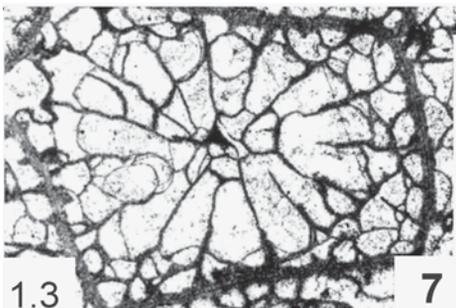
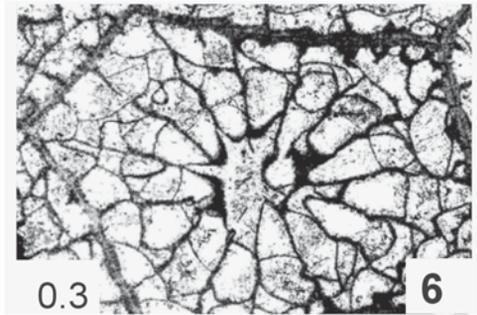
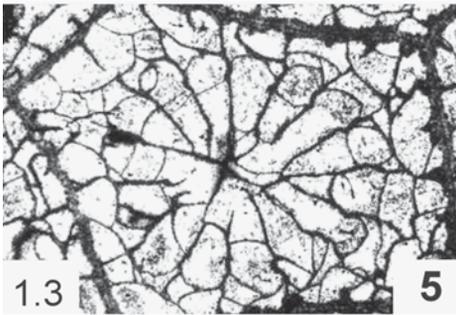
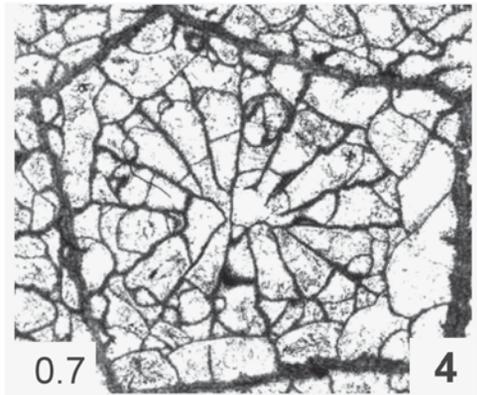
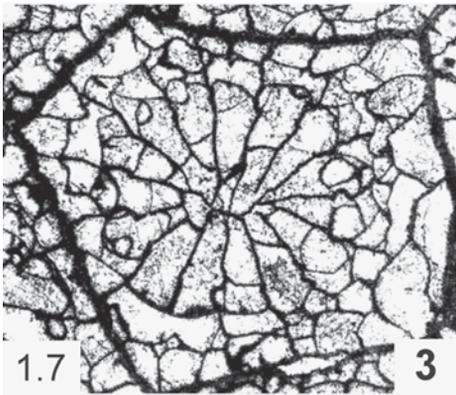
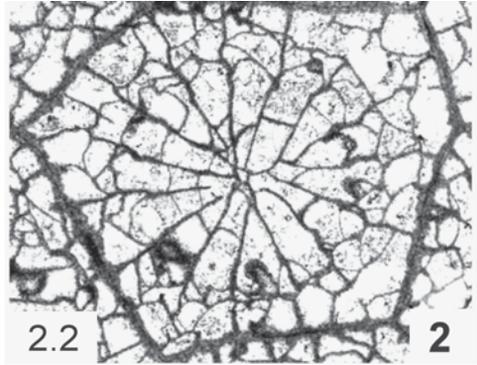
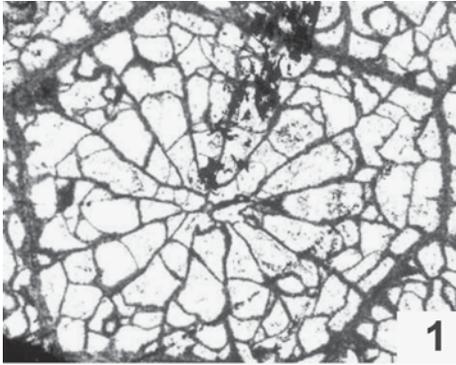


Plate 49

Figs. 1-8. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype. Corallite "A." Serial transverse acetate peels through hystero-brephic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Pl. 50).

All figures $\times 15$.

