

Dividocorallia, a new subclass of Palaeozoic Anthozoa

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Abstract

The new concept of taxonomy and phylogeny of some extinct Devonian and Carboniferous Anthozoa is supported by an increase in septa distinct from other Anthozoa and common for all members of the *Dividocorallia* n. subclass. Presence or absence of calices permits to divide the subclass into the orders *Calycorallia* and *Heterocorallia* respectively. Presence or absence of the dissepimentarium is a family level feature in the *Calycorallia*, whereas the microstructure of an external wall plays that role in the *Heterocorallia*. Primitive, calyculate Lower Devonian *Rugosa* were most probably ancestral to the *Dividocorallia*. This idea is supported by insertion of a single septum at the beginning of septogenesis in both subclasses. Deviation towards the *Heterocorallia* took place already during the Lower Devonian time, perhaps through neoteny.

Key-words: Devonian, Carboniferous – *Dividocorallia* n. subclass (Anthozoa) – Phylogeny – Taxonomy.

Streszczenie

Zaproponowano nową koncepcję taksonomii i filogenii niektórych wymarłych dewońskich i karbońskich Anthozoa. Wprowadzono nową podgromadę *Dividocorallia* z dwoma rzędami: *Heterocorallia* i *Calycorallia* n.ordo. Sposób przyrastania septów, jednakowy w całej podgromadzie *Dividocorallia* i odmienny niż u innych Anthozoa, jest jej główną cechą wyróżniającą, podczas gdy obecność (*Calycorallia*) lub brak kielicha (*Heterocorallia*) umożliwia wyodrębnianie rzędów. Obecność lub brak dissepimentarium stanowi kryterium wydzielenia rodzin wśród *Calycorallia*, natomiast mikrostruktura ściany zewnętrznej spełnia tę rolę wśród *Heterocorallia*. Przodkami *Dividocorallia* były zapewne prymitywne, dolno-dewońskie *Rugosa*. Wskazuje na to wydzielenie pojedynczego septum na początku ontogenezy w obydwu podgromadach. *Heterocorallia* oddzieliły się już w dolnym dewonie, zapewne w wyniku neotenu.

Key-words: Dewon, Karbon – *Dividocorallia* n. subclass (Anthozoa) – Filogeneza – Taksonomia.

Introduction

The first corals now included in the *Dividocorallia* n. subclass were described by MCCOY (1849) as the new rugose coral genus *Heterophyllia*. DYBOWSKI (1873) set them apart as the new rugose coral subfamily *Heterophyllinae*. YABE & SUGIYAMA (1940) were the first to recognize the distinctness of these corals from the rest of

the rugose coral families, but only SCHINDEWOLF (1941) distinguished them formally as a new order, the *Heterocorallia*, parallel to the *Rugosa*. HILL (1956) accepted that distinction at the ordinal level, whereas SOSHKINA, DOVROLYUBOVA & KABAKOVICH (1962) included the *Heterocorallia* as an order within the *Rugosa*. HILL (1981) later accepted such a position with some doubt, but wrote (p. F424): "Possibly the *Heterocorallia* should be regarded as a subclass of Anthozoa rather than as a doubtful order of the *Rugosa*". I fully agree with the last opinion as far as the distinction of *Heterocorallia* from the *Rugosa* is concerned, but I propose here a new concept of a whole group of animals that the *Heterocorallia* are only a part of.

The initial purpose of this study was to describe two peculiar coral colonies of Strunian age found in core drilled by the State Geological Institute, Lower Silesian Branch in the Sudetes (Poland). Closer examination of these and morphologically similar specimens made it clear that none of the so far existing classifications and morphogenetic reconstructions of *Heterocorallia* is satisfactory. The present study is a result of many attempts to achieve at least some satisfactory conclusions.

Terminology

CREATIVE SEPTUM (new term) – the septum of any generation that has already produced a new generation of septa.

FOSSA (new term) – large septal loculum formed due to the arrangement of septa starting in the earliest ontogenetic stages; the suspected duct for removing out the water lacking in food and enriched in waste products.

GENERATIONS OF SEPTA (new term) – all septa comparable to each other by their distance from an oblique septum (Fig. 1).

HETEROTHECA (after SCHINDEWOLF, 1941, modified herein) – the mostly lamellar external wall of some *Heterocorallia* composed of alternating septal and interseptal sectors.

OBLIQUE SEPTUM (after LAFUSTE, 1979, modified herein) – the first scleroseptum, inserted not due to peripheral dichotomous division, but to the simple folding of the

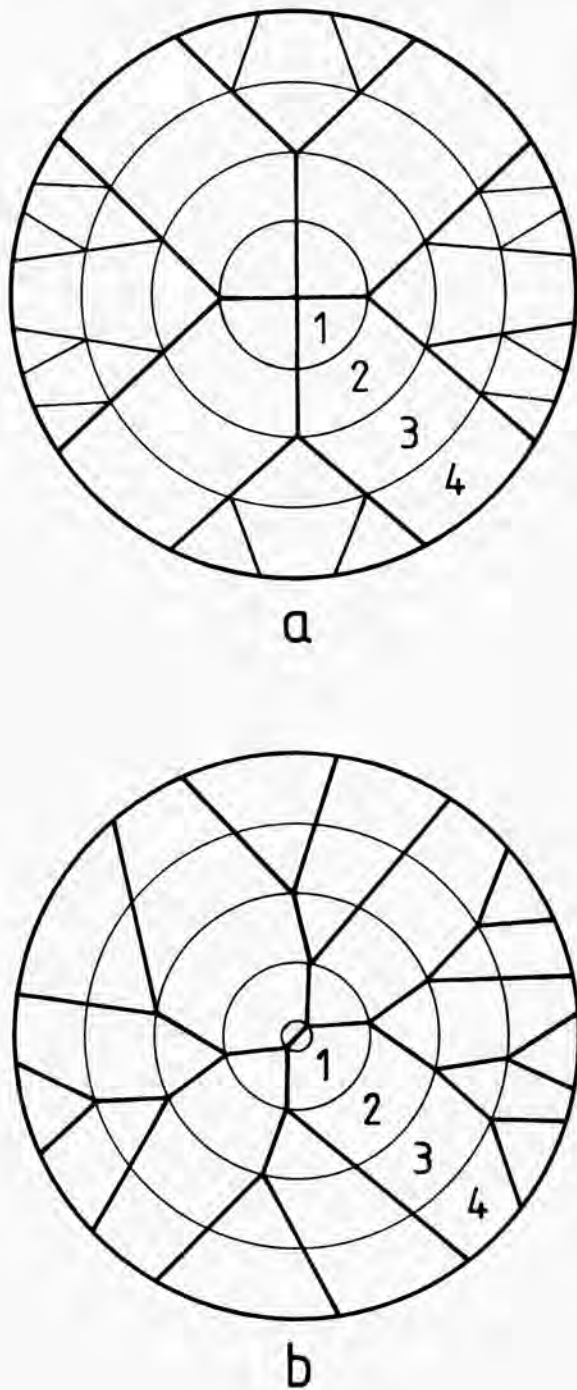


Fig. 1. – a. SCHINDEWOLF's (1941, fig. 22) idealized scheme of insertion of septa in cycles; b. Scheme of insertion of septa in generations proposed in this paper. Potentially creative septa present in peripheral part of a corallite may belong to different generations (marked by numbers).

ectoderm of the basal disc during or just after larval metamorphosis.

PERIPHERAL DICHOTOMOUS DIVISION (new term) – increase in septa due to the formation of two peripherally directed forks, derived from previously existing septum (creative septum) due to the dichotomous division of the

peripheral part of the septal pocket. The oblique septum is the first to fork in this way.

PERIPHERAL LONGITUDINAL TRENCHES (new term) – low, septal furrow-like depressions following vertical projections of peripheral parts of septa and corresponding to primary septa (Fig. 11C, p. 38).

POTENTIALLY CREATIVE SEPTUM (new term) – any septum that reaches the periphery of a corallite prior to the formation of a new generation of septa.

PROTOHETEROTHECA (new term) – the primitive external wall in which the peripheral parts of septa (primary septa and secondary sheets of septa) are restricted to the inner part of the external wall. The wall otherwise has lamellar microstructure (Fig. 11A, p. 38).

RADICITHECA (new term) – partly or mostly trabecular external wall of some Heterocorallia, composed of two layers (inner trabecular and outer solid) in phylogenetically more advanced and/or ontogenetically older forms, or partly trabecular partly fibrous (lamellar?) in ontogenetically younger or phylogenetically less advanced ones; clear sectors absent (Fig. 11D, p. 38).

RETICULOTHECA (new term) – external part of a corallite homologous in position to the external walls of other families of heterocorals; composed of vesicular, nearly vertically arranged tabulae supplemented by centrifugally arranged parts of fragmented septa. These two structural elements form a net distinct in morphology from the inner tabularium, denser at the periphery of the corallite, where individual septal elements become non-correlative with the continuous septa of the inner part of the corallite.

SYSTEM OF SEPTA (new term) – all septa derived due to the peripheral dichotomous division from the first fork of the oblique septum. The so called Y-septa in *Hexaphyllia* formed the simplest system existing.

Previous models of the insertion of septa and their critique

Only the order Heterocorallia has formally been distinguished until now, although representatives of the Calyxcorallia n. ordo have already been occasionally described or informally mentioned (see below). Therefore, all models and/or discussions of septal insertion in the Dividocorallia n. subclass have been restricted so far to representatives of the Heterocorallia. The three main models have already been reviewed by SUTHERLAND & FORBES (1981), who supplemented RÓZKOWSKA's (1969) pioneering study on the ontogeny in *Oligophylloides* RÓZKOWSKA, 1969. However, neither RÓZKOWSKA nor SUTHERLAND & FORBES proposed new models. YABE & SUGIYAMA (1940) were the first who recognized the substantial difference in septal insertion between that observed in the family Heterophyllidae DYBOWSKI, 1873 and those in the Scleractinia and Rugosa. They proposed (*op. cit.*, p. 85) the division of all tetracorals into two groups: Dicoelia, solely devoted to the Heterophyllidae, and Tetracoelia comprising all the other families of tetra-

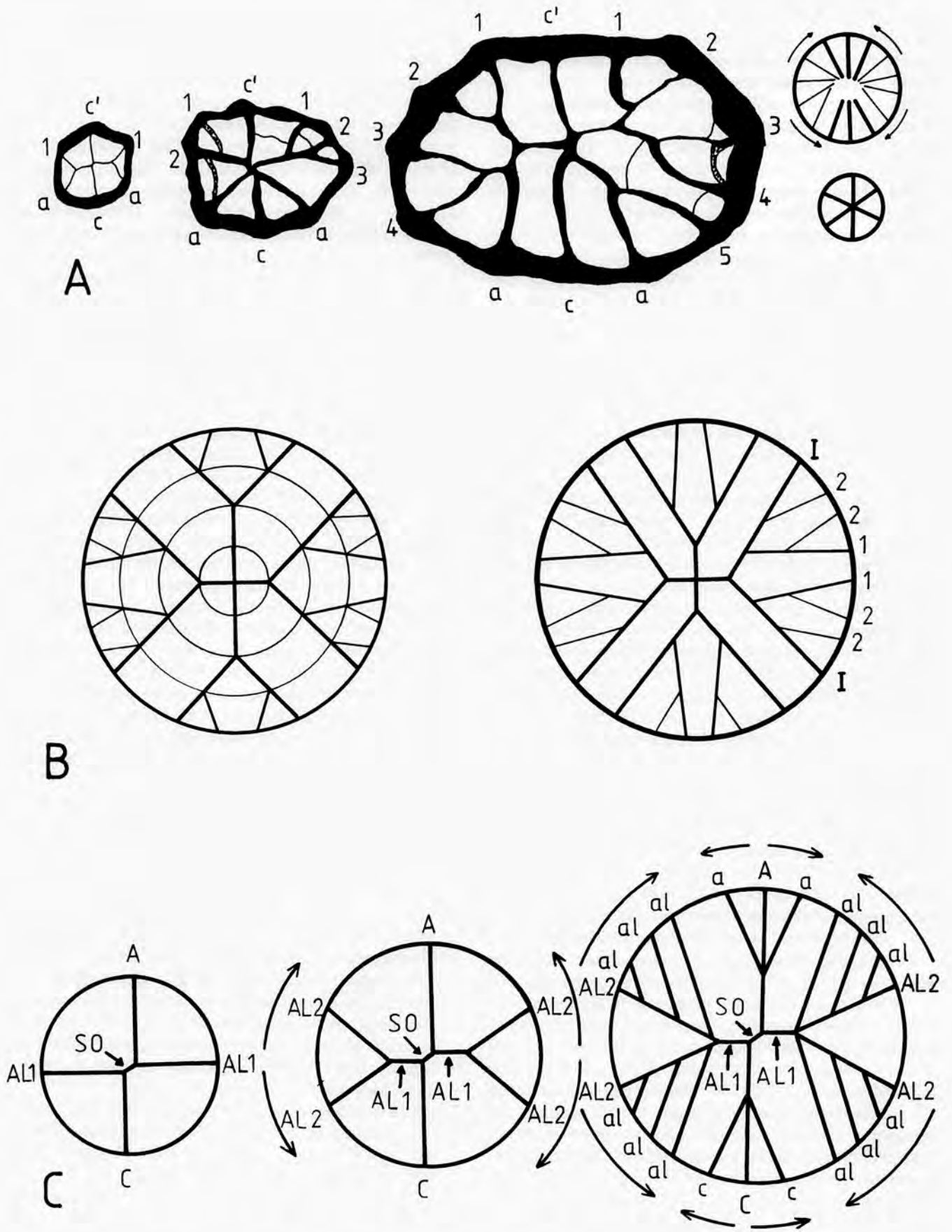


Fig. 2. - Comparison of earlier proposed reconstructions of increase in septa in Heterocorallia. A. YABE and SUGIYAMA (1940); B. SCHINDEWOLF (1941); C. POTY (1981).

corals. Such a classification was based on the suspected insertion of septa in only two of the original sextants in the Heterophyllidae, and in four of the original sextants in the remaining families of Tetracorallia. Sextants adjacent to both the cardinal and counter septa were reconstructed in Heterophyllidae as being barren of metasepta (YABE & SUGIYAMA, 1940, fig. 2: 3). Although detecting such a clear distinction, YABE & SUGIYAMA (1940) did not make a formal taxonomic distinction. They retained heterophyllids as a family within the Rugosa and compared the first septa inserted in this family to protosepta in the Rugosa (YABE & SUGIYAMA, 1940, fig. 1: 1). A comprehensive critique of YABE & SUGIYAMA's (1940) ideas published by SCHINDEWOLF (1941) and some remarks by SUTHERLAND & FORBES (1981) make it possible to omit this model from further discussion in the present paper.

SCHINDEWOLF (1941) rejected YABE & SUGIYAMA's (1941) model and introduced his own model of septal insertion in Heterophyllidae on which he based the introduction of the new suborder Heterocorallia, parallel to Rugosa and Scleractinia. In SCHINDEWOLF's (1941) model four primary septa were considered to be inserted first. These septa were called "Primär Septa" or "Protosepta". Two of them (in *Hexaphyllia*) or all four (in *Heterophyllia*) were afterwards split (aufgespalten) into four or eight forks respectively. All metasepta, if present, were inserted within loculi bordered by these eight forks (SCHINDEWOLF, 1941, fig. 22). In contrast to the protosepta, the metasepta were regarded (SCHINDEWOLF, 1941: 245) as inserted not by the splitting ("Aufspaltung") of older septa, but by the attachment ("Einschaltung") of new ones to them. Thus, two kinds of septa, i.e. four protosepta (two or all four of which split), and one to a few cycles of metasepta (only in the genera other than *Hexaphyllia*) were recognized. Insertion of these metasepta was reconstructed in such a manner that four interseptal loculi, called fossulae, that originated between the first four metasepta, remained undivided by any further septa (SCHINDEWOLF, 1941, figs. 22, 30). This model was fully accepted by HILL (1981, F422-F424) who included it in the diagnosis of the order Heterocorallia SCHINDEWOLF, 1941 and the family Heterophyllidae DYBOWSKI, 1873.

POTY (1978a) accepted the nomenclature of earlier authors, i.e. the names protosepta and metasepta, as well as some parts of the model proposed by SCHINDEWOLF (1941), namely the earliest four-septal stage of growth and the split of "alar" septa into two forks, called by him (POTY, 1978a: 235) "septes alaires secondaires". The latter formed the double "Y" structure perpendicular to the cardinal and counter septum. In this way the six protosepta (cardinal, counter, and two pairs of alars), four primary interseptal loculi and two additional interseptal loculi (between secondary alar septa) were formed. All further septa (called metasepta by POTY, 1978a, 1978b, 1981) were inserted in sequence by splitting of six protosepta, but mostly of the "alaires secondaires". The whole process took place exclusively in the four primary interseptal loculi (POTY, 1978a, pp. 235, 236, figs. 2, 3),

i.e. exactly opposite to the process as envisaged in SCHINDEWOLF (1941).

None of the models discussed above appears fully acceptable when compared to direct observations on the genera *Hexaphyllia*, *Heterophyllia Mariaephyllia* n. gen., *Stylostroton* and *Sudetiphyllia* n. gn. This is independent of the fact, pointed out by SUTHERLAND & FORBES (1981: 501) that except for *Oligophylloides* (at that time) "none are based on serial sections but, of necessity, on deductive postulations". The latter inconvenience, although important, is essential to details rather than to the general model. Any transverse section of a mature specimen of the Heterocorallia provides adequate information, containing in the septal apparatus the preservation of all the basic ontogenetic stages. The whole process of increase in septa can thus be easily read by tracing individual steps from the corallite axis towards its periphery. Thus it is maintained that deductive postulations based on various genera are adequate for proposing such a general model, especially when confirmed to some extent by the fairly detailed study of the ontogeny of *Oligophylloides* by RÓZKOWSKA (1969) and SUTHERLAND & FORBES (1981), in *Mariaephyllia* n. gen. (in this paper), and by some short ontogenetic series of other genera (KHOA, 1977; Sugiyama, 1984). Although the basic models of septal insertion in the Heterocorallia have been discussed by other authors, a further detailed discussion of two of them is necessary. SCHINDEWOLF's (1941) model was unanimously accepted until POTY's (1978a) paper, but even then HILL (1981) chose the former and omitted the latter from her account of the characteristics of Heterocorallia. Some parts of SCHINDEWOLF's model are supported by the material studied for the purpose of the present paper or by data in the literature, and thus have been accepted herein, although in modified version. These are:

1. The peripheral division (but not splitting) of earlier inserted septa. However, this process started not from four primary septa, but from a single septum located in the medial part of a young corallite, and not exactly in the manner reconstructed by SCHINDEWOLF (1941). Also, it was not restricted to eight septa, but was continued to the end of septal insertion. The unequal development of quadrants of septa derived from the four septa (first septa in SCHINDEWOLF's model) was interpreted by that author as retrogressive evolution. Such an interpretation formed the basis for the introduction of the subgenus *Heterophylloides* SCHINDEWOLF, 1941. Rejection of this concept by POTY (1978a) is fully accepted in this paper.
2. The formation of four main interseptal loculi ("fossulae") in most heterocorals, but not in the way proposed by SCHINDEWOLF and not in alle representatives of the subclass Dividocorallia n. subclass.
3. The arrangement of septa suggesting cyclicity in their insertion; the latter interpretation is rejected and is replaced by the idea of generations of septa, but the symmetry recognized by SCHINDEWOLF (1941) is mostly acceptable.

Several other parts of SCHINDEWOLF's model have been rejected in this paper because they were unsupported both by illustrations published by that author and by comparative studies made for the purpose of the present paper.

The problem of the occurrence of protosepta in the Dividocorallia or only in the Heterocorallia should be discussed first. The real mutual relationships and location of the four septa called protosepta by SCHINDEWOLF (1941, figs. 21, 22, 30) differ from the idealized image reconstructed by that author and followed by several other authors. There is almost always a shorter or longer lamella, septal in morphology, that divides these "protosepta" into two oppositely directed Y-shaped pairs. The occurrence of such a lamella in the corallite axis has already been noted by LAFUSTE (1979), who called it the "oblique septum", the term accepted herein as possessing priority for the Heterocorallia and thus for the Dividocorallia n. subclass. LAFUSTE (1979) pointed out the role of an oblique septum in the asymmetrical arrangement of septa apparent in some genera of Heterocorallia. However, he did not mention its role in the insertion of the septal apparatus within this group of corals. KHOA (1977, p. 26: 5-7) and POTY (1978a, pl. 1: 1-4) have demonstrated the ontogenetically earliest stages of the hererocorals other than *Oligophylloides* and *Mariaephyllia* n. gen. One of POTY's specimens (1978a, pl. 1: 1) seems to support the occurrence of a four-septal stage and thus the beginning of septal insertion in heterocorals following SCHINDEWOLF's (1941) model. However, there occurs a short bar rather than a point of junction of the four early septa, i.e. the presence of a very short oblique septum can be accepted. The occurrence of the latter septum has been indicated by POTY (1981, fig. 61) in his modified model. Also, all other four (?) and five (?) septal specimens illustrated by POTY (1978a, pl. 1: 2-4) possess the oblique septum well developed. Thus, these specimens should be considered not four- and five- but five- and seven-septal respectively (see below for the interpretation).

There is a point in the study by SUTHERLAND & FORBES (1981) on the ontogeny of *Oligophylloides* that may explain the phenomenon of the apparent occurrence of four crossed septa in a corallite axis. In one of the specimens studied by those authors in detail (SUTHERLAND & FORBES, 1981, figs. 1A-1E, 2A; pl. 40: 1-17) the oblique septum, very well developed in earlier stages of growth, has been reduced in the course of ontogeny to a state suggesting a direct intersection of four septa in the corallite axis. The apparent four-septal stage of POTY (1978a) specimen can thus be compared to the axial part of the corallite of *Oligophylloides* discussed above, and an identical relationship of septa of both corallites can be deduced. The temporary disappearance of the oblique septum is not at all unique. On the contrary, this is quite a common phenomenon, occurring as far back in the history of dividocorals as in the Middle Devonian *Pseudopetraia* SOSHKINA 1951 (pl. 1: 2a, b; 3a, b). The discovery of *Tetraphyllia* YOH *et al.*, 1984 from the late

Early Devonian of SE Yunnan may provide some proof for the primary occurrence of the oblique septum. All specimens of that genus illustrated so far possess this structural element well developed. However, the ontogeny in none of these specimens has been studied. Nevertheless it is maintained that:

- the four-septal stage does not exist in Heterocorallia and in Dividocorallia n. subclass as a whole; its rarely observed occurrence is an artefact resulting from the reduction in length of the oblique septum;
- the appearance of the oblique septum at the very beginning of the insertion of septa in all Dividocorallia n. subclass seems more than probable. This can be easily deduced from its position in the system of septa and from the sequence in the appearance of remaining septa. The serial section of earliest ontogeny described in this paper supports that idea.

Both SCHINDEWOLF (1941) and POTY (1978a, 1981) accepted the idea of increase in septa by splitting. The former author restricted it only to the insertion of eight "protosepta", whereas the latter extended it to all but the four "first" septa. The term "splitting" suggests a kind of longitudinal break in the peripheral parts of septa, which is morphogenetically unacceptable and should be

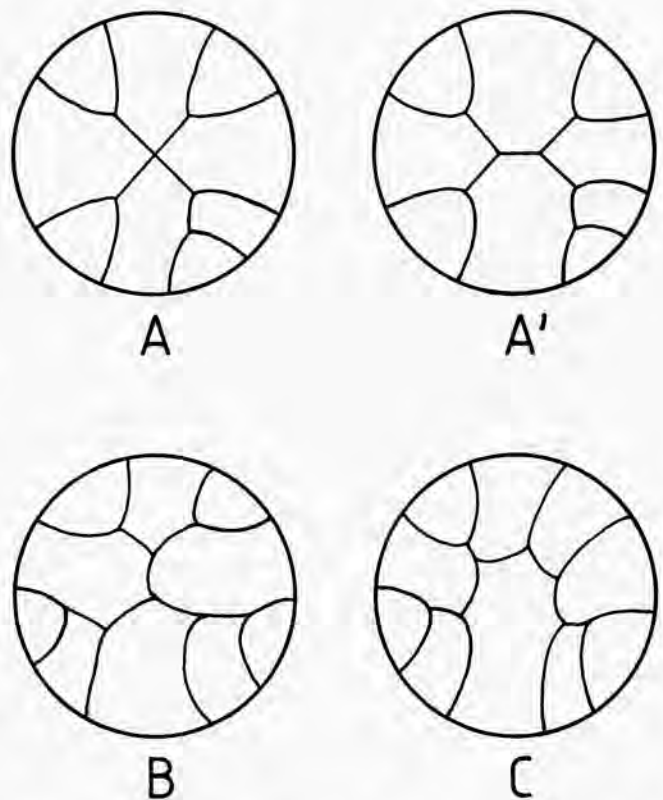


Fig. 3. – Transverse sections described by SUTHERLAND and FORBES (1981: 499) as "irregular septal developments". Such a temporary irregularity, resulting mainly from modifications of the oblique septum, is exemplified by fig. A' drawn from the transverse section made just above that illustrated by SUTHERLAND and FORBES (1981, fig. 2A) and re-illustrated here as fig. 4A.

abandoned as misleading. Increase in septa in the *Dividocorallia* n. subclass is discussed later in this paper.

There is no difference in the morphology, microstructure, septal insertion and mutual relationship of all septa in *Dividocorallia*. Thus the distinction by SCHINDEWOLF (1941: 245) of septa being inserted by "Aufspaltung" and "Einschaltung" is not accepted in this paper. Consequently, the term "protosepta" is not accepted in *Dividocorallia* despite the fact that it has been unanimously accepted for the *Heterocorallia* as the representative of this group of corals. In the new model proposed later in this paper there are no septa in the *Dividocorallia* comparable to the protosepta in the *Rugosa* other than the oblique septum. The latter is homologous to the axial septum, inserted at the very beginning of growth in most, if not all, *Rugosa*. Thus, it should perhaps be called not the oblique, but simply the axial septum. Such a solution is not proposed herein for three reasons: the term "oblique septum" has priority in the *Heterocorallia* and thus in the *Dividocorallia* as well; it has already been used a few times; the oblique position of this septum is to some extent characteristic of such genera as *Hexaphyllia*, *Heterophyllia* or *Stylostrotion*. The morphogenetically similar insertion, as well as equal value and role of all septa other than the oblique septum is confirmed by two facts:

1. The absence in *Tetraphyllidae* of septa comparable to the "cardinal" and "counter septum". Thus this family would be lacking of two of the main protosepta.
2. In *Hexaphyllia*, *Stylostrotion*, *Radiciphyllia* and all other genera possessing several generations of septa, the stage and place of the insertion of these septa, as well as the direction of insertion of the new septa were not subordinated to the rules suggesting any particular septa to be more important than the others, as it is observed in the *Rugosa*. A simple analysis of the septal apparatus of any specimen belonging to such genera will confirm this observation. Thus, it is proposed herein to reject the term "protosepta" as inapplicable in the *Dividocorallia* n. subclass, or to restrict it to the oblique septum, which is the only true protoseptum in this group of organisms.

The individual value of the septa, with some appearing especially important, can be superficially demonstrated in individual specimens or sections of specimens, which is discussed later in this paper. This was the basic idea of SCHINDEWOLF's (1941) and POTY's (1978a, 1981) models, whereas an absence of this character is one of the main reasons for these models to be rejected herein.

The model introduced and later slightly modified by POTY (1978a, 1981) in accordance with LAFUSTE's (1979) recognition of the "oblique septum", is often characterised above as being opposed to SCHINDEWOLF's (1941). The following parts of POTY's (1978a, 1981) model are not acknowledged herein, although they have been fully accepted by SUGIYAMA (1984):

1. A single septum, not four septa were inserted at the beginning of the formation of septa.
2. None of the specimens investigated both for compari-

son (*Hexaphyllia*, *Heterophyllia*, *Oligophylloides*) and in this paper (*Mariaephyllia* n. gen., *Stylostrotion*) show septal insertion as proposed by POTY (1978a, 1981). Also, in the specimens he illustrated, the insertion of septa outwards from the so called "septes alaires secondaires" and towards four "fossulae" is correct only for the second generation of septa in the nomenclature introduced here. The insertion of further generations of septa towards the fossae, if observed, is not dependent on the rule introduced by POTY, but results from the production of advanced generations of septa (see the model introduced here).

3. It has been postulated (POTY, 1978a, 1981) that each new septum was split from one of four secondary alar septa in such a way that the first inserted metaseptum was located near the periphery, whereas the subsequent ones form a series towards the corallite axis with the last septum inserted being located in the transverse section closest to the axis (POTY, 19781, fig. 2). Such a concept cannot be supported on the basis of any specimen observed so far. The corallite with the "protosepta" marked by POTY himself (1981, pl. 34: 5) in which the last formed septa in quadrants are not united with A2 but with septa preceding them in appearance, speaks against the theoretical figure 61 of that author. Some other points of disagreement with POTY's (1978, 1981) model were discussed above together with the critical review of SCHINDEWOLF's (1941) model and do not need to be repeated.

Illustrations and description of septal insertion by SUGIYAMA (1984), who declared them as being fully in support of POTY's (1978, 1981) model, cannot be accepted as such. This is first of all because the insertion of septa of only three generations was demonstrated for sure (SUGIYAMA, 1984, p. 6). Also, there are the following disputable points concerning the interpretation by SUGIYAMA (1984, p. 6: 1a-e versus 1a'-e') of his serial sections and drawings: [SUGIYAMA's (1984) nomenclature of septa is followed in this part of discussion]

1. The insertion of septum "m2". In pl. 6: 1d the peripheral part of the lower right septum "a1" showed a division suggesting inwards, i.e. in SCHINDEWOLF's (1941) sense rather than outwards insertion of the new septum. This can be confirmed by the free septum located in the closed loculum formed by the narrow Y-septum (pl. 6: 1c). The transverse section of the tabula inwards of this free septum confirms that the septum is just being inserted above the surface of this tabula, and thus is not seen beneath it. The next section (pl. 6: 1b), obviously made above the tabula mentioned, exhibits the relationship here suspected of the two septa in question. Both these facts confirm at the same time the model proposed in this paper. Thickenings at the base of the septum "m2" and of the upper right fork of the septum "a1" (pl. 6: 1a) may suggest an early stage of further division of these two septa.

2. The septum seen in pl. 6: 1a as being inserted from "ml" appeared quickly and one cannot be certain whether or not the shade seen between it and the C-septum is really the free septum being cut beneath the tabula in the manner discussed above. However this was formed, the position of this septum next to "ml" is in contradiction to POTY's (1978a, 1981) model, in which no further development of septa derived from the "cardinal" septum is hypothesised.
3. The lower left metaseptum (pl. 6: 1c, d) may or may not be inserted in the direction reconstructed by SUGIYAMA as no evidence is apparent in the earlier growth stage of this division (pl. 6: 1c).
4. The position of the septa next to the so called "anti-cardinal septum" (a) changes from section to section, but is never clear. Thus this question is left without comment. These brief remarks show that contrary to SUGIYAMA's (1984) suggestion, his specimen analysed in detail does not confirm POTY's (1978a, 1981) model of septal insertion in the Heterocorallia.

There is one point concerning septal insertion in the Heterocorallia that should be discussed: the free septa at the early stage of their insertion. The mode of occurrence of such septa is simple and was well documented, although not explained, by SUTHERLAND & FORBES (1981, pl. 40: 8-12). The two free septa in question, as for any other septa in corals, were inserted above the basal disc of the polyp, i.e. above the last tabula in this case. Septa that are seen in transverse sections as being permanently attached to preceding septa either extend high above the level of the tabula, or the latter is not steeply inclined, or both. Almost any transverse section passes through the junction area of such septa. In contrast to these, the septa that extend only slightly above the surface of a steeply, upward-inclined tabula are rarely sectioned through their point of junction or division. Sectioning of such elements will most commonly show at least two growth stages of the corallite: a less advanced stage, located closer to the corallite axis (below the tabula), and a more advanced stage at the periphery (above the tabula). Septa inserted in the more advanced stage of growth will be absent below the tabula (Fig. 4a). They will be seen as terminating at the section of the latter, whereas in fact their parts have been cut off together with their area of division and the upper part of the tabula (Fig. 4b). The comparison of individual transverse sections illustrated by SUTHERLAND & FORBES (1981, pl. 40: 8-12) and SUGIYAMA (1984, pl. 1: 1b, c) confirms this reconstruction. Thus, there is nothing unusual in this as well as in other phenomena observed by SUTHERLAND & FORBES (1984, fig. 2; pl. 40: 17; 41: 15, 16) in the early ontogeny of *Oligophylloides*, called by them "irregular septal development". The apparent disappearance of the oblique septum is the most important of these variants. Close examination of sections illustrated by these authors (pl. 40: 14-17) shows, however, that this septum underwent a step by step reduction in length, but did not disappear. Also, the insertion of septa and their mutual relationships in the other specimen mention-

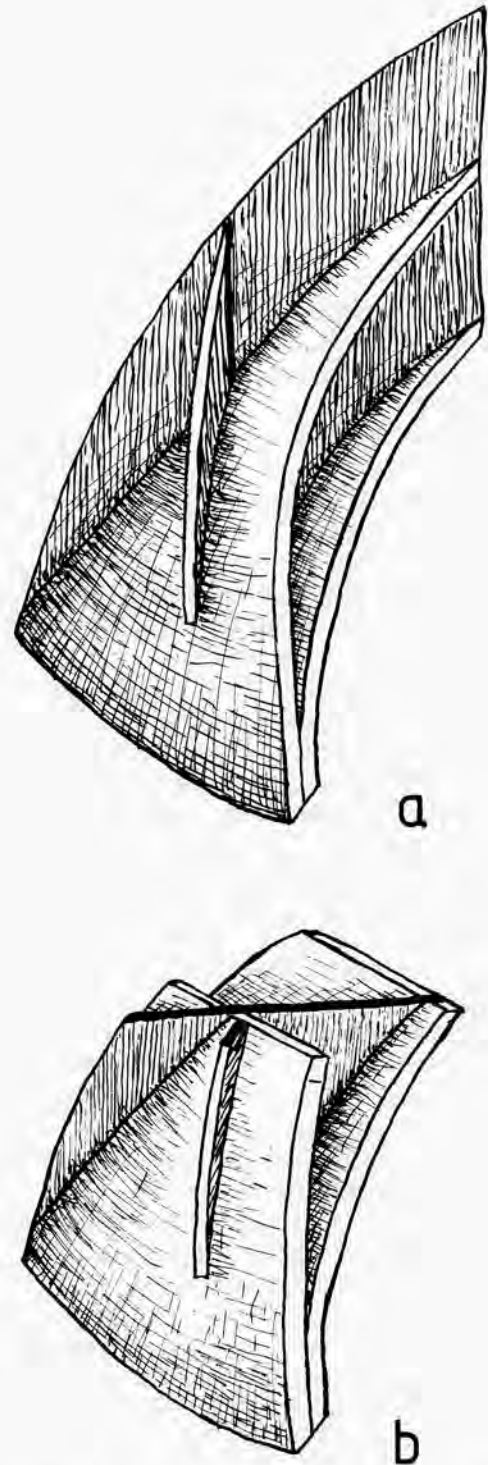


Fig. 4. – Tabulae/septa relationship in reconstruction; a. Complete structural elements; b. Cross section. Shortening of newly inserted septum is seeming; it has been inserted above the level of a tabula.

ed by SUTHERLAND & FORBES (1981, pl. 41: 15, 16) is easy to explain once the position of the oblique septum is correctly established. The similarity of the latter variant to the variants commonly observed within *Stylos-*

tration is of some broader value. It points to another character common to two orders of the *Dividocorallia* n. subclass, i.e. the similar modifications of their septa.

The new model of septal insertion in the *Dividocorallia* n. subclass

MORPHOGENETICAL INTERPRETATION AND DISCUSSION

The following facts should be pointed out first:

1. All septa in the *Heterocorallia* and all major septa in the *Calyxcorallia* n. ordo are permanently, or at least in the early stage of their presence, united by their mid-lines.
2. The development of a new septum starts near the peripheral end of a given septum, called here the creative septum. This peripheral part of the creative septum is often (e.g. SUGIYAMA 1984, pl. 6: 1d-b, left) but not always, thickened.
3. Any septum, except for one septum in "*Pentaphyllia*.. and two septa in *Hexaphyllia*, if these genera are valid, can create a new septum.
4. Observations of any septal system in transverse sections of the *Dividocorallia* n. subclass indicate a succession of more or less symmetrical bifurcations of septa. They start at both ends of the oblique septum and end at the periphery of a corallite in the form of the last two forks of a given generation of septa.

The following morphogenetic interpretation of these facts is proposed: The more or less peripheral part of the septal pocket in which a given creative septum was secreted commenced division into two septal pockets at the very beginning of formation of a new septum. This process in the *Heterocorallia* is often preceded by the thickening of the peripheral part of the creative septum, resulted from the widening of the peripheral part of the septal pocket. Creation of a new septum in at least some *Heterocorallia* possibly took place inwards of the peripheral wall, i.e. not exactly at the lowermost part of the creative septum, but slightly above that point (Fig. 5b). This reconstruction, confirmed by the position of the newly inserted septum in relation to the external wall (e.g. SCHINDEWOLF, 1941, pl. 12: 1a, 1b) may mean that this is not a true division, i.e. the simultaneous appearance of two equal forks, but rather a partition, i.e. the insertion of a new fork from the axially-lateral part of the creative septum (Fig. 5b). The fork created in this way elongated quickly up to the length and thickness of its partner, becoming indistinguishable from it. In the *Calyxcorallia* n. ordo the point of division at the very beginning was located close to, but perhaps not at the calice rim, and was transferred inwards in the course of further growth of the corallite. This supposition is speculative and is based only on the smooth external surface of corallites, comparable to that in the *Diffingiina* (*Rugosa*) that also possess no septal furrows. It is not based on direct observations of calices in *Calyxcorallia* n. ordo.

The recognition of the peripheral division or partition of septal pockets in *Dividocorallia* n. subclass is the fundamental point of the reconstruction of septal insertion within the subclass. It explains all four points listed above.

The peripheral division of any creative septum may take place only once. It ends the occurrence of this septum near the periphery of the corallite. The two septal forks created due to that process form a new generation of septa called herein potentially creative septa. This is independent of whether we are dealing with an ideal division or only with partition. The distinction between these two can in fact be reduced to the size of the two forks at their inception. Thus each peripherally directed Y-system of septa is composed of the creative septum, corresponding to the inner, unitary part of the system, and of two potentially creative septa at its periphery (Fig. 6a, 6b). This means that each creative septum produced two potentially creative septa of the next generation. The whole process of formation of new generations of septa started from the oblique septum, which is at the same time the first creative septum. It differs

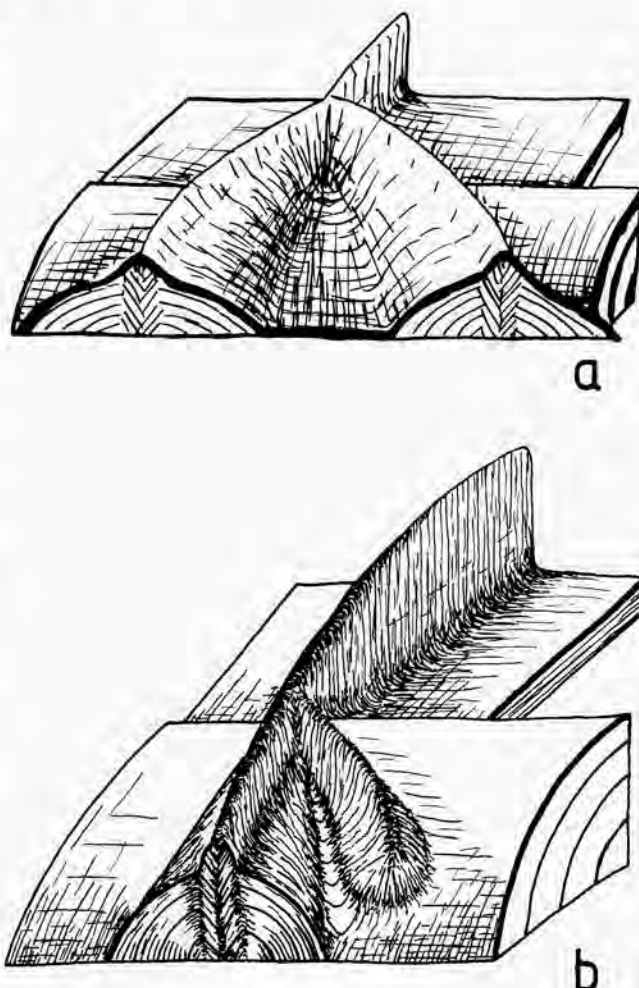


Fig. 5. – Reconstruction of peripheral dichotomic division of septa. a. symmetrical; b. asymmetrical, with one fork dominating in early stage of growth.

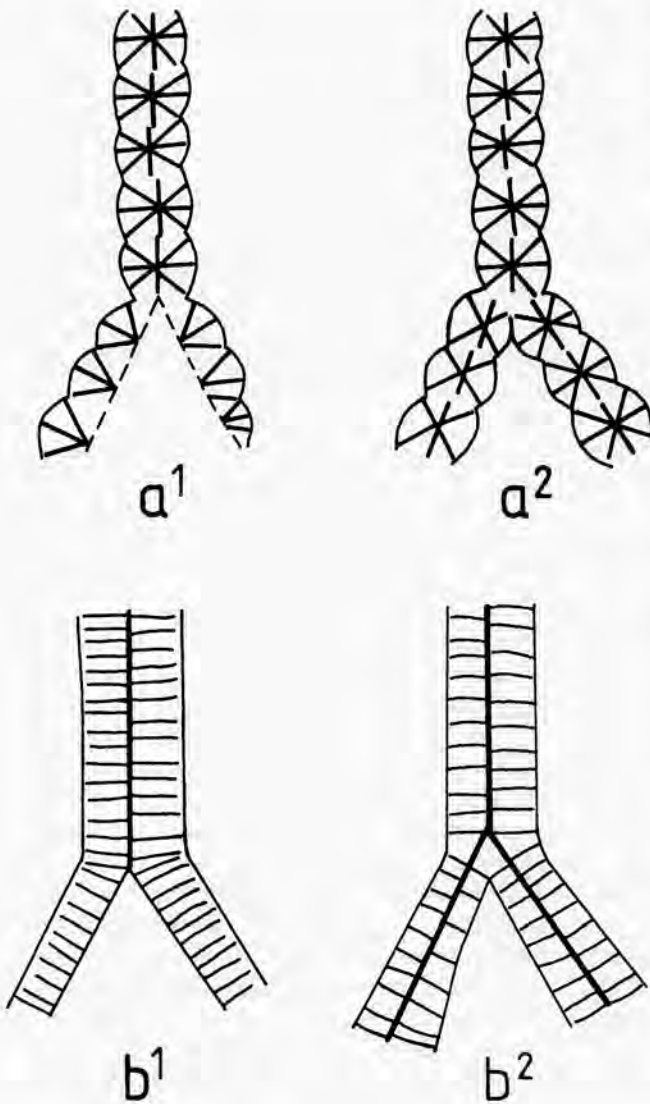


Fig. 6. — Reconstruction of differences in microstructure of "Y" systems of trabecular (a) and fibro-normal (b) septa. a^1 , b^1 . Hypothetical splitting; a^2 , b^2 . Peripheral dichotomic division comparable to Pl. 2: 1-3.

from all its descendents by creating one pair of forks at either end. All septa located between the oblique septum and the most peripheral septal forks are nothing but the former Y-systems of septa, with the oblique septum being in this interpretation just a common creative septum for the two first Y-systems. In all these systems, forks were initially potential and afterwards the true creative septa with the exceptions mentioned below. SCHINDEWOLF's (1941, fig. 22) idealized reconstruction, slightly modified for the purpose of this paper (Fig. 1, p. 22), illustrates this well. Thus the insertion of septa in the Dividocorallia n. subclass was carried out in geometrical progression, which explains their rapid increase in number.

Not all four septa created by the oblique septum are equal in their potential for developing generations of creative septa. Some never divide, which is discussed

later as having a potential taxonomic value. Also, among the septa of younger generations there may be arms of individual forks that remain only potential and not true creative septa (e.g. SCHINDEWOLF, 1941, pl. 15: 2a, 2b; 3a-3c; 6a, 6b; 7) I cannot point out a taxonomic value for such septa, although this should not be excluded.

Bearing in mind the basic point of the reconstruction discussed, i.e. the peripheral division of individual creative septa, all further peculiarities in the morphology and relationships of individual septa within the septal apparatuses in Dividocorallia n. subclass are fairly easy to explain. First of all it explains the union of the primary septa (= mid-lines of septa), observed e.g. in most of the Heterocorallia and in some Calyxcorallia n. ordo. The insertion of individual generations of septa in the peripherally divided septal pockets leave no room for any other possibility. Thus, this is not the area of union, but the area of division of these septa. The separation of individual septal pockets leads to the secretion of separated, often shortened, septa. The upward growth of septa in the Heterocorallia and the inward growth of the peripheral portions of major septa in the Calyxcorallia, with the simultaneous transmission of the point of division towards the corallite axis in both instances, explains the elongation of the peripheral septal forks, i.e. the potentially creative septa, the simultaneous shortening of the creative septa themselves and the permanent junction of mid-lines of septa of both generations, i.e. of the Y-system of septa. The same process observed in all generations of septa present in any given corallite explains why the older, i.e. located closer to the oblique septum, generation of creative septa is short and the potentially creative septa belonging to the same older generation are long. Some of the latter may be located at the border of fossae, which perhaps misled SCHINDEWOLF (1941) in his interpretation of the increase in septa in the Heterocorallia.