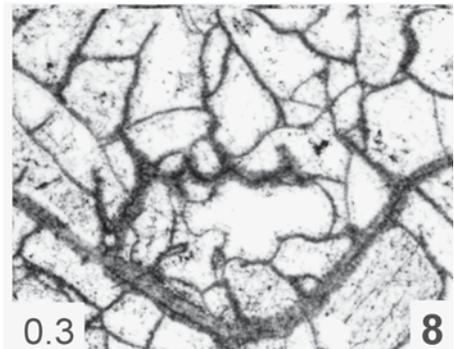
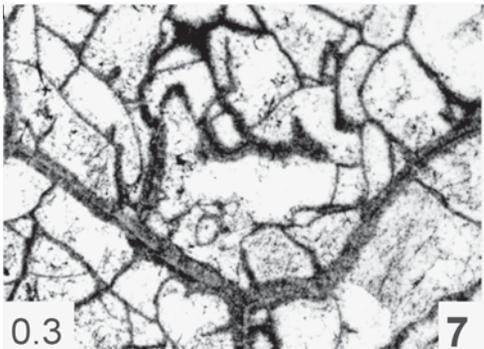
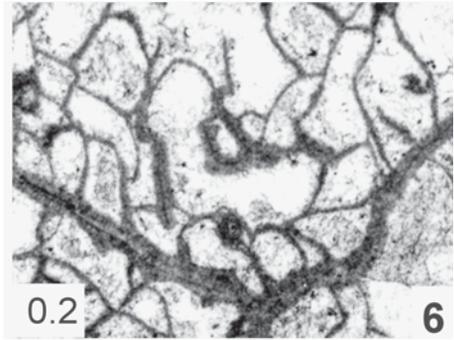
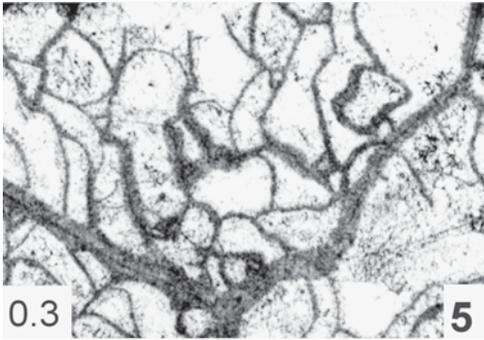
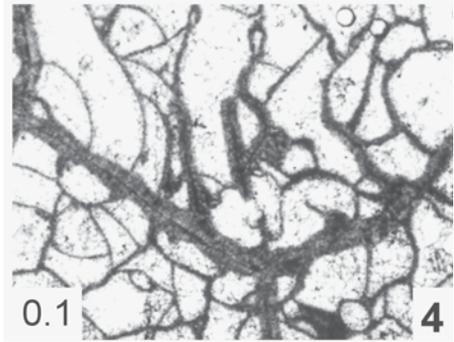
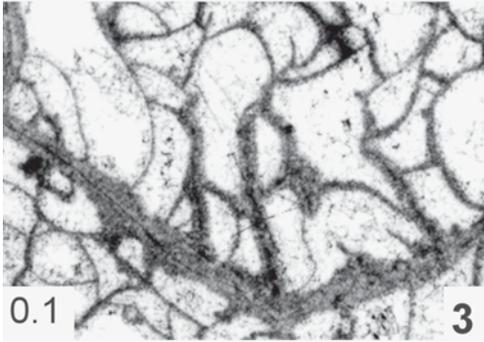
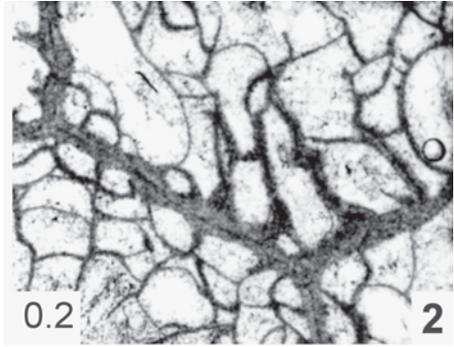
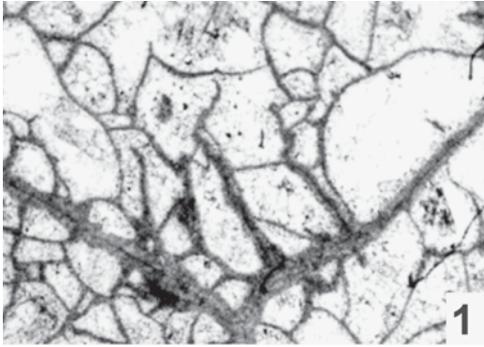


Plate 50

Figs. 9-16. Continued from Plate 49. Hystero-brephic (9-10), early hystero-neanic (11-12) and hystero-neanic (13-16) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 15$.