The reconstruction proposed herein allows new septa to be created by peripheral division, without any particular direction to their increase, which is still in full agreement with the morphology of the specimens observed so far by various authors, but in contrast both with SCHINDEWOLF's (1941) and POTY's (1978a, 1981) reconstructions, as has already been discussed above.

The development of secondary sheets of septa in all Dividocorallia is reconstructed in a way similar to but not identical with that proposed by SCHOUPE & STACUL (1955, figs. 5, 6) for the Rugosa. Peripheral division and a common upward growth of septa in many dividocorals do not contradict that reconstruction because it assumed action of the basal disc or the lower part of septal pockets in the secretion of that secondary stereoplasm, whereas points of division of individual generations of creative septa are located higher within septal pockets, i.e. above the basal disc (Fig. 13a-13c, p. 43).

The junction point of the three parts of any Y-system, or strictly speaking, the point of the division, was perhaps critical for the recognition of split septa by SCHINDEWOLF (1941) and POTY (1978a, 1981). Indeed, the

Y-systems in the Heterocorallia appears to have been split longitudinally. Closer examination shows, however, that the microstructure of the mid-lines (= primary septa) of the secondarily thickened septa, or the non-thickened primary septa is identical in both the peripheral forks (i.e. the potentially creative septa) and in the inner part of the Y-system (i.e. the creative septum) (Pl. 2: 1-3). The development of such a microstructure is possible only in regular septal pockets, whereas a split must by definition lead to the longitudinal division of a septum along the axis of symmetry of the primary septum. Thus we should have all fibres in the peripheral forks (i.e. the potentially creative septa) directed unilaterally outwards from the locus between these forks, whereas the symmetrical arrangement of these fibres would be seen only in the creative septum (Fig. 6a², b²). This has never been observed. Thus, the term "split septa" should be omitted as misleading.

These remarks are applicable in general to any dividocoral discussed so far in the literature, whereas the sequence in septal insertion may perhaps be diagnostic of component groups of the Dividocorallia n. subclass. Any discussion of the latter problem should start from a discussion of the cyclicity in septal insertion emphasized by SCHINDEWOLF (1941), and best exemplified in his figure 22. Indeed, the study of mature specimens of most genera seem to support this hypothesis. However, detailed studies of serial sections (SUTHERLAND & FORBES, 1981; SUGIYAMA, 1984, and in this paper) show that individual septa in *Oligophylloides*, *Radiciphyllia*, and *Mariaephyllia* n. gen. were inserted in series, not in cycles, and formed the characteristic heterophylloid symmetry due to the subsequent addition of new elements. This can easily be proven when particular stages of growth observed in separate specimens of a particular taxon are compared. For instance, some septa in *Heterophyllia*, *Radiciphyllia* or *Stylostrotion* remain single, whereas neighbouring ones have already undergone several generations of forking and form together with them septal system. It is obvious that the eventual division of the long unforked septum, although comparable to the earliest steps in the division of other septa, could not be treated as belonging to the same cycle.

The process of attainment of the symmetry in the septal apparatus characteristic of a particular taxon within the Dividocorallia n. subclass and the obvious steps in the division of septa observed in any dividocoral has led to the conclusion that these episodes of division should be called generations of septa rather than cycles, which they are not. As in the common meaning of the word "generation", it is not the moment of appearance, but the relationship of the individual (the septum in this case) to the preceding and following individuals which determines its status. It is unimportant for their relationships within a family whether brothers and sisters are children or mature individuals having their own children and grand-children. It is unimportant within the Dividocorallia n. subclass when a particular septum appeared in comparison to other septa. Its relationship to the

preceding septa, the oblique septum included, will remain the same. I therefore propose the term "generation" for each level of septal division that has the appearance of a cycle in cross sections of mature specimens. There are many factors, extrinsic (somatic) and genetic that determined the arrangement of septa, sometimes quite differentiated, during the course of growth of individual corallites. In general, however, septa tend to be arranged in such a way that comparisons of individual generations can be by connecting the points of division with more or less regular circles. This phenomenon perhaps led SCHINDEWOLF (1941) to his idea of the cyclic appearance of septa in the Heterocorallia.

THE SEQUENCE OF SEPTAL INSERTION IN DIVIDOCORALLIA N. SUBCLASS

SCHINDEWOLF's concept of septal increase exclusively in four locked original loculae cannot be confirmed and is rejected in this paper. His ideas about cyclicity in septal increase, best exemplified in his fig. 22, although not accepted herein in its original sense, was partly an inspiration for the model proposed in this paper. The basic idea of this model is very simple and can be described briefly as a successive, dichotomic peripheral division of septa. Two stages in the development of the septal apparatus can be distinguished: the initial stage and the stage of division. The initial stage took place immediately after larval settlement, and was restricted to the development of a single septum on the basal disc of the larva or the newly metamorphosed polyp, i.e. the oblique septum. It is thought that the earliest skeleton was inserted in a manner observed in Scleractinia (e.g. JELL, 1981), except for the number of septa being inserted at the beginning. This might be the major analogy between the Scleractinia, Rugosa and Dividocorallia n. subclass, whereas the number of septa inserted on the basal disc, the sequence and manner of their insertion form one of the fundamental characteristics distinguishing between them. The presence of the single septum stage in *Mariaephyllia* n. gen. is confirmed in this paper. Also, its presence has been clearly shown in the Rugosa by many authors. The three septal stage found in *Oligophylloides* by RÓZKOWSKA (1969) and confirmed by SUTHERLAND & FORBES (1981) allows one to assume that a single septum did exist at the beginning at the development of the septal apparatus in that genus as well. Observations on many dividocorals support the view that there is no other possibility for the insertion of the oblique septum, positioned in the middle of the corallite, and in a key position for all remaining septa, than to appear at the very beginning of septal development. Thus, the name Dicoelia informally proposed by YABE & SUGIYAMA (1940) to include the single family Heterophyllidae in order to contrast it with the rest of the Rugosa, explains the earliest morphology of the polyp and its skeleton better than the name Heterocorallia formally introduced by SCHINDEWOLF (1941). It is presumed here that the basal part of the interior of a newly metamorphosed larva was in some sense divided

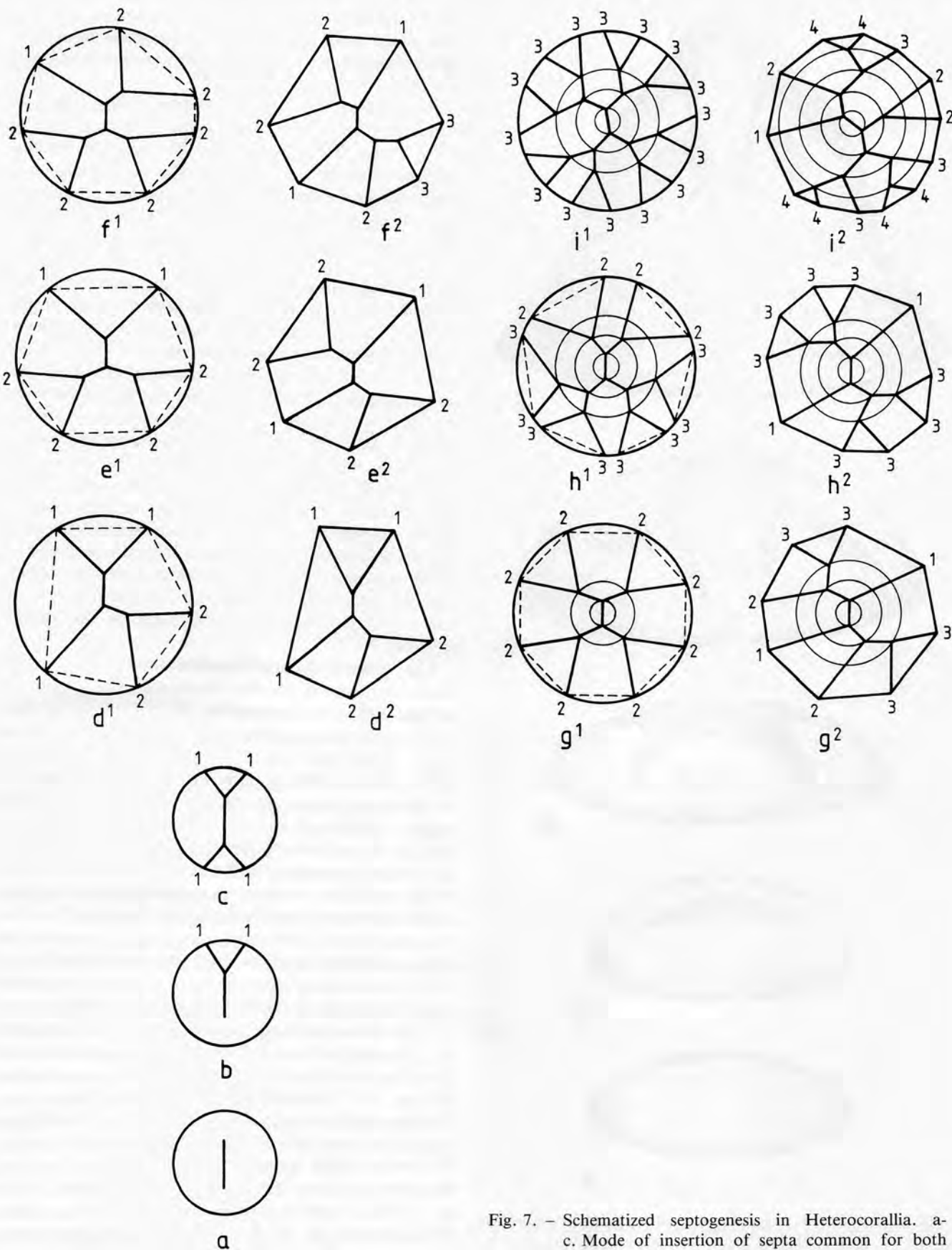


Fig. 7. - Schematized septogenesis in Heterocorallia. a-c. Mode of insertion of septa common for both suborders; d¹-i¹. Further development in Tetracyclina n. subordo; d²-i². Further development in Heterocorallia (suborder). Individual generations of septa marked by numbers.

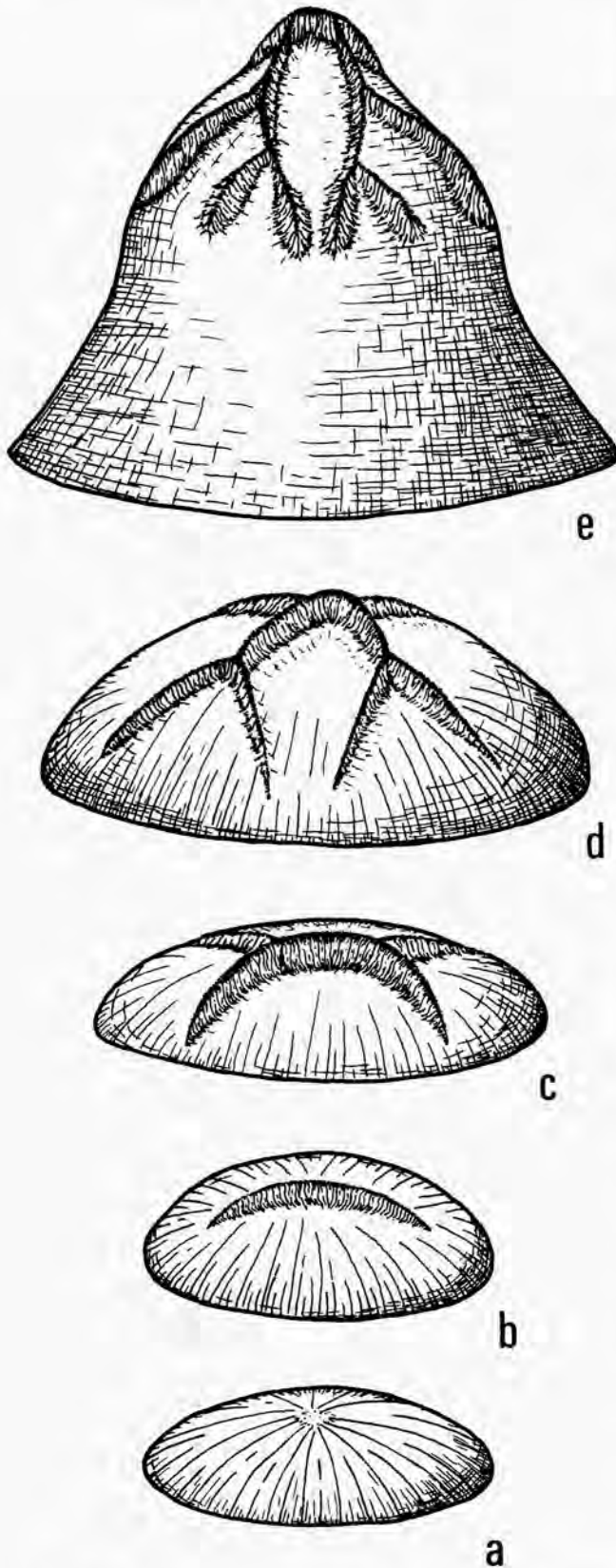


Fig. 8. – Idealized reconstruction of successive stages of growth of skeleton in Heterocorallia (based on *Oligophylloides*). a. Aseptal basal disc; b-d. Insertion of the oblique septum and two first generations of septa; e. Young corallite that just started its cylindrical portion of growth.

into two major loculi, although this division was incomplete due to the limited upward protrusion of the primary septum (the oblique septum) and its assumed short length (Fig. 8b).

The development of the oblique septum, preceded perhaps by the development of the hard basal disc on which it was formed, ended the first stage of development of septa in the *Dividocorallia* n. subclass. It is presumed herein that this stage was typical of all specimens of the subclass irrespective of both their further growth and the polyp-skeleton relationship. This important problem is discussed separately in one of the following chapters. Considering the data available so far, and comparing them to deductions discussed earlier in this chapter, it is proposed herein that the second stage of septal insertion in the *Dividocorallia* n. subclass began with the division of the oblique septum. The latter process started most probably asymmetrically as is shown by the three-septal stage of *Oligophylloides* and *Mariaephyllia* n. gen. (Fig. 19, p. 54). Then the opposite end of the oblique septum was divided and the five-septal stage was formed. The four-septal stage has already been concluded above to be lacking. The five-septal stage is herein accepted to be characteristic of all *dividocoralloid* genera, because it can be deduced from the arrangement of the axial parts of the septal apparatuses of all of them. The oldest five-septal *dividocoral* *Tetraphyllia* from the late Lower Devonian of China confirms this reconstruction.

The further division of the septa is herein treated as the most important diagnostic criterion for the subdivision of the subclass into orders (Fig. 7). In *Tetraphyllia* there are no more than just five septa. This is at least what we know about this genus as yet. In *Oligophylloides* (RÓZKOWSKA, 1969; SUTHERLAND & FORBES, 1981) and in *Mariaephyllia* n. gen. (in this paper) the five-septal stage is simple and more or less symmetrical. The two divided ends of the oblique septum formed the basis for the further appearance of the next generations of septa, which are rather restricted in number. Lack of the septa called elsewhere in the literature the "cardinal" and the "counter" septa is the most characteristic feature of the genera discussed, and the most important criterion for their distinction as separate taxa. The main taxonomic remarks are included in the systematic part of this paper.

Truly five-septal stages in genera other than *Tetraphyllia*, *Oligophylloides* and *Mariaephyllia* n. gen. have only been illustrated three times in the literature known to me (KHOA, 1977, POTY 1978a, 1981). In all of these cases, this stage has been called four-septal, because the oblique septum has not been counted. The apparently five (i.e. the seven) septal stage is better known and has been illustrated by KHOA (1977), POTY (1978a, 1981), YU *et al.* (1978), and SUGIYAMA (1984). It has been distinguished by YU *et al.* (1978) as the new genus *Pentaphyllia*. The occurrence of the "cardinal" and/or "counter" septum in this stage of growth or in the genus (?) *Pentaphyllia* is the most substantial difference when compared to the *Tetraphyllidae*. The septal apparatus in

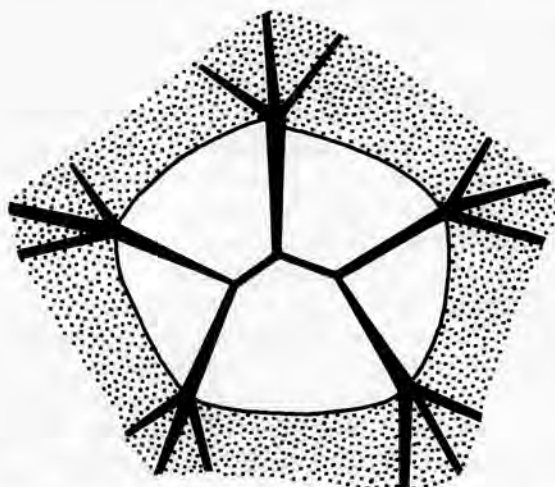


Fig. 9. – *Pentaphyllia regulare* YU, LIN, HUANG and TSAI 1978. Holotype, redrawn from YU *et al.* (1978, p. 56, fig. 7a), not to scale.

this stage (or genus) is composed of the following septa: the oblique septum, two pairs of forks of this septum, and two forks of the second generation of septa. Thus, among four forks of the oblique septum three are potentially creative septa. Two of them are fairly short and are located at the periphery (Fig. 9, left). The third one is comparatively long and is called the “cardinal” or “counter” septum. The fourth fork of the oblique septum forms the inner portion (the creative septum) of the Y-system (Fig. 9, right). Thus, this is a seven-, not five-septal stage. Although all the elements mentioned are clearly seen in the original drawing by YU *et al.* (1978, fig. 7a), the moment of the division, leading towards the appearance of two forks of the second generation is best demonstrated by KHOA (1977, pl. 27: 7a-d; fig. 43: 9a-c) in serial sections.

There are two theoretical possibilities concerning the further growth and development of corals having seven septa:

1. It represents a genetically determined limite of septal insertion and the generic name *Pentaphyllia* YU *et al.*, 1978 is truly valid.
2. It is a stage of growth leading towards *Hexaphyllia* (HILL, 1981) and perhaps towards *Heterophyllia* (POTY, 1978). The latter is not only theoretically possible, but can be demonstrated in the septal apparatuses of mature *Heterophyllia*. However, lack of a complete ontogenetic study leaves this deduction open for further discussion. It is maintained herein that the seven-septal stage is characteristic of all Heterocorallia excepting *Tetraphyllia* and perhaps of the Calyxcorallia n. ordo as well.

In the further development of the septal apparatus one of the two first generation septal forks, located opposite to the first formed potentially creative septum of the second generation, divided (Fig. 8, 19). This is the stage best illustrated by KHOA (1977, pl. 25: 12). The corallite shows the right septum at the initial stage of division,

allowing the upward directed septum to be recognized as the “counter” and the downward directed one as the “cardinal” or vice-versa. Further growth of the two incipient forks leads to the appearance of the common morphology of *Hexaphyllia*. The septal apparatus of the hexaphyllid stage of growth or of the genus *Hexaphyllia* is in fact composed of:

1. The oblique septum.
2. A first generation fork at either end; one fork of each pair remains a potentially creative septum and they have been recognized by previous authors as the “cardinal” and the “counter” septum; the other fork of each pair is a true creative septum.
3. Two pairs of second generation septa, i.e. the potentially creative septa derived from the creative septa mentioned in point 2.

Thus, the stage discussed (or *Hexaphyllia*, if its independent generic status is confirmed) is in fact composed of nine septa. Specimens possessing seven septa (eleven, if the here proposed model is applied) have been described by RODRIGUEZ (1989) from the Namurian deposits of the Cantabrian Mountains in Spain, making at least some specimens of *Hexaphyllia* only a growth stage of *Heterophyllia*. Such a solution has already been postulated by POTY (1978a). This cannot be generalized, however, because the occurrence of a genetically determined, i.e. independent genus *Hexaphyllia* cannot be excluded. The same is true of the specimens from the Cantabrian Mountains mentioned above, i.e. they may well be either growth stages of *Heterophyllia* or belong to the independent genus. Such a solution suggests the possibility of the creation of a new genus for each case of insertion of a new generation of septa, but it can not be excluded at the present level of our knowledge. Both solutions are shown as equally possible in theory and not yet proven in practice.

Further development of the septal apparatus is highly variable in detail, which perhaps can be important for lower level taxonomy. It is subordinated only to two general rules:

1. Each septum is potentially capable of division.
2. One of the forks of each end of the oblique septum is often much more productive than the other of further generations of septa. This is especially clear within the suborder Heterocorallia.

The second rule is obvious and can easily be recognized in almost any transverse section of a dividocoral that possesses septa axially united. Its taxonomic implication is large, as has already been pointed out. In such genera as *Oligophylloides* and *Mariaephyllia* n. gen. there may be almost no difference in the development of the individual septal quadrants, or differentiation in the number of generations developed in individual quadrants is random. The situation within the suborder Heterophyllina is different. There are always septa that have been recognized formerly as the „cardinal” and/or the “counter” septum that remain either simple or initiate fewer generations of septa than other two forks of the oblique septum.

The first rule is simple as well and it is easily demonstrated. However, it contradicts both SCHINDEWOLF's (1941) and POTY's (1978, 1981) interpretations, and should thus be more fully explained. Any analysis of a transverse section of, for instance, *Heterophyllia* will show several dividing points of septa initiated at either end of the oblique septum. At each dividing point two septal forks have begun to develop. Both these forks may be equal in length and both may be creative septa (Fig. 7). If such a potentially creative septum belongs to as early as the second or even the first generation of septa, which is possible to find among the suborder Heterocorallia, and if it borders the quadrant next to the fossa, one may easily consider it a protoseptum in SCHINDEWOLF's (1941) sense. Consequently, all septa of the neighbouring quadrant that have developed from the other twin fork of the potentially creative septum mentioned above, may appear to have been inserted inside the primary locus between the two twin forks discussed, i.e. exactly in accordance with SCHINDEWOLF's (1941) hypothesis. There is one substantial difference between this hypothesis and the pattern confirmed by any observation of the material: the potentially creative septum borders only one side of the quadrant whereas there is a sequence of subsequently younger generations of septa, not bordered by any potentially creative septum on the other side of the same quadrant. Also, the process of septal increase is not due to adding (Einschaltung) a new septum to the earlier existing one, as postulated by SCHINDEWOLF (1941), but due to the peripheral dichotomous division resulting in the production of two equally important new forks. The fact that one of these forks divides again and the second may retain undivided does not mean that either the first or the second of them is more important or represents a higher rank of septa. The literature is full of examples of this arrangement, but it is best to refer to SCHINDEWOLF's (1941) paper (e.g. pl. 15: 3a-c, right; 5a, b, left) to show it illustrated.

Also, there exists no leading septum that all further septa were derived from, as postulated by POTY (1978a, 1981), although the asymmetrical arrangement of septa, rarely seen in *Heterophyllia*, may sometimes suggest it. Again, it is best to refer to POTY's (1978a, 1981) papers in order to show that there are many examples illustrating the model proposed here, but none supporting the model of that author. To avoid a long description, the postulated rule in septal increase, i.e. the peripheral dichotomous division of septa into still higher generations, as well as some variants of this process, are shown in Figs. 1b, 7. The illustrated and unillustrated theoretical variants may be treated as hypothetical diagnostic characters for taxa of different rank (genera and species). However, establishing such characters can be done only on the basis of a restudy of the original material in the light of variability in ontogeny superimposed on intraspecific variation. A brief examination of the literature seems to demonstrate that the systematic importance of the variability discussed should not be exaggerated. This concerns both sys-

tems advanced in the insertion of septa, and rudimentary systems. Some of the latter may not even be formally called systems because they consist solely of potentially creative septa of the first generation, whereas their twin forks may at the same time initiate up to 2-3 generations. Also, there may appear to be no dichotomous divisions, but a form of triad seen in some specimens (e.g. KHOA, 1977, pl. 27: 7). A close analysis and comparison with the lower part of the specimen mentioned show that we are in fact dealing with two generations of septa that were separated from each other by a very reduced remnant of the creative septum of the preceded generation. This short septum is aligned with the creative septum of the previous generation it was derived from. Thus, the structure discussed is again of no taxonomic value.

The coral growth in *Dividocorallia* n. subclass

Two modes of skeletal growth can almost certainly be distinguished among dividocorals: centrifugal and centripetal. The differences between these two modes in the polyp-skeleton relationship and in the suspected morphology of the former are so large that two distinct orders are proposed herein for the genera representing each of these models.

The morphogenesis in *Heterocorallia*

The centrifugal growth has already been reconstructed for *Hexaphyllia*, *Heterophyllia*, *Oligophylloides* and *Mariaephyllia* n. gen. (SCHINDEWOLF, 1941; SUTHERLAND & FORBES, 1981; WRZOLEK, 1981; and in this paper), and can well be suspected in *Radiciphyllia*, *Longlinophyllia* and *Vassiljukaephyllia* n. gen. In the case of *Tetraphyllia* the situation is not so clear, because many details of its morphology are either uncertain or unknown. It was placed within the Heterocorallia for the reasons discussed in more detail elsewhere in this paper. Thus, perhaps all representatives of the order Heterocorallia described so far can be characterised by that peculiarity. Such a direction of growth and the tabulae-external wall relationship may lead either to the misinterpretation of the life position of polyps or to the conclusion that the polyp was not protected by a calice. SCHINDEWOLF (1941) and POTY (1978) considered concavity of up-side down oriented tabulae to be bases of calices. HILL (1956) correctly re-oriented the life position of the heterocoral polyps, but she omitted any comments, morphogenetic discussion or the re-interpretation of SCHINDEWOLF's (1941) ideas. Her orientation of heterocorals was generally accepted afterwards (e.g. FONTAINE, 1961; RÓŻKOWSKA, 1969; KHOA, 1977; IGO & KOBAYASHI, 1980; LAFUSTE, 1979, 1981; POTY, 1981; WRZOLEK, 1981; SUGIYAMA, 1984; KARWOWSKI & WRZOLEK, 1987, etc.).

The morphogenesis of the heterocorals was only seldom discussed. The excellent analysis by SCHINDEWOLF

(1941: 259-265) has not been mentioned by subsequent authors in spite of the fact that his idea concerning the centrifugal growth of skeletons in *Hexaphyllia* and *Heterophyllia* was fully accepted by WRZOLEK (1981, SUTHERLAND & FORBES (1981) and KWARWOWSKI & WRZOLEK (1987).

The coral growth in the Heterocorallia was most completely reconstructed by WRZOLEK (1981). His reconstruction was afterwards confirmed by KARWOWSKI & WRZOLEK (1987) on the basis of the microstructure of skeletal elements. General ideas of those authors are accepted in the present paper, but a new reconstruction of individual growth stages is proposed (Fig. 8a-8e). Absence of calices in the Heterocorallia opens a question of the origin of skeleton: epi-, or endo-dermal? This is a substantial problem, because only the epidermal origin of the heterocoral skeleton allows to place this group, together with Calyxcorallia n. ordo, in the common subclass. The microstructure of septa in *Oligophylloides* resembles that in the Rugosa (compare fig. 5G of KARWOWSKI & WRZOLEK, 1987). Similar conclusions of LAFUSTE (1981) and WANG ZHIPING (1988) concerning heterocorals other than *Oligophylloides* allow to consider this character common for at least some Heterocorallia. Thus, from this point of view the skeleton should be considered epidermal. Relationship of the tabulae to the external wall and the microstructure of the former (KARWOWSKI & WRZOLEK, 1987, fig. 5E) are the most convincing proofs of the epidermal origin of those bodies and, indirectly, of identical secretion of septa as the closely related structural elements.

The preceding remarks seem obvious and useless, but they are not if one accepts the reconstruction of a coral growth in *Oligophylloides* proposed by WRZOLEK (1981) and generalized for all heterocorals in this paper (Fig. 8a-e). *Oligophylloides* skeletons found so far are up to 8 cm long and none of them is complete. Thus, the total length of specimens belonging to this genus, as well as to *Hexaphyllia* and *Heterophyllia* is considerable. In spite of that all heterocorals are generally thought to have grown perpendicular to but not resting on a sea floor. Even the simple length/width ratio of fragments of skeletons opens a question of the relationship between the polyp's body and such a narrow but enormously elongated skeleton. The body must have covered the whole talon-like structure in *Oligophylloides*, which has already been pointed out by SUTHERLAND & FORBES (1981). This is true of *Radiciphyllia* and *Mariaephyllia* n. gen. as well. Such parts of the skeleton could not have been secreted otherwise. Also, the polyp must have covered at least a part of the cylindrical portion of the skeleton. This is confirmed by the occurrence of growth lamellae in the external wall. These lamellae, called "tangential-konzentrischen Anwachslamellen" (= growth lamellae) by SCHINDEWOLF (1941) and "tabulae" by RÓŻKOWSKA (1969) and WRZOLEK (1981) are oblique to the surface of the external wall and such must have been position of the polyp's body. The origin of both the growth lamellae and tabulae is similar, i.e. basal. However, the continuous

secretion of the calcium carbonate that took place in the first instance should be opposed to the periodical secretion in the second. Such a distinction is adequate for reserving the term "tabulae" to bodies arranged at some distance from each other. Consequently, the term "heterotheca" proposed by SCHINDEWOLF (1941: 265), but not the "tabulotheca" introduced by RÓŻKOWSKA (1969) and indirectly proposed by WRZOLEK (1981: 514) is accepted herein with some restrictions. These restrictions mainly concern the so called "Balken" of SCHINDEWOLF (1941) and their recognition as elements similar to trabeculae. SCHINDEWOLF's (1941: 262) description of these "structural elements" (?) as "kleines Syringaxon-Stadium" permits to compare them to holacanth's, i.e. original skeletal structures that underwent diagenetic alterations (HILL, 1981: F8, F34). SCHINDEWOLF's photographs (1941, pls. 10: 2b, 12: 1a, b, 13: 1a, b, 2a, b) are very suggestive, although some (pl. 13: 2b) were obviously retouched. His interpretations were not accepted herein for three reasons:

1. The external wall in *Heterophyllia* was proven to be lamellar.
2. "Balken" pass from the external wall to the lamellar parts of septal "maces" but not to the trabecular primary septa.
3. There are no marks of these bodies on the corallite surface. This has already been mentioned by SCHINDEWOLF (1941), who left question of the origin of "Balken" half open.

The septa/external wall relationship is another question that was widely discussed and differently interpreted. SCHINDEWOLF (1941: 260, 261) came to two important conclusions:

1. Mid-lines of adjacent septa are united adaxially. This leads eventually to the union of all those septa.
 2. Triangular or mace-like structures embedded in the external wall are parts of the latter. The first of those conclusions is fully acceptable. The disconnection of septa in some taxa restricts that conclusion, but does not discredit its morphogenetic importance. SCHINDEWOLF's (1941) second conclusion must be reconsidered. Continuity observed by him between "Sockeln" (socles) or "Keulen" (maces) and remaining parts of the external wall was fully confirmed by LAFUSTE (1981, KARWOWSKI & WRZOLEK (1987), and by my own studies. These results allow to focus on the following questions:
1. Septa in the tabularium may or may be not covered by secondary sheets, whereas their peripheral portions embedded in the external wall are always thickened.
 2. Continuous growth lines between "Sockeln" or "Keulen" and the rest of the external wall do not prove the non-septal origin of the former. On the contrary. Strong curvature of those growth lines mark limits of wide, peripheral portions of septal pockets that transmit abruptly into the flat epidermis that secreted the external wall.
 3. In some genera or species, especially in *Hexaphyllia*, the primary septa may extend almost to the periphery,

whereas they do not in the others (e.g. *Oligophylloides*). Four following examples were selected to explain the most important variants of the mutual connection between the vertical and basal skeletal elements among the Heterocorallia.

Oligophylloides exemplifies taxa possessing peripheral part of the external wall outside septal terminals well developed. This is clearly demonstrated by KARWOWSKI & WRZOLEK (1987, figs. 3F, 4B, 5B) and needs no further photographic illustrations. The following steps in appearance of individual portions of the skeleton can be reconstructed:

1. The preseptal stage of secretion of the hard basal disc (Fig. 8a). This stage was deduced as being comparable to that in Scleractinia (e.g. JELL, 1981).
2. In the second stage the oblique septum was secreted in a way similar to the appearance of the first septum in the Rugosa or first six septa in the Scleractinia (Fig. 10). Four septa of the first generation appeared due to the peripheral dichotomous division of both ends of the oblique septum. This process may lead to the extreme shortening of that septum, resulting in the appearance of the seeming four septal stage recognized in some specimens.

All five earliest inserted septa (the oblique septum and two pairs of the potentially creative septa) are homologous to the mid-lines of septa in mature corallites. Their appearance ends the second stage of development of the

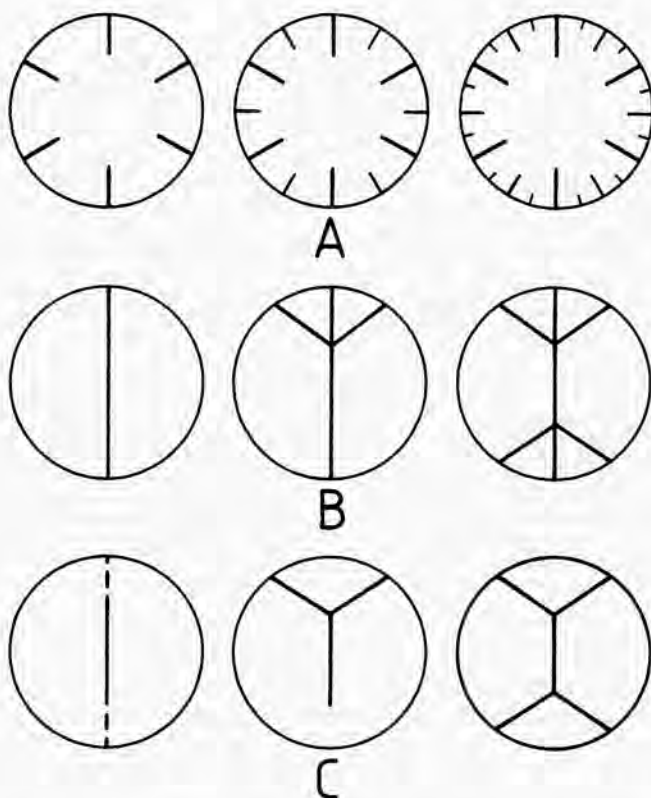


Fig. 10. – Idealized drafts of early septogenesis in Scleractinia (A), Rugosa (B) and Dividocorallia n. subclass (C).

skeleton in the Dividocorallia n. subclass. WRZOLEK (1981, fig. 1a) recognized such a seemingly four septal stage of growth as the earliest stage of development of *Oligophylloides*. WRZOLEK's reconstruction has not been acknowledged for two reasons:

1. Because four septa were predicted to occur at the very beginning of the skeletogenesis.
2. Because those septa were supposed to grow up from a large, flat basal disc, equal in size to the future talon-like structure. Such a reconstruction is morphogenetically unreal. The earliest basal disc could not have been larger than the earliest corallite lumen plus the first layer of the external wall.

It has been arbitrarily accepted in this paper that the third stage of growth in *Oligophylloides* started with the formation of the clearly established tabularium and ended with the appearance of the protoheterotheca. Several processes took place during this stage, some of which are permanent. An upward growth of the oblique septum and the first generation of septa should be considered first. Such a direction of growth has been recognized herein as one of the two main factors that caused the upward growth of the whole skeleton, with the gas pressure being the second one (see discussion on the talon-like structure). Permanently upward growing septa caused some tension between the epidermis of their ridges and that of a tabula. The stretched polyp might have contracted its body by leaving the old tabula and starting secretion of the new one. Accumulation of gas beneath its basal disc made that contraction easier. This mechanism is closely comparable to that reconstructed by WELLS (1969), but with more emphasis to the upward growth of septa. Tension caused by such an upward growth of septa was differently distributed, being the largest in the area adjacent to the septa. Thus, peripheral part of the polyp's body did not suffer disconnection from the skeleton. However, secretion of calcium carbonate in the external wall was reduced at the time when the remaining part of the basal disc left the tabula. This break was afterwards marked as a growth line of an external wall, corresponding to the tabula.

It seems necessary to remind that a polyp of a caliceless animal must have looked like a soft, leather bag with the opening (mouth) tied around the uppermost part of septa (Fig. 14). This is the only possible reconstruction, if the morphological, microstructural, and other skeletal characteristics discussed elsewhere in this paper are considered correct.

The talon-like structure, called the talon by RÓŻKOWSKA (1969) was recognized by her as the attachment body. Both the name and interpretation were accepted by subsequent authors. Indeed, this is a structure that attached an organism to the substrate, but its origin differs from that of the true talon in the Rugosa. Thus, the name "talon" is not accepted in the present paper. Its morphogenetic reconstruction must involve several factors. Gravity made lateral expansion of the structure possible, whereas its strength was dependent on water turbidity. The upward growth of this structure was pro-

pulsed by the upward growing septa supplemented by pressure of the carbon dioxide released in the process of chemical reaction, predicted for the skeletogenesis in Anthozoa (e.g. SORAUF, 1972). A part of the carbon dioxide was liquidized to form the carbonic acid, whereas the rest of it saturated liquid existing between the skeleton and the layer of calycolasts. Increasing volume of gas caused an increase of pressure beneath the epidermis up to a critical point. Tension generated by the upward growing septa may have helped in starting the process of disconnection of the basal disc from the skeleton when that critical point was achieved.

Processes deduced above formed perhaps the main propulsive mechanism causing the upward movement of the polyp's floor in any anthozoan taxon and, consequently, mechanism of development of any kind of the vesiculate structural element, such as tabulae, dissepiments, or vesicles that form the talon-like structure in *Oligophylloides*. How, if at all, this process was genetically controlled, is a different question.

There exists a possibility that the increasing acidity of the liquid between the layer of calycolasts and the skeleton reached a level making further secretion of calcium carbonate impossible, or even causing some dissolution of the earlier secreted skeleton. At least some of the so called growth lines may have resulted from this process.

In the case of permanently growing skeletal elements, such as a solid external wall or septa, there must have been mechanisms in all Anthozoa allowing removal of the carbon dioxide released in the process of skeletogenesis. The same is true for secondary stereoplasmic sheets laid down on any structural element. A kind of "bubbles" in secondary sheets of septa observed in some Rugosa resulted perhaps from the temporary and local cease of acting of that removal mechanism. The size of the talon-like structure was most probably dependent on the turbidity of water. It certainly reflected the size of the polyp. To cover all this structure by the polyp's body was the only possibility of its creation in the calice-lacking Anthozoa. Thus, the polyp must have been large in the early stage of its existence. There are two speculative options concerning its further growth:

1. It became reduced in size starting from a stage of insertion of the lowermost peripheral vesicle of the talon-like structure.
2. It became more slender but not smaller when started to produce the cylindrical, upper portion of growth.

The first option may have involved either resorption of a part of soft tissue, which seems more probable, or autotomy of the lowermost portion of a body. Reduction of the polyp's size is documented by comparison of size of cones produced by growth lines in the cylindrical portion of a corallite to size of the talon-like structure. The way of achieving this reduction is unknown and may well have been differentiated. The cylindrical portion of growth of a corallite, surrounded by the protoheterotheca, has been distinguished herein as the fourth and the last stage of growth of *Oligophylloides*. Development of

septa, their thickenings, and the septa/external wall relationship are fully documented only on this level of growth.

Secretion of the stereoplasmic thickenings can be characterised by two axioms and four factors. The former are:

1. Epidermis of a polyp forms a continuous sheet irrespective of its shape.
2. There is a surplus of calcium carbonate available for a polyp.

The four factors are as follows:

1. Formation of the obliquely upward directed tabulae and growth lines of the protoheterotheca that compose cone-shaped upper portion of the skeleton.
2. Absence of the calice.
3. Centrifugal, but generally upward growth of septa.
4. Acting of gravity which, although reduced in water, cannot be omitted.

The shape of stereoplasmic thickenings of the peripheral, i.e. lower portions of septa, resulted from all those factors and can be compared to the down-hanging drop of a dense liquid. Such a shape is characteristic of the majority, if not of all, Heterocorallia. Some reduction in size of a "drop" may have resulted from fairly flat position of tabulae in some taxa, inadequate supply with calcium carbonate or other secondary factors. Distribution of stereoplasmic thickenings, and drop-like shape of the lowermost septa are fully understandable when the insertion of septa, their position on a skeletal cone, and direction of growth are considered. The axial part of the whole system of septa, i.e. the oblique septum, and the first generations of the potentially creative or creative septa, located on the top of the cone, and growing mainly upward, are the thinnest. This is well documented in the cross sections of specimens. Septa inserted lower on the cone, and thus growing more or less perpendicular to its surface are the thickest. This stronger widening resulted perhaps from the polyp's shape, position on the cone, and connection to the flat portions of the epidermis (Fig. 11A, B). The above deduction is confirmed by the morphogenetic interpretation of microstructure of individual portions of septa. Fibres and/or fine trabeculae seen in the middle portions of cross sections of septa could have been produced exclusively in narrow septal pockets. This ability disappeared in lower parts of septal pockets, where they became too wide, thus allowing only lamellar, i.e. one way secretion, homologous to that of the tabulae and external wall. Both the drop-like shape and the arrangement of individual layers in those lower parts of septa are well illustrated by KARWOWSKI & WRZOŁEK (1987, figs. 3E, F; 5B). Gently rounded growth layers of secondary sheets of septa changed their direction abruptly at the border with tabulae and/or external wall (SCHINDEWOLF, 1941; WRZOŁEK, 1981; KARWOWSKI & WRZOŁEK, 1987). This phenomenon is connected with change of shape of the epidermis that became flattened outside the drop-like septal pockets (Fig. 11A). The transmission of growth layers between septa and the external wall, although

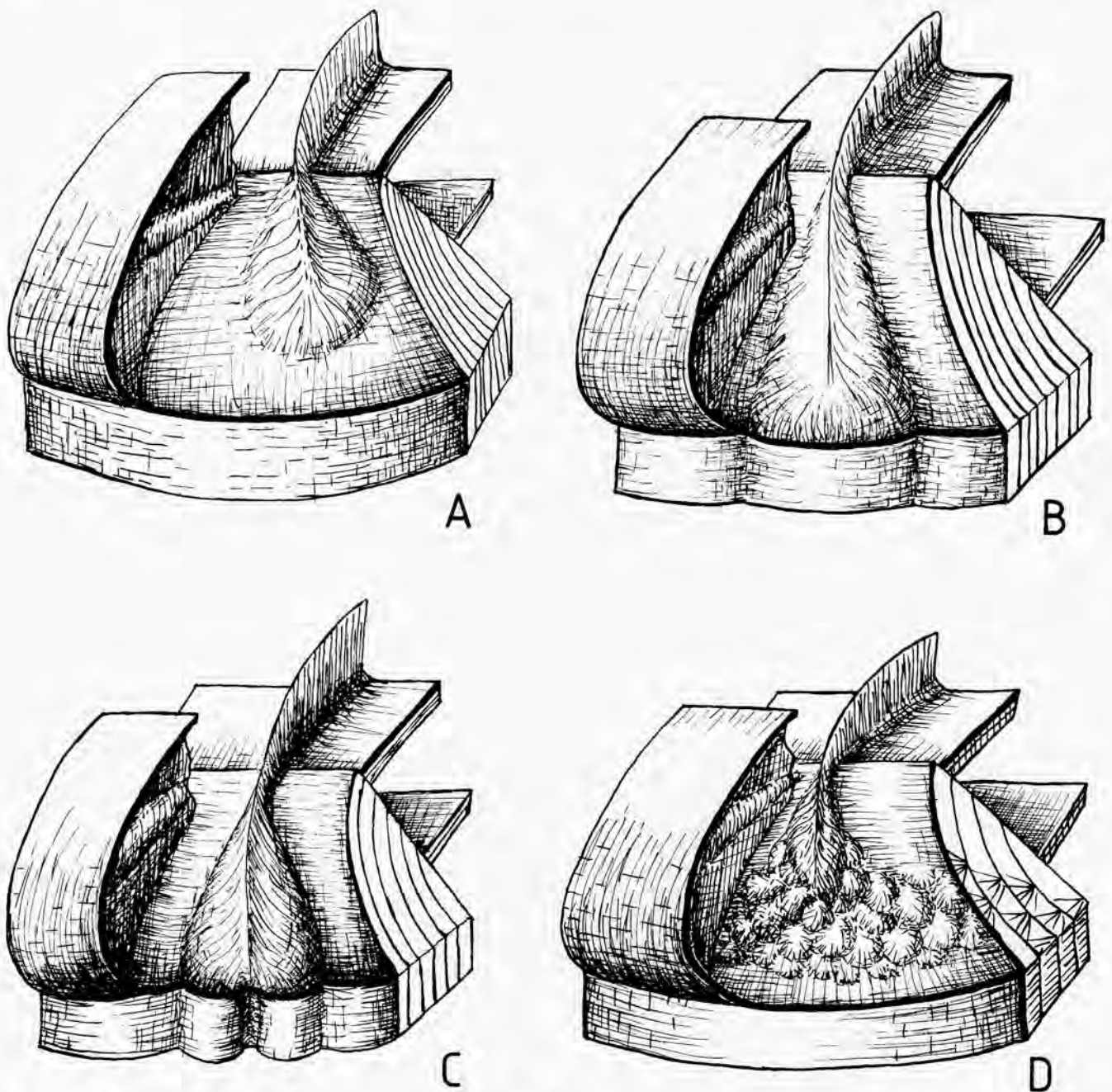


Fig. 11. – Reconstruction of peripheral portion of heterocoralloid polyp showing morphology of peripheral parts of septa and their bearing of the structure of the external wall. A. Protoheterotheca formed due to restriction of septa to inner portion of the external wall (e.g. *Oligophylloides*). B. Heterotheca and peripheral protrusions of septa formed due to continuous peripheral growth (e.g. *Heterophyllia*). C. Heterotheca and peripheral, longitudinal trench formed between peripheral lobes of septa (e.g. *Hexaphyllia*). D. Radicitheca formed due to scattering of trabeculae derived from peripheral parts of septa (e.g. *Radiciphyllia*).

disturbed a little, allows to accept the widened, peripheral portions of septa as components of the external wall. They are considered herein ancestral and homologous to “Keulen” and “Sockeln”, established by SCHINDEWOLF (1941) in *Hexaphyllia* and *Heterophyllia*. Thus, the conclusion proposed in this paper is opposite to that of SCHINDEWOLF (1941).

Septal pockets did not reach the lower limit of a

polyp's basal disc, but were transformed into the flat epidermis that secreted a few flat layers of an external wall outside peripheral limits of septa (Fig. 11A). Transmission from the three-dimensional septal pockets into the flat peripheral epidermis was gentle and did not cause any major disturbances. However, the incorporation of septa entirely in the external wall led to the distinction of such a wall from the heterotheca (see below).

Morphogenetic relationship of septa to tabulae and the external wall is similar. The only obvious difference, i.e. an absence of the drop-like shape of most of septa near the surface of tabulae resulted from the inner position of the latter, where septa are weakly thickened. Growth lamellae of septa located next to tabulae are directed in a manner similar to that in the external wall.

Hexaphyllia, *Heterophyllia* and *Mariaephyllia* n. gen. can be indicated as the second example of growth and relationship of septa to the external wall. According to SCHINDEWOLF (1941), insertion of a new septum in *Heterophyllia* took place near or at the inner surface of the external wall. This observation is confirmed by some transverse sections illustrated by authors and by my own studies. Also, a similar mode of the insertion of septa is characteristic for *Mariaephyllia* n. gen. In the course of growth septa "sink" into the external wall up to eventually crossing it through. That centrifugal growth of septa was accompanied by their widening, leading to the formation of "socles" and "maces". Flattening of the epidermis in *Oligophylloides* has been deduced above as the effective cause for morphology of the external wall in that genus (Fig. 11A). Consequently, the permanent activity of septal pockets that were widely rounded at the periphery resulted in formation of septal parts ("socles" and "maces") of the external wall in *Heterophyllia* (Fig. 11B) and *Hexaphyllia* (Fig. 11C). The mutual relationship of septal and interseptal portions of the external wall is in this case identical to that in the inner part of the external wall in *Oligophylloides*. Permanent growth of peripheral portions of septa may lead to their outward extension. Such a hypertrophy was most frequently observed in *Hexaphyllia*. Wide spacing of the tabulae allowed long upward and outward growth of septa and/or their secondary sheets. Densely spaced tabulae reflect more frequent upward movement of the basal disc of a polyp. This may perhaps be correlated with lesser stretching of the latter and with shorter upward and outward growth of septa.

Extension of peripheral parts of septa in some hexaphyllids may lead to the formation of two parallel, vertical combs on a corallite surface separated by a long, furrow-like depression that can be mistaken with true septal furrows in the Rugosa. The origin of that furrow-like depression was totally different, and cannot serve as a proof of the relationship between the Rugosa and Heterocorallia. Whereas the origin of septal furrows in the Rugosa can be reduced to the process of weaviness of a calice margin, the origin of peripheral, longitudinal septal ditches in the Heterocorallia was much more complex. It is classified herein as the most advanced development of peripheral portions of septa.

The development and morphology of those ditches and peripheral lobes of septa can be reconstructed as resulted from the contemporaneous and complementary acting of two factors:

1. Tightness of the uppermost portions of septal pockets and partly centrifugal, but mostly upward directed growth of primary septa.
2. Connection of all septa that form a system on the terminal portion of a corallite, with the oblique septum on the top (Fig. 8a).

These two factors created a kind of restraint against unlimited widening of septal pockets. Such a restraint system acted along the whole length of septal pockets, but was most effective in their middle portions that produced the primary septa. Their lateral and peripheral portions were more readily exposed to gravity, thus producing peripheral protrusions of septa. As a result, longitudinal ditches corresponding to primary septa, and peripheral lobes corresponding to secondary sheets of septa were formed (e.g. SCHINDEWOLF, 1941, pl. 9: 2, 3, 11b, 12; Fig. 11C in this paper). In some instances (e.g. POTY, 1981, pl. 34: 10, 13) not the stereoplasmic sheets of septa, but interseptal portions of the external wall protruded peripherally. Thus, the whole septal portion of external wall formed the ditch. In many other instances there are no septal ditches present on the corallite surface, the outline of which is smoothly rounded although the drop-like shape of peripheral portions of septa can be easily recognized. Taxonomic value of the characters discussed should therefore be treated with caution.

Protrusion of peripheral portions of septa in *Hexaphyllia* and *Heterophyllia* may have led to the formation of six- to multi-angular outline with sharply rounded septal parts alternating with more gently rounded intermediate sectors. There was no major difference in the secretion of both portions of the heterotheca, except for the hemispherical arrangement of growth lamellae in its septal parts versus more flattened arrangement of them in the remaining sectors. Two other peripheral structures seen in some specimens of the Heterocorallia, i.e. knobs and spikes were not studied herein. Judging from the literature (especially SCHINDEWOLF, 1941 and SUGIYAMA, 1984) the former may either be peripheral extensions of trabeculae (if they follow peripheral projections of primary septa) or are simple stereoplasmic bodies that served as peripheral supporting elements. Careful examination of the longitudinal sections along those bodies may help in the final establishing of the microstructure of septa in the Heterocorallia.

In contrast to knobs, the origin of spikes must have been peripheral. Some of them are pipes located against the primary septa and opened toward the periphery (e.g. SUGIYAMA, 1984, pls. 2: 1c, 3a, b; 3: 6; 4: 7). An explanation of the origin of those structures cannot be proposed without studying them in detail.

Radiciphyllia has been selected herein as the third example of growth and mutual relationship of the basal and vertical structural elements. This has been done without the re-examination of the original material. Thus, the remarks that follow only supplement and summarise earlier conclusions.

The position of *Radiciphyllia* within the higher rank taxa should be considered first. Reasons for distinguishing the family Radiciphyllidae n. fam. is discussed in the systematic part of this paper. Here the original placing of that genus within the Heterocorallia (SUGIYAMA,

1984) is supported. The arrangement of crystals in peripheral parts of septa (e.g. IGO & KOBAYASHI, 1980, pl. 15: 1, 2; SUGIYAMA, 1984, pl. 5: 1a; pl. 7: 1a, 2c, 4) is the most convincing proof of their centrifugal growth. Position and morphology of the talon-like structure, similar to that in *Oligophylloides*, and shape of peripheral parts of tabulae, are additional proofs. Thus, the genus discussed exposes the main diagnostic character of the order, i.e. lack of the calice.

Analysis of descriptions and illustrations of IGO & KOBAYASHI (1980) and SUGIYAMA (1984) allow to establish two regularities in septa of *Radiciphyllia*:

1. Development of comparatively narrow and compact periaxial portions of septa and a strong widening of their peripheral parts that look like being composed of scattered skeletal elements.
2. Disconnection of many septa in the corallite axis.

This is to some extent accompanied by more intensive scattering of skeletal elements of peripheral portions of septa. However, the disconnection is mostly observed in the stratigraphically youngest species. Thus, the latter character may have some phylogenetic value, whereas the former permits to accept a schema of development of septa in *Radiciphyllia* similar to that in *Heterophyllia*.

There is no difference between the axial part of septal apparatus in *Oligophylloides* or *Heterophyllia* and less advanced species of *Radiciphyllia*. Also, the upper portions of septa acted in all three instances as a restraint system for the lower, widened parts of septal pockets. However, in the phylogenetically advanced species of *Radiciphyllia* septa became disintegrated axially, which seems to contradict the reconstruction presented above. Morphology of the tabularium should in this case be pointed out as an explanation. Tabulae are vesiculate and form a flat axial area (SUGIYAMA, 1984, pls. 5: 2b; 7: 6a, b) making strong restraint against gravity unnecessary. Nevertheless the inner portions of septa remain thin and grow mainly upwards, thus playing the same role as they do in *Oligophylloides*, *Mariaephyllia* g. gen., *Heterophyllia* or *Hexaphyllia*. Similarity in the arrangement of septa, i.e. the mutual relationship of individual generations of septa in all heterocoralloid genera can easily be established. Analysis of the microstructure of peripheral parts of septa in individual genera included in that order exhibits differences that have been classified herein as generic and family. *Radiciphyllia* differs from all other taxa in having its lateral parts of septa not lamellar, but most probably trabecular. This conclusion is supported by comparison of illustrations of *Radiciphyllia* (IGO & KOBAYASHI, 1980; SUGIYAMA, 1984) to those of *Lophophyllidium* GRABAU, 1928 (FEDOROWSKI, 1974; SORAUF, 1977). Asymmetrical, small trabeculae found in that rugose coral genus can be compared directly to bunches of fibres seen in peripheral parts of septa in *Radiciphyllia*.

The conclusion above can to a large extent be supported by the opinion of IGO & KOBAYASHI (1980: 160), who wrote: "Trabeculae are not distinct but recognized in some parts of this stereozone", i.e. the external wall.

The following morphogenetic reconstruction of the structure and growth of septa and then of their relationship to the external wall can be proposed: The septal pockets, narrow and uniform in their upper (= inner) portions became widened at the periphery of a corallite due to both gravity and an absence of a calice. Those widened parts must have been secondarily folded. Peripheral, asymmetrical trabeculae and their bunches would not have been able to appear otherwise. No reason for this secondary folding can be pointed out in this moment. Formation of peripheral trabeculae must have been genetically controlled. They would not have been so constant otherwise.

Trabecular pyramids built in peripheral parts of corallites are mostly incorporated in the external wall. Their relationship to the remaining portions of the latter differ slightly from species to species. Pyramids of trabeculae in *R. akiyoshiensis* are narrow, whereas the interseptal, lamellar portions of the external wall are fairly large. In contrast to this there are almost nothing but the scattered trabeculae or bunches of fibres present in some portions of the external wall in *R. toriyamai*. The outline of corallites is in such an instance rounded or delicately ribbed (e.g. SUGIYAMA, 1984, p. 7: 4). In the case of the occurrence of more compact bunches of trabeculae or fibres, a clear septal ribbing, corresponding to that in *Hexaphyllia*, *Heterophyllia*, or *Mariaephyllia* n. gen. occurs (e.g. IGO & KOBAYASHI, 1980, pl. 15.2, lower part). Secondarily folded septal pockets are the only places of secretion of such structures, whereas sectors of the external wall between these septal structures were fibrous (IGO & KOBAYASHI, 1980; SUGIYAMA, 1984). Being secreted by flattened part of the epidermis, these sectors may well be fibro-lamellar or even lamellar. Such laminated, peripheral portions of the external wall may sometimes occupy large part of the whole circumference of a corallite. Structures of that kind were most frequently observed in *Radiciphyllia toriyamai*, in which SUGIYAMA (1984: 63) discovered that "microstructure of the outer stereoplasmic zone (= the external wall in the herein accepted meaning) is composed of two layers, an internal septal, stereoplasmic layer and a peripheral massive layer".

Three steps of development of the external wall can thus be distinguished in *Radiciphyllia*:

1. Septal and interseptal portions are almost equally developed.
2. Septal portions overwhelmingly prevail.
3. Septal or mixed inner part of the external wall is covered externally by the lamellar or fibro-lamellar "peripheral massive layer" of SUGIYAMA (1984).

The main differences between those three types of the external wall can be reduced to the following points:

1. In the first case the interseptal part of the external wall was secreted by a flat epidermis of the peripheral, down-hanging polyp's body. Its septal part is restricted to narrow pyramids outside primary septa (Fig. 11D; compare SUGIYAMA, 1984, fig. 15; pl. 6). Relationship of those pyramids to the neighbouring

interseptal parts of the external wall is identical to that in the Rugosa and can be reduced to the idea of the complete lateral flatness of a given septal pocket. The centrifugal growth in the Heterocorallia forms the only difference between these two instances.

2. In the second case the external wall developed perhaps from the first one due to widening of the zone of peripheral septal pockets. Expanding laterally those pockets did not lose their ability to produce short and scattered trabeculae or elongated, hemispherical bunches of fibres.
3. In the third case the external wall resulted perhaps from a complex process. The inner, trabecular part of the external wall was formed first. Then, its medial part, composed of scattered trabeculae was secreted by a less distinctly folded epidermis. The completely flattened epidermis, restricted to the peripheral part of a polyp, secreted individual layers of the solid, peripheral portion of the external wall.

The reconstruction above may generate doubts concerning rejection of trabecular origin of "Balken" of SCHINDEWOLF (1941). However, "Balken" were recognized both in the peripheral portions of septa ("Sockeln" and "Keulen"), and in the interseptal sectors of the heterotheca. Several of them passed from one of these structures to the other. The identical lamellar microstructure established both in peripheral parts of septa and in the external wall (e.g. KARWOWSKI & WRZOŁEK, 1987) is conclusive. Moreover, centripetal "growth" of "Balken" is opposite to the centrifugal growth of the whole skeleton, making this idea unsupported. Structures found in *Radiciphyllia*, although not studied in detail, exhibit striking similarity to the arrangement of trabeculae in the columella of *Lophophyllidium* GRABAU, 1922, the centrifugal growth of which seems certain (Compare FEDOROWSKI, 1974, pls. 64: 1a, b; 67: 1, 2, 3b; 69: 2).

Differences in the morphology and origin of the external wall between *Oligophylloides* - *Heterophyllia* - *Hexaphyllia* on one side and *Radiciphyllia* on the other, open some terminological questions. The term "heterotheca" has already been accepted herein as valid for Heterocorallia, although it has been modified in accordance with the new interpretation (see terminology, p. 21). The morphology of heterotheca is opposed herein to the wall in *Radiciphyllia*, which is proposed to be called "radicitheca" (a new term).

The morphogenetic interpretation of some characters of *Vassiljukaephyllia* n. gen. seems necessary both for the better understanding of some features of that genus seen in sections (e.g. VASSILJUK, 1964, p. 8: 7a, b) and the relationships within the order Heterocorallia. The morphology of septa, their relation to the tabulae and the external wall, as well as the morphology of the latter, are of special value for such an interpretation. The morphology and mutual relationship of early generations of septa seen in the axial portions of transverse sections do not differ from the analogous portions of the typical heterophyllids and do not need a different morphogenetic interpretation. The same is true for the small (young?)

specimens illustrated by VASSILJUK (1964, pl. 8: 6a, b, 8), if they belong to that genus and not to *Heterophyllia*. Having no answer to the latter question all remarks that follow are referred exclusively to the holotype of *V. fragmentoseptata* VASSILJUK, 1964.

The shape of tabulae (VASSILJUK, 1964, pl. 8: 6v) indicates that the pedal disc formed a wide, low cone that was slightly protruded axially due to the higher exposition of the oblique septum and the first generation of septa. Peripheral part of the cone was inclined steeply down, terminating with a fairly narrow, but perhaps solid external wall. The insertion of septa was fast early in the ontogeny, but slow later on. This resulted in the formation of short creative septa next to the corallite axis, and long potentially creative septa at the periphery. Several of the latter were peripherally disintegrated. All septa are fairly thin and have low blades. Their pockets must have been weak and easy to flatten. This was perhaps the reason of their differentiation into rows of isolated, small pockets developed next to steeper parts of tabulae, where the disintegrated septa were formed. Disintegration of septal pockets may have resulted from the higher tension in those areas or from the need for stronger support of the down-hanging polyp's body. Development of septal knobs instead of the solid septal blades may have had not only a purely mechanical, but also a physiological origin. Better distribution of water, its easier access to peripheral portions of the gastro-vascular cavity and easier removal of waste can be in this case listed on the first place. However, both options are purely speculative.

The morphology and morphogenesis of *Longlinophyllia* are to some extent similar to these in *Vassiljukaephyllia* n. gen. The axial portions of septa can be omitted from the discussion, as being closely comparable to most of heterocorals. The morphogenesis of basal and vertical structural elements that form the peripheral zone, i.e. the reticulotheca, can to some extent be compared to the morphogenesis of the talon-like structure in *Oligophylloides*. The following succession of morphogenetic events can be established: Axial and periaxial parts of septa, typical for heterocorals, grew mostly upward. This can be reconstructed from the almost horizontal position of periaxial parts of tabulae. The peripheral zone is composed of flat, vertical vesicles alternated with septal rods that are oriented perpendicular to the corallite surface. Those vertical vesicles originated perhaps due to gas pressure of the oversaturated water. The mechanism of disconnection of a polyp's epidermis perpendicular to the direction of growth of corallites remains uncertain. The vesicular zone discussed is the only example of this kind among heterocorals known so far. The introductory stage of its development in *Vassiljukaephyllia* n. gen. is the only exception. The origin of the reticulotheca must have resulted from a unique physiology. In *Longlinophyllia* there must have been mechanisms controlling storage of the carbon dioxide between peripheral parts of a polyp's body and the calcium carbonate crystals of vertical vesicles. In contrast to this there must have been

mechanisms removing that gas in other taxa. Such contrary acting mechanisms must have been genetically controlled. This seems adequate for the distinction of *Longlinophyllia* on the family level, a solution proposed by LIN & WU (1985) but without a morphogenetic analysis.

Septal rods, positioned normally to vesicles, form the next structural element of the reticulotheca. As any septa, these rods must have been secreted in septal pockets. Some of them were located close to each other and arranged in rows following the solid, inner parts of septa. Rows of septal rods originated perhaps in once regular septal pockets segmented afterwards into individual sacs. Both vesicles and rods were simultaneously secreted by the epidermis. Shape of the latter and growth of individual skeletal elements: permanent in the case of rods and interrupted (pitchy) in the vesicular tissue, form the only difference between these bodies. Thus, presence of long rods must be referred to the period of the occurrence of given septal sacs, but not to the high protrusion of the rod above the surface of a corallite. It may have been exposed slightly higher only just before the formation of a vesicle adjacent to it. In the peripheral portion of corallite occur additional rows of rods that can be interpreted as septa of younger generations.

In addition to the fairly regularly arranged rods there are rods not traceable towards any particular solid septa or rows of septal rods. These disconnected rods may have appeared in narrow sac-like protrusions of the epidermis that covered surfaces of tabulae or vesicles. The reconstruction proposed herein is supported by the relationship of rods to the surfaces of the basal elements. The occurrence of random septal rods was dependent not only on the formation of septal sacs, but also on the introduction of a mechanism allowing removal of the carbon dioxide from this particular portion and not from the adjacent part of the epidermis, where further formation of vesicles was available.

The last layer of peripheral vesicles may have been slightly thicker than the inner ones, if the peripheral portion of the polyp's pedal disc rested long enough on it. Also, it was knobby because of the exposition of the peripheral ends of septal rods.

The upward growth of the reticulotheca was perhaps generated in a purely mechanical way by the upward growth of the axial and periaxial septa and tabulae. Growing upwards, either permanently in the case of septa or pitch by pitch in the case of tabulae, the axial and periaxial parts of a polyp's floor carried upwards its lower, down-hanging rim, responsible for the formation of the reticulotheca. It can be assumed that the differentiated relief of a corallite surface, originated both from the convexity of vesicles and from knobs of septal rods. Such a differentiated relief allowed the mechanical support for the down-hanging polyp's body and better distribution of water within this very narrow area of the gastro-vascular cavity.

The reticulotheca in *Longlinophyllia* was light and strong, a reminder of the skeletal constructions in the Scleractinia. Its construction required much lesser ex-

pense of the building material than the external walls of other heterocorals.

To sum up the foregoing discussion of growth of corallites in the Heterocorallia attention should be drawn to the general similarity, i.e. the centrifugal growth of all genera included in this order and to the differences in details, allowing further subdivisions within the order (see the systematic part).

The morphogenesis in the Calyxcorallia n. ordo

Development of regular calices distinguishes Calyxcorallia n. ordo from Heterocorallia. All other characters of representatives of the former, such as the commonly observed disjunction of the inner ends of major septa, especially next to a corallite axis; the appearance of minor septa and the dissepimentarium; differentiation of the latter towards the interseptal and lonsdaleoid dissepiments and other less important characters can at least to some extent be considered consequences of development of calices.

One important question must be solved at the beginning of this analysis: was growth in Calyxcorallia n. ordo centripetal or centrifugal, or both? Presence of well developed calices, easily confirmed by any longitudinal section speaks in favour of the first option whereas the insertion of septa by means of peripheral dichotomic division may be interpreted as proof of the second. Indeed, the insertion of septa in *Stylostroton* does not differ from that in heterophyllids. A new septum appeared due to dichotomic division of an earlier existing, potentially creative septum. This process can be deduced back to the oblique septum, from which it started. Unfortunately, the sequence in the insertion of septa in the Calyxcorallia n. ordo has not been confirmed by direct observations of development of septa starting from the very beginning of this process.

The complex growth of septa in Calyxcorallia n. ordo must be correlated to the shape of all parts of a calice. Minor septa and peripheral parts of major septa, mainly those included in the dissepimentarium, are all directly or indirectly connected to the vertical external wall and, therefore, must have grown centripetally. This is confirmed by the incorporation of peripheral parts of con-

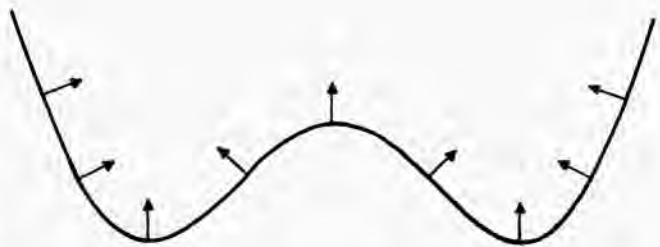


Fig. 12. – Idealized outline of calyxcoralloid calice; arrows indicate directions of growth in its individual portions.

tinuous septa in the external wall (Pl. 6: 2b), and by the direction of growth of crystals in the latter. The downward arranged rows of interseptal dissepiments in the longitudinal section (Pls. 3: 1e; 7: 1b) is centripetal. Thus, growth of septa cannot be opposite. The arrangement of trabeculae (Pl. 6: 1c) forms the final confirmation of the centripetal growth of peripheral parts of major septa and of the minor septa. The lonsdaleoid dissepiments form the next important proof on the centripetal growth of this part of the skeleton. They must have been developed after secretion of the external wall, but before the insertion of septa attached to them. This is true for the temporarily appearing lonsdaleoid dissepiments as well. Thus, there can be two sequences in the appearance of individual peripheral structural elements: either external wall - septa, or external wall - lonsdaleoid dissepiments - septa. The convex, axially elevated tabularium, reflecting the position of the inner portion of the polyp's pedal disc, allows a reconstruction of inner parts of septa as growing centrifugally. Such a concept is only seemingly contradictory. It is enough to refer to the uniformity of the epidermis and to examples of the long-septal Rugosa that possess the inner part of a convex tabularium, to find an explanation. Being formed in a long, single septal pocket that follows the shape of a pedal disc, such a long septum grew simultaneously in all its parts, although the rate of growth and its direction differ in individual portions (Fig. 12). In case of high elevation of peripheral and axial portions of the calice, such a continuous, long septum possesses its intermediate portion located deep in the calice. It may look interrupted when transversally sectioned. As in the Rugosa, the simultaneous growth of major septa in the Calyxcorallia n. ordo was as follows: centripetal near the calice wall - directed upwards in the lowermost portion of the calice - centrifugal in the periaxial part - and directed upwards near the corallite axis (Fig. 12).

Three problems should be solved in the analysis of increase in septa in the Calyxcorallia n. ordo: direction of growth, area of division of septa, and mode of their insertion. The preceding discussion made the first point clear. The centripetal growth of peripheral parts of septa focuses on a calice rim as a starting point of insertion of younger generations of septa. It seems possible, however, that the oblique septum and first generations of septa were inserted directly on a calice floor, i.e. in the manner observed in the Rugosa. Lack of adequate material makes the solution of this problem impossible. Mode of insertion and arrangement of septa in the Calyxcorallia n. ordo do not differ from those in Heterocorallia. This striking similarity makes a detailed analysis unnecessary.

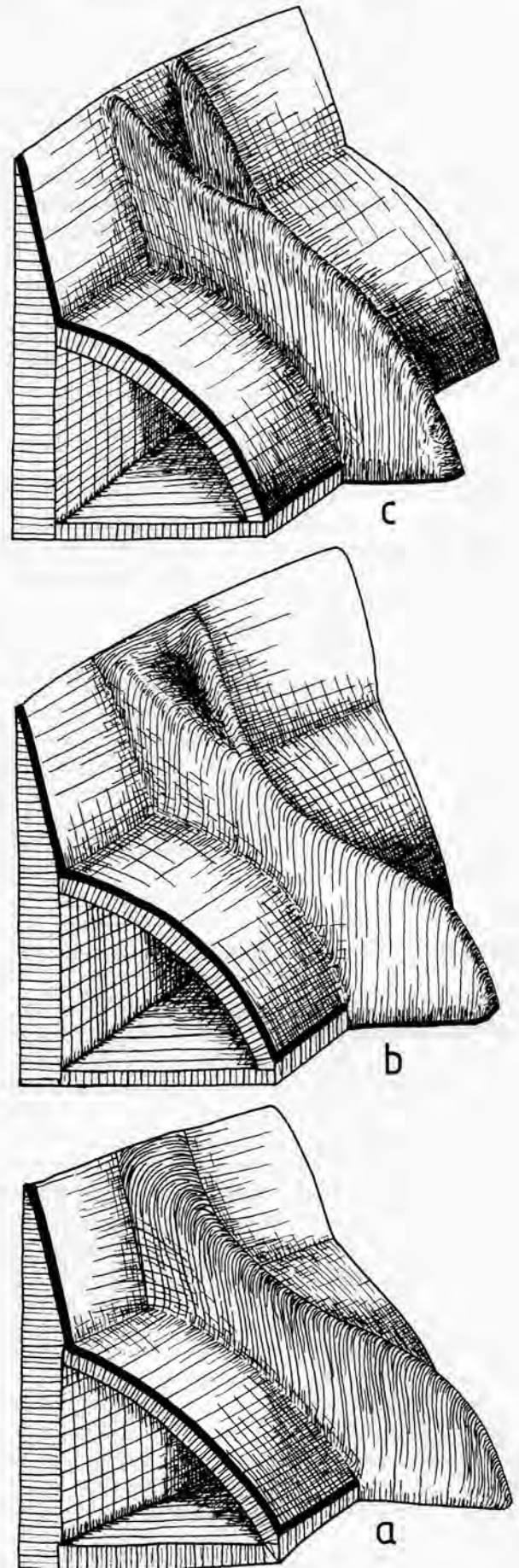


Fig. 13. — Reconstruction of three stages of peripheral dichotomic division of septa in Calyxcorallia n. ordo. a. Widening of upper, peripheral portion of septum; b. Formation of middle depression due to cease of upward growth of that area; c. Complete division of two forks of next generation of septa.

It should be pointed out that the centripetal, not centrifugal direction of division (but not growth) of septa occurs in both orders. Some observations by SCHINDEWOLF (1941) in *Heterophyllia* and detailed studies by SUTHERLAND & FORBES (1981) in *Oligophylloides*, by SUGIYAMA (1984) in *Radiciphyllia* and by myself in *Mariaephyllia* n. gen. prove this clearly. The major difference between the Heterocorallia and the Calyxcorallia n. ordo is exposed not in the mode of increase in septa, but in the direction of growth of their peripheral portions, caused by the presence or absence of calices. Disjunction of the major septa in the axial part of some corallites of the Calyxcorallia n. ordo requires some additional discussion. Such a disjunction, resulting in the formation of a large axial depression, is absent from most of the Heterocorallia, except for some *Radiciphyllia*. The only specimen of *Heterophyllia* exhibiting some axial disjunction of septa (SCHINDEWOLF, 1941, pl. 11: 1) was perhaps diagenetically altered rather than naturally developed that way. No *Hexaphyllia*, *Mariaephyllia* n. gen. or *Oligophylloides*, with axially disjuncted septa have been found so far. Even in the *Radiciphyllia* the disjunction of septa is indistinct, and no wide, open axial area was formed, whereas some "dematophylla" strikingly resemble *Rugosa*. This is well seen both in the length of septa and shape of the tabularium (WU *et al.*, 1981, p. 4: 7-9). The obviously amplexoid character of major septa in such rugosa-like specimens, as well as a distinct shortening of major septa above the surface of a tabula, leave no doubt as to the inward growth of their inner ends. The relationship of individual pairs of septa may be the only basis of distinction of such specimens from the *Rugosa*.

The suspected behaviour of *Dividocorallia* n. subclass

The suspected behaviour of the Heterocorallia has already been discussed by SCHINDEWOLF (1941), RAMSBOTTOM (1978), SUGIYAMA (1984) and in the indirect way by RÓZKOWSKA (1969) and WRZOŁEK (1981). Appearance of hooks in some species, especially in *Hexaphyllia*, allowed to consider such species to be either epiplanc tonic (SCHINDEWOLF, 1941) or attached by those hooks to seawood (RAMSBOTTOM, 1978, fig. 45). None of the authors preceding SUGIYAMA (1984) accepted the suspected behaviour as a diagnostic character adequate for distinguishing separate groups which, although informal, have been suggested to be phylogenetically distinct. SUGIYAMA (1984: 33) wrote: "... unfortunately, phylogenetic relations between Group 2 and Group 1 are not clear because of rarity of these groups".

"*Pentaphyllia*", *Hexaphyllia*, and *Heterophyllia* were included by SUGIYAMA (1984) in the group of attached genera, whereas *Pseudopetraia*, *Oligophylloides* and *Radiciphyllia* were suggested to form the group of sessile genera. Lack of outer projections of septa in *Oligophylloides* and *Radiciphyllia* was selected by SUGIYAMA (1984) for placing these two genera in the same

group. Solutions proposed by that author are not acknowledged in the present paper. This resulted from a different taxonomic evaluation of individual characters.

Firstly *Pseudopetraia*, a calyculate genus, cannot be placed together with *Oligophylloides* and *Radiciphyllia* that almost certainly were naked. Secondly, the taxonomically much more important morphogenetical differences can in no way be overbalanced by the sessile behaviour. Thirdly, an absence of peripheral projections of septa in *Oligophylloides* and *Radiciphyllia* cannot be equalized and accepted as a common character, because the morphogenesis of these structures is totally different on the microstructural level. Also, the synonymy of "*Heterophyllia*" (= *Mariaephyllia*, n. gen.) *famenniana* RÓZKOWSKA, 1969 with *Oligophylloides*, postulated by SUGIYAMA (1984) cannot be acknowledged, if morphology of the external wall is accepted as an important taxonomic character.

There seems to be no doubt concerning the growth position, but not necessarily the behaviour, of all *Dividocorallia* n. subclass described so far. All *dividocorallid* genera, except for *Heterophyllia*, *Hexaphyllia*, *Longlinophyllia*, and *Vassiljukaephyllia* n. gen., the ontogenetically youngest portions of which are unknown, must have been sessile organisms. This is demonstrated either by presence of attachment abilities, of calices, or both (*Pseudopetraia*). The lithofacies wherefrom the discussed genera derived have only rarely been described in a way which allows close comparisons. It seems, however, that there were no facies to which those organisms were restricted. *Oligophylloides* has been found in deposits varying from the quiet and rather deep water regime in Łagów to the high energy regime in Gałęzice. *Mariaephyllia* n. gen., although most common in Gałęzice, is also present in the much quieter regime of Zaręby. *Radiciphyllia* is said by SUGIYAMA (1984) to be present in the reef complex of the Akiyoshi Limestone, whereas IGO & KOBAYASHI (1980) found a phylogenetically advanced species of that genus in the deeper water nodular limestone. Polish representatives of *Stylostrorion* occur in biomicrites containing crinoid columbals, small Foraminifera, Algae, and Stromatoporoidea that can characterise shallow, well aerated and rather turbulent waters. *Pseudopetraia* found in red, bioclastic limestone, together with cephalopods, was considered by SOSHKINA (1951) to have been washed out and redeposited. Deep calices present in the latter genus are characteristic for corals living in a low rate sedimentation environment (HUBBARD & POCOCK, 1972), thus rather a quiet regime may be indicative of their original environment. The occurrence of *Hexaphyllia* and *Heterophyllia* is most diversified. RAMSBOTTOM (1978) and SUGIYAMA (1984) described them from the reefoidal facies of Britain and Japan respectively. Bioclastic limestones are the main matrix of their occurrence in Belgium, whereas in Poland they are present both in high energy regime deposits in the Holy Cross Mountains and in lower energy regime limestone and marly lenses in the Sudetes. Similar quiet water deposits occur in the Lublin area (KHOA, 1977).

Thus, there is no direct relationship between the given morphology of corallites (e.g. taxa with *versus* taxa without calices) and the lithology of deposits. Also, the taxa reconstructed as resting directly on a sea floor cannot be distinguished from the genera considered by SCHINDEWOLF (1941), RAMSBOTTOM (1978), and SUGIYAMA (1984) as being attached to other objects. Lack of talons or talon-like structures in the ontogenetically youngest portions of specimens known so far of the *Heterophyllia* – *Hexaphyllia* – *Tetraphyllia* group of genera cannot be conclusive, because the initial parts of growth of those taxa remain unknown. They were perhaps attached to the sea floor at the period of metamorphosis, but their further direction of growth and life position remain unknown. Upwards directed hooks, correctly recognized by SUGIYAMA (1984), look useless for the upwards growing organism. They may have been effective supporting elements only in the case of downward growth. However, the latter supposition opens two questions:

1. How did these hooks support a body, if they were secreted by the epidermis that surrounded their axial channels? A delicate polyp's body could not have survived on hooks surface resting on a supporting objects. Thus, their lower surfaces should have suffered deformations, which they did not.
2. What were channels in the hooks formed for?

Having no satisfactory explanation, I leave both these questions open.

Recognition of vertical, upwards directed growth position in Dividocorallia n. subclass generates another problem, i.e. the reconstruction of the morphology and physiology of polyps. Everything is obvious as far as the calyculate genera of Calyxcorallia n. ordo are considered. Polyp's morphology and behaviour of these corals can fairly closely be reconstructed as similar to hypothetical polyps in the Rugosa, and to a lesser degree, in some solitary Scleractinia. This part of the problem is therefore omitted from the discussion below. Lack of external support for the polyp's body (the calice walls) in Heterocorallia makes the reconstruction much more complex. Mutual relationship of the oral disc and the mouth to the rest of the body must be considered first, presence and role of tentacles next, and the problem of mesenteries in the third place.

In calyculate genera the pedal and oral discs of polyps are located at a larger or shorter distance from each other, leaving enough room for the development of the gastro-vascular cavity. The strength of such a construction has been especially obvious since discovery of the attachment scars in the Scleractinia (WISE, 1970; SORAUF & PODOFF, 1977; RONIEWICZ & MORYCOWA, 1987), and in the Rugosa (FEDOROWSKI, 1985, 1990). Attachment scars have not been found in Calyxcorallia n. ordo. This is perhaps a matter of lack of proper material. Well preserved, empty calices of those corals have never been studied. There occur no facts contradicting their close similarity in this respect to the subclasses mentioned above.

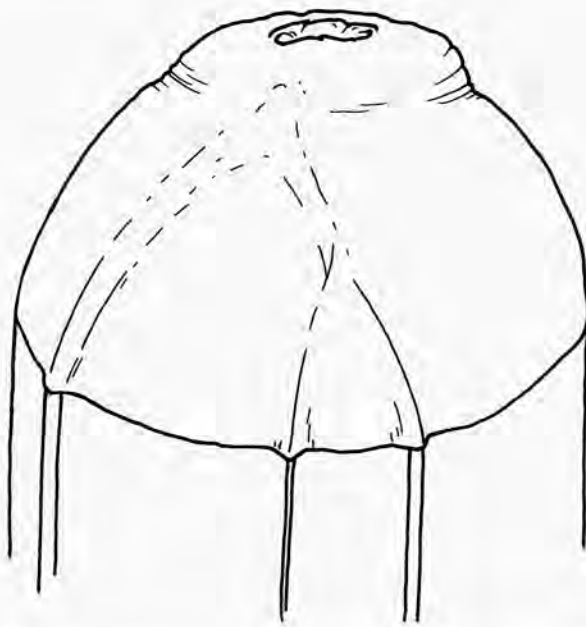
The reconstruction of Heterocorallia accepted in this paper means that the basal disc rests on the skeleton, whereas the rest of the body lacks any attachment to the hard parts. Growth lines of the external walls make clear that the polyp must have been hanging considerably down along that wall. Tentacles, present in all Anthozoa, cannot be hypothesized as lacking in the Heterocorallia. Thus, the additional weight on the oral disc should also be considered, whereas the muscle system in Anthozoa is very primitive and rather ineffective. Moreover, in order to work properly, any muscle must possess good attachments at both sides. A circumpharyngeal ring of strong muscles seems to be the only solution. Such a musculature may have formed a basis for muscle attachments at the oral disc, supporting at the same time a ring of tentacles and the peripheral part of a polyp's body in the right position (Fig. 14C). Any attempt to reconstruct a whole muscle system in the Heterocorallia must be purely speculative. The reconstruction herein is therefore limited to the most obvious and necessary remarks. Muscle action must have allowed tentacles to spread and to hide themselves fairly quickly. In modern Actinia and Scleractinia such an action is connected with the retraction of the whole body. A similar possibility can theoretically also be accepted in Heterocorallia. The following muscles were probably fundamental for the functioning of a naked body:

1. The circumpharyngeal ring of strong muscles; these muscles opened and closed a mouth and acted as a base for the attachment of some other muscles.
2. Muscles allowing a simple hiding of tentacles; these were perhaps specialised muscles of the circumpharyngeal ring.
3. Mesenterial muscles allowing the whole body to retract.

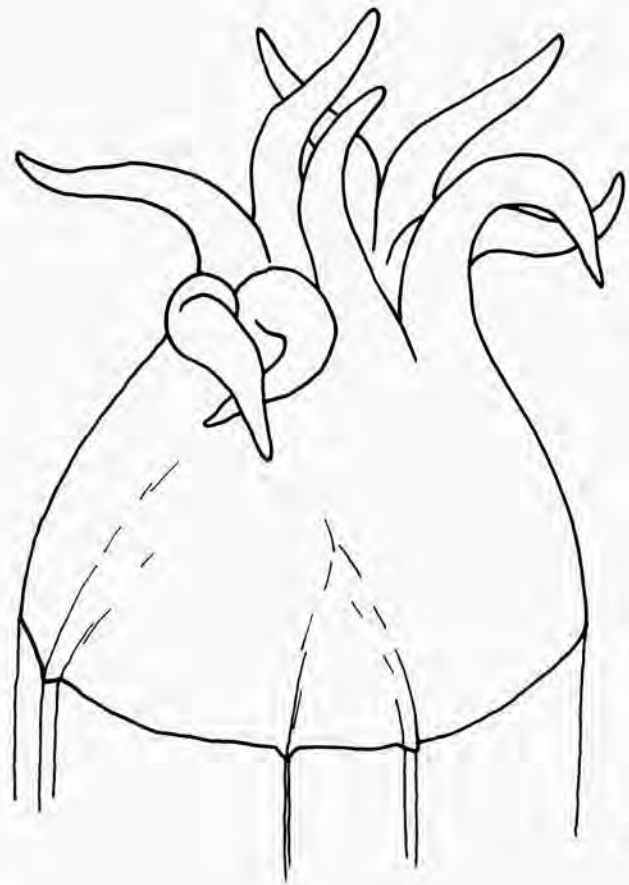
An action of all those and other muscles must have been controlled by a nervous system. They were able to act only one way: by retraction. Diastole was nothing but the lack of retraction. Recent Anthozoa demonstrate a good effectiveness of that passive system. Peculiarity in the insertion and arrangement of septa in the Dividocorallia n. subclass made the reconstruction of tentacular system practically impossible. Tentacles must have been present as the necessary feeding organs but both their number and shape cannot be reconstructed in a satisfactory way.

Mesenteries are basic organs for the anthozoan physiology. Lack of them in the Rugosa, postulated by BIRENHEIDE (1965) has already been criticized by SCHINDEWOLF (1967) and has not been accepted by other authors. The presence of mesenteries in the Dividocorallia n. subclass seems axiomatic, but their development parallel to the insertion of sclero-septa by means of the peripheral dichotomic division is poorly understood. Two ways of development of mesenteries in the Heterocorallia can be reconstructed:

1. A mesenterium or two mesenteria located in a given septal loculum became doubled prior to, or simultaneously with, the division of a given sclero-septum.



A



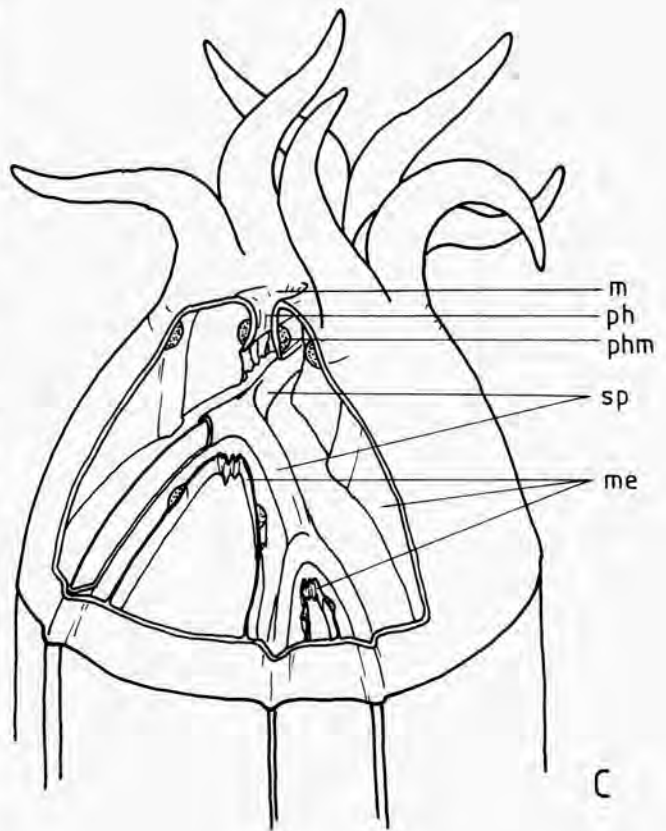
B

Fig. 14. – Reconstruction of polyp/skeleton relationship in Heterocorallia. A. Retracted position. B. Feeding position. C. Most important soft parts; m: mouth, me: mesenteries, ph: pharynx, phm: pharyngeal muscles, sp: septal pockets.

Division of the mesenterium could have been similar to that of the scleroseptum, i.e. dichotomic, with one fork (or a pair of forks) remaining in the parietal loculum, and the other one becoming shifted to a loculum being actually formed. Such a way in the formation of new mesenteries, although theoretically possible, would have led to the formation of a net of axially united mesenteries hanging between and above the septa: each newly inserted mesenterium must have overcrossed a newly inserted scleroseptum. It is difficult to imagine such a system as effectively acting. Its attachment to an oral disc would have been possible exclusively through the first inserted mesenteries.

2. The insertion of a new mesenterium (a pair of mesenteria) followed the insertion of a given scleroseptum. Its (their) formation was due to the independent folding of the peripheral part of a polyp's body. The downward hanging of that body, postulated herein for the Heterocorallia (Fig. 11) produces the main difficulty in accepting this reconstruction. On the other hand, the mesenterial connection of that down hanging part with the inner portion of the body would have been helpful in its effective restraint.

Both alternatives accept gradational system of development and effectiveness of mesenteries. It has been presumed that two first mesenteries or two pairs of mesenteries were inserted either simultaneously with or prior *versus* after the insertion of the oblique septum, but before its first division. Insertion of the next mesenteries followed that of scleroseptata. Their earliest gener-



C

ations were located closer to a polyp's mouth and were working most effectively in retraction of the body and in distribution of food and waste products carrying waters inside the gastro-vascular cavity.

Like any conclusion in this part of the paper, the reconstruction of water distribution within the gastro-vascular cavity is purely theoretical. It seems proper to presume that the food-rich water should not be mixed with the food-less, waste products carrying water. The complex system of septa, with the main fossae more or less clearly marked suggest that the inflowing water was distributed from the mouth down along the interseptal loculi toward the periphery and then back upwards along the fossae. Such a system may have been especially effective in those Heterocorallia that possess all septa united and arranged in a kind of pyramid. Septa of the earliest generations may have been projected so high as to reach the level of the mouth or even being projected above it when completely open during the most effective feeding period. Deep fossae would have allowed removal of used water below the stream of the incoming water. To make this system more effective some passages through the ring of tentacles, corresponding to "fossae", can be hypothesized. In some instances the whole septal system is modified in such a way that a single, large fossa is formed. This is not a constant character, however, and cannot be accepted for taxonomic purposes.