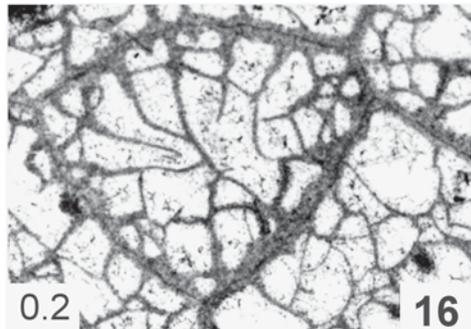
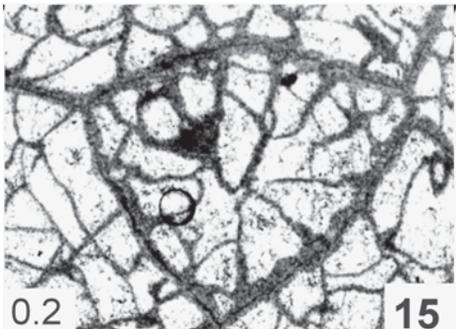
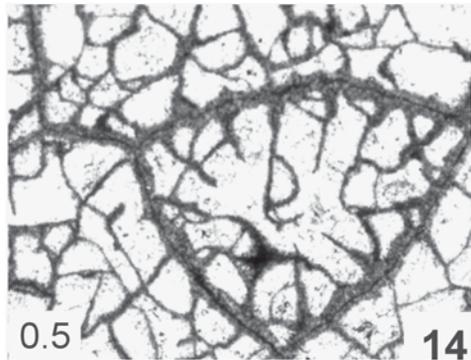
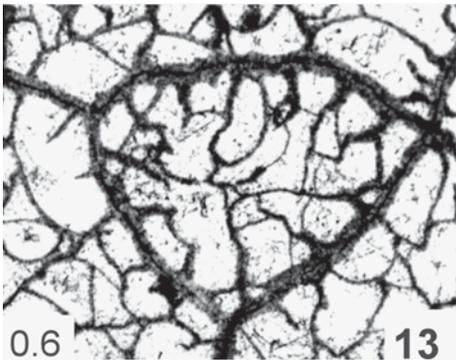
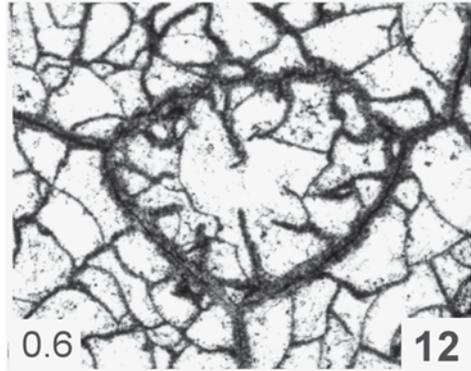
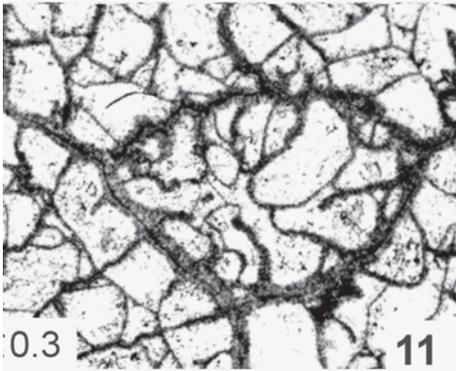
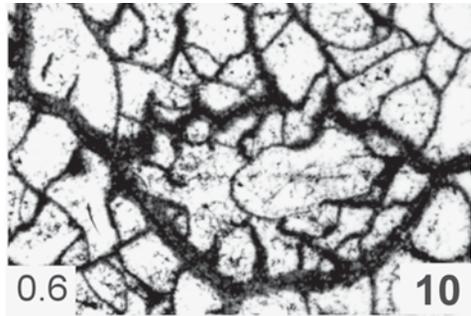
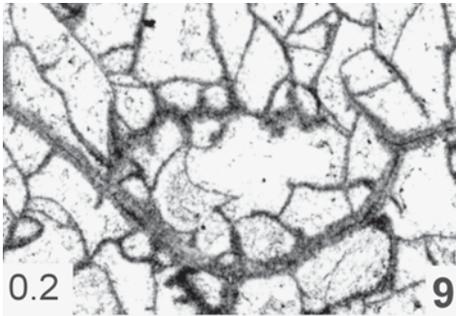


Plate 51

Figs. 1-9. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype, corallite "B". Serial transverse acetate peels through hystero-brephic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Pl. 52).