The microstructure

The microstructure in the Dividocorallia n. subclass has been discussed by SCHINDEWOLF (1941), RÓŹKOWSKA (1969), LAFUSTE (1981), SUGIYAMA (1984), KARWOWSKI & WRZOŁEK (1987), and others, but only as far as the Heterocorallia are concerned. My own observations on this group are in agreement with those of the previous authors who accepted the trabecular microstructure of the primary septa and the fibrous or lamellar microstructure of the external wall (except for *Radiciphyllia*), tabulae and secondary sheets of septa.

Specimens of the Calyxcorallia n. ordo discussed in this paper are recrystallized and permit only a rough microstructural studies in the transmitted and non-polarised light. In the best preserved portions of septa two areas are distinguishable: the middle line, i.e. the primary septa, and peripheral, stereoplasmic sheets of septa. Dark, more or less isolated fragments of the primary septa, arranged either in narrow, almost straight (Pl. 6: 1a) or slightly scattered rows (Pl. 6: 2b) are herein interpreted as trabeculae. This interpretation is supported by the occurrence of elongated bodies seen in the longitudinal section (Pl. 6: 2a) that are closely comparable to typical trabeculae. Therefore the microstructure of primary septa in *Stylostrotion* is considered trabecular, although a detailed description of the trabeculae is not possible. Peripheral sheets of septa in *Stylostrotion* may be either fibrous or lamellar, or fibro-lamellar. None of these variants can be selected for sure. The same is true

as far as the microstructure of dissepiments, tabulae, and the external wall are concerned. In the case of the latter a possibility of the occurrence of the lamellar microstructure can be considered. This may be indicated by fairly sharp boundaries between peripheral ends of septa and the external wall (Pl. 6: 2b) comparable to "socles" in the Heterocorallia. This is not a constant structure within individual corallites. The instability may have resulted entirely from the diagenesis. Also, there are corallites in which the diagenetic alterations of separate portions of the external wall imitate individual septa (Pl. 6: 1b).

The presumed phylogeny of Dividocorallia n. subclass and their position within the Anthozoa

The insertion and arrangement of septa has traditionally and through a long experience been considered the most important character within the Anthozoa and the main basis for their subdivision into individual lower rank taxa. This traditional approach is accepted in the present paper. Simplified relationship of individual subclasses is shown in Figure 15. This simple figure needs no wider explanation, except for the following remarks: Rugosa are generally accepted as derived from Tabulata, and Auloporida are often indicated as their direct ancestors which may or may not be accepted. However, the Tabulata themselves represent perhaps a group of superficially similar skeletal organisms, but not a biological taxon.

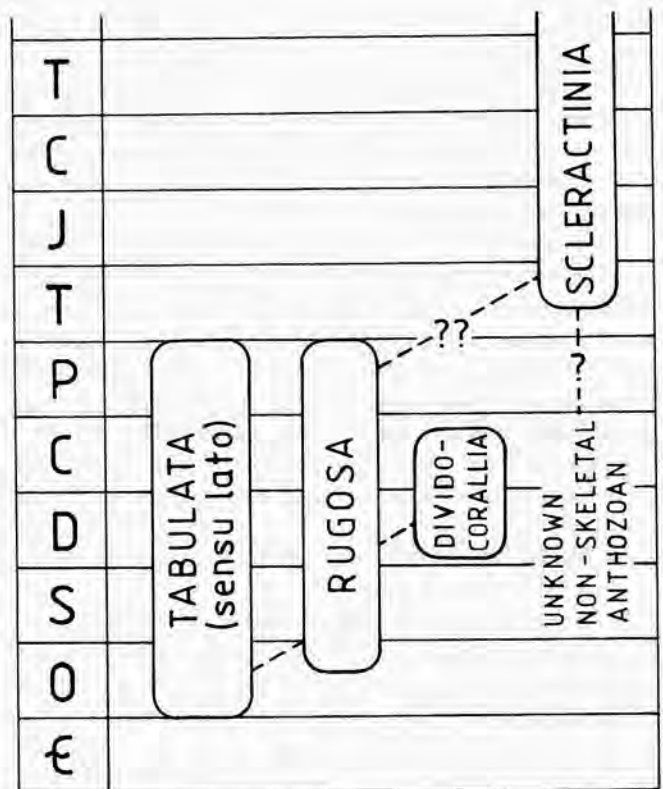


Fig. 15. - Probable relationship and range of anthozoan subclasses.

Some taxa, such as Heliolitida or Chaetetida have already been removed from the Tabulata. For some others a transfer into the Sponges has been proposed (KAŹMIERCZAK, 1987). This is not discussed in detail here. I would only like to point out that herein the name Tabulata is used in the traditional sense. The problem of the Tabulata-Rugosa relationship is discussed in more detail in SCRUTTON (1979). No new arguments can be added to the discussion concerning the Rugosa-Scleractinia relationship. The summary by OLIVER (1980) remains perhaps the most comprehensive. Two question-marks used in the linkage of Scleractinia from the Rugosa and one from the unknown non-skeletal anthozoan (Fig. 15) means that we possess quite a few arguments against the origin of Scleractinia from the Rugosa, whereas lack of data is the main argument against the second option. In the case of non-skeletal organisms such an argument is not really decisive.

In contrast to the very doubtful Rugosa-Scleractinia relationship, a close phylogenetic connection between the Rugosa and Dividocorallia n. subclass is at least very probable. This, despite the fact that two main characters in common between these taxa, i.e. the calcitic skeletons and similarity in the earliest skeletogenesis were not decisively proven. The mineralogy and diagenetic alterations in dividocoralloid skeletons are very similar to those in the Rugosa. The calcitic mineralogy of the latter is univocally accepted. Also, most students consider this mineralogy primary. There are some (e.g. OEKENTORP 1984) who argued for it being altered from the aragonitic. OEKENTORP's ideas, based on the Permian Rugosa from Timor Island did not find a general support and were critically reviewed by FEDOROWSKI (1986) and SORAUF (1984) on the basis of the same or similar Timor Island material. Doubts created by these opposite options remain, but they are equally applicable to both subclasses discussed thus providing an indirect argument for their primary microstructural identity.

Data concerning the early skeletogenesis, i.e. the second argument speaking in favour of close Rugosa-Dividocorallia relationship are unequally distributed between these subclasses. Numerous studies of the early ontogeny in the Rugosa, conducted since the pioneering work of DUERDEN (1902) by means of cross sections were supplemented by restricted observations in etched calices (e.g. SANDO, 1961; FEDOROWSKI, 1987). The following facts, important in the context of this discussion were documented:

1. A single axial septum was formed at the very beginning of septal insertion.
2. It crossed a whole corallite lumen.
3. At least in some Rugosa the axial septum as well as the alar and counter-lateral septa were inserted on a calice floor with no connection to septal furrows. All these septa reach a corallite wall, but are not elongated onto it at the very beginning of the septogenesis.
4. Stop of growth of the axial septum in its middle part led to the formation of the cardinal and the counter septum.

5. Alar and counter-lateral septa appeared laterally to the axial septum.

The early skeletogenesis in the Calyxcorallia n. ordo is unknown. In the Heterocorallia it has been studied by means of serial sections in a single corallite of *Mariaephyllia* n. gen. (Fig. 19: 1). That study is supplemented by observations started from the three-septal stage in *Oligophylloides* (RÓŹKOWSKA, 1969; SUTHERLAND & FORBES, 1981). The following events of that ontogeny should be considered most important from the phylogenetic point of view:

1. A single septum was formed at the very beginning of septal insertion.
2. It may or may not cross a whole corallite lumen at the very beginning of septogenesis, but it is restricted to a corallite axis since the insertion of the first septa descendent from it.
3. Septa following the axial septum in the appearance were inserted at peripheral ends of the former. Only those four septa reached the external wall. Thus, homologs of the cardinal and counter septum do not exist in the Heterocorallia, nor in the whole new subclass Dividocorallia.
4. The oblique septum in many (most?) dividocorals is continuous. In some instances it may temporarily or permanently disappear or is divided into axially located rudiments. Thus, division of the oblique septum does not lead towards insertion of the cardinal and counter septum.

The preceding brief summary of early septogenesis in the Rugosa and Dividocorallia n. subclass exposes their main connecting and distinguishing characters. Insertion of a single septum at the very beginning of septogenesis forms the fundamental argument for the direct, phylogenetic connection between these two subclasses. The predicted identity in the mineralogy of their skeletons provides only an additional proof. The divergence towards the Dividocorallia took place in a very early growth stage due to the insertion of new septa at both ends of the axial septum but not at its lateral sides. Two fundamental dividocoralloid characters, i.e. the primarily continuous axial septum (= the oblique septum), and the peripheral dichotomic division of septa were attained that way. The oblique septum did not produce the cardinal and the counter septum, because deviation towards the Dividocorallia n. subclass took place prior to the appearance of those protosepta in the ontogeny of the ancestral form. The division or disappearance of the oblique septum in some Carboniferous dividocorals resulted from their own, independent phylogeny, thus being only analogous to that process in the Rugosa.

The appearance of the axial septum and four first lateral septa on a calice floor in some Rugosa and the restriction of these septa to the calice floor at the very beginning of septogenesis pointed to the Calyxcorallia n. ordo as ancestral for the whole subclass Dividocorallia n. subclass. This interpretation assumes the monophyletic origin of the subclass. Insertion of septa, their increase and microstructure, common for both orders, are argu-

ments favouring such an interpretation. Following this deduction based on facts provided both by the Rugosa and Dividocorallia n. subclass, it seems logical to consider a possibility of deviation from the Calyxcorallia n. ordo towards the Heterocorallia immediately after insertion of the first two pairs of the potentially creative septa in the former order. This way a fundamental dividocoralloid character, i.e. the peripheral dichotomic division could have been continued in both orders. Besides, the five-septal stage either proven or deduced as present in all dividocorals, could have been inherited by heterocorals.

An upward growth of a corallite's axial portion with a contemporaneous relinquishment of secretion of the external wall seems to be the most probable way of deviation from the Calyxcorallia n. ordo towards the Heterocorallia. Such a mutation must have happened early in an ancestor's ontogeny, because two models of insertion of the next generations of septa, i.e. the symmetrical and asymmetrical model seem to occur only in the latter order. Besides, an inconstant but commonly large size and a primitive septal apparatus in *Tetraphyllia*, the earliest known heterocoral, may indicate neoteny as a way of the origin of Heterocorallia. An occurrence of *Tetraphyllia* and *Pseudopetraia* in the Upper Emsian pointed to the Early Devonian as the level of appearance of the dividocoralloid's ancestors. Primitive metriophyllids with their axially united, weakly differentiated or non-differentiated major septa are the most possible ancestors of the Dividocorallia n. subclass although any particular genus or species of that suborder cannot in this moment be specified.

However, an independent origin of the Calyxcorallia n. ordo and the Heterocorallia cannot be excluded. In this option, the Calyxcorallia n. ordo would have originated as postulated above, whereas Phillipsastraeidae or their ancestors would have given rise to the Heterocorallia. This option is supported by the occurrence of the so called everted calices in Phillipsastraeidae, which can be considered as leading towards the calice-less forms. However, all Phillipsastraeidae known so far are phylogenetically advanced, dissepimentate taxa. The retrogressive evolution from such taxa in all but one character, i.e. the everted calice, and the achievement by them of a stage so primitive as *Tetraphyllia* seems most unlikely. This option is therefore rejected from further discussion.

Tetraphyllia is either an ancestor of all the Heterocorallia or stays very close to it. The primitive five-septal morphology and the inconstant but commonly large size speaks in favour of the first option. Lack of date made the Middle and a part of the Upper Devonian heterocoralloid phylogeny unknown. The diversified Famennian faunas from Poland (RÓZKOWSKA, 1969; SUTHERLAND & FORBES, 1981; WRZOLEK, 1981; KARWOWSKI & WRZOLEK, 1987), Germany (WEYER, 1989), Belgium (POTY, 1978, 1986; DREESEN *et al.*, 1985), Afghanistan (VACHARD, 1980), and perhaps also, though their faunas are not always studied in adequate detail, from the Ural Mts., could have developed two different phylogenetic lines leading towards the Carboniferous *Hexaphyllia* or *Heterophyllia*:

1. *Tetraphyllia* – *Oligophylloides* – *Mariaephyllia* – *Heterophyllia*.
2. *Tetraphyllia* – *Pentaphyllia* (?) – *Hexaphyllia* – *Heterophyllia*.

Both options started with *Tetraphyllia*. This approach is fully supported by the primitive and generalized morphology of that genus. Further, it seems to expose the monophyletic relationship of all genera under discussion. It would thus only be a matter of establishing lineages between the individual general and of evaluating the taxonomic ranks of individual lineages to make the history of the order Heterocorallia clear. Such an optimistic version is not supported by the facts accumulated so far. The absence of Middel and lower Upper Devonian heterocorals is the first obstacle and results in making this part of the heterocoral phylogeny largely deductive and open to several theoretical interpretations. The first option established above is supported by a sequence of stratigraphical occurrences of individual genera. This straight phylogenetic line, based on the increasingly enlarged number of the symmetrically arranged septa and on the increasing complexity of the external wall, gets broken when its last segment, i.e. *Heterophyllia* is considered. Possessing the number of septa and the morphology of the external wall similar to *Mariaephyllia* n. gen., it differs from the latter in its ontogeny and in the asymmetrical arrangement of septa. Differences in these high rank characters eliminate *Heterophyllia* from the phylogenetic line discussed. They do at the same

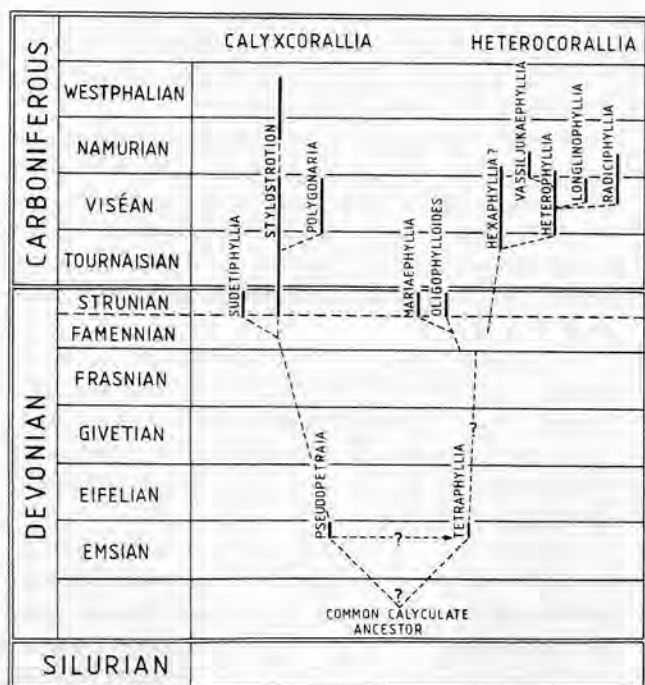


Fig. 16. – Probable phylogeny of Dividocorallia n. subclass and ranges of individual genera.

time show that the three first segments of this line are closely related. All of them are restricted to the Devonian.

A cladistic approach allows to predict an occurrence of the Middle and Early Upper Devonian morphotypes or genera intermediate between *Tetraphyllia* and *Oligophylloides*. A line leading through the seven-, nine-, and eleven-septal taxa or morphotypes is one option and the appearance of an *Oligophylloides*-like coral is the second one. Early growth stages in the ontogeny of *Oligophylloides* may be indicative for the predicted morphology of those intermediate forms. As in the case of Carboniferous genera (?) *Pentaphyllia* and *Hexaphyllia*, discussed elsewhere in this paper, a given number of septa may or may not be genetically controlled. The first option is possible in those forms, in which it is ultimate in their ontogeny. Thus, we may be dealing with two parallel phylogenetic lines: Devonian and Carboniferous operating similarly due to the restriction of possibilities offered by a simple morphology of heterocorals. The Devonian line, characterised by symmetrical arrangement of septa, is distinguished herein as the suborder *Tetraphyllina* n. suborder.

The phylogenetic line leading from *Tetraphyllia* through the Lower Carboniferous *Pentaphyllia* (?) and *Hexaphyllia* to *Heterophyllia* and other genera of a complex morphology and asymmetrical arrangement of septa form the suborder *Heterocorallia*. This option is yet unsupported for the time span from the Emsian to the Upper Tournaisian (?) or Lower Viséan. *Heterophyllia* sp. described from the Lower Famennian of Thuringia (WEYER, 1989) is herein included in *Mariaephyllia* together with *H. famenniana* RÓŻKOWSKA, 1969.

A long stratigraphic gap in the occurrence of heterocorals may have resulted either from lack of findings or from the non-existence of the asymmetrical heterocorals during that period of time. This means either a monophyletic or polyphyletic origin of the order. The arrangement of septa in the innermost parts of the Carboniferous heterocorals identical to *Tetraphyllia* forms the main argument for the first option available up to now. One may argue, however, that such a simple arrangement must occur early in the ontogeny of any dividocoral. Presence of non-skeletal ancestors of the suborder *Heterocorallia* prior and during the stratigraphic gap mentioned – the only way to support the second option – is unacceptable for two reasons. First, a physiological operation of such a form is highly improbable. Secondly, the whole subclass *Dividocorallia* must then be considered to be polyphyletic, because there would be rather a weak reason to consider the appearance of *Tetraphyllia*-like forms in a way discussed earlier in this chapter. The cladistic correctness of the first approach may have resulted from an improper evaluation of individual diagnostic characters, but this must always be taken into account in any analysis.

In conclusion it is only right to say that facts and deductions favour the monophyletic status of the *Dividocorallia* n. subclass, but the polyphyletic option cannot

in this moment be totally excluded. The Carboniferous history of the suborder *Heterocorallia* is equally unclear. The early ontogeny or arrangement of septa of all genera that actually occur in that suborder exhibit a hexaphylloid arrangement for early generations of septa, but the independent generic status of *Hexaphyllia* is uncertain. Thus, it may be either *Hexaphyllia* or *Heterophyllia* that gave rise to the phylogenetically more advanced genera.

Radiciphyllia originated most probably from *Heterophyllia* because it repeated the heterocoralloid morphology and arrangement of septa early in its ontogeny, but introduced a new feature, i.e. the disintegration of the inner ends of septa afterwards. This new character was achieved parallel to the development of the radicitheca. The latter is a solid wall characterised by the disintegration of trabeculae within peripheral parts of septa. These disintegrated trabeculae replaced the lamellar microstructure of peripheral parts of septa first, and then expanded into the interseptal portions of the external wall to form the advanced radicitheca. The disintegration of trabeculae is observed in a course of ontogeny (SUGIYAMA, 1984, pls. 5: 1, 6), being best accentuated in *R. toriyamai* (SUGIYAMA, 1984, pl. 7). Strong peripheral scattering of trabeculae may not have appeared the most progressive achievement because in the stratigraphically younger species *R. tokyoensis* bunches of trabeculae are restricted mostly to the inner part of the external wall, whereas small peripheral projections of septa may occur at its periphery (IGO & KOBAYASHI, 1980, p. 15: 2). *Radiciphyllidae* n. fam. was perhaps a short-ranging, morphologically advanced, blind offspring of *Heterophyllidae*.

The probable access to *Radiciphyllidae* of ? *Lithotrotion* cf. *tereense* PICKETT, 1966, described by PERRET & SEMENOFF-TIAN-CHANSKY (1971) from the Pyrenees, is discussed with remarks on *Calyxcorallia* n. ordo. Only the following should be noticed here:

1. Although appearing high in the stratigraphical column (V3a-V3c) the species discussed may well find its ancestors in the Asiatic parts of the Carboniferous Ocean because of its "right" geographical occurrence. Recognition of such an eastern rugose coral genus such as *Kizilia* as far West as France, may confirm this thesis.
2. ? *L.* cf. *tereense* has been described as a colonial species. This recognition is confirmed by specimens collected by the present author in the type locality. Thus, this is the species that developed a character weakly accentuated by some of the Asiatic species of *Radiciphyllidae* n. fam.
3. It exhibits some features in the peripheral parts of corallites comparable both to *Radiciphyllia* and *Vassiljukaephyllia* n. gen. Those common features may illustrate a similar way of development rather than its intermediate character. The species requires restudy prior to drawing any final conclusions. The foregoing remarks are included in order to show a close similarity to *Heterocorallia* and *Calyxcorallia* n. ordo not

only in the arrangement and development of their septa, but also in the form of growth.

Two options for the origin of *Longlinophyllia* are possible. *Heterophyllia* is considered ancestral for this genus in both options, but there may be either a direct connection between those two genera or with an intermitance of *Vassiljukaephyllia* n. gen. The main characteristics of the latter genus are discussed here for composition purpose. These are:

1. Large size; up to 12 mm in the diameter.
2. Up to 42 potentially creative septa.
3. Irregular arrangement of septa; individual quadrants are almost indistinguishable.
4. Disconnection of inner ends of several septa.
5. Peripheral thickenings of septa, called carinae by VASSILJUK (1964: 95), but recognized as trabeculae.
6. Peripheral disintegration of septa.
7. Almost vertical position of densely located tabulae at the periphery.

The characteristics listed can be divided into three groups. The first four are attributed to the phylogenetically advanced taxa. The fifth character, i.e. large trabeculae, is distinctive for the genus. The last two are new for Heterophyllidae. Their appearance together with the first four ones, as well as the high stratigraphic position of *Vassiljukaephyllia* n. gen. are interpreted here as resulted from peragenesis, i.e. adding of new qualitative features to the pre-existing mature morphology of the ancestral taxon.

The taxonomic position of *Vassiljukaephyllia* n. gen. and its relationship to *Longlinophyllia* may be interpreted in two ways:

1. It forms an intermediate step towards *Longlinophyllia*.
2. It forms a blind ultimatum of the *Hexaphyllia* – *Heterophyllia* – *Vassiljukaephyllia* n. gen. line.

The second option is accepted in this paper as being supported by facts available up to now. These are:

1. A more advanced development of the inner parts of septa in *Vassiljukaephyllia* than in *Longlinophyllia*.
2. Geographical and stratigraphical distribution of both taxa. Occurrence of morphologically less advanced species higher in the stratigraphic column in the Donetz Basin than in China contradict a predicted direction of the Carboniferous equatorial palaeocurrent. Although not belonging to Longlinophyllidae, *Vassiljukaephyllia* n. gen. is important as a taxon illustrating a possible way of transmission from *Heterophyllia* to *Longlinophyllia*. A true intermediate taxon should be expected to occur in strata older than the Lower Namurian and in the area of occurrence of *Longlinophyllia*.

Phylogeny within the Calyxcorallia n. ordo can be reconstructed only in a very generalized way. This results from a poor record, inadequate level of knowledge and geographical and stratigraphical dispersal of the order. Its oldest known representative *Pseudopetraia devonica* SOSHKINA, 1951 possesses deep calices and thin septa, i.e. characters attributed by HUBBARD & POCKOCK (1972)

to inhabitants of a low sediment rate regime. The irregular arrangement of septa and their permanent axial union, as well as the morphology of calices, focus on Metriophyllina as the possible ancestral group of that genus and the whole subclass Dividocorallia n. subclass.

Corals exhibiting calyxcoralloid characteristics have not been recorded from the Eifelian to Strunian strata. Diversified calyxcoralloid faunas appeared during the Strunian in places so far apart as Poland and China. Both those faunas consists of exclusively colonial forms. In China dendroid and subcerioid colonies occur, whereas dendroid and thamnasterioid – aphroid forms were recognized in Poland. Questions substantial for this discussion are:

1. Was any direct connection between the Chinese and Polish faunas possible?
2. Where they related to the Emsian *Pseudopetraia* from Southern Ural?

These two questions cannot be solved without considering a global Devonian geography. During the Lower and Middle Devonian there were large land masses that separated Western European seas from the Uralian geosyncline, but there was a direct connection between the latter seas and Pre-Tethys. Thus the relationship between *Pseudopetraia* and Asiatic representatives of *Stylostrotion* is at least probable, whereas any connection between that Uralian genus and Central and Western European stylostrotionids should be excluded. The Upper Givetian – Frasnian transgression and generally westward expansion of Eastern European seas made westward migration of coral faunas possible. It is therefore postulated that the Chinese Strunian representatives of Calyxcorallia n. ordo derived from descendants of *Pseudopetraia* and migrated as far west as to Poland in the Strunian and to the Ardennes and Montagne Noire in the Viséan. The genus *Stylostrotion* is abundant in Vietnam, China and Central Asia up to the Upper Viséan and is present there up to the Weiningian (Upper Bashkirian – Lower Moscovian). It was rare in Central and Western Europe but it has been documented up to the Upper Viséan in the Ardennes. Also, it occurred in the Donetz Basin up to the Upper Moscovian under the name *Donophyllum*.

Three features of species attributed to the latter genus draw attention:

1. Small size of corallites.
2. Lack of lonsdaleoid dissepiments.
3. A tendency of major septa to disintegrate in a corallite axis.

The first two characters are frequently considered primitive, whereas the third seems to be progressive. Similar characteristics are true for the Chinese *Stylostrotion intermedium* although none of the five corallites illustrated by CHI (1931, pl. 1: 1a-e) is fully diphyphylloid and similar in this respect to *Donophyllum diphyphylloideum* FOMICHEV, 1939. Why these primitive characters appeared in the stratigraphically youngest taxa is difficult to explain. Also, the long gap in occurrence between the Upper Viséan and Upper Bashkirian –

Moscovian taxa may speak in favour of distinguishing *Stylostrotion* from *Dematophyllum*. Such a solution is not postulated herein due to reasons discussed in the systematic part of the paper.

Geographical occurrence and stratigraphical position of the youngest Chinese and Eastern European species of *Stylostrotion* speak in favour of their close relationship. Also, it seems right to consider the far Asiatic seas as a "creative" region for the Carboniferous calyxcoralloid fauna.

Sudetiphyllia n. gen. is considered an endemic Polish genus. Its migration from the East has not been confirmed, whereas its direct relationship with the Chinese Upper Viséan *Polygonaria* FAN in H.D. WANG, 1978 should be excluded. The latter conclusion is documented by much more advanced integration within colonies of the Polish genus, contrasting to its early stratigraphical occurrence and geographical isolation. However, both genera in question belong probably to the same family, which is postulated in the systematic part of this paper. Their independent origin from separate Chinese and Polish species of *Stylostrotion* seems most probable.

Taxonomy

Phylum Coelenterata FREU & LEUCART, 1847

Class Anthozoa EHRENBERG, 1834

Subclass Dividocorallia n. subclass

TYPE ORDER

Heterocorallia SCHINDEWOLF, 1941.

DIAGNOSIS

Anthozoa possessing septa developed due to peripheral dichotomic division; the process started from a single oblique septum, located axially and inserted on pedal disc.

REMARKS

Septal insertion established herein for the Dividocorallia n. subclass plays a double role. First this criterium allows to distinguish dividocorals from all remaining groups of Anthozoa. Secondly, the oblique septum inserted at the very beginning of the formation of septa can be considered homologous to the axial septum in the Rugosa, focusing on the latter subclass as the most probable ancestor of the Dividocorallia n. subclass. The extensive discussion which precedes the taxonomical part of this paper makes more specific remarks unnecessary.

Order Heterocorallia SCHINDEWOLF, 1941

EMENDED DIAGNOSIS

Dividocorallia without calices

REMARKS

The morphogenesis and mutual relationship of all major

skeletal elements of heterocorals were discussed in the general part of this paper. The discussion that follows is focused on uncertainties in the classification on the suborder and family level. Two characters should be considered most important for the classification within the order:

1. Model of the insertion of septa.
2. Morphology of the external wall.

The first criterium is distinct in two groups, within the frames of which it is constant. It may be: a) symmetrical, i.e. all quadrants are more or less equally developed in the number of septa and the volume of a corallite lumen; b) asymmetrical, i.e. one or two quadrants are underdeveloped. These two groups of taxa are classified herein as suborders. Morphology of the external wall is less well established in some taxa, and may be less constant. It has been accepted as characteristic for the taxa below the ordo level and is discussed with remarks on individual suborders and families.

Suborder Tetrephyllina n. subordo

TYPE FAMILY

Tetrephyllidae YOH, JIN, ZHEN & XIE, 1984.

FAMILIES ASSIGNED

Monotypic.

DIAGNOSIS

Heterocorallia possessing septa arranged symmetrically.

REMARKS

The necessity of the introduction of this suborder became clear when individual diagnostic characters were cladistically evaluated. Two genera included in the suborder, i.e. *Oligophylloides* and *Mariaephyllia* n. gen. exhibit its diagnostic features clearly. Also, both these genera are fairly completely investigated. The third genus – *Tetrephyllia* – is rather poorly known and some important characters of its type species can only be suspected or deduced. Nevertheless, its characteristics established so far allow to place it, together with the other two, in the same family. The introduction of the family Tetrephyllidae by YOH *et al.* (1984), correct from the formal point of view, made an application of that name necessary unless the distinction on the family level between *Oligophylloides* and *Mariaephyllia* n. gen. on one side and *Tetrephyllia* on the other is documented. This is impossible in this moment. To rise the taxonomic rank of Tetrephyllidae to the suborder level and to accept this suborder as monotypic for the time being, is the only solution possible in a situation discussed. The relationship between Heterocorallia and Tetrephyllina n. subordo are discussed in remarks on the phylogeny.

Family Tetrphyllidae YOH, JIN, ZHEN & XIE, 1984

TYPE GENUS

Tetrphyllia YOH, JIN, ZHEN & XIE, 1984.

SYNONYM

Heterophyllidae RÓZKOWSKA, 1969; SUTHERLAND & FORBES, 1981; WRZOLEK, 1981; KARWOWSKI & WRZOLEK, 1987 (e.p.); WEYER, 1989. Non DYBOWSKI, 1873.

GENERA ASSIGNED

Tetrphyllia YOH *et al.*, 1984, *Oligophylloides* RÓZKOWSKA, 1969, *Mariaephyllia* n. gen.

EMENDED DIAGNOSIS

Tetrphyllina possessing external wall of either protoheterotheca or heterotheca kind; weak colonies may occur.

REMARKS

Morphology of the external wall is differently evaluated within suborders of Heterocorallia. This is in part caused by the inadequate knowledge of this character in *Tetrphyllia*. Illustrations of YOH *et al.* (1984, pl. 1: 1-6) allow to state that:

1. The outline of corallites is rounded.
2. Some rudimentary structures can be interpreted as comparable to peripheral parts of septa and the external wall in *Oligophylloides*, i.e. the protoheterotheca (e.g. YOH *et al.*, 1984, pl. 1: 2a, upper left; pl. 1: 4a, down; pl. 1: 5a, left).
3. Some septa strongly thickened at the periphery, look like only touching the inner surface of the external wall (YOH *et al.*, 1984, pl. 1: 2a, septa other than the upper left septum; pl. 1: 3a; pl. 1: 5a, right). To state that the external wall in *Tetrphyllia* is possibly not of the heterotheca kind and can perhaps be closely comparable to the protoheterotheca, is all one can deduce from the above observations. To sum up the discussion on the external wall in Tetrphyllina n. subordo it is only right to say that the protoheterotheca is perhaps the most common structure in that suborder. Being characteristic for *Oligophylloides*, it is developed in some parts of growth in *Mariaephyllia* n. gen. and is suspected in *Tetrphyllia*.

Genus *Tetrphyllia* YOH, JIN, ZHEN & XIE, 1984

TYPE SPECIES

T. devonica YOH, JIN, ZHEN & XIE, 1984.

SPECIES ASSIGNED

Monotypic.

EMENDED DIAGNOSIS

Tetrphyllidae possessing septal apparatus restricted to oblique septum and two pairs of potentially creative septa.

REMARKS

The original diagnosis was emended in accordance to the here established arrangement and development of septa. Also, the absence of tabulae, emphasized in the original diagnosis by YOH *et al.* (1984) and considered by those authors a basis for the distinction of both genus and family, is rather superficial and was most probably diagenetic. At least some perpendicular bars seen in the longitudinal sections illustrated by those authors (e.g. pl. 1: 3b, 5b) may well be interpreted as tabulae or pseudomorphoses of these bodies. Thus, tabulae were most probably present in *Tetrphyllia*, but the distinction of this genus from other genera of Tetrphyllidae is based on the number of generations of septa. The morphology of the external wall is not discussed, because data provided by the original description and illustrations made such a discussion almost baseless.

Genus *Oligophylloides* RÓZKOWSKA, 1969

TYPE SPECIES

O. pachytheucus RÓZKOWSKA, 1969.

SPECIES ASSIGNED

O. pachytheucus RÓZKOWSKA, 1969; *O. tenuicinctus* RÓZKOWSKA, 1969.

EMENDED DIAGNOSIS

Tetrphyllidae possessing protoheterotheca and more than one generation of potentially creative septa; weak colonies may occur.

REMARKS

Oligophylloides has been studied a few times in detail (RÓZKOWSKA, 1969; SUTHERLAND & FORBES, 1981; WRZOLEK, 1981; KARWOWSKI & WRZOLEK, 1987) thus becoming one of the best known heterocorals and making extensive discussion unnecessary.

Genus *Mariaephyllia* n. gen.

TYPE SPECIES

Heterophyllia famenniana RÓZKOWSKA, 1969.

SYNONYM

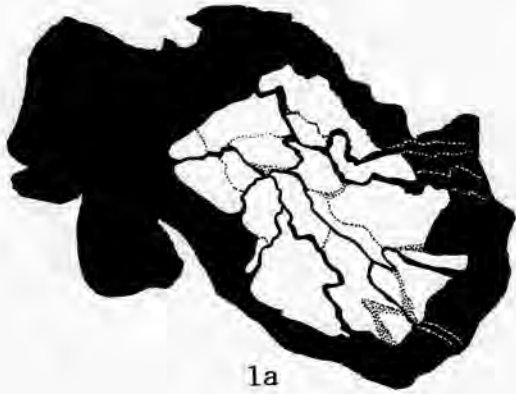
Heterophyllia RÓZKOWSKA, 1969; WEYER, 1989, non MCCOY, 1849.

DERIVATION OF THE NAME

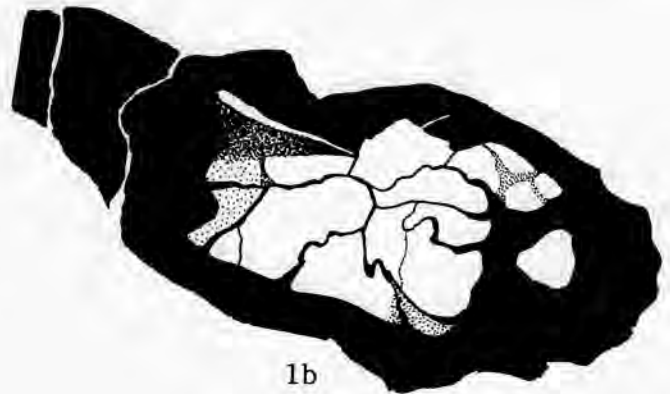
After the first name of both my late Mother and the late Professor Maria RÓZKOWSKA.

SPECIES ASSIGNED

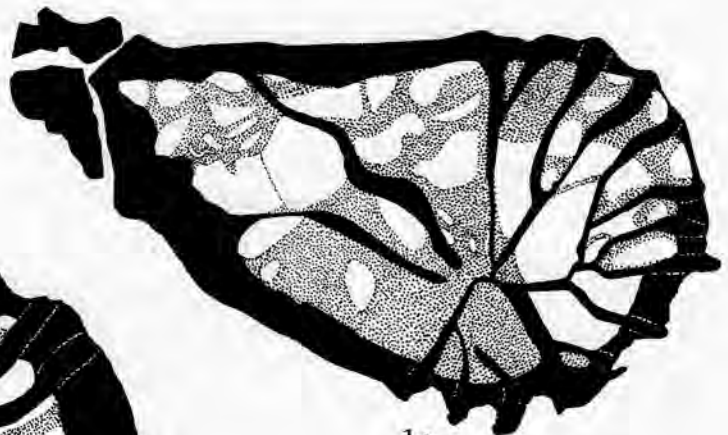
Monotypic.



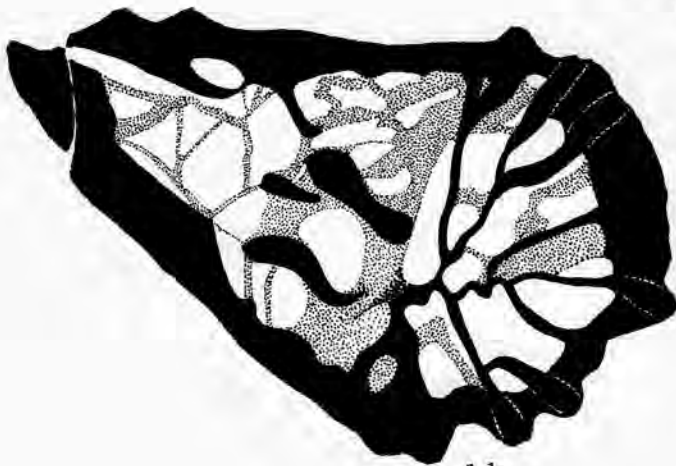
1a



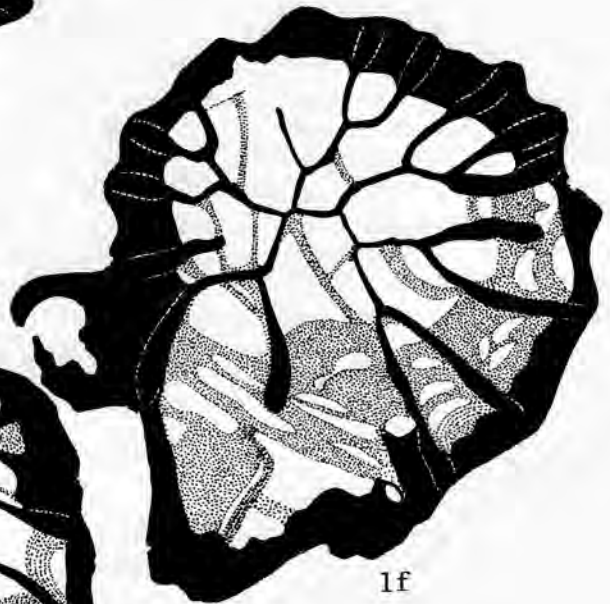
1b



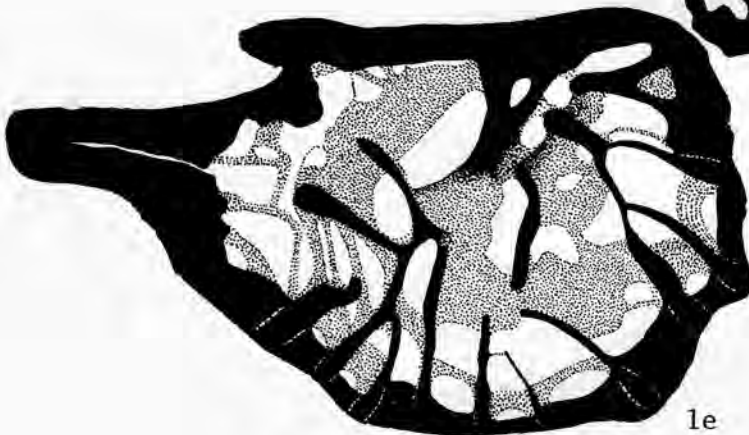
1c



1d



1f



1e

DIAGNOSIS

Tetraphyllidae possessing inconstant heterotheca and several generations of potentially creative septa.

REMARKS

The morphology of the external wall is the main qualitative character distinguishing *Mariaephyllia* n. gen. from *Oligophylloides*. Restriction in the number of septa to 12, pointed out in the original diagnosis of *Oligophylloides* (RÓŻKOWSKA, 1969: 161) must be re-evaluated because the calculation has been made in accordance to SCHINDEWOLF'S (1941) scheme, i.e. all septa of the peripheral part of a corallite were counted independently of their generations. Indeed, the species of *Oligophylloides* described so far possess only up to 12 septa, but these are all potentially creative septa of last generations in individual quadrants. Assignment by RÓŻKOWSKA (1969) of Polish Famennian specimens to the Carboniferous genus *Heterophyllia* has already been questioned by some authors (e.g. SUGIYAMA, 1984; WEYER, 1989). Reinvestigation of the original collection of RÓŻKOWSKA (1969) with the supplementary sectioning and peeling made for the purpose of this paper, allows to confirm the objections mentioned and to create a new genus *Mariaephyllia* with "*H.* *famenniana*" as its only representative known so far, if the informal taxon *Heterophyllia* sp. of WEYER, 1989 is not counted. Collision in the evaluation of arrangement of septa versus morphology of the external wall in *Oligophylloides* and *Mariaephyllia* on one side, and *Heterophyllia* on the other, is apparent. The symmetrical arrangement of septa is a primitive high rank character that gave rise to more progressive and constant asymmetrical arrangement. Contemporaneously to that event the morphology of the external wall became subordinated to several changes. Some of them were parallel in both groups that were identified by the arrangement of septa. Moreover, in *Mariaephyllia* n. gen. one can observe fragments of typical heterotheca replaced by fragments of pseudoheterotheca, whereas in *Heterophyllia* the heterotheca is permanent. Occurrence of the well developed heterotheca in *Hexaphyllia* and presence of hexaphylloid stage in the ontogeny of *Heterophyllia*, but not in *Oligophylloides* and *Mariaephyllia*, helped in the evaluation of characters and made the introduction of new genus *Mariaephyllia* necessary.

Mariaephyllia famenniana (RÓŻKOWSKA, 1969)

(Pls. 1: 1-11; 2: 1-5; Figs. 17-23)

* *Heterophyllia* (*Heterophyllia*) *famenniana*
RÓŻKOWSKA, 1969, pp. 170-173, text-fig. 72A-J; pl. 6,
figs. 11, 12.

MATERIAL

The original collection of RÓŻKOWSKA (1969), from which many new thin sections and peels were prepared.

EMENDED DIAGNOSIS

Mariaephyllia possessing up to 5 generations of septa and up to 21 septa at periphery; maximum diameter 4.5 mm.

DESCRIPTION OF THE HOLOTYPE

The holotype has been rather unfortunately chosen by RÓŻKOWSKA (1969) because its inner morphology is, in several portions of growth, camouflaged by thick and recrystallized stereoplasm and by the talon-like structure. Thus, only the upper portion of growth (Fig. 18: 1c-1f) exhibits septa only slightly influenced by extrinsic or diagenetic factors. In the last four sections the oblique septum is long and may bend a little, whereas septa of the first and next generations diverged almost symmetrically. This resulted in the formation of two distinct fossae separated from each other by the oblique septum. Individual quadrants differ both in number of generations and number of septa at the periphery. The latter character is perhaps constant in the ontogeny, but this is only deduced from remnants of septa in the ontogenetically earlier sections.

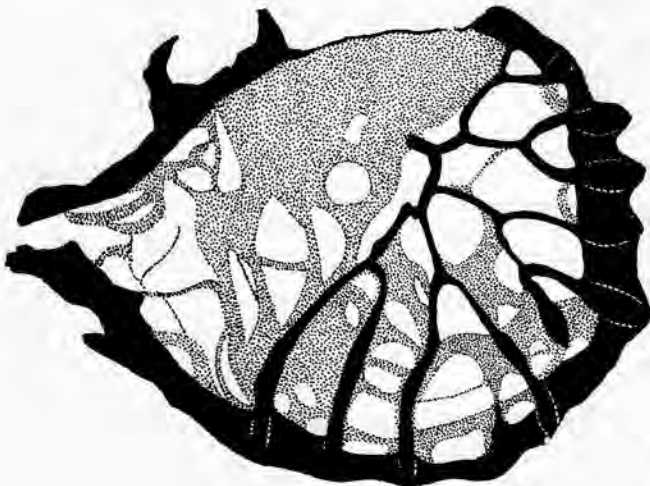
Increase in septa has perhaps been fast early in the ontogeny. Preservation of the specimen does not allow to establish a precise succession in their appearance. Also, the position of the oblique septum in the earliest two and in some higher sections is not quite clear (Figs. 17: 1a, 1b, 1d, 1e; 18: 1a). It is very short in all but the last four sections.

There exists a striking difference in thickness and shape of septa between the ontogenetically earliest (Fig. 17: 1a, 1b) and subsequent sections. The unthickened septa seen in the earliest portions of growth are probably primary, but their irregular shape may illustrate some diagenetic alterations. Distinctly increased thickness of septa corresponds to the thickest secretion of stereoplasm elsewhere in the corallite lumen. This may be explained as either temporary increase in the calcium carbonate available for the coral or as strengthening of the skeleton in its portion attached to the sea floor. Thinning of the skeleton above the talon-like structure supports the second option. The heterotheca consists of differently arranged septal and interseptal portions. Peripheral parts of septa may form external protrusions (Fig. 17: 1c, 1d, 1f) or disappear in the thickness of the external wall.

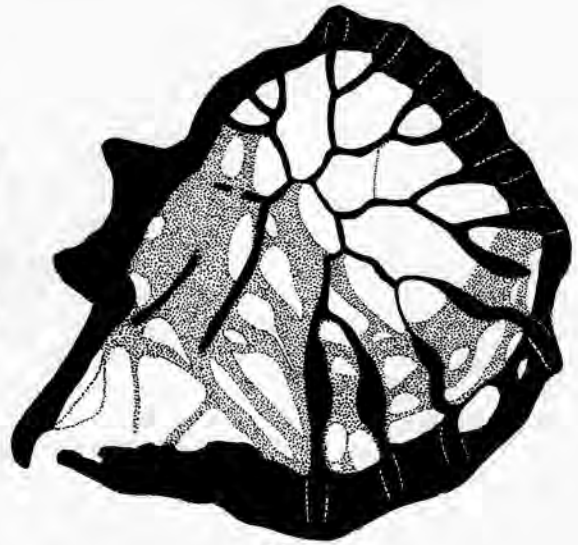
INTRASPECIFIC VARIABILITY

The holotype shares several characteristics with the paratypes. Lack of a direct correlation between the number and/or generations of septa and a corallite diameter is

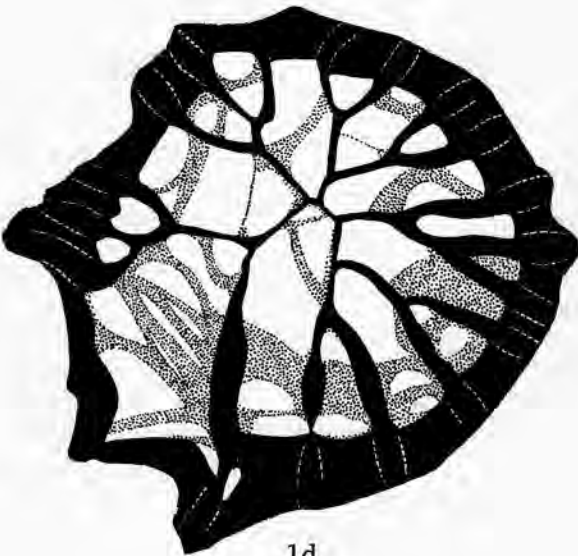
Fig. 17. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). Specimen Z.Pal.P.Tc-3/2026. Holotype. Gałęzice, Holy Cross Mountains. Upper Famennian *costatus* and *velifera* Zones. Transverse sections of successive ontogenetic stages. Stereoplasmic infillings and tabulae dotted. Early growth of the corallite. A11 × 20.



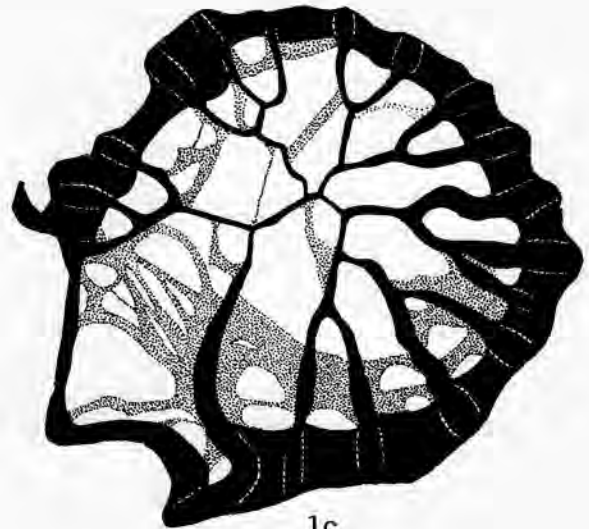
1a



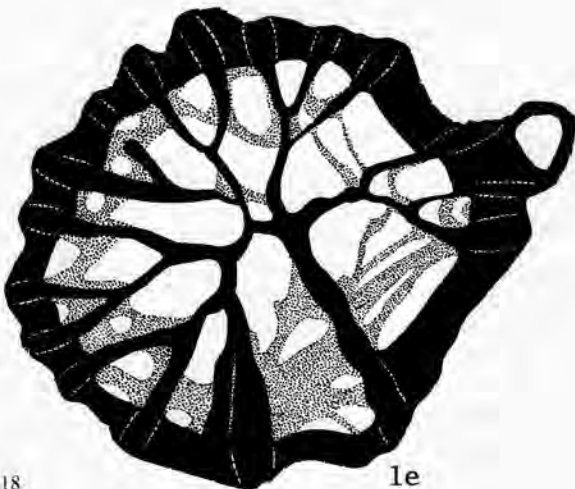
1b



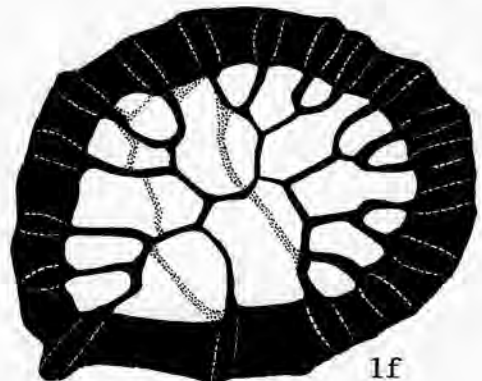
1d



1c



1e



1f

Fig. 18

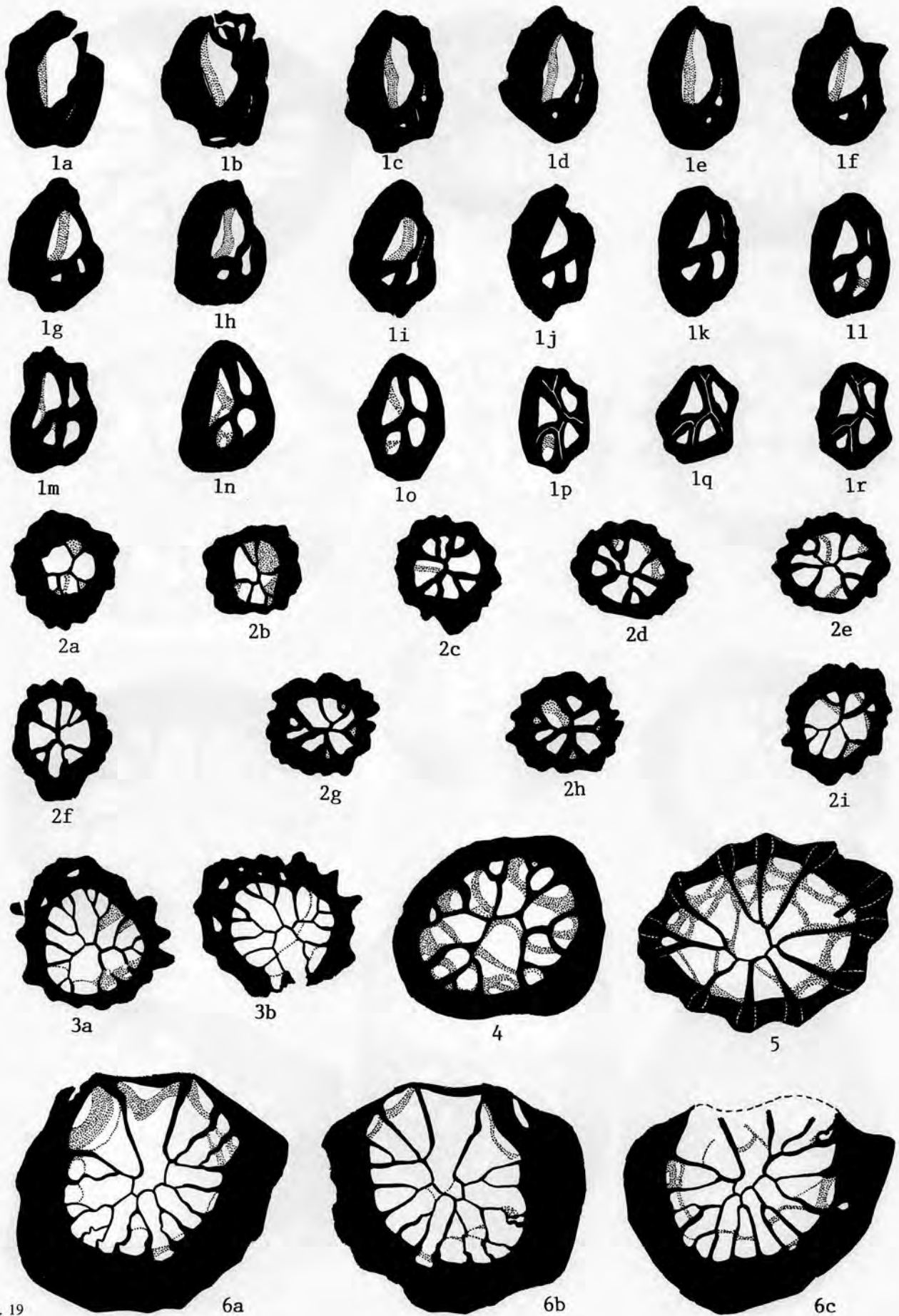


Fig. 19

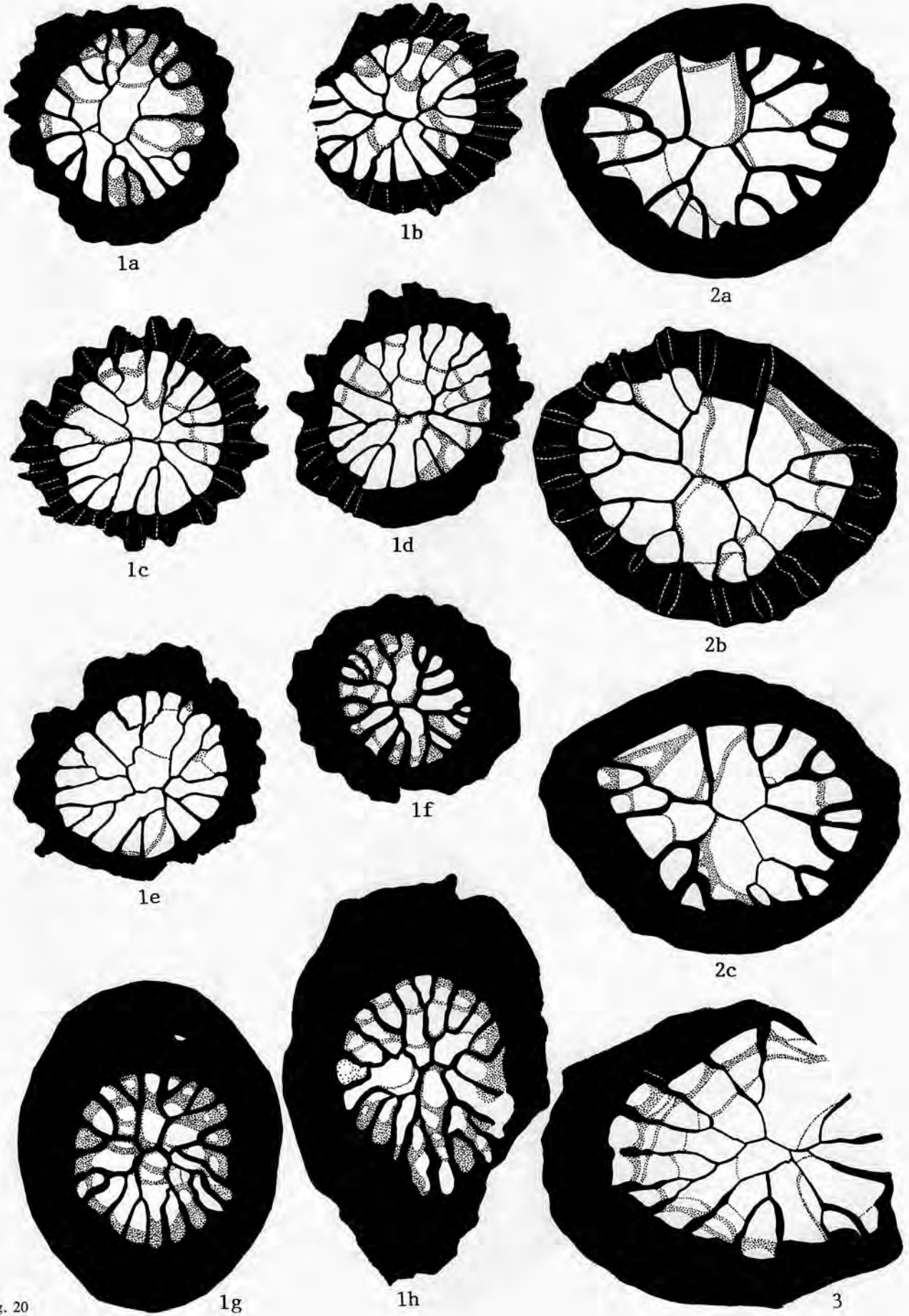


Fig. 20

1g

1h

3

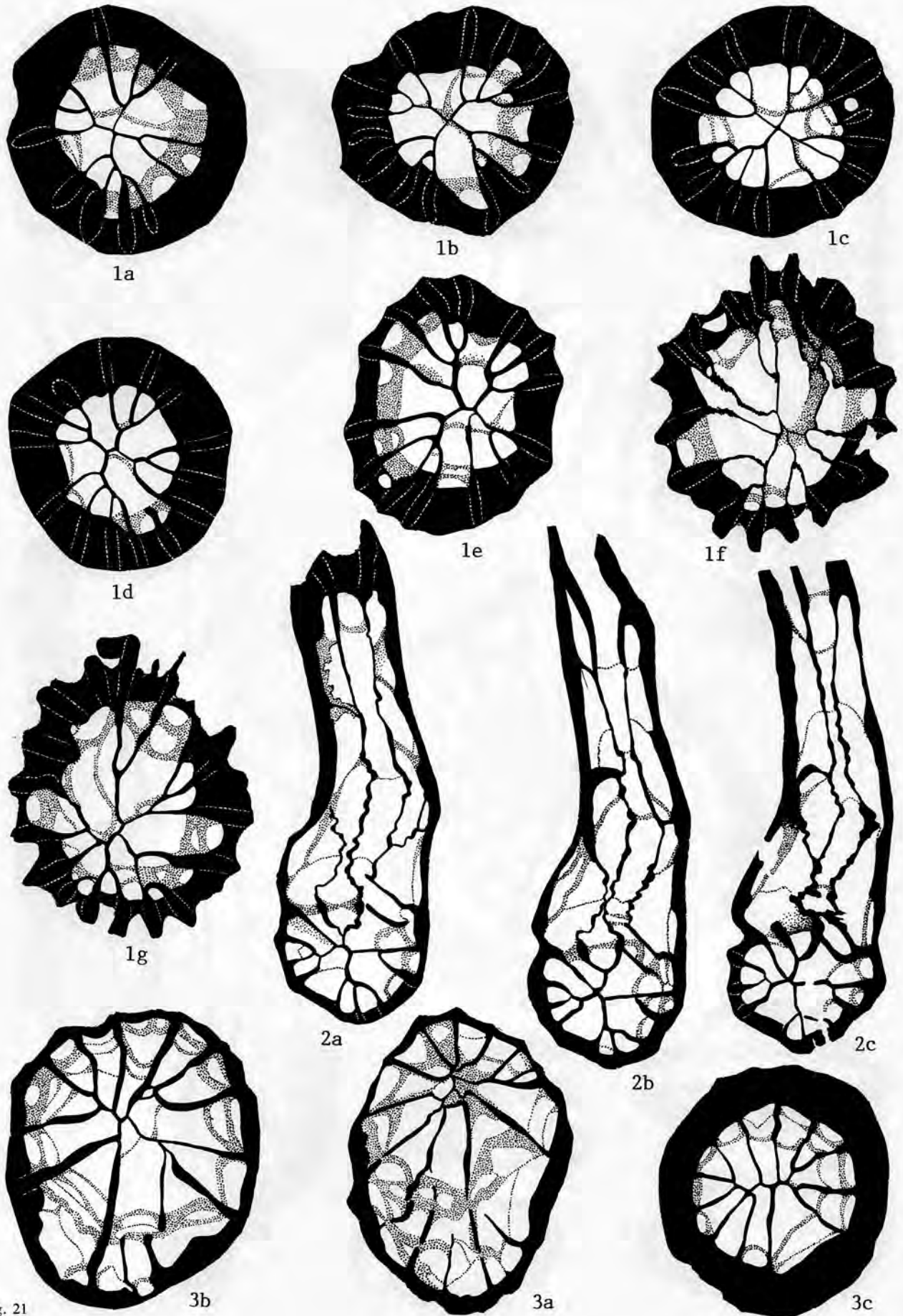


Fig. 21

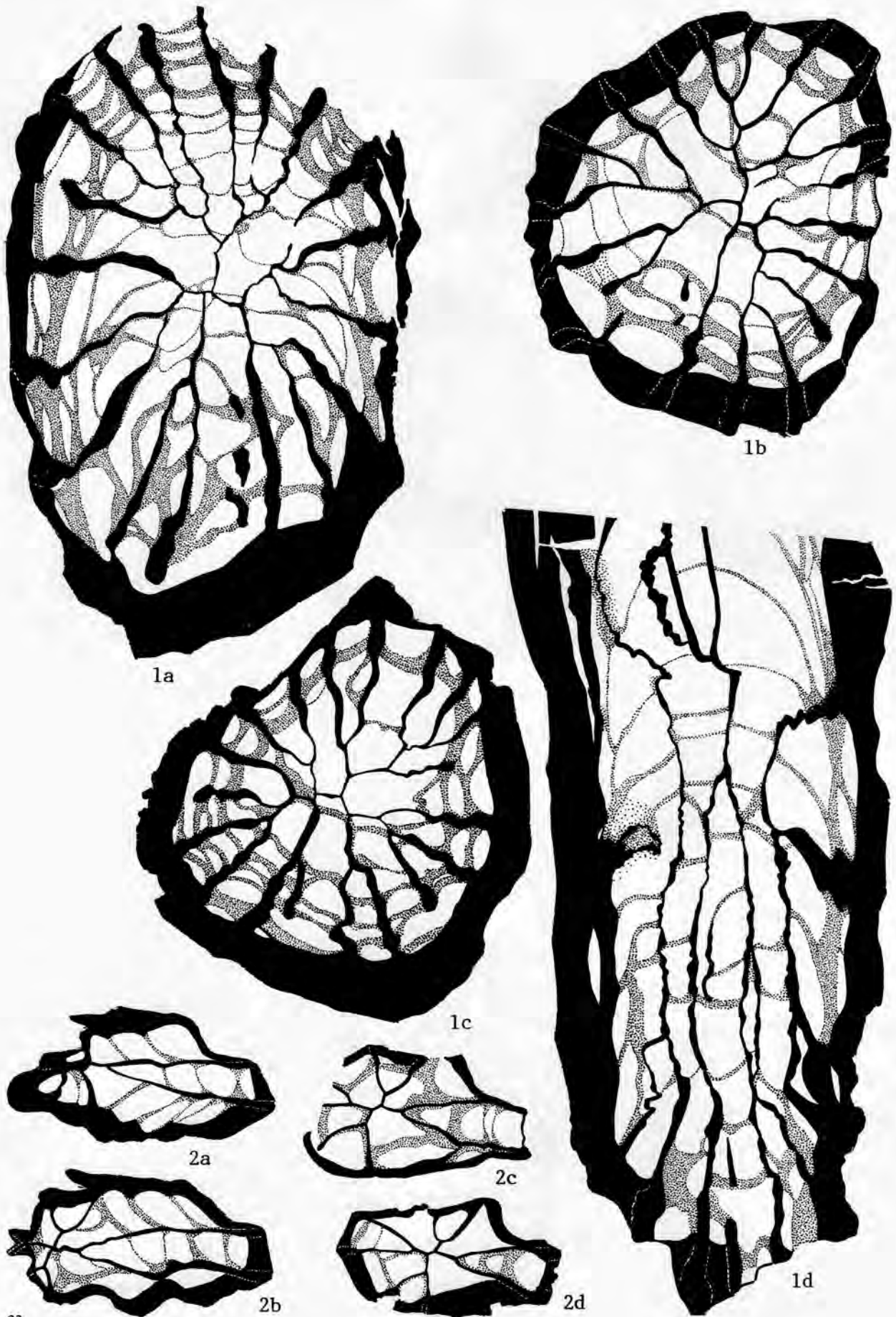
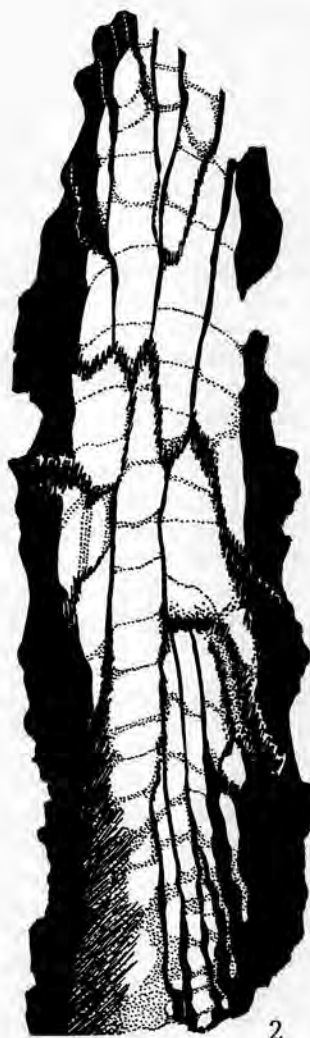


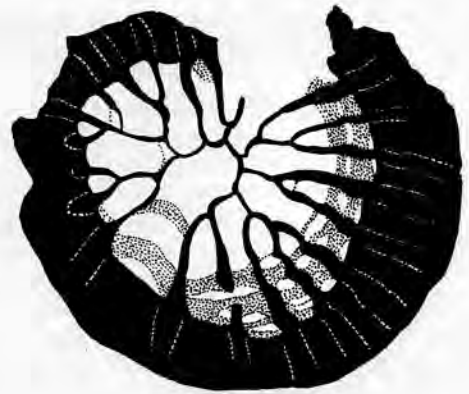
Fig. 22



1



2



3a



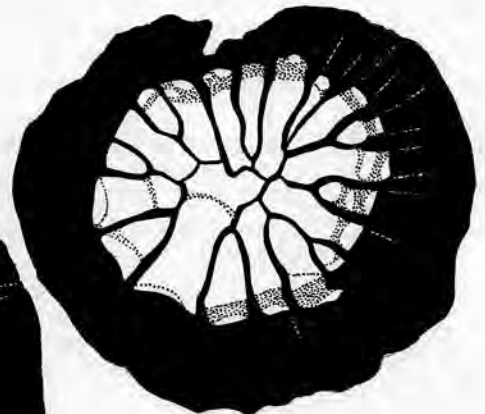
3b



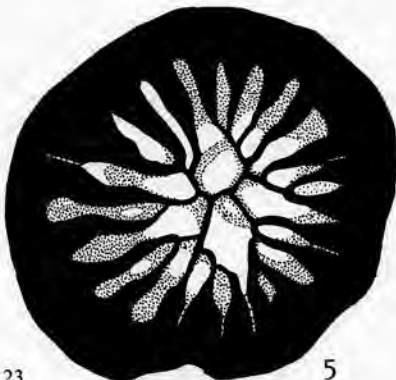
4a



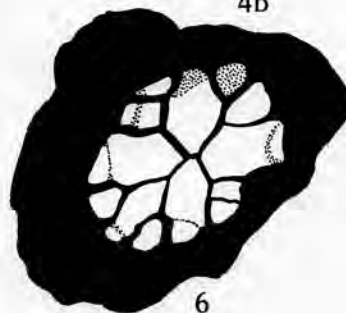
4b



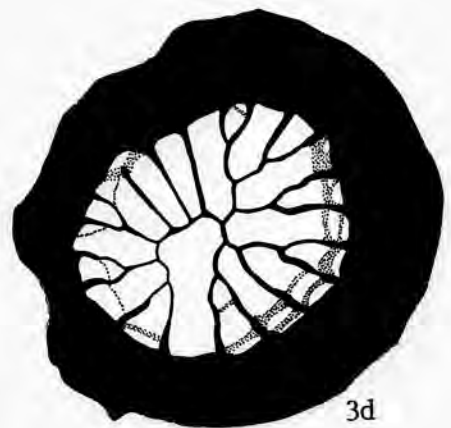
3c



5



6



3d

Fig. 23

- Fig. 18. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). Specimen Z.Pal.P.Tc-3/2026. Holotype. Transverse sections of upper portion of growth. Explanations as for fig. 17 except middle and late portions of growth of the corallite. A11 × 20.
- Fig. 19. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). All specimens from Gałęzice, Holy Cross Mountains. Upper Famennian *costatus* and *velifera* Zones. Transverse sections. 1a-1r. Specimen Z.Pal.P.Tc-3/2022a. Successive stages of very early ontogeny. Eccentric position of septa in figs. 1a-1i resulted from the obliqueness of sections. 1a-1b. Septal apparatus restricted to the oblique septum; 1c-1j. Appearance and growth of first pair of first generation of potentially creative septa; 1k-1o. Appearance and growth of second pair of first generation of potentially creative septa (upper). Note comparatively large size of ontogenetically youngest portion of the corallite resulted from development of the talon-like structure. A11 × 30. 2a-2i. Specimen Z.Pal.P.Tc-3/2096. Successive ontogenetic stages of a very small corallite. A11 × 20. 3a-3b. Specimen Z.Pal.P.Tc-3/2319. Corallite showing strong peripheral protrusions of some septa. Both × 20. 4. Specimen Z.Pal.P.Tc-3/2331. Corallite possessing septa regularly arranged and the heterotheca smooth. 5. Specimen Z.Pal.P.Tc-3/2027. Corallite possessing septa irregularly arranged and the heterotheca with septal protrusions, × 20. 6a-6c. Specimen Z.Pal.P.Tc-3/2230. Corallite possessing septa irregularly arranged and the heterotheca thick and smooth, A11 × 20.
- Fig. 20. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). Gałęzice, Holy Cross Mountains. Transverse sections. 1a-1h. Specimen Z.Pal.P.Tc-3/2073. Successive stage of growth. The heterotheca changes from moderately thick with strong septal protrusions in earlier sections to very thick and smooth in higher portion of growth. Figures 1b-1e in mirror position comparing to the remaining pictures. 2a-2c. Specimen Z.Pal.P.Tc-3/2023. Successive sections of corallite possessing strong oblique septum. 3. Specimen Z.Pal.P.Tc-3/2329. Corallite possessing one septum seemingly disconnected from the periphery. A11 × 20.
- Fig. 21. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). 1a-1g. Specimen Z.Pal.P.Tc-3/2003. Gałęzice, Holy Cross Mountains. Upper Famennian, *costatus* and *velifera* Zones. Transverse sections of successive growth stages. Note changes in size of the oblique septum and development of strong septal protrusions in the upper portion of growth. 2a-2c. Specimen Z.Pal.P.Tc-3/2301. Occurrence as above. Successive sections of strongly curved corallite showing morphology in both transverse and longitudinal section. 3a-3c. Specimen Z.Pal.P.Tc-3/2312. Zaręby, Holy Cross Mountains. Upper Famennian, Successive transverse sections Irregular morphology in ontogenetically younger sections was caused by the talon-like structure. A11 × 20.
- Fig. 22. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). Gałęzice, Holy Cross Mountains. Upper Famennian, *costatus* and *velifera* Zones. 1a-1d. Specimen Z.Pal.P.Tc-3/2397. The largest corallite present in the collection. 1a-1c. Successive (downward) transverse sections. Note seeming disintegration of some septa. 1d. longitudinal section. 2a-2d. Specimen Z.Pal.P.Tc-3/2070. Successive oblique (2a, 2b) and transverse sections of small, regular corallite. A11 × 20.
- Fig. 23. – *Mariaephyllia famenniana* (RÓŻKOWSKA, 1969). Gałęzice, Holy Cross Mountains. Upper Famennian, *costatus* and *velifera* Zones. 1. Specimen Z.Pal.P.Tc-3/2329. Oblique septum. 2. Specimen Z.Pal.P.Tc-3/2604. Oblique septum. 3. Specimen Z.Pal.P.Tc-3/2332. Transverse sections of successive growth stages of corallite possessing septa irregularly arranged and one fossa very well developed. 4a, 4b. Specimen Z.Pal.P.Tc-3/2022. Regular corallite possessing external wall extremely thick. 5. Specimen Z.Pal.P.Tc-3/2001. Transverse section of regular corallite possessing structural elements strongly thickened. 6. Specimen Z.Pal.P.Tc-3/2307. Regular corallite. A11 × 20.

among the most important. It resulted from the strength of the talon-like structures and their influence on the inner morphology of corallites. Thus, the n:d ratio, a character so important in the Rugosa, is of rather restricted taxonomic value in the Heterocorallia. Ontogenetically more advanced portions of growth of some corallites are smaller than their early portions of growth.

The holotype is a fairly large specimen starting from the beginning of its growth whereas many paratypes are much smaller. However, size of a corallite may not be accompanied by a correlative number of potentially creative septa and/or generations of septa. For instance, the largest specimen found so far (Fig. 22: 1a-1d), measuring 4.5 mm in diameter and possessing 5 generations of septa in one of its quadrants, has only 19 potentially creative septa. At the same time one of the smallest specimens in the collection (1.7 mm in diameter) possesses 16 potentially creative septa and 5 generations of septa (Fig. 19: 3a, 3b).

There is one point related to a corallite diameter that should be briefly discussed; how this character, if at all, is connected with the size of a larva in a given species. Larvae in the modern Scleractinia do not show a large variability in size and there is no reason to consider the heterocoralloid ones to have been different. Thus, size of corallites may appear as a diagnostic character of species. This character has not been applied in the present paper because almost all of the restudied corallites were derived from the same locality and from closely corresponding beds. Also, all are fragmentary corallites, offering no opportunity for complete ontogenetic studies and precise comparisons of individual stages of growth.

The arrangement of septa may be fairly regular although the number of generation in individual quadrants may differ (e.g. Figs. 19: 3a, 3b; 20: 2a-2c; 22: 2c, 2d; 23: 5, 6). Also, the arrangement of septa may vary in the course of growth of individual corallites (e.g. Fig. 21: 1a-1g) with some stages showing almost an ideal cross of septa in the corallite axis. Some corallites are so irregular that the position of their oblique septa can hardly be established (e.g. Figs. 19: 5, 6a-6c; 21: 3a-3c; 23: 3a-3d). Also, there are corallites in which only a single fossa can be distinguished (e.g. Figs. 19: 5, 6a-6c; 23: 3a-3d).

The heterotheca varies considerably both between corallites and, sometimes, in the course of growth of a given specimen. In some corallites (e.g. Pl. 1: 1, 7, 8, 10) most of septa do not reach corallite surface and the external wall is comparable to the protoheterotheca. It may happen, however, that such a smooth pseudoheterotheca-like external wall is replaced by a typical heterotheca with distinct septal protrusions (Pl. 1: 9a-9e).

Development of the talon-like structure may influence the inner morphology of corallites, width of the tabularium included. Two sections of a specimen made in the distance of approximately 1 mm illustrate this well (Fig. 23: 4a, 4b). The lower section can well be mixed with *Oligophylloides*, whereas the upper one exhibits the morphology of regularly built *Mariaephyllia* n. gen.

Morphology in the longitudinal section is simple and exhibits little variability (Figs. 21: 2a-2c; 22: 1d; 23: 1, 2). All tabulae are rather widely spaced and dome-shaped; they may be slightly uplifted next to sections of septa.

Early ontogeny. The series of peels illustrated in Fig. 19: 1a-1r have been taken from approximately 1.5 mm of growth of the corallite. Most sections, and especially those illustrated in Fig. 19: 1a-1i are oblique. Septa look therefore like being inserted from the external wall. The incidentally discovered specimen did not permit a proper orientation. The corallite is larger at the beginning of its growth than at the end of its preserved portion. This resulted from development of the talon-like structure. The oblique septum appeared in a form of a long body (Fig. 19: 1a, 1b) that soon produced first a pair of potentially creative septa of the first generation (Fig. 19: 1c). Two opposite septa of this generation appeared after some shortening of the oblique septum (Fig. 19: 1j, 1k). Arrangement of septa in some sections (e.g. Fig. 19: 1i, 1j) clearly resembles that of the three-septal stage in *Oligophylloides*. The five-septal stage (Fig. 19: 1k-1o) differs in the arrangement of septa from section to section, with some possessing the oblique septum almost totally reduced. Also, the diameter of individual sections differs a little. This depends on the width of the external wall and the talon-like structure.

In the uppermost portion of growth of the corallite available for study (Fig. 19: 1p-1r) the protoheterotheca appeared, the oblique septum got elongated, and the second generation of septa became inserted at the end of one septum of the first generation. All three sections mentioned are the smallest, being probably made already above the talon-like structure.

OCCURRENCE

Holy Cross Mountains, Gałężice (Besówka), Upper Famennian, *costatus* and *velifera* Biozones. Zaręby, goniatite zones III and IV.

Suborder Heterocorallia SCHINDEWOLF, 1941

TYPE FAMILY

Heterophyllidae DYBOWSKI, 1873.

FAMILIES ASSIGNED

Heterophyllidae DYBOWSKI, 1873; Longlinophyllidae LIN & WU, 1985; Radiciphyllidae n. fam.

EMENDED DIAGNOSIS

Heterocorallia possessing septa asymmetrically arranged; microstructure of septa trabecular; weak colonies may occur.

REMARKS

In contrast to Tetraphyllina n. subordo, morphology of the external wall forms a basis for the further subdivision of the suborder discussed. This has been motivated by three reasons:

1. Clear difference between individual structures.

2. Stratigraphical gradation in the appearance of still more advanced structures.
3. Presence of a given external wall structure in more than one taxon.

Family Heterophyllidae DYBOWSKI, 1873

TYPE GENUS

Heterophyllia MCCOY, 1849.

SYNONYM

Crepidophyllidae YU, LIN, SHE, HUANG & YU, 1983.

GENERA ASSIGNED

Pentaphyllia (?) YU, LIN, HUANG & TSAI, 1978; *Hexaphyllia* (?) STUCKENBERG, 1904; *Heterophyllia* MCCOY, 1849; *Vassiljukaephyllia* n. gen.

EMENDED DIAGNOSIS

Solitary Heterocorallia; peripheral and axial parts of septa solid, tending to disintegrate in the phylogenetically most advanced taxa; external wall: heterotheca tending towards reticulotheca.

REMARKS

YU *et al.* (1983) introduced a new family Crepidophyllidae based on the genus *Crepidophyllia* YU *et al.*, 1978. Both family and genus are not acknowledged in the present paper. This is conditioned first of all by the, at least theoretical, impossibility of development of true septal aulos in the Dividocorallia n. subclass. The half-aulos, i.e. the structure surrounded partly by septa and partly by tabulae does not have a taxonomic value on the generic level. Besides, the temporary arrangement of axial parts of septa in the Dividocorallia n. subclass frequently resembles the half-aulos. This may appear in solitary as well as in colonial species. In colonies the corallites having the half-aulos developed may be located next to the regular specimens. Also, the true aulos has not been documented in the longitudinal section of *Crepidophyllia*. The seeming aulos illustrated by YU *et al.*, (1983, fig. 387b, c) resulted from the cross section of the tabula that supplemented the half-aulos. The diagnostic value of such a character is practically nil.

Morphology of the external wall forms the basic difference between Heterophyllidae and the remaining two families of the suborder. It is not uniform, however, and exposes such differences as development versus lack of peripheral longitudinal trenches, or disintegration versus firmness of peripheral parts of septa. Permanently united inner ends of septa distinguish this family from individual representatives of the remaining two families.

Genera (?) *Pentaphyllia* and *Hexaphyllia* were included in this family with the question mark because their independent taxonomic status is uncertain. This has already been discussed elsewhere in the present paper.

The species problem of genera included in the Heterophyllidae is omitted from this discussion. It should only

be pointed out that diagnostic criteria accepted by authors for *Pentaphyllia* (?) and *Hexaphyllia* (?) as well as for *Heterophyllia* must be reconsidered. In the case of the first two genera (?) such characters as the diameter of corallites, more or less convex interseptal portions of the external wall, more or less exposed peripheral portions of septa, presence or absence of spines, and more or less densely packed tabulae, may well have either genetic or somatic, environmental origin. Distinction between these two options has never been analysed in terms of intraspecific variability, advanced ontogenetic studies or palaeogeographical distribution. Thus, the Recent level of knowledge makes suggestions based on the literature date premature.

In the case of *Heterophyllia* the problem is even more complex. All species (?) of this genus, like those of the formerly discussed genera (?) have been established on the basis of fragmentary specimens. As a result nobody knows whether small corallites possessing numerous septa are early ontogenetic stages of large corallites or whether they belong to a different species. Presence or absence of "Balken", differentiation in number and arrangement of septa in quadrants, variable density and composition of the tabularium, inconstant thickness of structural elements, are characters making a complete analysis of the latter genus impossible.

Genus *Heterophyllia* MCCOY 1849

TYPE SPECIES

H. grandis MCCOY, 1849.

SYNONYMS

Heterophylloides SCHINDEWOLF, 1941 (subgenus)

Crepidophyllia YU *et al.*, 1978

? *Hexaphyllia* STUCKENBERG, 1904 (perhaps partim)

? *Pentaphyllia* YU *et al.*, 1978 (perhaps partim)

non *Heterophyllia* VASSILJUK, 1964; RÓZKOWSKA, 1969; IGO & KOBAYASHI, 1980; WEYER, 1989.

SPECIES ASSIGNED

Not established in this paper.

DIAGNOSIS

Heterophyllidae having more than six potentially creative septa at periphery; peripheral longitudinal trenches may occur.

REMARKS

Most problems concerning this genus are discussed with remarks on the family. Uncertain taxonomic status of the genera (?) *Pentaphyllia* and *Hexaphyllia* discussed in the general part of this paper, makes this section of the paper inconsistent. The genera mentioned are, in part and with a question mark, placed in synonymy with *Heterophyllia*, whereas the number of potentially creative septa of these genera was excluded from the diagnosis of *Hetero-*

phyllia. At present, such an ambiguous solution seems to be the only one possible. Two subgenera of *Heterophyllia* were introduced by SCHINDEWOLF (1941); they have been very generally accepted since. In some handbooks they have even received rank of independent genera. Neither of those approaches are accepted in the present paper. POTY (1978, 1981) and LIN & WU (1985) were already of the same opinion.

Genus *Vassiljukaephyllia* n. gen.

TYPE SPECIES

Heterophyllia fragmentoseptata VASSILJUK, 1964.

SYNONYM

Heterophyllia VASSILJUK, 1964; non MCCOY, 1849.

DERIVATION OF THE NAME

In honour of Dr. N.P. VASSILJUK from Donetsk University, USSR.

DIAGNOSIS

Heterophyllidae possessing inner ends of septa often disconnected in maturity; some septa and tabulae form incipient reticulotheca; solid wall present at periphery.

REMARKS

Characters mentioned in the diagnosis and especially morphology of the peripheral portion of a corallite can be considered intermediate between *Heterophyllia* and *Longlinophyllia*. The ambiguous taxonomic position of this genus is discussed in more detail in the phylogeny chapter of this paper.

Family Longlinophyllidae LIN & WU, 1985

TYPE GENUS

Longlinophyllia LIN & WU, 1985.

GENERA ASSIGNED

Monotypic.

EMENDED DIAGNOSIS

Heterocorallia with peripheral septal parts divided in septal rods; external wall: reticulotheca.

REMARKS

The distinction of *Longlinophyllia* at the family level has been based solely on the morphology of the external portion of the corallites. The high taxonomic evaluation of this character is discussed elsewhere in this paper. *Vassiljukaephyllia fragmentoseptata* is so far the only species described that is comparable to the Chinese species of *Longlinophyllia*. The most striking character which they have in common is the loosely constructed peripheral portions of the corallites. Such a similarity may either lead to placing the Donetsk Basin species in

Longlinophyllia or to the introduction of a new genus. The latter option has been selected here because of the following characteristics of *Vassiljukaephyllia* n. gen. but absent in *Longlinophyllia*:

1. Incipient morphology and inconstant character of the reticulotheca.
2. Occurrence of a solid external wall at the periphery.
3. Commonly disconnected inner ends of septa.
4. Higher position in the stratigraphic column, contradicting with a less advanced morphology.
5. Geographical position west of the occurrence of *Longlinophyllia*, i.e. excluding the possibility of migration of a more primitive genus towards the area of existence of a more advanced genus. All these facts resulted in considering *Vassiljukaephyllia* n. gen. as the phylogenetically most advanced member of the Heterophyllidae, rather than as a member of the Longlinophyllidae.

Genus *Longlinophyllia* LIN & WU, 1985

TYPE SPECIES

L. ditabulata LIN & WU, 1985.

SPECIES ASSIGNED

Monotypic.

EMENDED DIAGNOSIS

Longlinophyllidae with inner ends of septa connected; reticulotheca well developed up to periphery.

REMARKS

As for the family.

Family Radiciphyllidae n. fam.

TYPE GENUS

Radiciphyllia SUGIYAMA, 1984.

GENERA ASSIGNED

Monotypic.

DIAGNOSIS

Heterocorallia possessing radicitheca; microstructure of primary septa and parts of radicitheca trabecular; weak colonies may occur.

REMARKS

Numerous and almost symmetrically arranged septa in mature *Radiciphyllia* focus on *Oligophylloides* or *Mariaephyllia* n. gen. as its potential ancestor. Such a conclusion contradicts with hexaphylloid and asymmetrical arrangement of septa in earlier growth stages of that genus, which is considered conclusive for its phylogenetic relationship. Substantial re-arrangement in morphology of the external wall and peripheral portions of septa resulted perhaps from the enlargement of trabeculae and

from their ability to disperse, is achieved in *Radiciphyllia*. Such morphological change was possible only at an early stage of individual growth of the ancestral form, i.e. before lamellar peripheral sheets of septa appeared. Early growth of *Heterophyllia* or primitive species of *Hexaphyllia* should therefore be accepted as a potential ancestor of *Radiciphyllia*. Ability to form weak colonies and talon-like structures in both *Oligophylloides* and *Radiciphyllia* was accepted by SUGIYAMA (1984: 33) conclusive for placing these two genera in the same informal group (subfamily?). Such a position contradicts with differences in ontogeny and microstructure of septa, i.e. features which are taxonomically much more important. SUGIYAMA's (1984) point of view is therefore not accepted in this paper.

There seems to occur a considerable distinction between *Radiciphyllia akiyoshiense* SUGIYAMA, 1964 and "*Heterophyllia*" ? *tokyoensis* IGO & KOBAYASHI, 1980 in morphology and, perhaps in increase in septa. Further comments on this peculiar group of corals are not proposed because the original material must be restudied first. The literature data indicate that specimens described so far and included by SUGIYAMA (1984) in *Radiciphyllia* may belong to two distinct genera.

Order Calyxcorallia n. ordo

TYPE FAMILY

Stylidophyllidae n. fam.

FAMILY CONTENT

Stylidophyllidae n. fam., Pseudopetraiidae n. fam.

DIAGNOSIS

Dividocorallia possessing normal calices.

REMARKS

Corals included in this order look so distinct from the Heterocorallia and so close to the Rugosa that their taxonomic status has not been recognized for sixty years of studies, i.e. since the paper by CHI (1931) who described peculiar specimens from the Weiningian of SW China and called them *Stylostrotion intermedium*. YU (1933) described similar corals from the Tournaisian and Viséan of the same region, calling them *Diphyphyllum* ? *vesiculosum*. He did not refer his findings to those of CHI (1931), but recognized their distinction from typical diphyphylla.

FOMICHEV (1939, 1953) introduced a subgenus *Diphyphyllum* (*Donophyllum*) for the Bashkirian colonial corals from the Donetz Basin. FOMICHEV's generic name has been used several times for corals exhibiting a heterocoralloid arrangement of septa accompanied by such rugose coral characteristics as calice and dissepimentarium (e.g. WANG, 1978, KHOA, 1984; WU & ZHAO, 1989). Further records of calyxcoralloid corals, i.e. by IVANOVSKY (1967) and POTY (1981) are discussed later on. WU *et al.*, (1981) proposed a new genus *Dematophyllum* for

corals similar to CHI's (1931), YU's (1933) and FOMICHEV's (1939) specimens, but derived from deposits attributed to the Strunian. In May 1988 Dr. N.P. VASSILJUK from Donetz University, USSR kindly informed me about an abundant occurrence in Central Asia of corals similar to the Chinese *Dematophyllum*. Their morphology and their range (Tournaisian – Lower Viséan) are comparable to those pointed out by YU (1933) for his *Diphyphyllum*. In all published records known to me these colonial corals were included in the family Lithostrotioniidae. Indeed, several of their characteristics can be interpreted as typical for that rugose coral family:

- the fasciculate form of growth;
- the occurrence of minor septa and of a dissepimentarium;
- the shape of the tabularium.

None of the earlier authors drew attention to the arrangement and insertion of major septa – a key character for the identification of these corals. The union of major septa in a corallite axis was interpreted as a weak columnella, and the heterocoralloid arrangement of septa as bunches. The more or less frequent withdrawal of major septa from a corallite axis was considered sufficient for calling such specimens *Diphyphyllum*. The morphogenetic interpretation of septal systems proposed in this paper permits the recognition of the relationship of these corals with the Heterocorallia. *Pseudopetraia* SOSHKINA, 1951 from the Emsian of the Ural Mts. is the oldest known taxon of the Calyxcorallia n. ordo. It has been introduced as a rugose coral genus and included in the Lindstroemiidae POCTA, 1902. Only HILL (1981) correctly recognized *Pseudopetraia* as a heterocoral, i.e. a dividocoral in the herein accepted meaning. WEYER (1989) did not accept Hill's (1981) interpretation, but her opinion is fully supported by the present author's restudy of the type material of *Pseudopetraia*.

Family Pseudopetraiidae n. fam.

TYPE GENUS

Pseudopetraia SOSHKINA, 1951.

GENERA ASSIGNED

Monotypic.

DIAGNOSIS

Solitary, nondissepimentate Calyxcorallia possessing well developed major and minor septa; microstructure of septa is fine trabecular.