All figures $\times 15$.

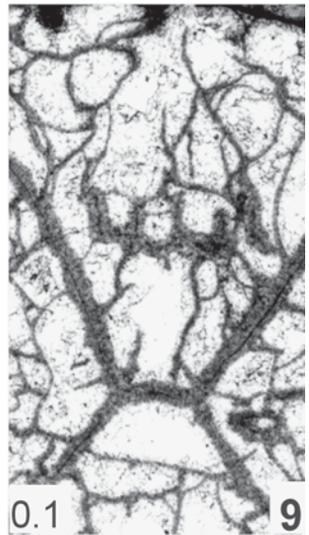
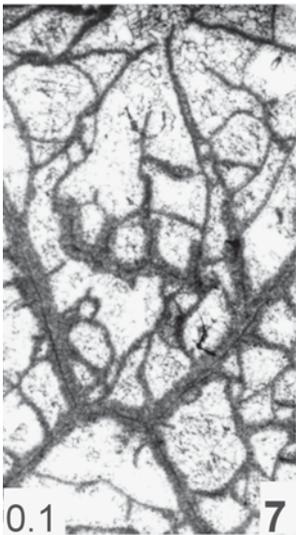
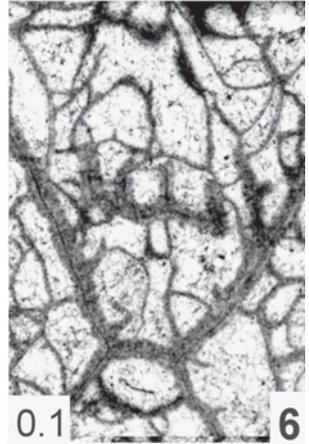
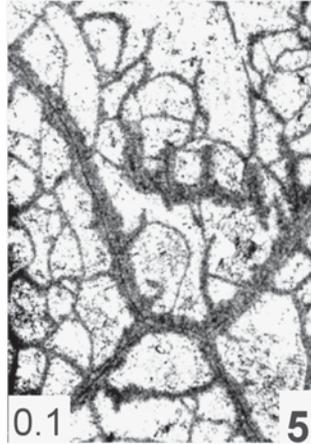
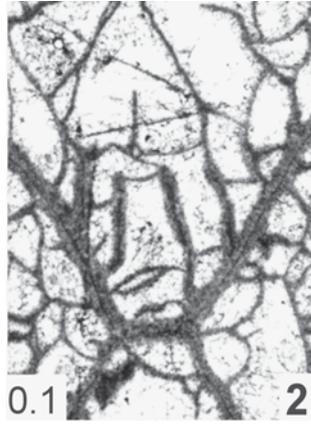
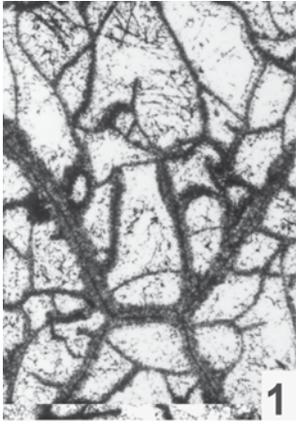


Plate 52

Figs. 10-15. Continued from Plate 51. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype, corallite "B". Hystero-brephic (10-13) and early hystero-aneic (14-15) growth stages.

Figs. 1-4. *Arctocorallium trimorphum* (de Groot, 1963), RGM 112599, holotype, corallite "C". Serial transverse acetate peels through hystero-brephic growth stage. Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Pl. 53).

All figures $\times 15$.