REMARKS

A brief restudy of the type thin sections of *Pseudopetraia devonica* SOSHKINA, 1951 fully confirmed a relationship of this species and genus with the Heterocorallia (*sensu lato*) as postulated by HILL (1981). Development of deep calices focuses on the Calyxcorallia n. ordo. The necessity of rising the taxonomic rank of *Pseudopetraia* to the family level is confirmed by its solitary form of growth

and lack of dissepiments. Not all specimens illustrated by SOSHKINA (1951, 1952) under the name *Pseudopetraia devonica* belong to this species, genus and the Calyxcorallia n. ordo. Some of them, and perhaps all specimens originally included in *P. geniculata* SOSHKINA, 1951, are rugose corals. Thus, thin sections of only three specimens, re-illustrated in this paper, were recognized as dividocorals. Also, the non-illustrated and non-sectioned "paratypes" of *P. devonica* must be re-investigated before considering them dividocorals. Stony material of SOSHKINA's (1951) collection was not available for the study.

Genus *Pseudopetraia* SOSHKINA, 1951

TYPE SPECIES

P. devonica SOSHKINA, 1951.

SPECIES ASSIGNED

Monotypic.

DIAGNOSIS AND REMARKS

As for the family.

Pseudopetraia devonica SOSHKINA, 1951

(Pl. 1: 12-14, Figs. 24: 1, 2; 25)

*e.p. *Pseudopetraia devonica* SOSHKINA, 1951, pp. 24-26, Pl. 2, figs. 1-3 only.

e.p. *Pseudopetraia devonica* SOSHKINA. SOSHKINA, 1952, p. 65, Pl. 1, fig. 2, only specimens selected above.

Pseudopetraia devonica SOSHKINA. SOSHKINA, 1960, text-fig. 4.

Pseudopetraia devonica SOSHKINA. SOSHKINA, DOBROLYUBOVA & KABAKOVICH, 1962, p. 321, Pl. 12: 2a, 2b.

Pseudopetraia devonica SOSHKINA. HILL, 1981, p. F425, fig. 280a-c.

non *Pseudopetraia devonica* SOSHKINA. SPASSKYI, 1960, pp. 22, 23, Pls. 1: 1, 2; 26: 1-3.

non *Pseudopetraia devonica* SOSHKINA. RÓZKOWSKA, 1979, p. 16, Pl. 1: 7a, b.

MATERIAL

Only thin sections were available for study. The holotype is represented by five thin sections, of which the longitudinal and the ontogenetically youngest and oldest ones were originally illustrated by SOSHKINA (1951, Pl. 2: 2a-c). All four transverse sections are in the ontogenetical sequence. It remains unknown, however, from which part of the corallite the longitudinal section has been made. Specimens accepted in this paper as paratypes were sectioned as follows: Specimen 6651 – one thin section made either from younger part of the corallite, or from the ontogenetically immature specimen. Specimen 6688 – three transverse thin sections; the middle one

has not been illustrated by SOSHKINA (1951). The holotype and two paratypes provided the only basis for the discussion that follows. Judging from the longitudinal thin section of the holotype, corallites of *P. devonica* were elongated and, perhaps, slightly curved, resembling solitary, nondissepimentate Rugosa.

DIAGNOSIS

Pseudopetraia possessing oblique septum short, variable, temporarily replaced by directly connected inner ends of septa of first generation; external wall thick; tabulae mostly complete, domed.

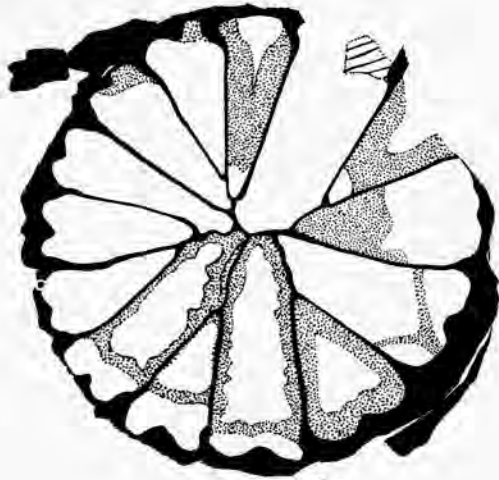
DESCRIPTION OF THE HOLOTYPE

Major septa are mostly straight and thin. Dispersal of stereoplasmic thickenings is random and striking. They are generally observed only on one side of all structural elements surrounding a given septal loculum (Pl. 1: 12a-12d; Fig. 24: 1a-1d). Regular arrangement of calcitic fibres within these thickenings contrasts with coarse secondary cement covering structural elements in other loculi, speaking in favour of the biological origin of the former. This question has not been finally solved. Peripheral ends of major septa are covered with stereoplasmic sheets that form thin layers, continued from periphery of a given septum down to the external wall and then upward to cover the adjacent minor septum, if present.

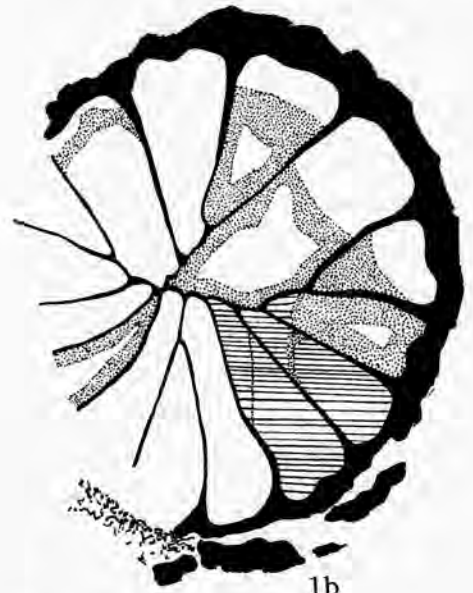
Increase in the major septa is due to the peripheral dichotomic division, resembling other dividocorals. However, several deviations and irregularities of this process have been established. The oblique septum is distinguishable only in three ontogenetically younger thin sections. It forms a short and indistinct blade (Fig. 24: 1a-1c). In the ontogenetically most advanced stage (Fig. 24: 1d) the sheet of stereoplasm (?) that stuffed two loculi located on the opposite sides of the corallite became united axially. Three options can be proposed to explain this phenomenon:

1. The oblique septum has been naturally (biologically) reduced and replaced by the stereoplasm.
2. The oblique septum has been mechanically destroyed and the stereoplasm filled in the lacking part of the skeleton.
3. The oblique septum has been diagenetically altered and the infilling is inorganic. None of these options can be fully proven.

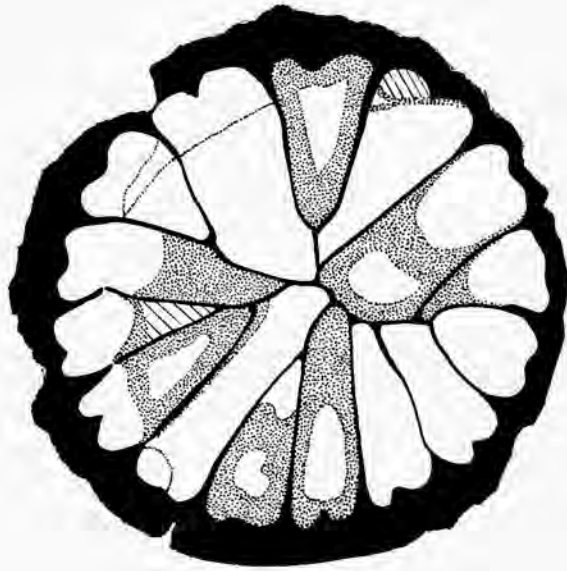
The major septa expose large variability in their mutual relationship, when individual quadrants in the course of growth of the corallite are compared. These changes are fully illustrated (Pl. 1: 12a-12d; Fig. 24: 1a-1d) and can be omitted from the further discussion. It seems only right to point out that the variable mutual relationship between the creative and potentially creative septa is typical for the holotype of *P. devonica* and, consequently, for the species. Minor septa are present in all four thin sections. Their development is individualized in particular loculi, but generally more advanced in the ontogenetically oldest portion of growth (Fig. 24: 1d). Tabulae are rare in cross sections, which is in some disagreement with



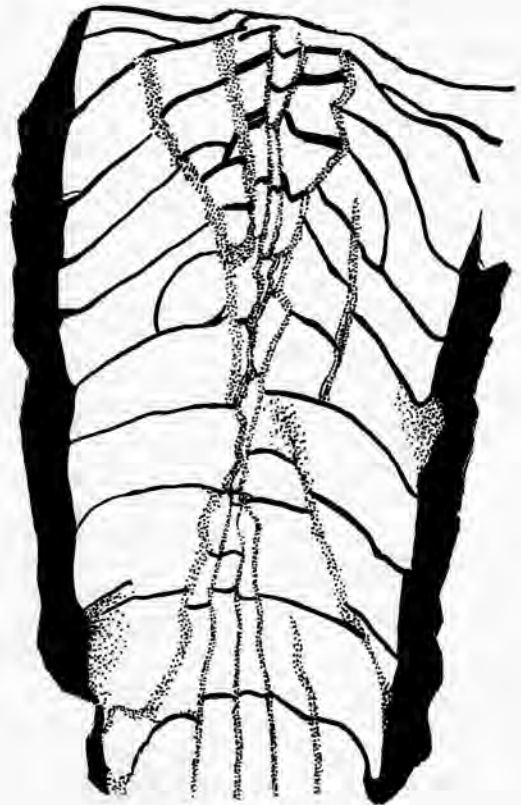
1a



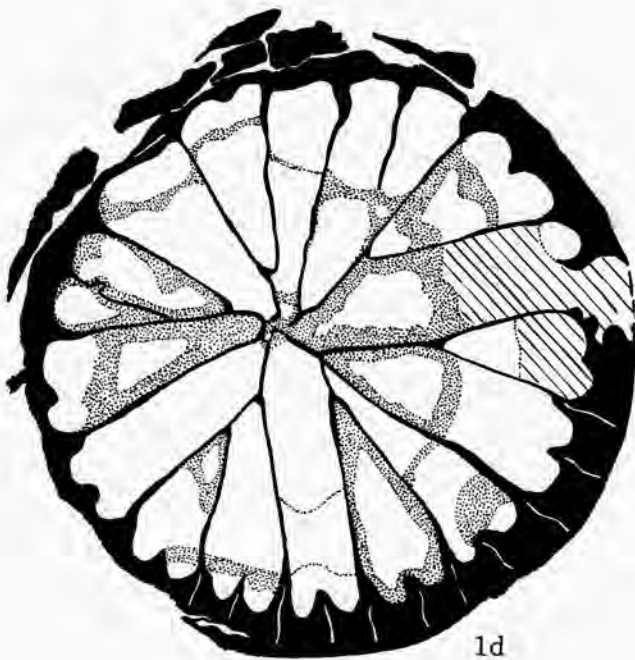
1b



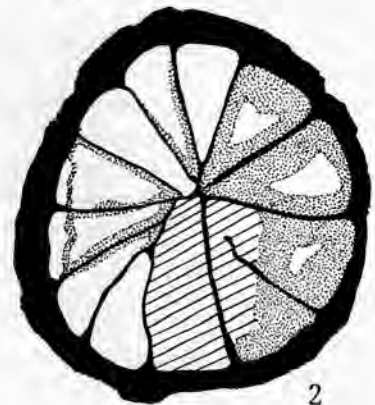
1c



1e



1d



2

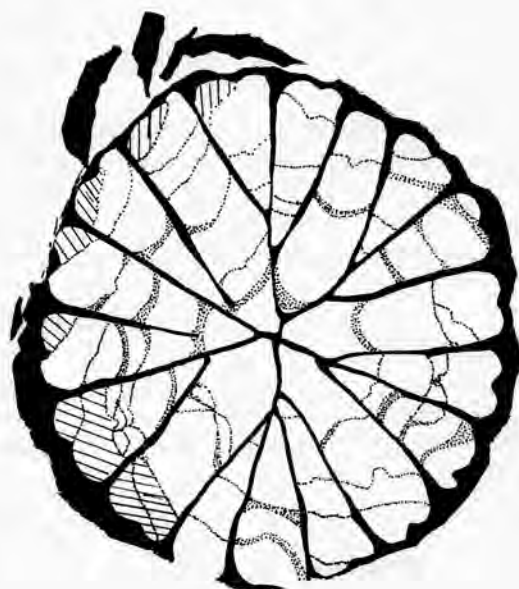
the morphology exposed by the slightly oblique longitudinal section (Pl. 1: 12e; Fig. 24: 1e). In the axially sectioned, middle part of the corallite, tabulae are complete, leaning at approximately 50° from the corallite wall to its axis. Rare tabellae may occur.

Complete intraspecific variability cannot be established because only two corallites accepted as paratypes, were available for study. One of them (Pl. 1: 13; Fig. 24: 2), illustrated by SOSHKINA (1951, p. 2: 1) represents juvenile portion of growth. Minor septa are not yet developed, dividocoralloid arrangement of the major septa is difficult to establish due to diagenetic alterations. Differences in volume and septal content of individual quadrants is partly secondary.

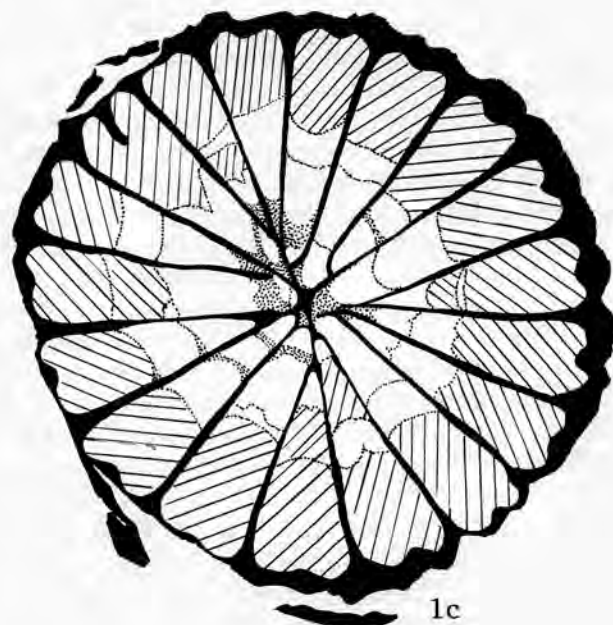
The second paratype (Pl. 1: 14a-14c; Fig. 25: 1a-1c) is represented by three thin sections, two of which were illustrated by SOSHKINA (1951, pl. 2: 3a, b). Individual quadrants differ in the number of septa, but this pattern is constant for all three sections. Representing different growth stages, the calice included, these three sections do not show any increase in septa. Like in the holotype, the mutual relationships of individual septa within quadrants differ (compare illustrations cited above). The oblique septum is clearly distinguishable only in the ontogenetically youngest thin section (Pl. 1: 14a, Fig. 25: 1a). It disappeared in the next thin section where four septa of the first generation meet axially. Stereoplastic infillings in the third section (Pl. 1: 14c; Fig. 25: 1c) camouflage a slight disconnection of some septa in the corallite axis. Major septa are most regularly arranged and fossae are best developed in the middle portion of growth of the corallite (Pl. 1: 14b; Fig. 25: 1b). Only two of the latter are easily correlative with the younger portion of growth and hardly with the uppermost one. Minor septa appear late in the ontogeny, being absent from the ontogenetically youngest section. The number of tabulae or tabellae must have been fairly large, and their spacing rather dense. This is indicated by large number of their sections in individual loculi. The thin section made partly through the calice (Pl. 1: 14c; Fig. 25: 1c) confirms the convex shape of the tabularium, but it is impossible to reconstruct shape and position of tabulae.



1a



1b



1c

△ Fig. 24. — *Pseudopetraia devonica* SOSHKINA, 1951. Prokrovskoe Village, Egorshinskiy Raion, Eastern slope of Middel Ural Mountains. Upper Emsian. 1a-1e. Specimen PIN 6661. Holotype. 1a-1d. Transverse sections of successive growth stages. 1e. Longitudinal section. 2. Specimen PIN 6651. Occurrence as above. Transverse section. A11 × 10.

Fig. 25. — *Pseudopetraia devonica* SOSHKINA, 1951. Occurrence as above. Specimen PIN 6688. Transverse sections of successive growth stages. Loculi filled in with strange fabric are dashed, × 10.

To sum up the morphological differences and similarities between all three specimens discussed, their inconstant morphology in the course of ontogeny must be pointed out on the first place. This variability does not concern all characters. For instance, the development of the minor septa, although reaching different level in individual corallites, exhibit at the same time a similar, increasing sequence. Also, the external wall is thick and the tabularium is convex in all specimens. The pattern of the major septa and their mutual relationship within and between the quadrants display the largest variability. This does not concern characters virtual for the subclass, such as increase in septa, which is realized by the peripheral dichotomic division, and their succession from the oblique septum down, but involves only mutual relationships of individual septa. Variability discussed is temporarily explained as connected to the early evolutionary step of development of the taxon.

OCCURRENCE

Pokrovskoe Village, Egorshinskiy Raion, Eastern slope of Middle Ural Mountains, Upper Emsian.

Family Stylostrotionidae n. fam.

TYPE GENUS

Stylostrotion CHI, 1931.

GENERA INCLUDED

Stylostrotion CHI, 1931; *Polygonaria* FAN in WANG, 1978; *Sudetiphyllia* n. gen.

DIAGNOSIS

Colonial Calyxcorallia possessing dissepimentarium well developed; microstructure of septa trabecular.

REMARKS

Distinction between Pseudopetraiidae n. fam. and Stylostrotionidae n. fam. is based mainly on the growth form (solitary versus colonial), on the absence of dissepiments in *Pseudopetraia* and on the large time span in the occurrence between the solitary, nondissepimentate member of the order (Emsian) and its colonial and dissepimentate relatives (Strunian). Morphological changes taking place during that time resulting in fixing fairly distant genotypes. By analogy to the Rugosa this large genetic span is considered characteristic for the family. Except for the colonial genera, the taxonomic position of which is more or less clear, there occurs a peculiar ? *Lithostrotion* cf. *tareense* PICKETT, 1966 described by PERRET & SEMENOFF-TIAN-CHANSKY (1971) from the Upper Viséan of Pyrenees. It most probably belongs to the Dividocorallia n. subclass, but several characteristics of it, seen particularly in the longitudinal section, are indicative for the calice lacking forms. Its fasciculate form of growth, pointed out in the original diagnosis, was confirmed by specimens collected by the present author from the type locality. This character as well as

the disconnection of septa in a corallite axis, and the trabecular microstructure of septa (e.g. PERRET & SEMENOFF-TIAN-CHANSKY, 1971, pl. 1: 1b) are adequate for considering this taxon a new genus of Heterocorallia. However, a formal generic name is not proposed because more careful and complete study should precede such a proposal.

Genus *Stylostrotion* CHI, 1931

TYPE SPECIES

S. intermedium CHI, 1931.

SYNONYMS

Diphyphyllum YU, 1933; WU & ZHAO, 1981, non LONSDALE, 1845
e.p. *Donophyllum* FOMICHEV, 1939
Dematophyllum WU & JIANG, 1981
Cionodendron IVANOVSKIY, 1967, non BENSON & SMITH, 1923

SPECIES ASSIGNED

Diphyphyllum ? *vesiculosum* YU, 1933; *Diphyphyllum antiquatum* WU & ZHAO, 1981; *Donophyllum reticulatum* FOMICHEV, 1953; *Donophyllum intermedium* FOMICHEV, 1953; *Donophyllum irregulare* WANG, 1978; *Donophyllum minor* ZUO, 1982; *Donophyllum grossum* KHOA, 1984; *Donophyllum guizhouense* WU & ZHAO, 1989; *Cionodendron* ? *primitivum* IVANOVSKIY, 1967; *Dematophyllum minor* WU & JIANG, 1981; *Dematophyllum hunanense* WU & JIANG, 1981; *Stylostrotion sudeticum* n. sp.

Notice: revision and detailed morphogenetic analysis of most species listed above have not been made. Some of them may well appear synonyms.

DIAGNOSIS

Stylostrotionidae possessing inconstant number of major septa in quadrants; simultaneous insertion of first minor septa precedes appearance of dissepiments.

REMARKS

The original description and illustrations of the type species of *Stylostrotion* CHI, 1931 (pp. 22, 23; fig. 6a, b; pl. 0: 1a-1f) are laconic and inadequate for the complete definition of the species and genus. This may have been one of the main reasons for either the neglecting of this genus or putting it in synonymy with *Lithostrotion* FLEMING, 1828 or *Siphonodendron* MCCOY, 1849. Indeed, some corallites illustrated by CHI (1931), e.g. fig. 1: 1a (right), 1c, 1e, can be confused either with *Siphonodendron* or with long-septal *Diphyphyllum*. On the other hand none of the specimens illustrated by CHI (1931), including those mentioned above, exhibits the typical rugosan arrangement of septa, whereas some (e.g. pl. 1: 1a, left, 1d) are almost typically dividocoralloid. This and the subsequent description of similar specimens (YU, 1933; FOMICHEV, 1939, 1953; WANG,

1978; WU *et al.*, 1981 and others) allow to consider *Stylostrotion* a member of Calyxcorallia n. ordo. Accepting this one has to accept its priority. The list of synonyms proposed above is temporary. It reflects the Recent level of knowledge of those taxa rather than their true relationship. Vesiculate or diphyphylloidal Strunian species from SW China may well appear distinct on the generic level from the Viséan or Bashkirian taxa with continuous, axially united septa. Also, *Donophyllum diphyphylloides* FOMICHEV, 1939 chosen as type species of *Donophyllum* by LANG, SMITH & THOMAS (1940) may either be a member of Stylostrotionidae n. fam. so far advanced in its development as to completely having lost its basic dividocoralloid character, i.e. peripheral dichotomic division of septa, or it belongs to the Rugosa. The restudy of its holotype made for the purpose of this paper by means of serial thin sections does not bring any solution. None of the corallites from the top and bottom section (Pl. 9: 2a, 2b), distant from each other for 13 mm, as well as from the four intermediate sections shows dividocoralloid division of septa. However, very young corallites were absent from the part of the colony restudied, leaving some hope for finding typically dividocoralloid specimen of this species. Distinction of genus *Donophyllum* would then be possible. ? *Cionodendron primitivum* IVANOVSKIY, 1967 from the Lower Carboniferous, perhaps Viséan, of Gornyi Altay, almost certainly belongs to Calyxcorallia n. ordo. Unfortunately, the original description and illustrations are inadequate for recognition of all generic features of that specimen, which may belong to a new genus. *Dematophyllum* WU & JIANG, 1981 exhibits large variety in characters that are considered diagnostic in the Rugosa on the generic level. Axially united versus shortened septa and interseptal versus lonsdaleoid dissepiments should be considered first. Two of the species included in this paper in *Stylostrotion* were originally described as *Diphyphyllum* LONSDALE, 1845. In the case of ? *Diphyphyllum vesiculosum* YU, 1933 there is no morphological support for such an identification. All specimens described and illustrated by that author are long-septal corallites, exhibiting typically dividocoralloid systems of septa. Also, none of the longitudinal sections illustrated by YU (1933, pls. 14: 5d; 15: 5b) displays a diphyphylloid character. *Diphyphyllum antiquatum* WU & ZHAO, 1981 is more typical diphyphylloid, especially when its longitudinal section is taken into account. Occurrence of lonsdaleoid dissepiments absent from *Diphyphyllum* can be ignored, if one wants to widen the diagnosis of that genus. This cannot be the case as far as the arrangement of septa is concerned. Three specimens illustrated by WU & ZHAO (1981, pls. 2: 24, 25; 4: 7-10) show all main steps from the typically dividocoralloid arrangement in the colony illustrated in pl. 4: 9 to the diphyphylloid colony illustrated in the same plate, fig. 7. Fortunately, in the latter colony there is a corallite (lowermost left), sectioned just above the surface of a tabula, exposing remnants of the dividocoralloid arrangement of septa. Strongly diphyphylloid colonies of *Dematophyllum* as well as *Donophyllum*

diphyphylloides may appear members of the same genus or parallel morphotypes belonging to separate genera. Interseptal versus lonsdaleoid dissepiments may be accepted a criterion of generic value. Indeed, there are corallites (e.g. YU, 1933 and in this paper) that developed almost exclusively the interseptal dissepiments. Lonsdaleoid ones, if present, occur only in the most elongated parts of corallites, tending to attach to their neighbours. Contrary to this, the specimens illustrated by WU & JIANG (1981) exhibit variety in development of both interseptal and lonsdaleoid dissepiments, with the latter being rare in *D. minor*, but dominating in *D. hunanense*. Therefore, this character is considered only as a supplementary feature for the time being.

Stylostrotion sudeticum n. sp.
(Pls. 3; 4; 5: 1; 6; 7. Figs. 26, 27)

HOLOTYPE

Specimen UAM Tc-2/1

TYPE LOCALITY

Sudetes, Zdanów borehole, depth 1803.2-1803.4 m.

TYPE HORIZON

Quasiendothya cobeitusana Biozone. Strunian.

DERIVATION OF THE NAME

Named after the Sudetes.

MATERIAL

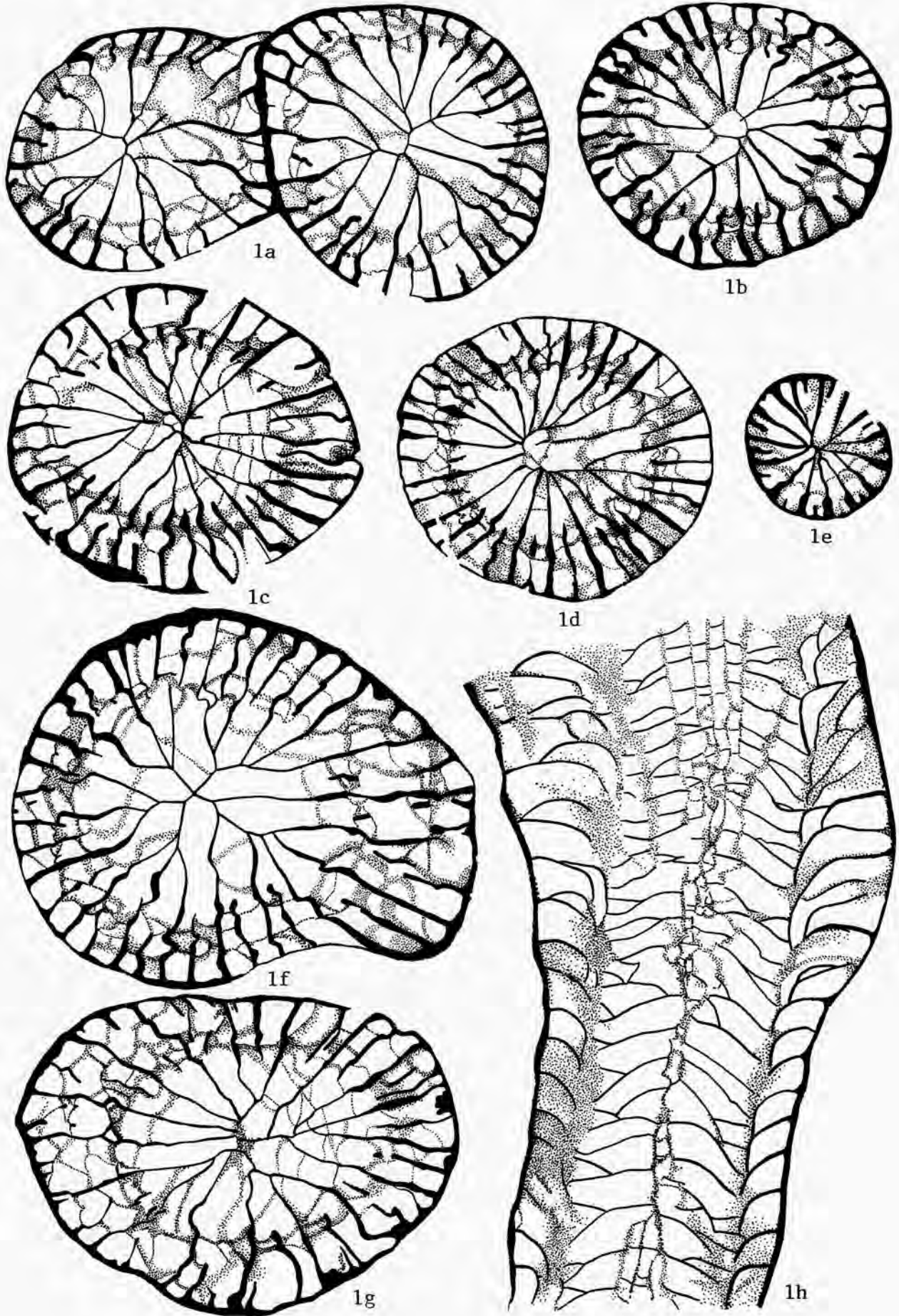
Large fragments of two colonies derived from cores.

DIAGNOSIS

Stylostrotion possessing up to 6 generations of septa at maximum diameter 7,2 × 9,0 mm; major septa arranged in unequal quadrants, most commonly meet near corallite axis; minor septa enter tabularium; dissepiments interseptal, in 1-3 rows.

DESCRIPTION OF THE HOLOTYPE

The colony is dendroid with corallites tending to form chains and/or groups. There are no connecting processes developed, but a given corallite may protrude towards one of its neighbours, up to joining it temporarily. Protrusions do not influence morphology of corallites, except for their peripheral parts. Dissepiments are always larger in that area and septa may be interrupted at the periphery. The calices were all destroyed due to postmortal transportation and diagenesis. In transverse sections the external wall is thin and slightly wavy, but this waviness does not exhibit regularity similar to that of septal furrows. Next to some septa the external wall is convex, whereas it is flat or concave next to others. Its microstructure is diagenetically destroyed in most corallites. Peripheral ends of septa are either embedded in the external wall (Pl. 6: 2b) or look like being only attached to its inner surface. There are no septa, except for deeply



altered diagenetically (Pl. 6: 1b) that reach the external surface of a corallite. The calice rim was perhaps smooth because septal furrows are lacking. Its permanent upward growth was contemporaneous with the thickening of the external wall and permanent growth of septa.

The arrangement of trabeculae (Pl. 6: 2a) indicates that septa bend smoothly around the rather sharp dissepimentarium/tabularium boundary (Pl. 3: 1e). Transverse sections show several details in the arrangement and morphology of major and minor septa. The former are thickened and continuous at the periphery and thin near a corallite axis, where secondary stereoplastic sheets are commonly underdeveloped. The arrangement of the major septa varies greatly, being slightly different in every corallite of the colony. The "classical" dividocoralloid arrangement is one of the rarest (e.g. Pl. 3: 1a; Pl. 5: 1a-1g, middle and left corallites) whereas the arrangement in which one fossa dominates and the irregular arrangement are the most common (Pl. 3: 1b-1d; Pl. 4: 2a-2c; fig. 26: 1a-1d, 1g). The ontogenetically less advanced corallites may exhibit a more regular dividocoralloid arrangement of septa (Pl. 6: 2c-2e; fig. 26: 1e), but this is not a rule. The irregularity and unstability in the arrangement of major septa observed both in the course of growth of the same corallite (Pl. 5: 1a-1g) and between corallites are therefore considered typical for the holotype colony. In the early growth stage (Pl. 6: 2c-e) minor septa are absent from the corallite lumen and the external wall. They appeared simultaneously when the number of major septa reached 12-15. Their further insertion is in sequence, following that of the major septa. Forming only small knobs at the beginning of their presence, they enter the tabularium later on. Some of them may be interrupted, although the major septa adjacent to them are continuous (e.g. Pl. 4: 2c, lower). First dissepiments were formed shortly after the first minor septa appeared. The width of the dissepimentarium varies. It may consist of 1-3 rows in the same transverse section. Walls of inner dissepiments are slightly thickened. In the longitudinal section (Pl. 3: 1e; fig. 26: 1h) the inner limit of the dissepimentarium is clearly marked by vertical position and slight thickening of inner dissepiments. Outer dissepiments or their peripheral parts are almost horizontal. The tabularium occupies slightly more than 1/2 of a corallite diameter. Tabulae are mostly complete, arranged obliquely; some of them bear peripheral tabellae that are either horizontal or resemble the clino-tabellae. Peripheral portions of tabulae are horizontal.

THE INTRA- VERSUS INTERCOLONY VARIATION

The most important intracolony variation is exposed in:

1. Random arrangement of septa (Pls. 3-7; fig. 26).

2. Reduction in many specimens of the oblique septum to the point of connection of four septa of the first generation.
3. Arrangement of major septa in such a way that a single fossa is formed.
4. Disconnection of major septa in a corallite axis.
5. Number of generations of septa in quadrants (see Table 1).
6. Underdevelopment of some quadrants; in extreme instances a quadrant may be reduced to a single septum of the first generation.
7. Prevailing occurrence of corallites possessing number of major septa in quadrants only slightly differentiated and showing fast increase in generations of septa early in the ontogeny.
8. Continuous or disconnected minor septa, with the first ones being much more common.

Table 1.

Dimensions in *Stylostrotion sudeticum* n. sp.

Number of specimen & corallite	Number of potentially creative septa	Number of generations of septa in quadrants	Diameter of corallites (in mm)
376: 1	18	1-6-1-5	6.5 × 5.7
	2	3-2-5-3	5.3 × 4.7
	3	2-4-4-4	6.2 × 5.2
	4	5-2-5-4	8.6 × 6.4
	5	5-5-2-5	8.0 × 6.7
	6	1-5-2-6	5.5 × 4.7
	7	4-5-4-2	7.3 × 6.5
	8	4-3-2-3	5.3 × 3.9
	9	3-4-6-4	9.2 × 7.4
	10	4-4-4-4	8.6 × 6.1
	11	4-1-5-4	6.7 × 5.3
	12	2-6-3-3	7.3 × 6.5
	13	1-5-4-4	6.1 × 5.2
374	18	2-5-3-4	5.0 × 4.8
	2	3-4-4-3	5.7 × 4.7
	3	2-4-3-4	4.1 × 3.8
	4	3-4-3-3	4.0 × 3.3
	5	3-4-6-4	7.0 × 5.0
	6	4-3-3-3	4.5 × 4.1
	7	2-3-5-3	3.5 × 3.1
	8	3-4-3-5	5.0 × 4.2
	9	5-3-3-3	5.6 × 4.8
	13	3-3-4-4	4.7 × 4.4
	17	1-4-1-4	2.0 × 1.8
	24	4-3-5-3	4.1 × 3.9
25	3-5-3-3	5.3 × 4.0	

Fig. 26. — *Stylostrotion sudeticum* n. sp. Specimen UAM Tc-3/1. Holotype. Sudetes. Zdanów borehole, depth 1803.2-1803.4 m. *Quasiendothyra cobeitusana* Zone. Strunian. 1a-1g. Transverse sections of individual corallites of dendroid colony showing intracolony variation; 1h. Longitudinal section. A11 × 10.

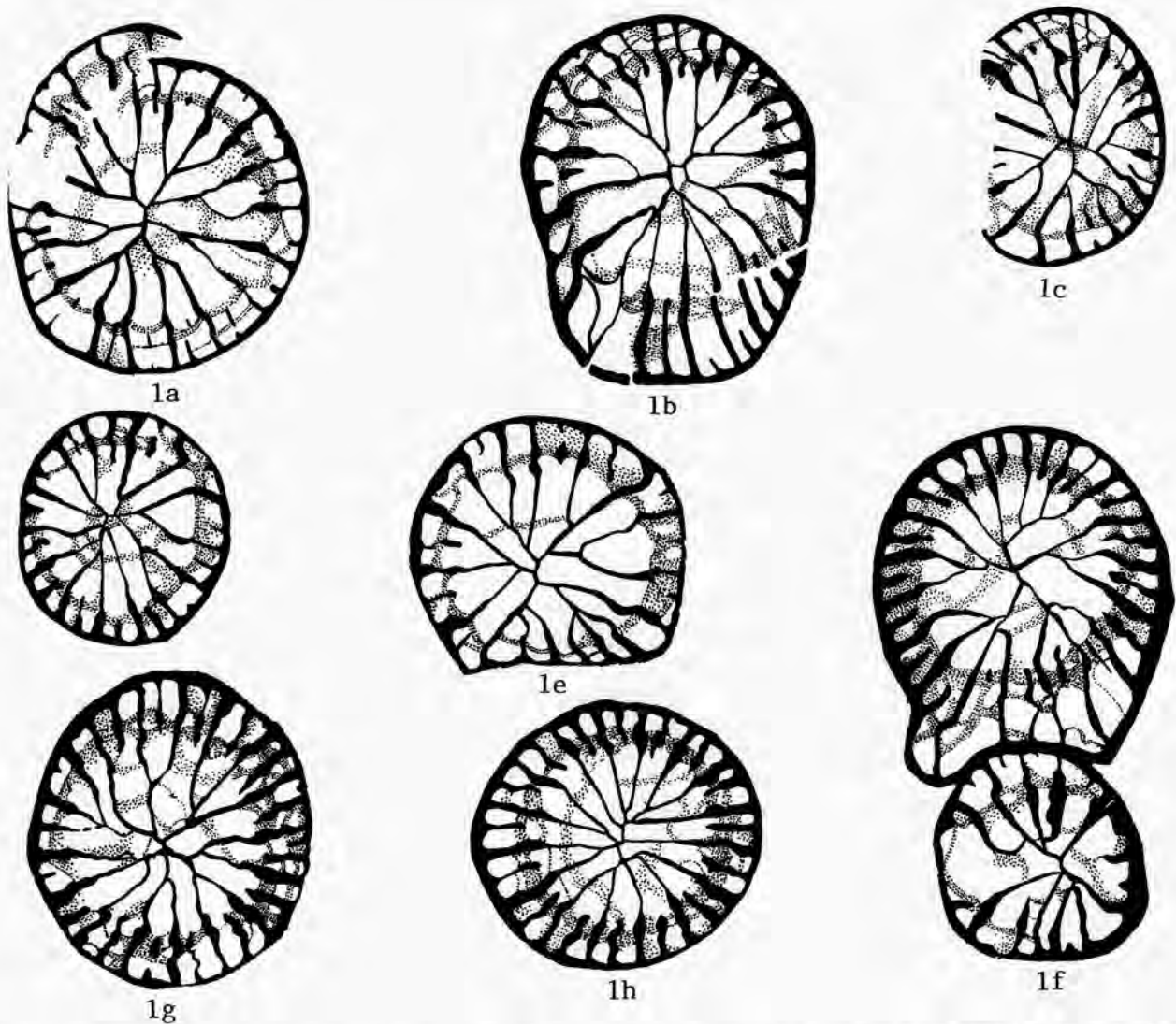


Fig. 27. – *Stylostroton sudeticum* n. sp. Specimen UAM Tc-3/2. Sudetes. Zdanów borehole, depth 1778.2 m. *Quasiendothyra cobeitusana* Zone. Strunian. Transverse sections of individual corallites of dendroid colony. A11 × 10.

All characters listed were observed in both colonies being therefore considered intracolony. The intercolony variability can be reduced to the diameter of corallites (Table 1). The ratio of the total number of potentially creative major septa to the corallite diameter is correlative in both colonies, whereas the number of generations is not. Small corallites of the paratype colony may have developed the number of generations of septa equal to large corallites of the holotype colony. Narrow dissepimentarium developed by corallites of the paratype colony (Pl. 4: 1a-1d; Pl. 7: 1a; Fig. 27: 1a-1h) is correlated to their smaller diameter.

REMARKS

The species described is strikingly similar to *Diphyphyllum* ? *vesiculosum* WU, 1933 in having its major septa mostly joining each other near a corallite axis and in developing interseptal, not lonsdaleoid, dissepiments. A narrower dissepimentarium and more irregular arrange-

ment of major septa, with only one fossa often dominating in the here described species, are its main distinguishing characters. *Donophyllum grossum* KHOA, 1984, another morphologically similar species, is readily distinguishable by its larger diameter and more regular arrangement of major septa. Much higher stratigraphical position and geographical occurrence of both species discussed eliminate them from being considered as closely related to *S. sudeticum* n. sp. allowing to accept an independent status of the latter species. Species of *Dema-tophyllum* described by WU & JIANG (1981) differ from *S. sudeticum* n. sp. first of all in developing lonsdaleoid dissepiments. In some corallites of the Chinese species this kind of dissepimentarium strongly prevails. This character, although distinct is not considered herein adequate for the generic distinction, at least on the recent level of the investigation. *Diphyphyllum antiquatum* WU & ZHAO 1981, possessing almost all major septa disconnected in a corallite axis, forms an extreme of the charac-

ter that is weakly, if at all, developed in the here described corallites. As in the former case this character is not considered adequate for the introduction of a new genus. Particular features of the Chinese species discussed above made them readily distinguishable from *S. sudeticum* n. sp. although the stratigraphic position of both Polish and Chinese specimens is similar.

OCCURRENCE

Sudetes, Zdanów borehole, depth 1778.2 and 1803.2-1803.4 m. *Quasiendothyra cobeitusana* Zone, Strunian.

Genus *Polygonaria* FAN in H.D. WANG, 1978

TYPE SPECIES

Donophyllum (Polygonaria) carbonica YU in H.D. WANG, 1978

SYNONYM

? *Prismatophyllum* YU, 1937, non SIMPSON, 1900.

EMENDED DIAGNOSIS

Ceriod Stylostrotionidae; major septa tend to loose mutual connection; lonsdaleoid dissepiments may occur.

REMARKS

See *Sudetiphyllia* n. gen.

Genus *Sudetiphyllia* n. gen.

TYPE SPECIES

S. prima n. sp.

DERIVATION OF THE NAME

Named after the Sudetes where all Polish representatives of this genus were found.

SPECIES ASSIGNED

S. prima n. sp., *S. aphroides* n. sp., *Sudetiphyllia* sp.

DIAGNOSIS

Thamnasterioid-aphroid Stylostrotionidae; major septa tend to loose mutual connection; in some or most corallites free.

REMARKS

Donophyllum (Polygonaria) FAN, in H.D. WANG (1978) raised herein to the generic rank, is the only genus described so far focusing directly toward the calyxcoralloid taxa of massive colonies. ? *Prismatophyllum* sp. YU, 1937, described by SMITH & YU (1943: 55) is herein regarded a member of *Polygonaria* in spite of the typically aulinid longitudinal section attributed to this taxon (SMITH & YU, 1943, Pl. 9: 16). The arrangement of septa and sections of tabulae exposed in the transverse section of that species (SMITH & YU, 1943, Pl. 9: 17) do not confirm a possibility of development of such a regular aulos. That

idealized reconstruction should be considered rather a longitudinal section of two inner ends of septa than a true aulos. Images similar to the one discussed are easily obtained by eccentrically sectioning a calyxcoralloid specimen. There are some other specimens or species included in genera such as *Lithostrotion*, *Siphonodendron*, *Aulina* and *Orionastraea* that expose calyxcoralloid characters in the arrangement of their septa. It will be possible to establish their true relationship by reinvestigating their type specimens and other stony material. This could not be done for this paper. However, specimens such as those illustrated by SMITH & YU (1943, pl. 8: 3; 4-6 respectively) as *Lithostrotion mccoynum* and *Aulina carcer* can be pointed out in the first place. Thus, it is possible to expect a much wider representation of massive Calyxcorallia n. ordo when some Carboniferous taxa shall have been carefully reinvestigated. The thamnasterioid and aphroid taxa may then appear to be members of *Sudetiphyllia* n. gen. and the cerioid ones to belong to *Polygonaria*.

Sudetiphyllia prima n. sp.

(Pls. 8: 1a-1f; 9: 1a-1d; 10: 1a-1c. Figs. 28: 2, 3a, b; 29)

HOLOTYPE

Specimen UAM Tc-3/3.

TYPE LOCALITY

Dzikowiec village, near Kłodzko, Sudetes.

TYPE HORIZON

Quasiendothyra cobeitusana Zone, Strunian.

DERIVATION OF THE NAME

lat. *primus*, *a*, *um* – first. First described and type species of the genus.