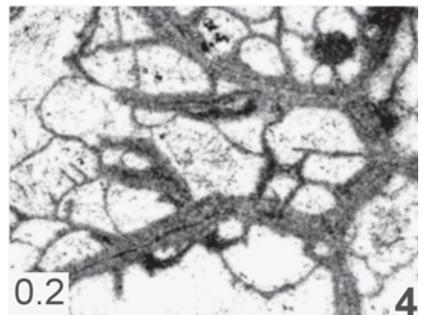
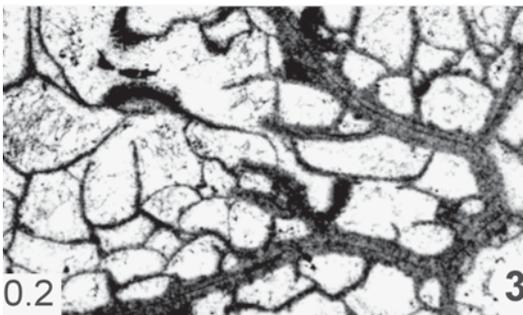
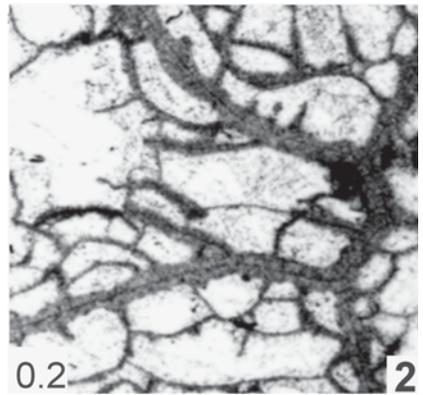
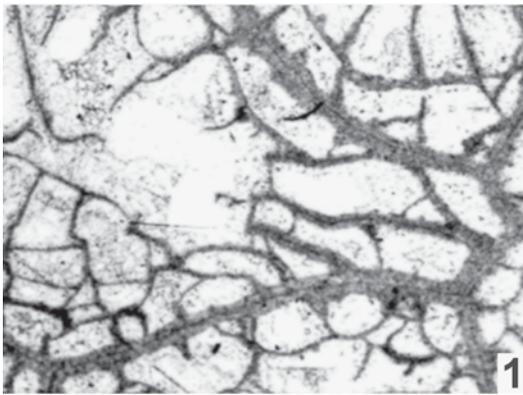
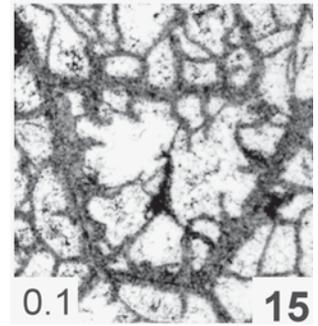
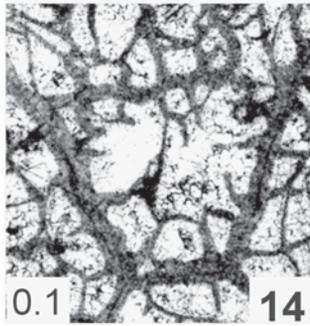
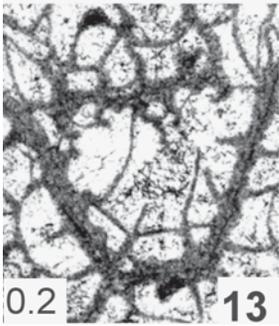
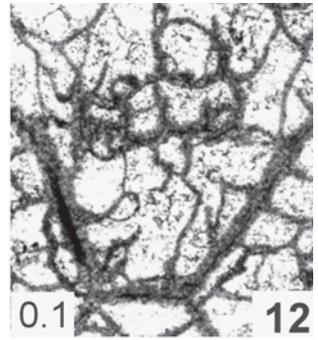
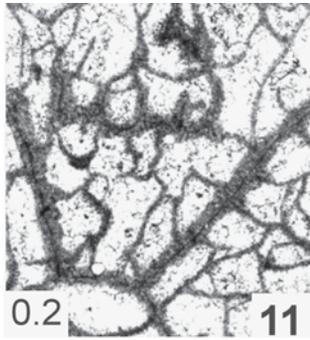
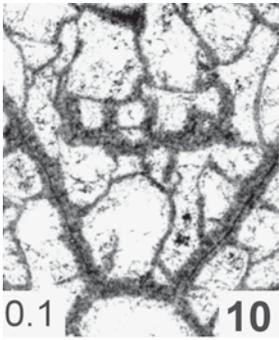


Plate 53

Figs. 5-12. Continued from Plate 52. Hystero-brephic growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm) (continued on Pl. 54).

All figures $\times 15$.