MATERIAL

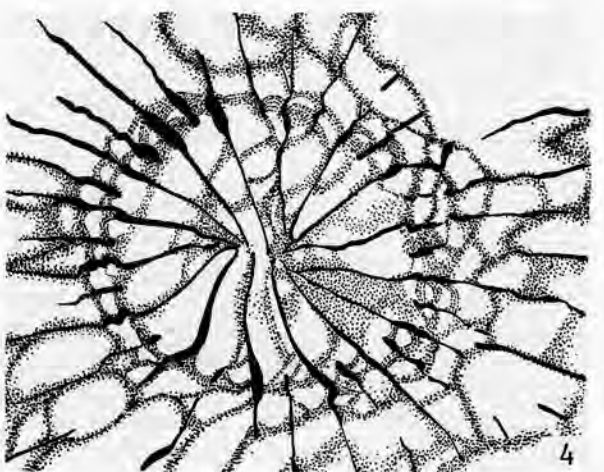
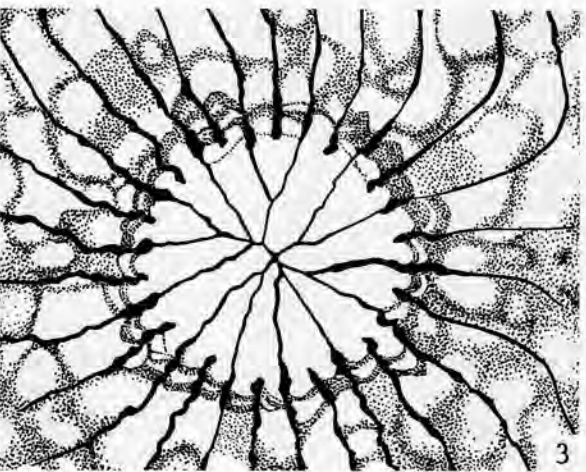
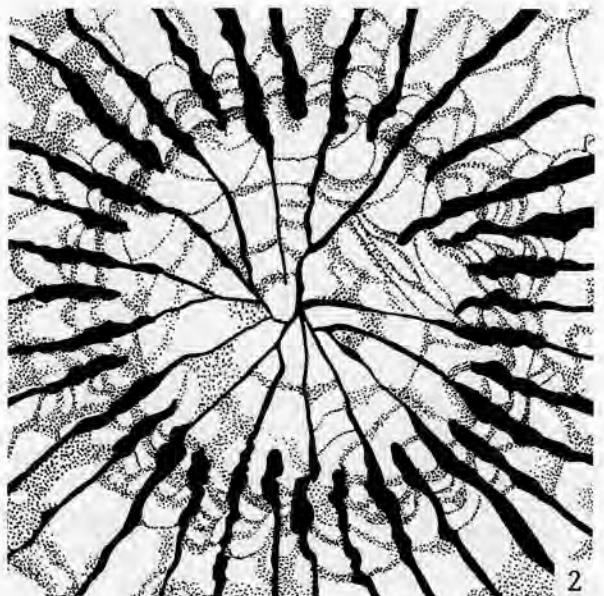
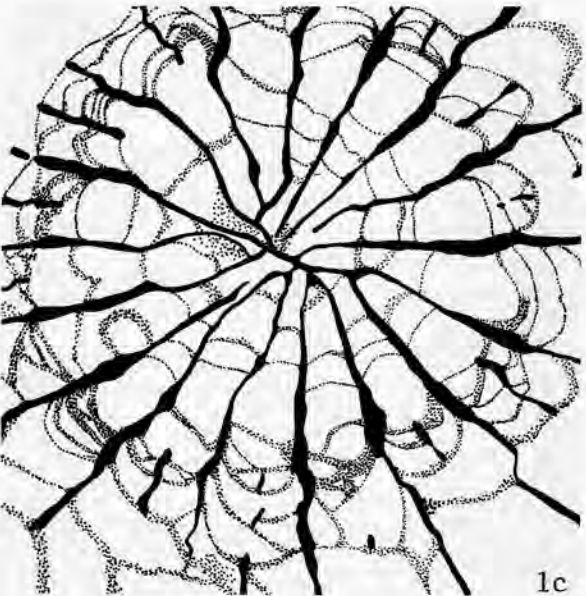
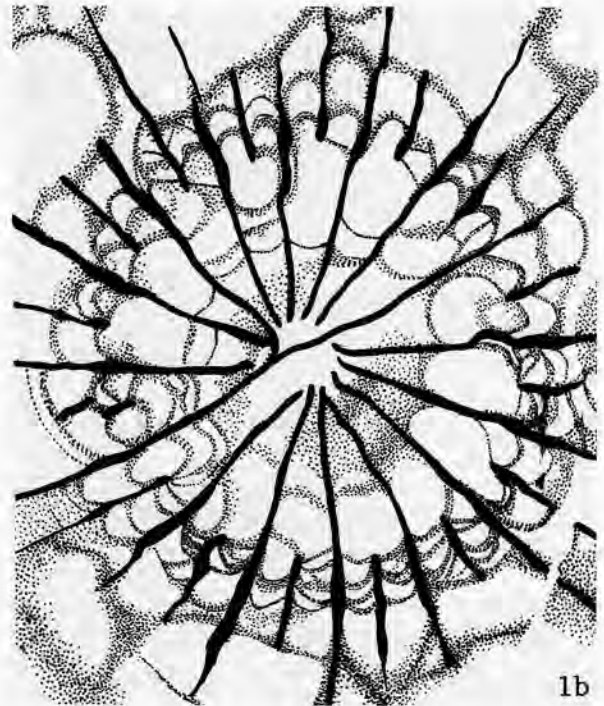
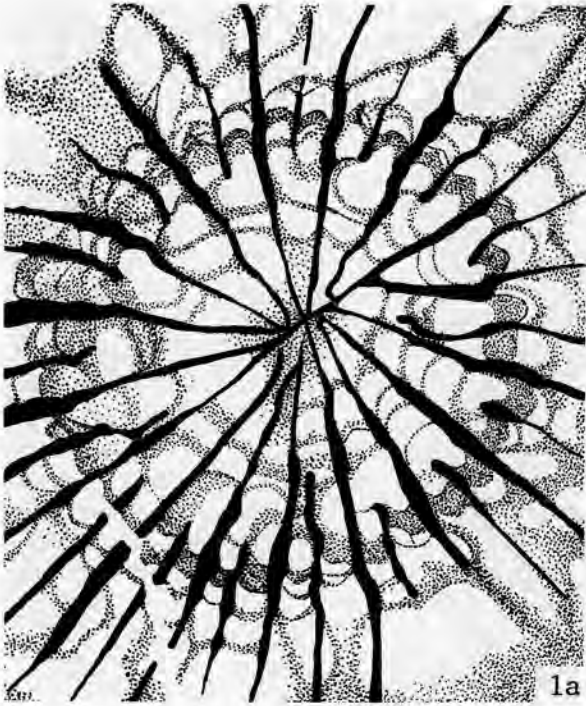
Two almost complete colonies, approximately 20 × 15 × 10 cm in size of which 11 thin sections were prepared.

DIAGNOSIS

Thamnasterioid towards aphroid *Sudetiphyllia* possessing up to 17 × 2 potentially creative septa; tabularium up to 4.2 mm wide, with densely packed tabulae (21/5 mm); major septa mostly united; minor septa well developed.

DESCRIPTION OF THE HOLOTYPE

The colony is thamnasterioid, but individual septa may be disconnected by coenenchymal vesicles in some areas. Spacing between individual neighbouring tabularia varies from 1.8 to 8.5 mm. Intertabular parts of septa, i.e. those connecting individual corallites, are slightly thickened or thin, whereas the adjacent to tabularia parts of septa are commonly thickened. The minor septa only slightly enter the tabularia, where their inner ends are free. Major septa are united in accordance to



generations. Their disconnection is mostly seeming and illustrates the oblique sectioning of specimens. Only in a few cases observed the major septa are truly disconnected. The arrangement of septa in quadrants can be clearly regular (e.g. Pl. 9: 1a, lower; Fig. 28: 3), which is manifested both by equal number and generations of septa. The irregular arrangement is much more common. In this case the oblique septum can be reduced to the size of apparent crossing of four septa of the first generation. Also, some quadrants are differentiated in size, number of septa and number of their generations. Fossae are often distinguishable. Dissepiments differ in size, shape and arrangement. Most of them are interseptal. Free dissepiments are rather uncommon, occurring only in the most distant portion of the coenosteum. The innermost ring of small dissepiments is thickened, which is fairly well accentuated in the longitudinal section. The major part of the coenosteum is composed of small, slightly convex or flat dissepiments, distributed horizontally. Such horizontally displayed dissepiments reach the dissepimentarium/tabularium border where they bend steeply downwards (Pls. 8: 1e, 1f; 10: 1a). Tabulae are densely packed, up to 21/5 mm, horizontal or slightly convex at the periphery and oblique in the periaxial portions. Their axial parts meet the oblique septum horizontally or under a wide angle. In the instance when not the oblique septum, but two periaxial parts of septa are sectioned, a false aulos may occur. Portions of tabulae located between such sections are horizontal (Pl. 10: 1a, lower).

INTERCOLONY VARIABILITY

Only one colony of the material studied can be considered as a paratype of the species discussed. It differs considerably from the holotype both in the morphology and dimensions of corallites. However, all those differences may appear intraspecific when more material is studied. Two clear peaks occurring when the number of specimens in particular classes are considered (Fig. 29), almost disappear when the mean $n:d$ ratio of specimens from both colonies is taken into account. With only two colonies available for study it seems only right to say that the variability in dimensions is restricted within colonies and comparatively large between colonies. Such a conclusion cannot form a basis for distinguishing those colonies on the species level. Much better accentuated aphroid character, more irregular arrangement of the major septa in individual corallites, wider zone of small dissepiments at the dissepimentarium/tabularium border in cross sections, and more distinct, almost diphylloid inner zone of the tabularium in the longitudinal section (Pl. 8: 1e) are further morphological characters distinguishing the paratype colony from the holotype.

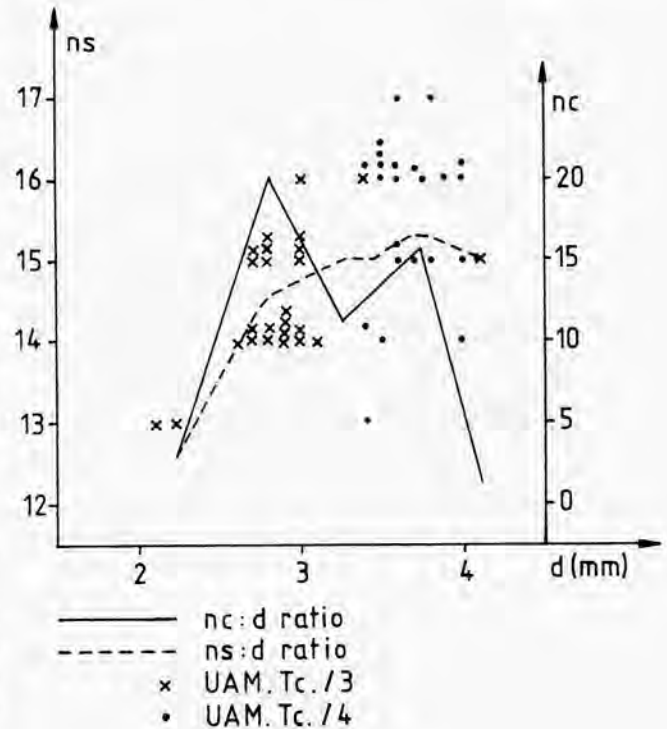


Fig. 29. – Statistical analysis of *Sudetiphyllia prima* n. sp. d: diameter of tabularium, nc: number of corallites, ns: number of septa.

However, like in the case of dimensions, all morphological differences listed may well be of only intraspecific value. The second option but not the introduction of two uncertain species seems more practical for the time being.

OCCURRENCE

As for the holotype.

Sudetiphyllia aphroides n. sp.

(Pls. 10: 2, 3; 11; 12: 2; Figs. 30: 1-3; 31)

HOLOTYPE

Specimen UAM Tc-3/5.

TYPE LOCALITY

Żdanów borehole (Sudetes), depth 1898.1 m.

TYPE HORIZON

Quasiendothyra cobeitusana Zone, Strunian.

DERIVATION OF THE NAME

Aphroides – after type of coloniality.

Fig. 28. – 1a-1c. *Sudetiphyllia* sp. Specimen UAM Tc-3/8. Sudetes. Dzikowiec quarry. *Quasiendothyra cobeitusana* Zone, Strunian. Transverse sections of individual corallites. 2. *Sudetiphyllia prima* n. sp. Specimen UAM Tc-3/4. Occurrence as above. Transverse section of individual corallite. 3a, 3b. *Sudetiphyllia prima* n. sp. Specimen UAM Tc-3/3. Holotype. Transverse section of the regular (3a) and irregular (3b) corallite. A11 × 15.

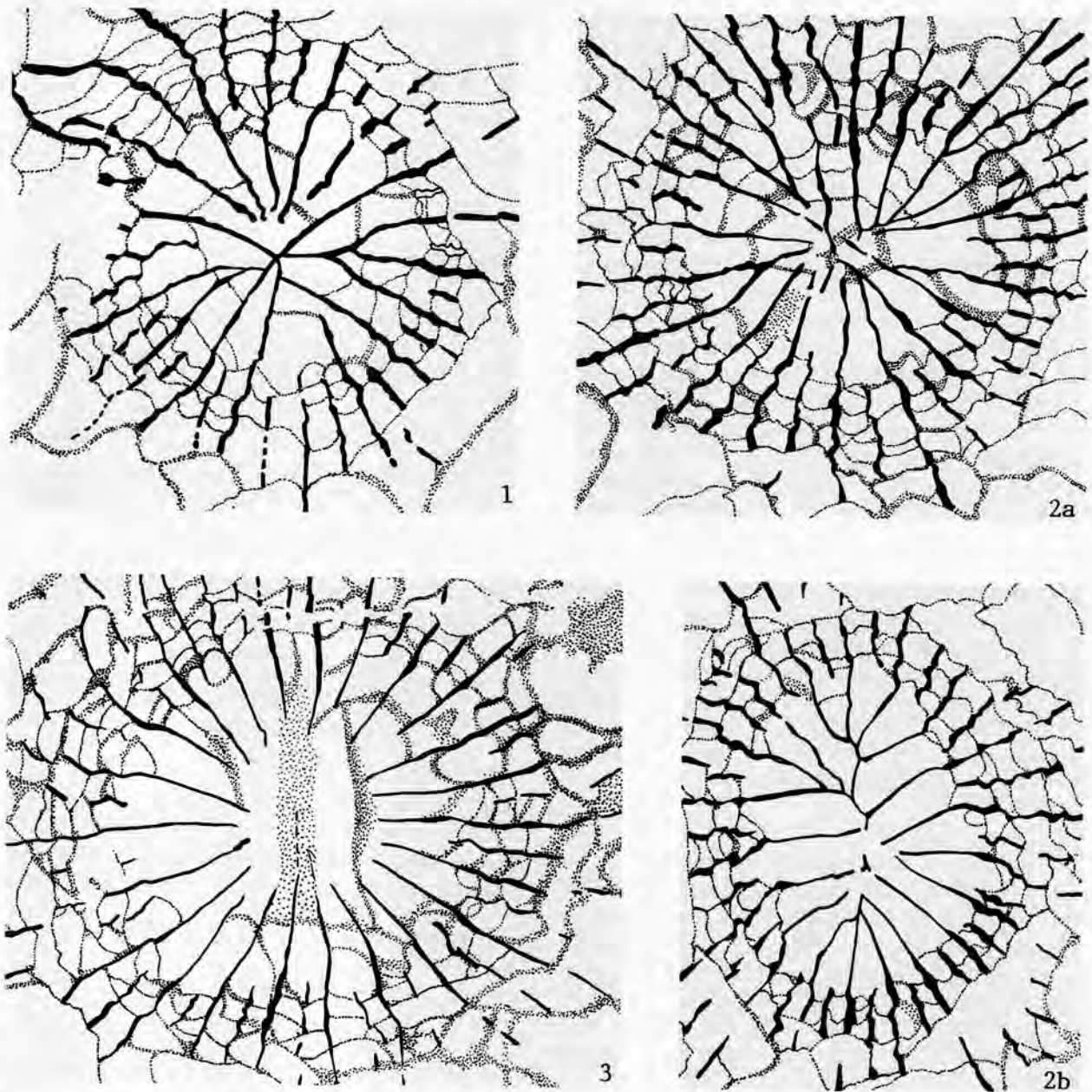


Fig. 30. – *Sudetiphyllia aphroides* n. sp. Transverse sections of individual corallites. All specimens from Sudetes, Zdanów borehole, depth 1898.1 m, 1891.9 m, 1898.8 m respectively. *Quasiendothyra cobeitusana* Zone. 1. Specimen UAM Tc-3/5. Holotype. 2a, 2b. Specimen UAM Tc-3/6. 3. Specimen UAM Tc-3/7. A11 × 15.

MATERIAL

Three fragments of colonies; all derived from the Zdanów borehole; depth 1891.9-1898.8 m. All fragments are recrystallized and dolomitized. Some morphological features are perhaps of diagenetic nature.

DIAGNOSIS

Aphroid *Sudetiphyllia*; n:dt ratio 16: 2.9 – 24:4.3; major septa commonly stop short of corallite axis; minor septa clearly enter tabularium; tabulae 7-12/5 mm at periphery, may bear long axial tabellae.

DESCRIPTION OF THE HOLOTYPE

The colony is clearly aphroid, with septa in individual corallites restricted mainly or entirely to their own, narrow zone of small interseptal dissepiments. Morphology of the common, vesicular tissue (coenosteum) is altered by recrystallization and dolomitization. It may be predicted that rather irregular and globose dissepiments were originally developed in that area. Completely integrated systems of major septa is very seldom present in individual corallites. Systems of septa are always irregular, when present, with the oblique septum being hardly dis-

tinguishable. Individuals possessing their septal apparatuses partly or completely disintegrated are most common. The arrangement of such free septa may be almost perfectly radial. Minor septa enter the tabularium, where their ends are slightly thickened. These slight stereoplasms thickenings are often extended to the dissepimental parts of major septa and the innermost dissepiments (Pls. 10: 3a; 11; Fig. 30: 1).

In the longitudinal section (Pl. 10: 3b) the common intracolony tissue consists of rather small, moderately convex dissepiments. Dissepiments adjacent to the tabularium are flattened and arranged steeply, sometimes vertically down. They resemble clino-tabulae in some parts of the section. Also, it may happen that the peripheral part of a tabula is arranged steeply upward at the periphery, imitating a dissepiment. Peripheral parts of tabulae are most frequently horizontal or slightly concave, whereas their periaxial and axial portions are horizontal, slightly convex or concave and are supplemented by long, flat axial tabellae.

INTERCOLONY VARIATION

All colonies included in *S. aphroides* n. sp. are strikingly similar to each other in dimensions of individual corallites and their morphology, as well as in scope of the intracolony variability. Both paratypes differ from the holotype in the frequent occurrence of corallites possessing the major septa completely disintegrated and radially arranged. That trend of development led to the appearance of diphyphylloid corallites, hardly comparable to typical *Calyxcorallia* n. ordo (Pl. 12: 2b; Fig. 30: 3). The ratio of corallites possessing major septa united axially to those having them free, as well as width of the free axial area differ slightly in individual colonies.

REMARKS

S. aphroides n. sp. is readily distinguishable from *S. prima* n. sp. by having aphroid colonies with larger corallites, the major septa of which are commonly disconnected. Also, wider ring of small, interseptal dissepiments, surrounding tabularia in transverse sections and more densely packed axial tabellae in longitudinal sections should be considered.

OCCURRENCE

Sudetes, Zdanów borehole, depth 1891.8-1898.8 m. *Quasiendothyra cobeitusana* Zone, Strunian.

Sudetiphyllia sp.
(Pl. 12: 1a-1e; Figs. 28: 1a-1c; 31)

MATERIAL

Single colony UAM Tc-3/8 of which one transverse and one longitudinal section were prepared, was available for study.

DESCRIPTION

The colony is aphroid with short, scattered and rare

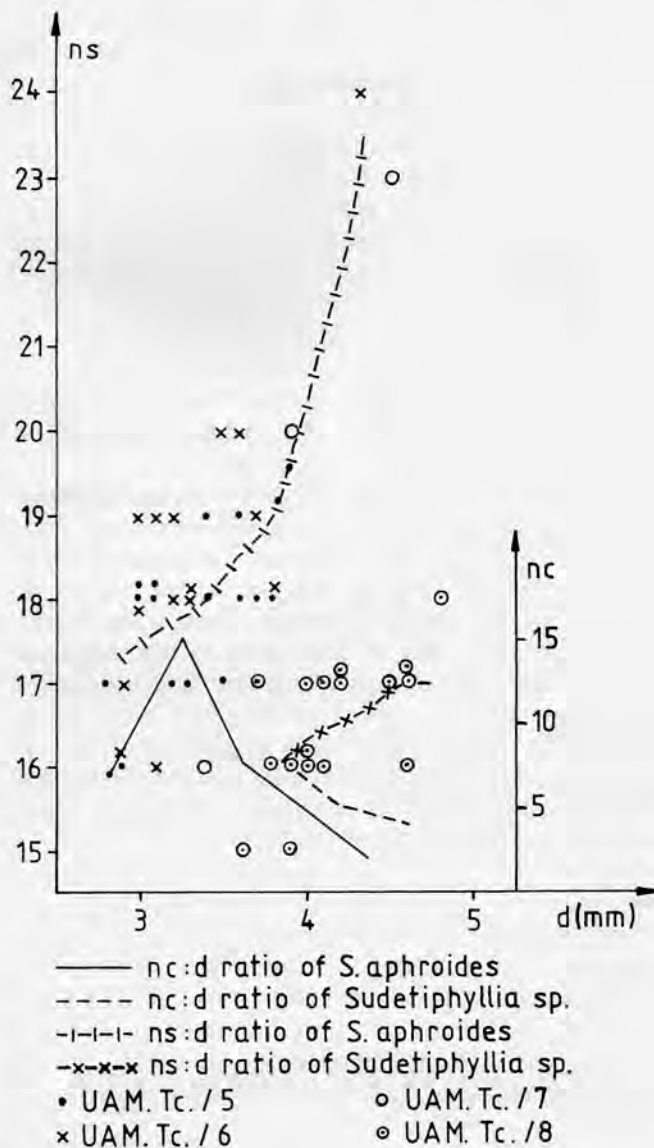


Fig. 31. - Statistical analysis of *Sudetiphyllia aphroides* n. sp. and *Sudetiphyllia* sp. d: diameter of tabularium (in mm); nc: number of corallites; ns: number of septa.

remnants of intercorallite walls present in places. Individual tabularia are 3.5-9.2 mm apart, but individualized portions of the skeleton are comparatively wide, making the colony rather densely packed with corallites (Pl. 12: 1d). The common colony tissue comprises large and irregular vesicles. It is fairly altered diagenetically, which may have influenced its morphology.

Morphology of individual corallites is very variable, with the morphotype allowing to identify the colony as a member of *Calyxcorallia* n. ordo being greatly subordinated. Only a single corallite (Pl. 12: 1b; Fig. 28: 1c) among 23 observed, exhibits this character advanced enough for easy recognition. Many corallites possess two opposite septa united to form a kind of columella. This morphotype (Pl. 12: 1a, 1d; Fig. 28: 1a, 1b) as well

as the morphotype with all major septa disconnected in a corallite axis (Pl. 12: 1d) are in the overwhelming majority, making the morphology of the colony rugosan rather than calyxcoralloid.

Minor septa in most corallites are well developed, entering the tabularium and being only slightly less thickened than the major septa in the interseptal dissepimentarium zone. They may disappear from some or most loculi in the thin-septal corallites. The interseptal dissepimentarium forms a distinct ring of small, interseptal dissepiments, surrounding the tabularium. Most dissepiments in this ring are concave; some are pseudo-herringbone. Inner dissepiments are thickened to form the inner wall. The latter is inconstant, being better developed in corallites possessing thickened septa.

Dissepiments in the longitudinal section are moderately large, elongated, rather flat; especially when long. Their arrangement in the common tissue is horizontal, but they became steeply, almost vertically oriented near the tabularium of individual corallites. These steep dissepiments are those seen as interseptal in the transverse section. Tabulae are regularly spaced and trapezoidal when their section is correctly oriented (Pl. 12: 1c, upper part). Their peripheral parts are slightly concave, axial parts flat and supplemented by long tabellae of the shape identical with that of inner portions of tabulae. Small tabellae may occur at the periphery.

REMARKS

Due to its aphyroid form of growth, the colony described resembles *S. aphyroides* n. sp. closer than *S. prima* n. sp. The different ratio of their dimensions (Fig. 31) and frequent occurrence in *Sudetiphyllia* sp. of corallites possessing two opposite septa connected axially, are the main distinguishing character of the latter taxon.

Conclusions

There are two distinct groups among the Late Devonian

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- and Carboniferous Anthozoa that were put together in this paper on the basis of their reinterpreted increase in septa. One of these groups – Heterocorallia – is almost equivocally accepted as distinct from the Rugosa, although the taxonomic level of this distinction was debated. The second group – Calyxcorallia n. ordo, is only herein distinguished as closely related to Heterocorallia. The general idea of this paper is that dividocorals, and especially Calyxcorallia were much more common in the Late Devonian and Carboniferous time than their actual record indicates. A careful examination of the increase in septa will perhaps allow to transfer several "lithostrotionids" and similar taxa to Calyxcorallia n. ordo. *Sudetiphyllia* sp. may serve as one of the best examples of such a possibility. The long time span between the Late Emsian and Strunian, seemingly barren from Dividocorallia n. subclass focuses on some Devonian taxa, actually placed within the Rugosa, as potential dividocorals. Closer examination, not possible for the purpose of this paper, may result in the recognition of the most striking parallel evolution, exemplified by the Rugosa and Calyxcorallia n. ordo. The latter developed all characters of the former, except for the increase in septa, invented at the very beginning of their independent phylogeny.

Acknowledgements

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PLATE I

- Figs. 1-11 – *Mariaephyllia famenniana* (RÓZKOWSKA, 1969). Gałęzice, Holy Cross Mountains. Upper Famennian *costatus* and *velifera* Zones. Transverse sections; those illustrated additionally by drawings are mentioned in parentheses. 1. Specimen Z.Pal.P.Tc-3/2001 (= fig. 7: 5). 2. Specimen Z.Pal.P.Tc-3/2003 (= fig. 5: 1c). 3. Specimen Z.Pal.P.Tc-3/2003 (= fig. 5: 1f). 4. Specimen Z.Pal.P.Tc-3/2230 (= fig. 3: 6b). 5a, 5b. Specimen Z.Pal.P.Tc-3/2096 (= fig. 3: 2a, 2b respectively). 6a, 6b. Specimen Z.Pal.P.Tc-3/2070 (= fig. 6: 2b, 2d respectively). 7. Specimen Z.Pal.P.Tc-3/2022 (= fig. 7: 4b). 8. Specimen Z.Pal.P.Tc-3/2232 (= fig. 7: 3a). 9a-9e. Specimen Z.Pal.P.Tc-3/2073 (Pl. 1: 9b-9d = fig. 4: 1c-1e respectively). 10. Specimen Z.Pal.P.Tc-3/2023 (= fig. 4: 2b). 11. Specimen Z.Pal.P.Tc-3/2397 (= fig. 6: 1b). A11 × 15.
- Figs. 12-14 – *Pseudopetraia devonica* SOSHKINA, 1951. Pokrovskoe Village, Egorshinskiy Raion, Eastern slope of Middle Ural Mountains, Upper Emsian. 12a-12e. specimen PIN 6662. Holotype. 12a-12d. transverse sections of successive growth stages; 12e. longitudinal section. 13. Specimen PIN 6651 – transverse section. 14a-14c. Specimen PIN 6688. Transverse sections of successive growth stages up to the calice. A11 × 5.

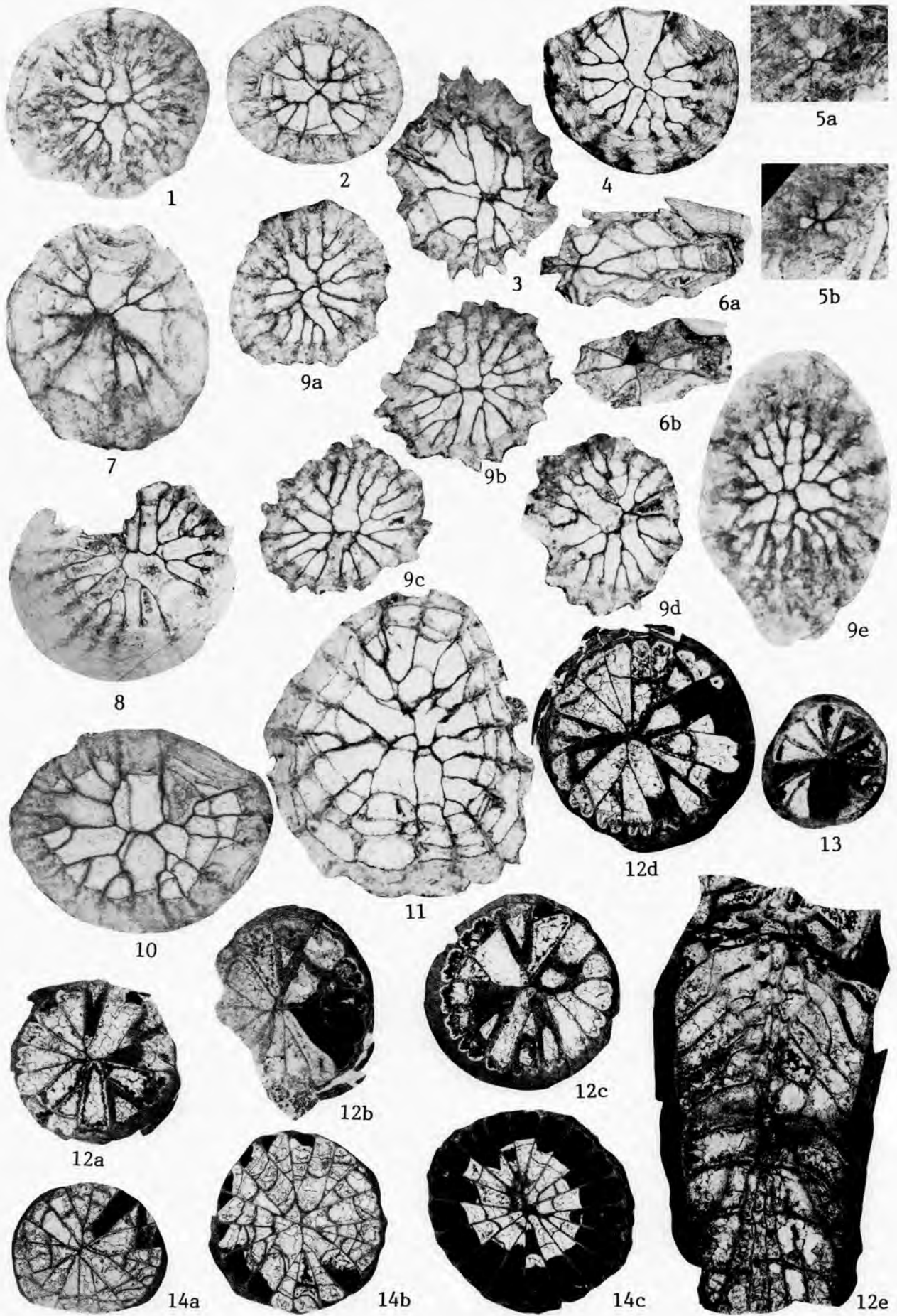


PLATE 2

- Figs. 1-5 – *Mariaephyllia famenniana* (RÓZKOWSKA, 1969). Transverse sections. Gałęzice, Holy Cross Mountains. Upper Famennian, *costatus* and *velifera* Zones. 1. Specimen Z.Pal.P.Tc-3/2023. Peripheral dichotomic division of septa; microstructure in all parts of the “Y” system is identical, × 200. 2a, 2b. Specimen Z.Pal.P.Tc-3/2070. Microstructure of septa as above, × 200. 3. Specimen Z.Pal.P.Tc-3/2073. Microstructure of septa as above, × 200. 4. Specimen Z.Pal.P.Tc-3/2332. Relationship between septa and the external wall, × 50. 5. Specimen Z.Pal.P.Tc-3/2230. Relationship between septa and the external wall, × 50.

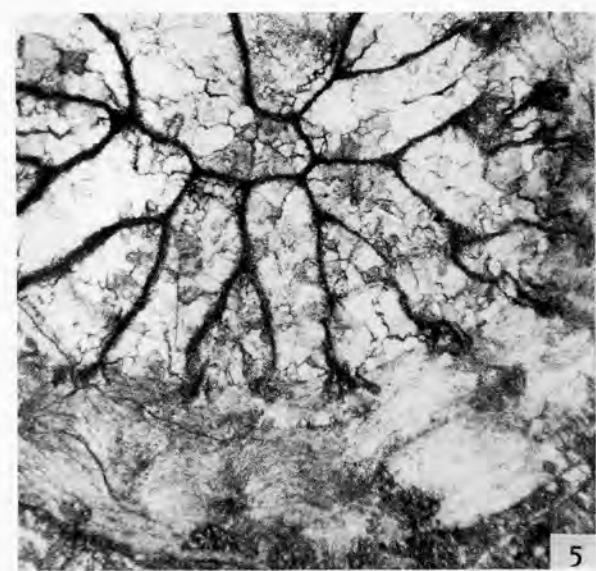
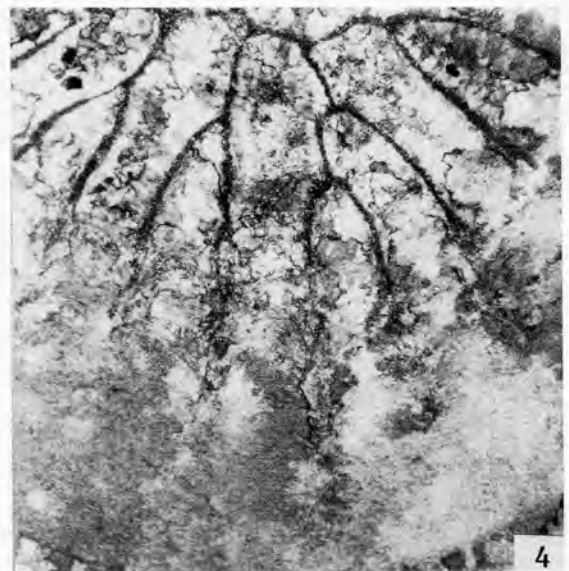
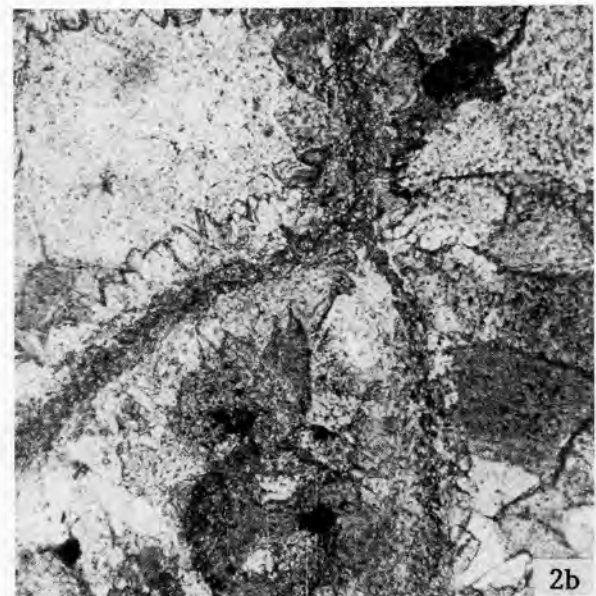
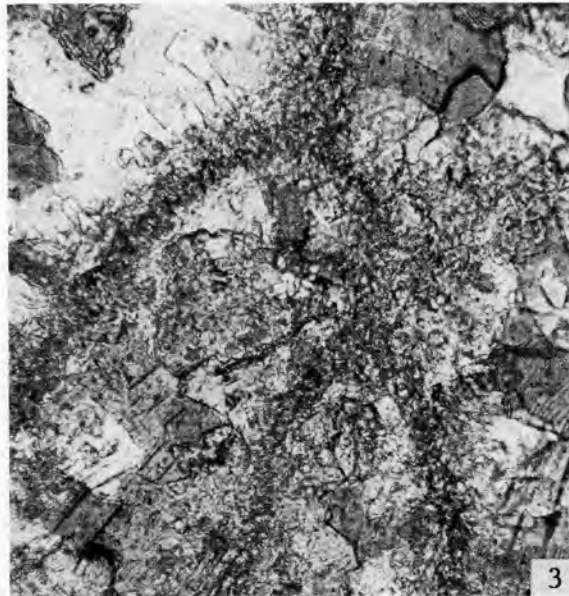
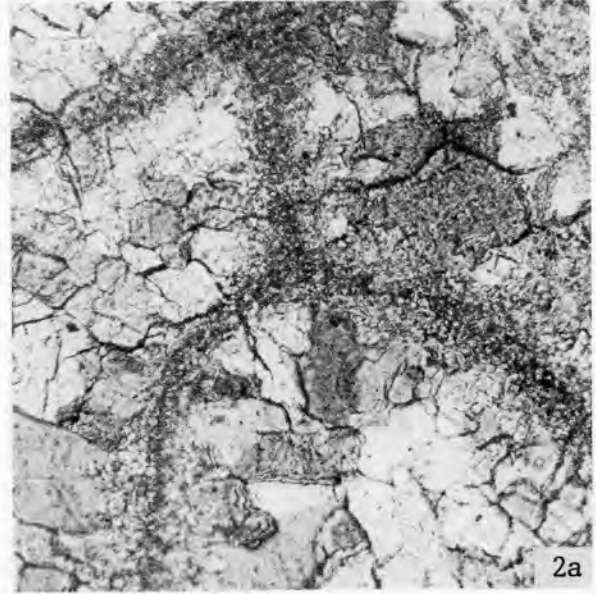
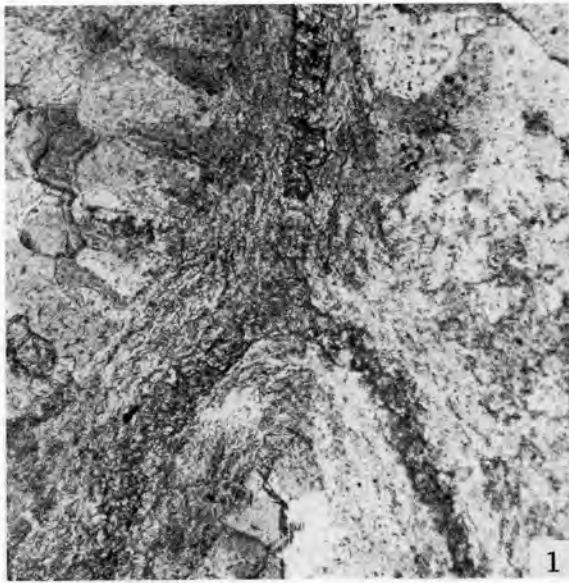


PLATE 3

Figs. 1a-1d. – *Stylostrothion sudeticum* n. sp. Specimen UAM Tc-3/1. Holotype. Sudetes, Zdanów borehole, depth 1803.2-1803.4. *Quasiendothyra cobeitusana* Zone, Strunian. 1a-1e. transverse sections of individual corallites of dendroid colony. 1e. longitudinal section. A11 × 10.

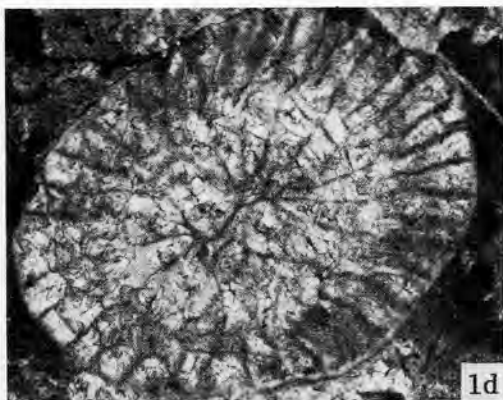
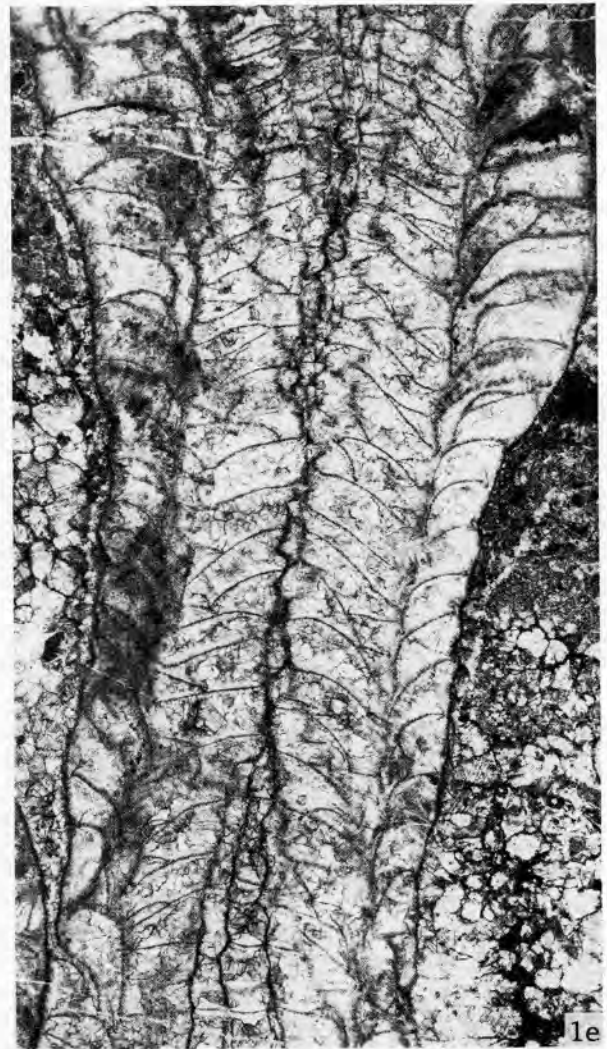
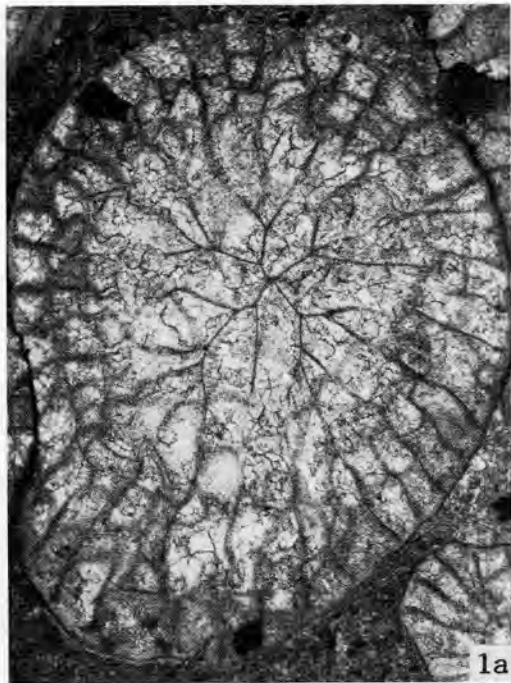
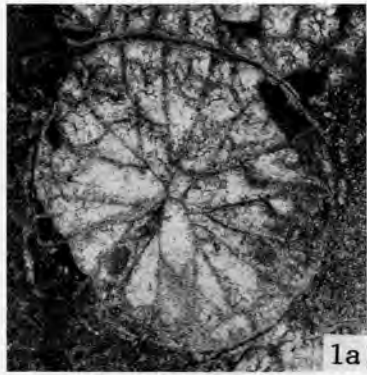
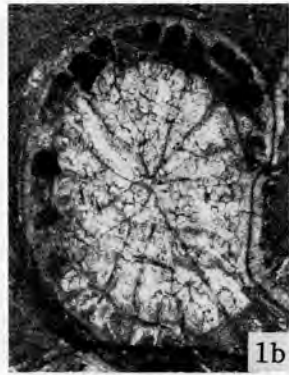


PLATE 4

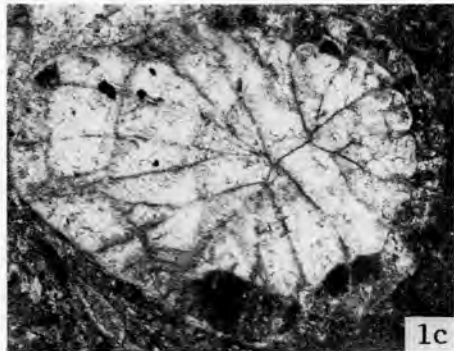
- Figs. 1-2. – *Stylostrothion sudeticum* n. sp. 1a-1d. Specimen UAM Tc-3/2. Sudetes, Zdanów borehole, depth 1778.2 m. *Quasiendothyra cobeitusana* Zone, Strunian. Transverse sections of individual corallites of dendroid colony. 2a-2c. Specimen UAM Tc-3/1. Holotype. Sudetes, Zdanów borehole, depth 1803.2-1803.4 m. *Quasiendothyra cobeitusana* Zone, Strunian. Transverse sections of fragments of dendroid colony. A11 × 10.