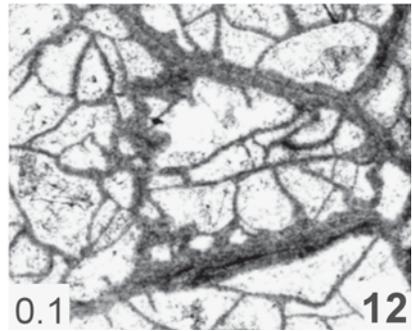
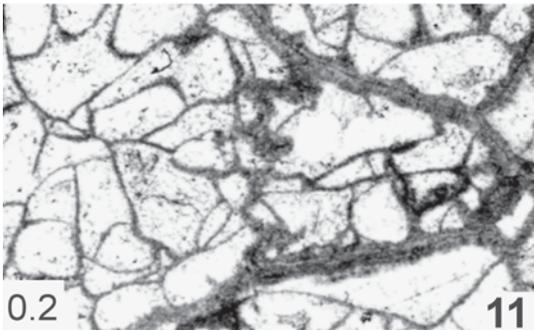
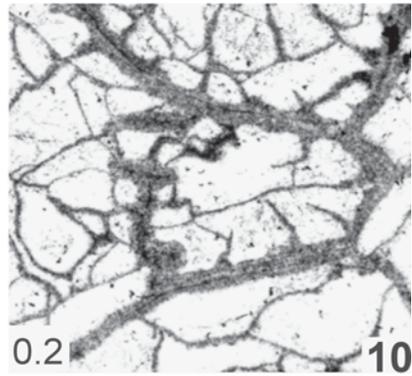
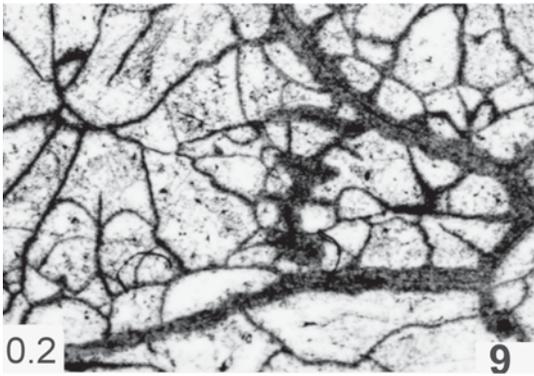
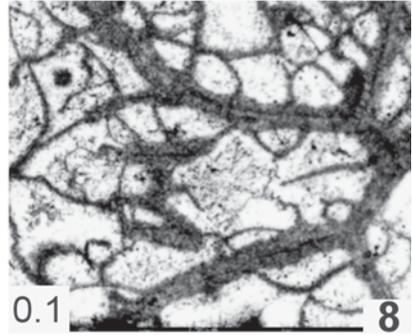
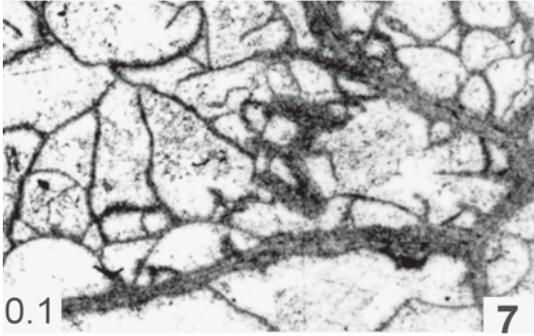
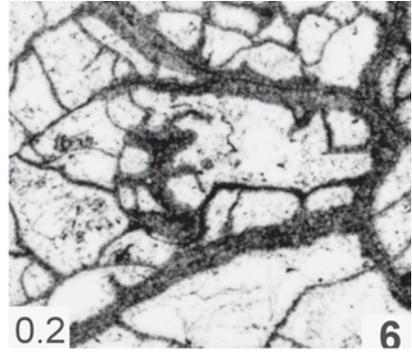
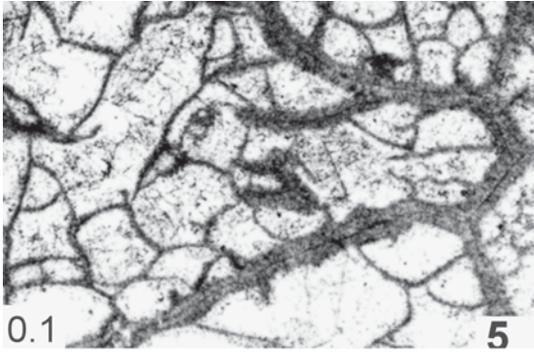


Plate 54

Figs. 13-20. Continued from Plate 53. Early hystero-aneanic (13-14) through hystero-aneanic (15-17) to early mature (18-20) growth stages. Numbers in lower left corners show distances between adjacent pictures (in mm).

All figures $\times 15$