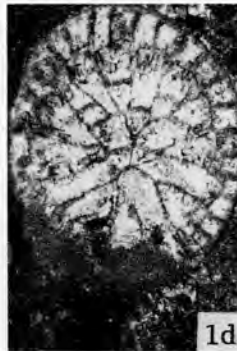
1a



1b



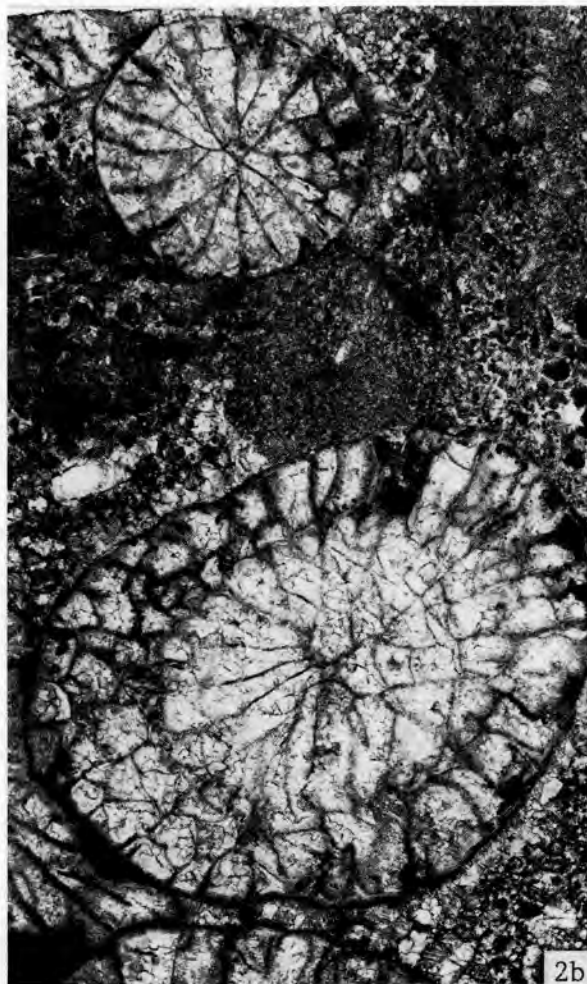
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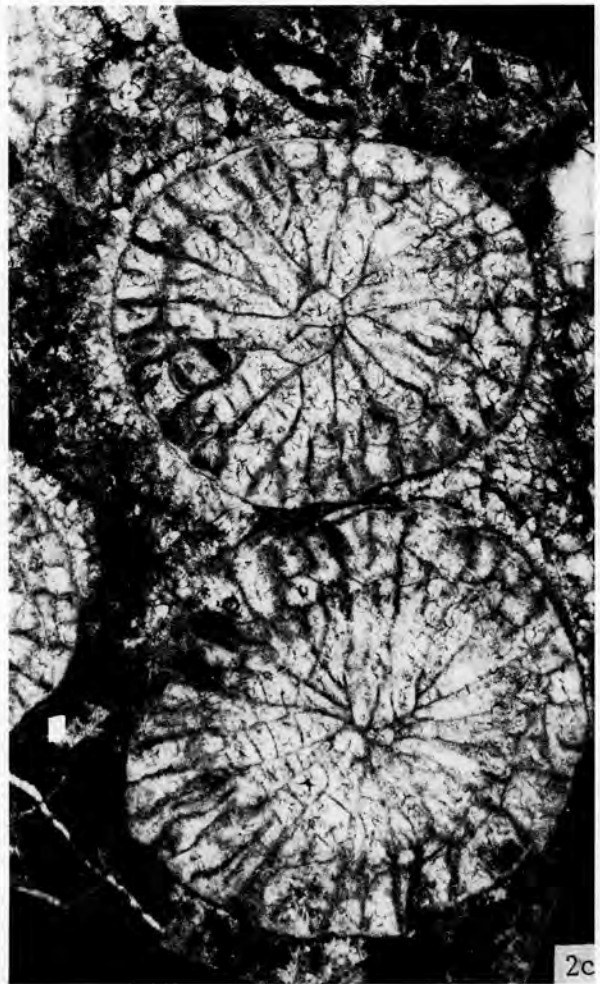
1d



2a



2b



2c

PLATE 5

- Figs. 1a-1g. – *Stylostroton sudeticum* n. sp. Specimen UAM Tc-3/1. Holotype. Sudetes, Zdanów borehole, depth 1803.2-1803.4 m. *Quasiendothyra cobeitusana* Zone. Successive transverse sections of part of dendroid colony.
- Fig. 2. – *Stylostroton grossum* (KHOA, 1984). Vietnam, Binhtrithien province, Viséan. Transverse section.
- Fig. 3. – *Stylostroton* sp. Pamir. Exact locality and age unknown (Upper Tournaisian or Lower Viséan). A11 × 3.

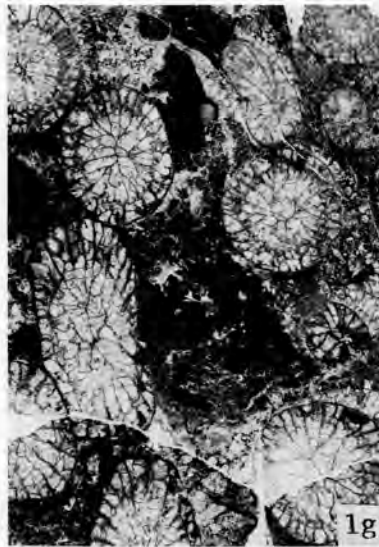
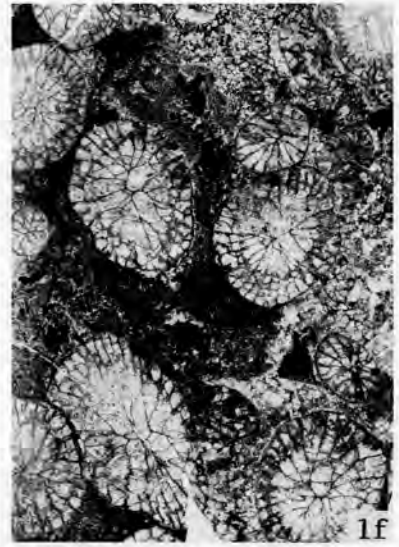
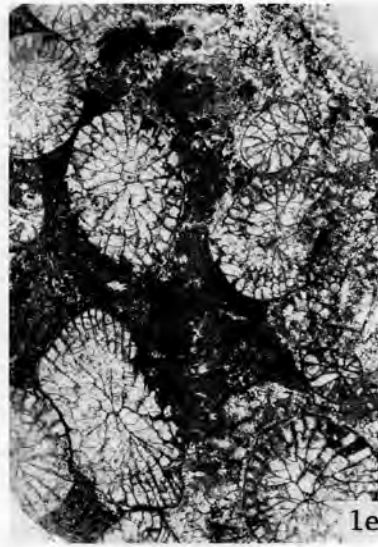
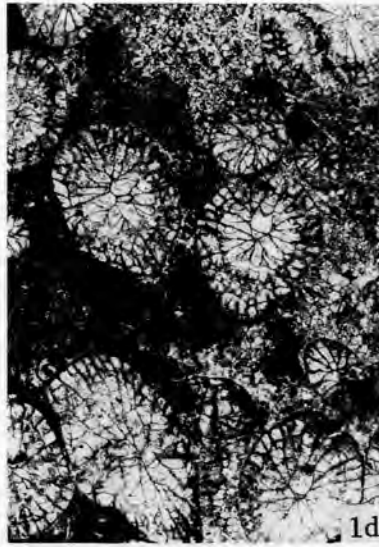
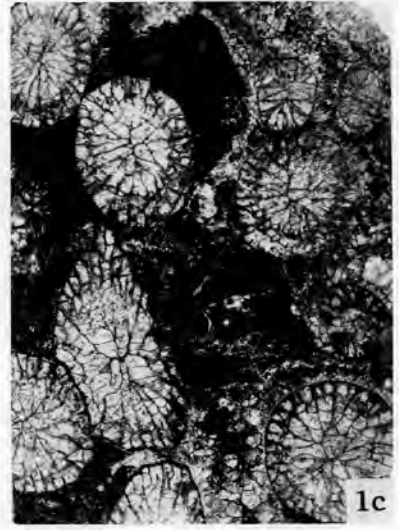
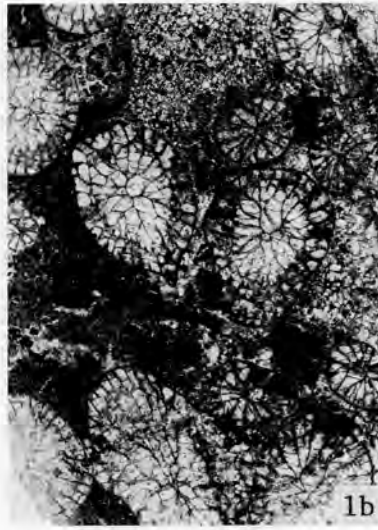
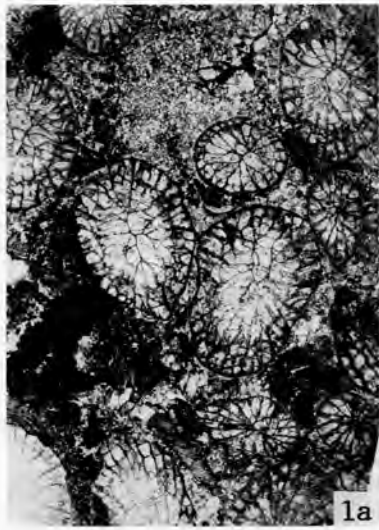


PLATE 6

- Figs. 1-2. - *Stylostrotion sudeticum* n. sp. 1a, 1b. Specimen UAM Tc-3/2. Sudetes, Zdanów borehole, depth 1778.2 m. *Quasiendothyra cobeitusana* Zone, Strunian. 1a. Transverse section showing trabecular microstructure of septa $\times 100$; 1b. Diagenetically altered microstructure of the external wall. 2a-2e. Specimen UAM Tc-3/1. Holotype. Sudetes, Zdanów borehole, depth 1803.2-1803.4 m. *Quasiendothyra cobeitusana* Zone, Strunian. 2a. Trabeculae in longitudinal section $\times 100$. 2b. Relationship of some septa to the external wall $\times 50$. 2c-2e. Transverse sections of successive growth stages of young corallite, $\times 25$.

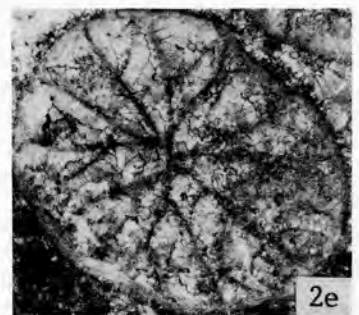
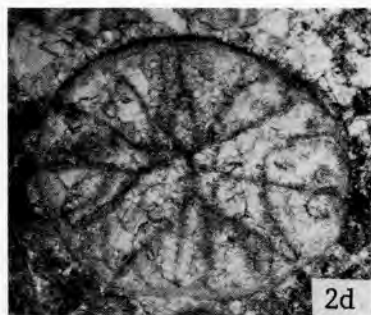
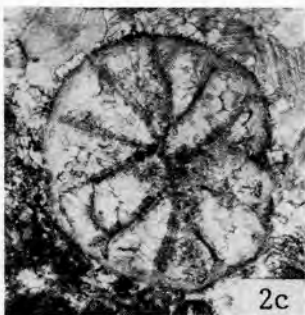
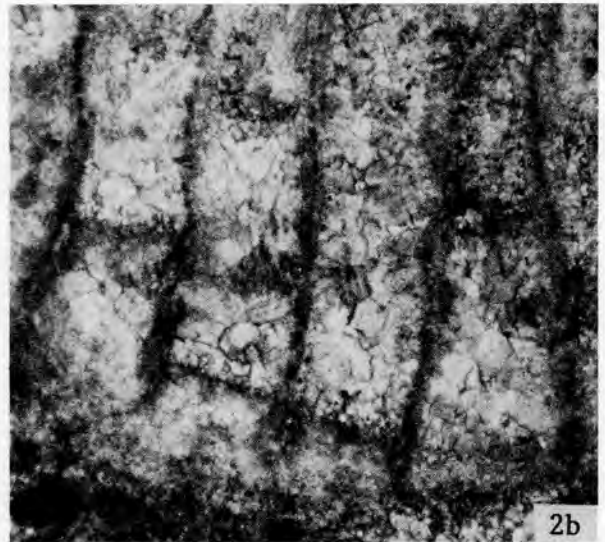
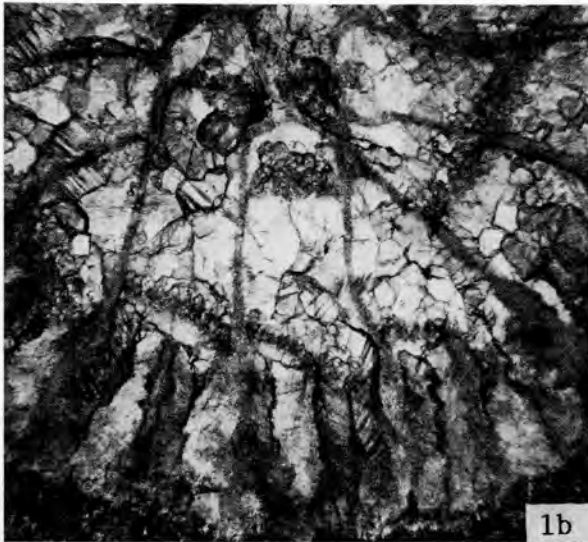
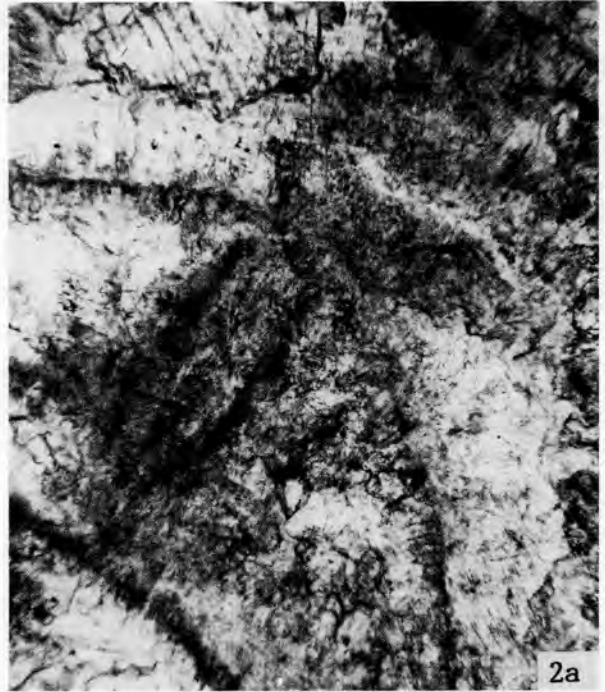
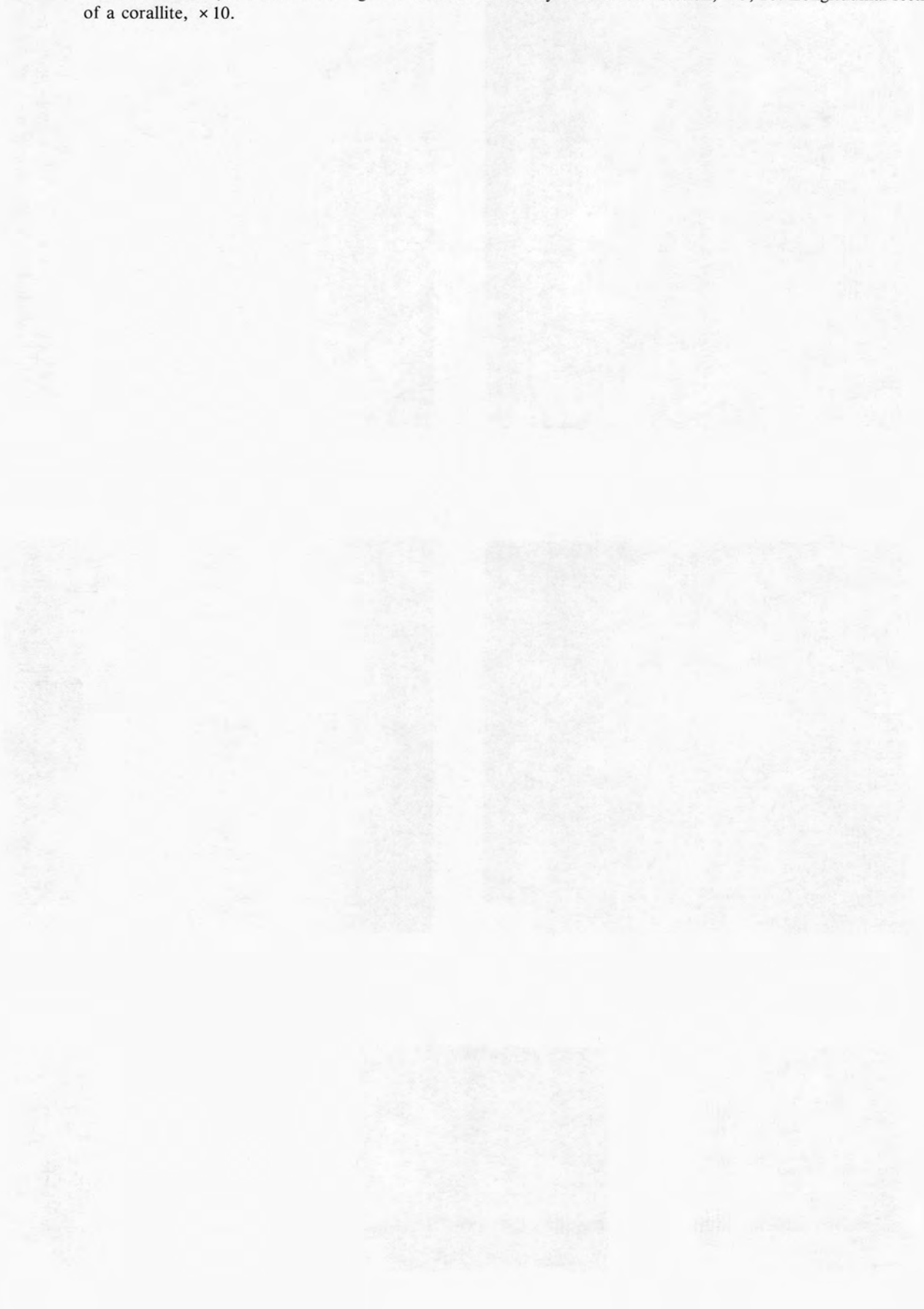


PLATE 7

Figs. 1a-1b. – *Stylostrotion sudeticum* n. sp. Specimen UAM Tc-3/2. Sudetes, Zdanów borehole, depth 1778.2 m. *Quasiendothyra cobeitusana* Zone, Strunian. 1a. Fragment of dendroid colony in transverse section, $\times 5$; 1b. Longitudinal section of a corallite, $\times 10$.



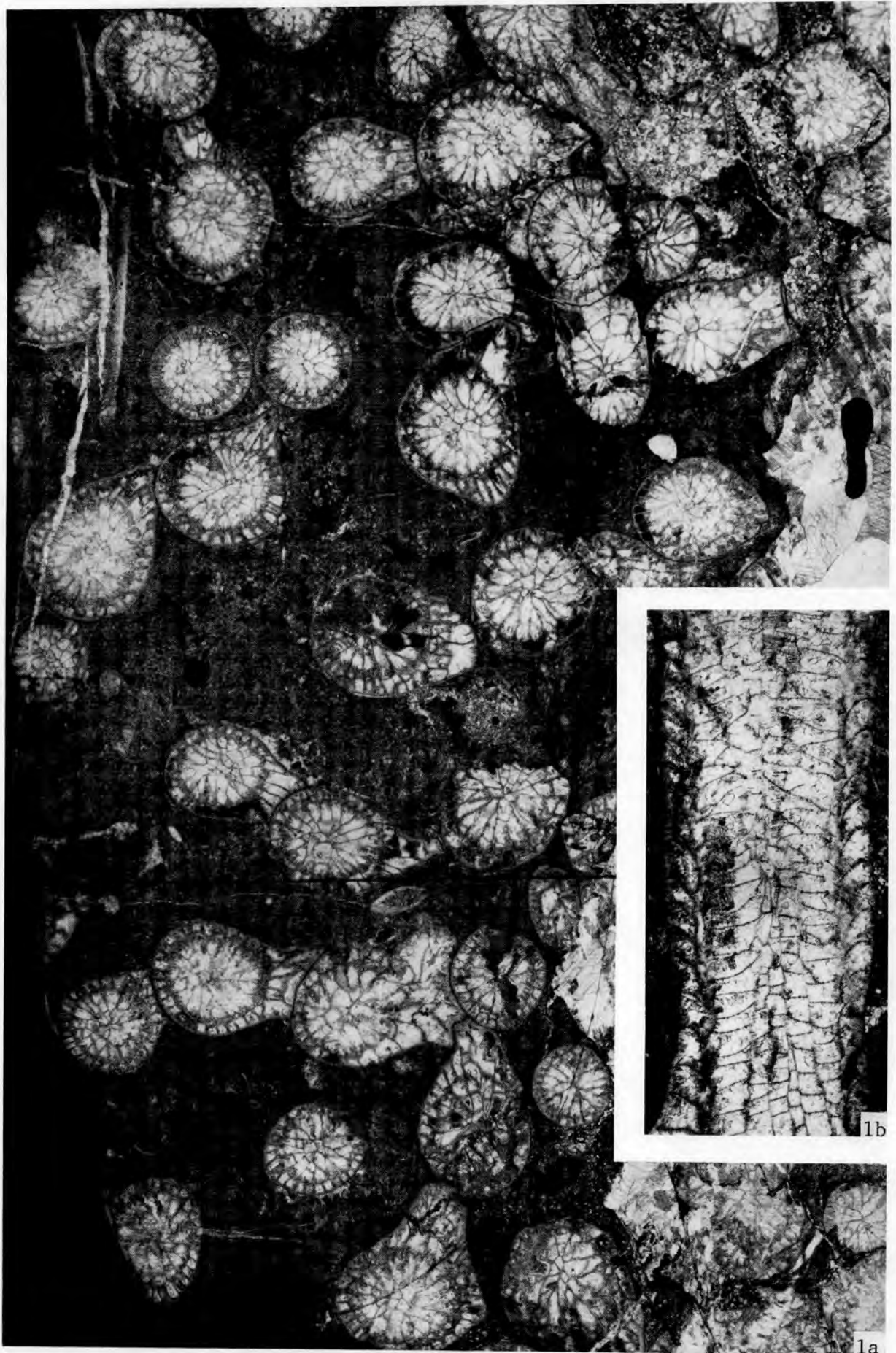


PLATE 8

Figs. 1a-1f. – *Sudetiphyllia prima* n. sp. Specimen UAM Tc-3/4. Sudetes, Dzikowiec quarry, *Quasiendothyra cobeitusana* Zone, Strunian. 1a-1d. Transverse sections of fragments of the colony, 1a, $\times 5$; 1b, 1c, $\times 10$; 1d, $\times 3$. 1e, 1f. Longitudinal sections. 1e, $\times 5$; 1f, $\times 3$.

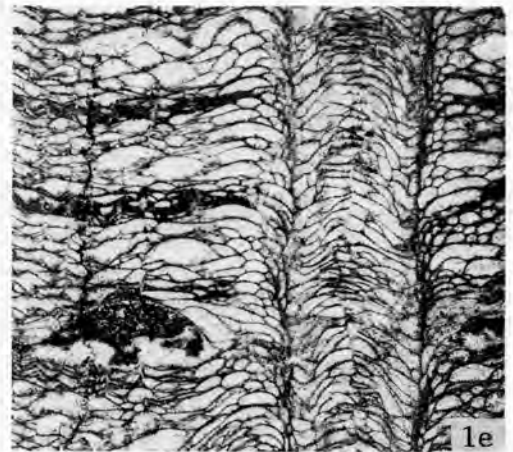
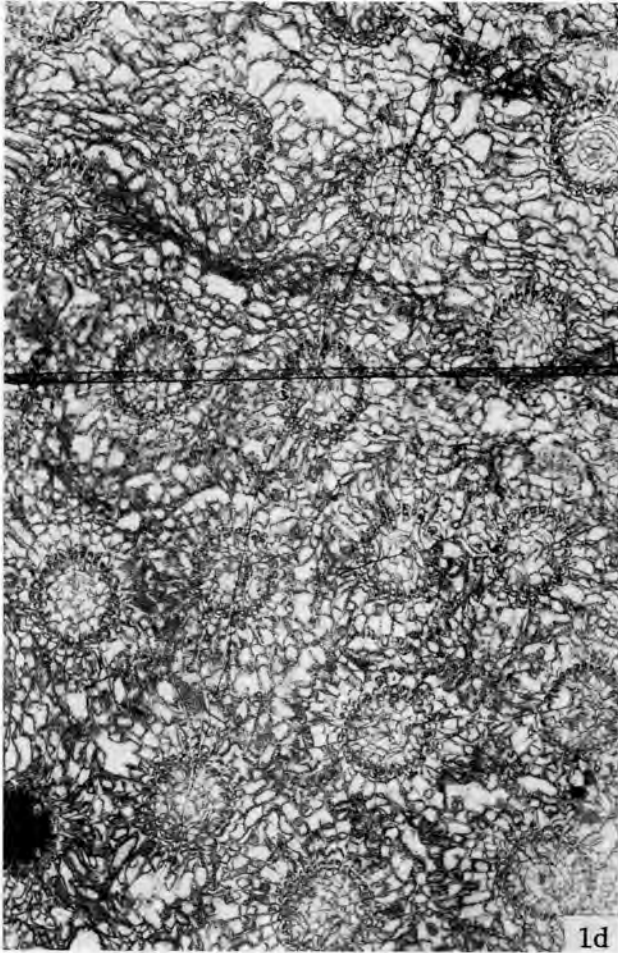
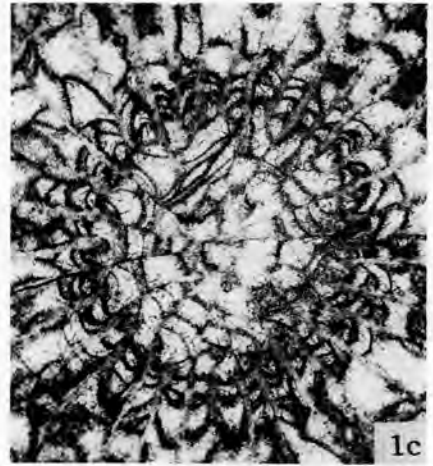
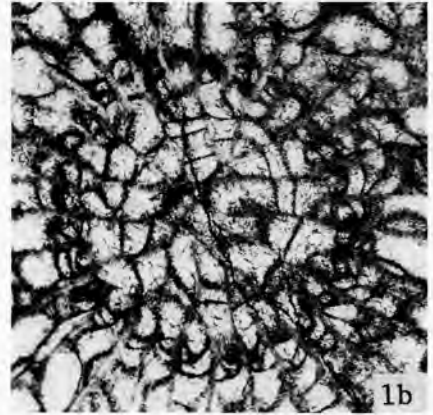
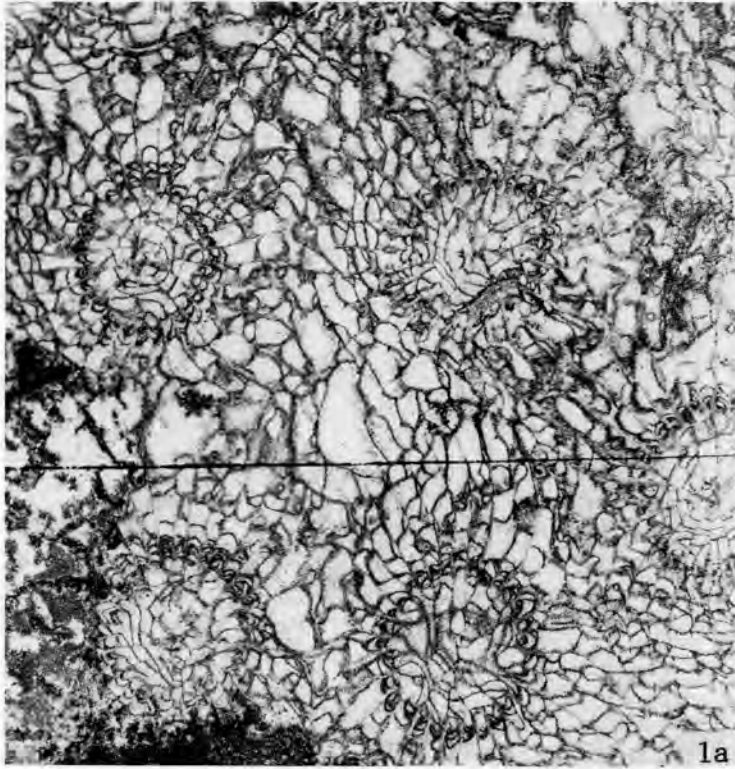
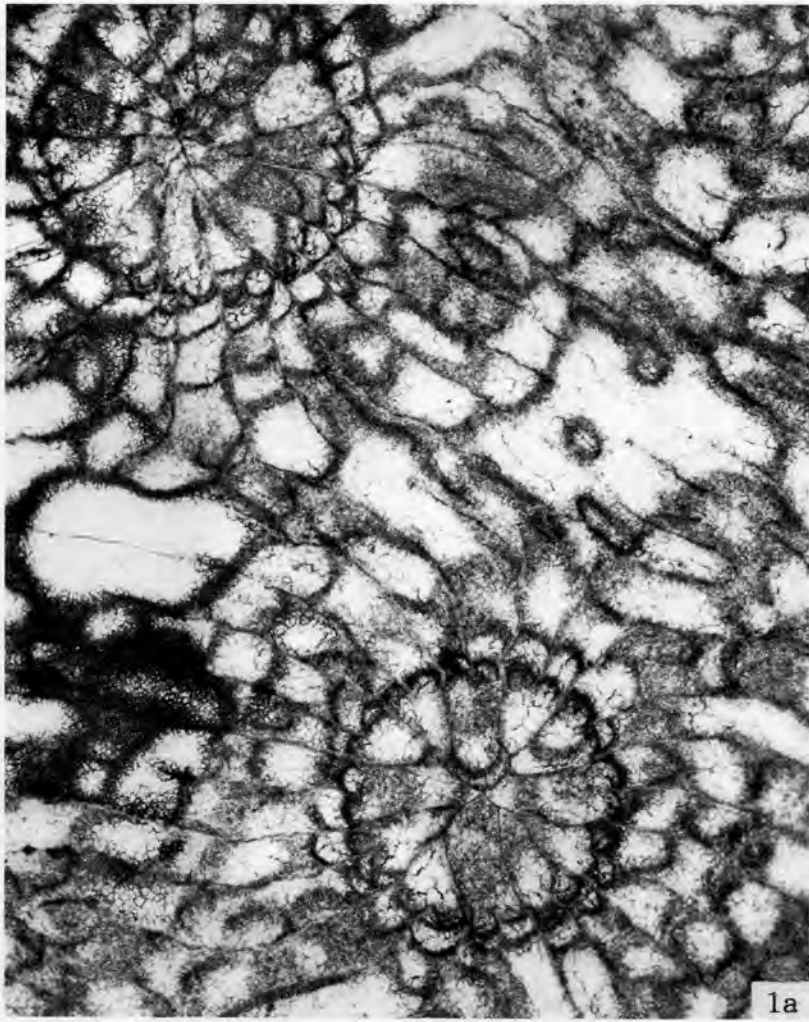
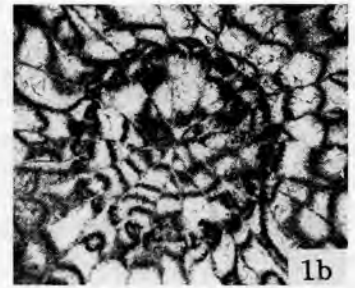


PLATE 9

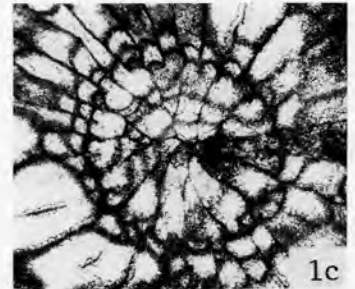
- Figs. 1a-1d. – *Sudetiphyllia prima* n. sp. Specimen UAM Tc-3/3. Holotype. Sudetes, Dzikowiec quarry, *Quasiendothyra cobeitusa* Zone, Strunian. Transverse sections. 1a, $\times 15$; 1b-1d, $\times 10$.
- Figs. 2a-2b. – *Donophyllum diphyphyloideum* FOMICHEV, 1939. Specimen 390/5030. Holotype. Donetsk Basin, Limestones K₈-L₅. Upper Bashkirian - Lower Moscovian. Transverse sections made 14 mm apart, $\times 3$.



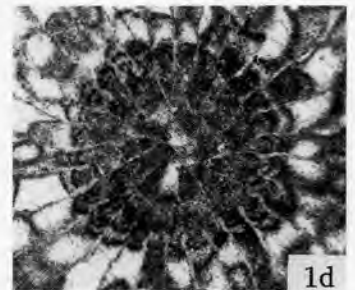
1a



1b



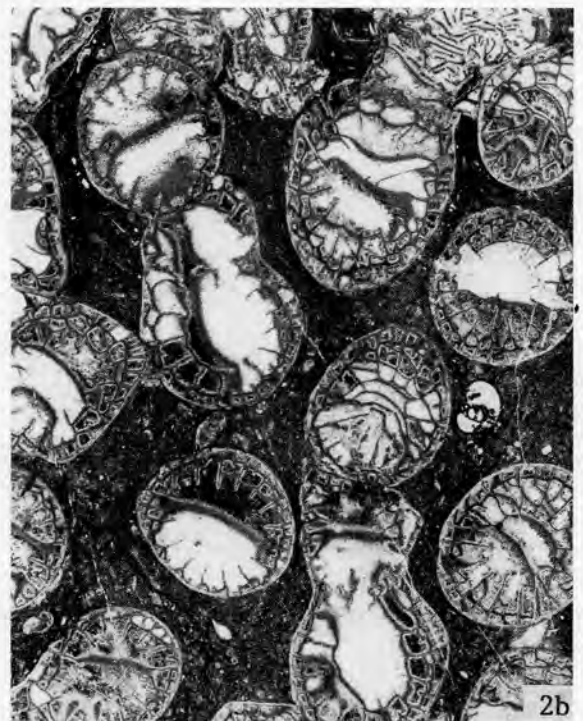
1c



1d



2a



2b

PLATE 10

- Figs. 1a-1c. – *Sudetiphyllia prima* n. sp. Specimen UAM Tc-3/3. Holotype. Sudetes, Dzikowiec quarry, *Quasiendothyra cobeitusana* Zone, Strunian. 1a. Longitudinal section, $\times 5$. 1b, 1c. Transverse sections, $\times 3$.
- Figs. 2, 3. – *Sudetiphyllia aphroides* n. sp. 2a-2c. Specimen UAM Tc-3/6. Sudetes, Zdanów borehole, depth 1891.9 m. *Quasiendothyra cobeitusana* Zone, Strunian. 2a, 2b. Transverse sections of individual corallites, $\times 10$; 2c. Longitudinal section, $\times 5$. 3a, 3b. Specimen UAM Tc-3/5. Holotype. Sudetes, Zdanów borehole, depth 1898.1 m. *Quasiendothyra cobeitusana* Zone, Strunian. 3a. Transverse section, $\times 3$; 3b. Longitudinal section, $\times 5$.

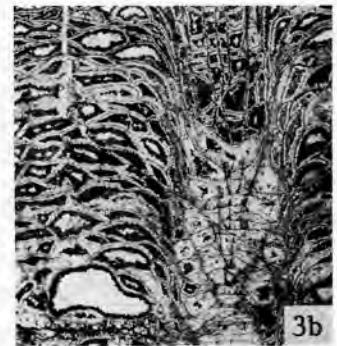
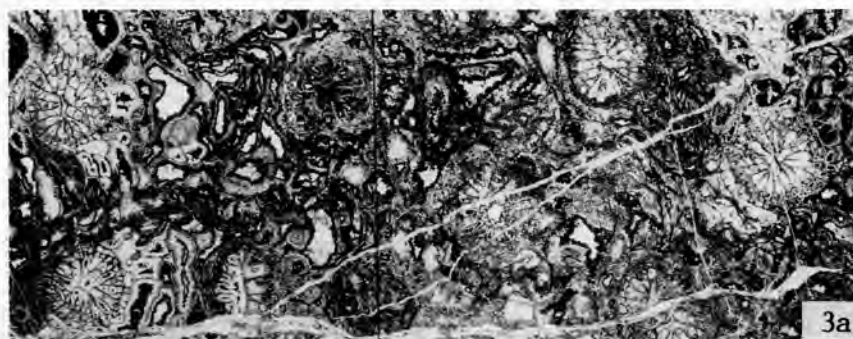
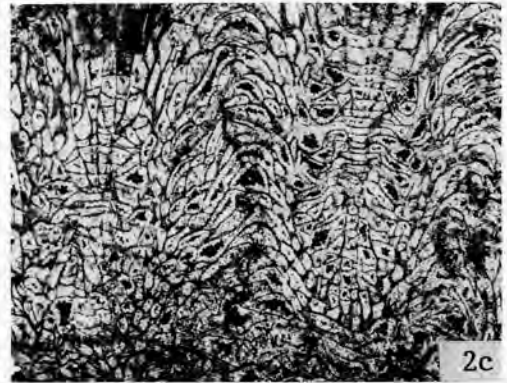
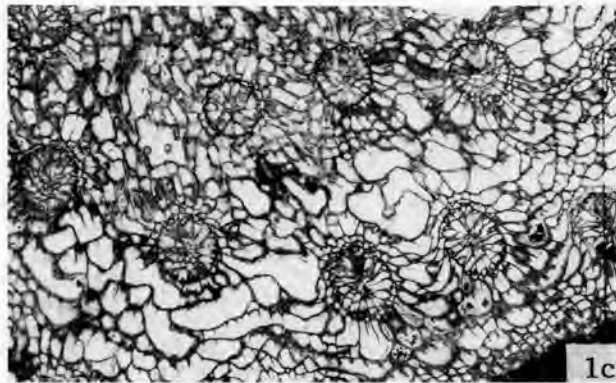
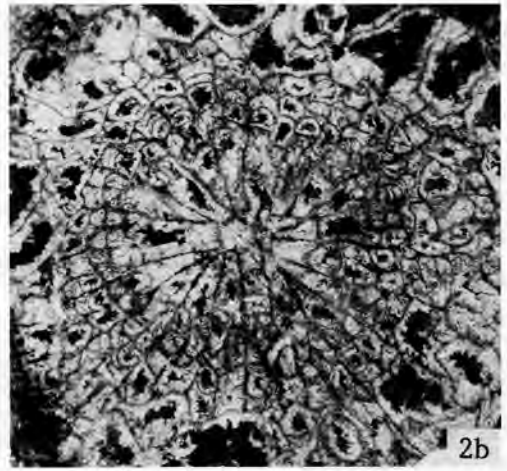
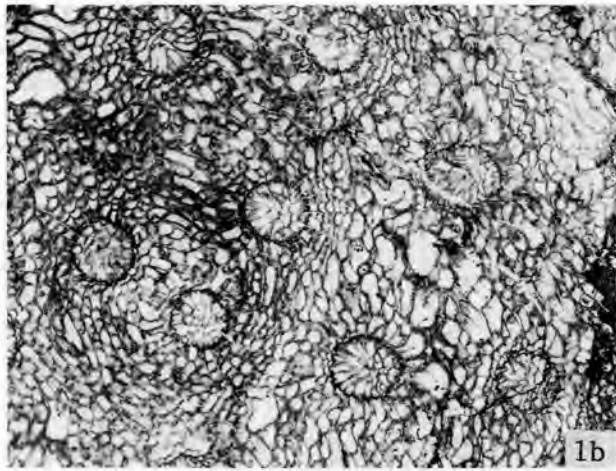
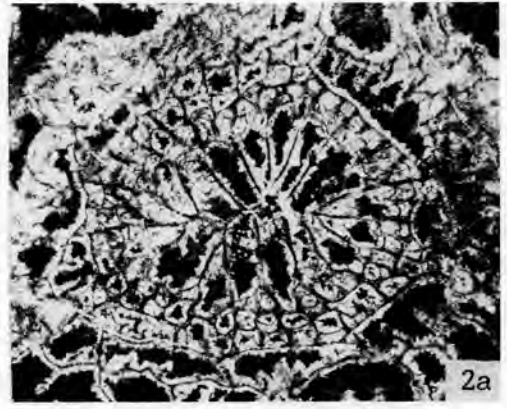
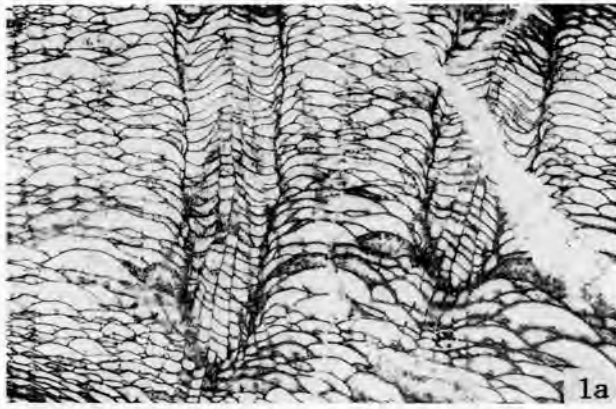


PLATE 11

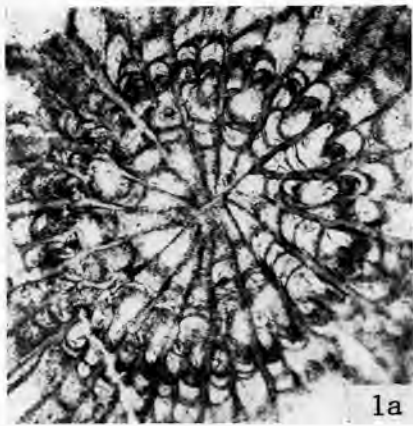
- Fig. 1. – *Sudetiphyllia aphroides* n. sp. Specimen UAM Tc-3/5. Holotype. Sudetes, Zdanów borehole, depth 1898.1 m. *Quasiendothyra cobeitusana* Zone, Strunian. Transverse section, $\times 5$.



PLATE 12

Figs. 1a-1e. – *Sudetiphyllia* n. sp. Specimen UAM Tc-3/8. Sudetes, Dzikowiec quarry. *Quasiendothyra cobeitusana* Zone, Strunian. 1a, 1b. Transverse section, $\times 10$; 1d. Transverse section, $\times 3$; 1c. Longitudinal section, $\times 5$; 1e. Longitudinal section, $\times 3$.

Figs. 2a-2b. – *Sudetiphyllia aphroides* n. sp. Specimen UAM Tc-3/7. Sudetes, Zdanów borehole, depth 1898.8 m. *Quasiendothyra cobeitusana* Zone, Strunian. 2a. Longitudinal section, $\times 3$; 2b. Transverse section, $\times 5$.



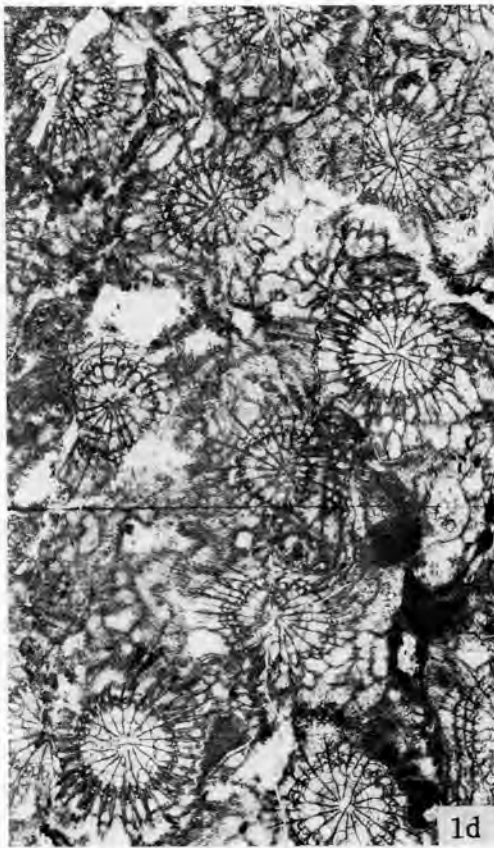
1a



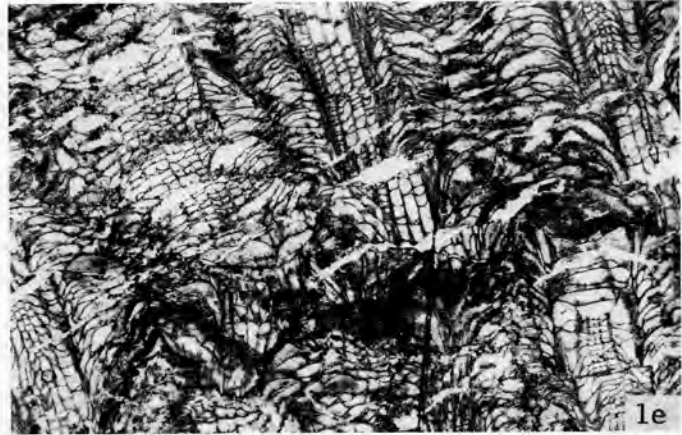
1b



1c



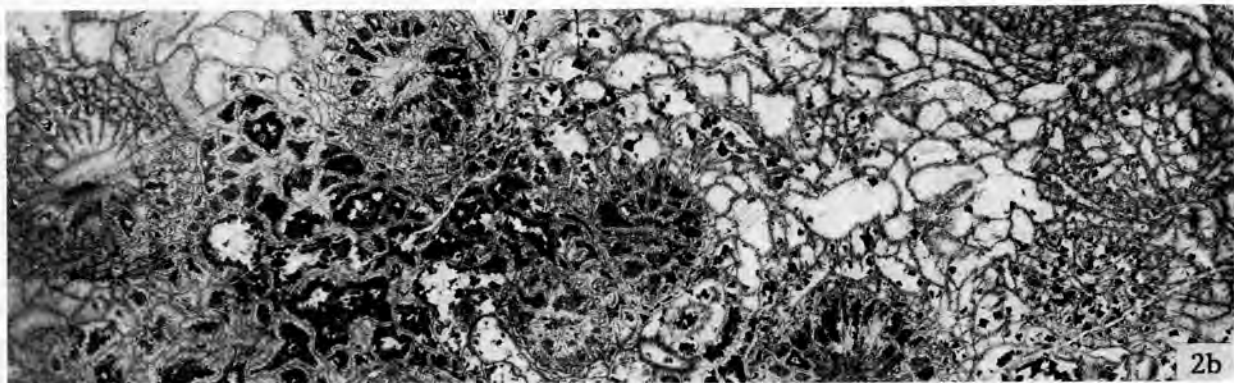
1d



1e



2a



2b

1910

1910

1910

1910