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# OFFSETTING OF POLYCOELIINA

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The composition of the suborder Polycoeliina is considered. This suborder includes mostly solitary corals, but colonial forms also occur. Mostly, they are small fasciculate colonies. Sometimes, only two or three offsets are developed. The basic mode of reproduction is intramural (lateral) increase, sometimes — intracalicinal offsetting and occasional division. Solitary and colonial coralites may be found within a single species. Offsetting in Lower Permian *Calophyllum dobrolyubovae*, in Upper Permian *G. kabakovitchae* and in Lower Carboniferous *Pentaphyllum dombaricum* is described. Division is observed in the two last species. Intramural offsetting, intracalicinal offsetting, division and rejuvenescence have been compared. Relationship between septal intensity and type of offsetting has been shown.

K e y w o r d s: corals, Rugosa, offsetting.

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## INTRODUCTION

The suborder Polycoeliina includes mostly solitary corals, but colonial forms also occur. I consider this suborder as consisting of two superfamilies and six families. The superfamily Plerophylliaceae Koker, 1924 includes the following families: Plerophyllidae Koker, 1924 (genera: *Oligophyllum* Počta, 1902; *Anisophyllum* Milne-Edwards et Haime, 1850; *Pentaphyllum* de Koninck, 1872; *Ufimia* Stuckenberg, 1895; *Pentamplexus* Schindewolf, 1940; *Paracaninia* Chi, 1973), Adamanophyllidae Vassiljuk, 1959 (genera: *Cystelasma* Miller, 1891; *Adamanophyllum* Vassiljuk, 1959; *Tachyphyllum* Dobrolyubova, 1966; *Flagellophyllum* Fan, 1962), Endotheciidae Schindewolf, 1942 (genus: *Endothecium* Koker, 1924). The superfamily Polycoeliaceae Roemer, 1883 includes the following families: Polycoeliidae Roemer, 1883 (genera: *Calophyllum* Dana, 1846; *Sochkineophyllum* Grabau, 1928; *Kinkaidia* Easton, 1945; *Pycnocoelia* Schindewolf, 1952), Prosmiliidae Ivanovsky, 1973 (genera: *Prosmilia* Koker, 1924), Numidiaphyllidae Flügel, 1976 (genus: *Numidiaphyllum* Flügel, 1976). In four of the six families mentioned above offsetting corallites or fasciculate colonies occur.

The family Adamanophyllidae contains offsetting corallites of *Cystelasma quin-*

*queseptatum* Stumm, 1948 from the Mississippian of North America (Stumm 1948) and small colonies of *Flagellophyllum shengi* Fan, 1962 from Lower Carboniferous deposits of China (Yü *et al.* 1962). Plerophyllidae reveals both solitary and offsetting corallites of *Pentaphyllum dombaricum* Iljina, 1980 from Lower Carboniferous deposits of the southern Urals (Iljina 1980). The family Polycoeliidae was also found to have colonial *Calophyllum dobrolyubovae* (Iljina, 1970) known from Lower Permian deposits of the south-eastern Pamirs and the Urals and *C. kabakovitchae* Iljina, 1977 — from the Upper Permian of the southern Primorie (Iljina 1970, 1977). The monotypic family Numidiaphyllidae is represented by the solitary and colonial forms of *Numidiaphyllum gillianum* Flügel, 1976 from Upper Permian deposits of Tunisia (Flügel 1976).

## MORPHOGENESIS OF COLONIES

The above-mentioned taxa did not develop colonies as large as those from the order Columnariida. Mostly, they are small fasciculate colonies. Sometimes, only two or three offsets are developed, as is the case of *Pentaphyllum dombaricum*. The latter should be regarded as microcolonies rather than true colonies.

*Calophyllum dobrolyubovae* and *C. kabakovitchae* form small fasciculate colonies reaching 5—10 cm in maximum height, and occupying 5—7 cm². The colonies are thinly-branched, with the diameter of corallites varying from 4 to 10 mm. In the first of the two species corallites are fairly parallel, while in the second one branching is rather irregular and offsets arising from the protocorallite are initially few in number. Then the intensity of offsetting increases progressively achieving its maximum in the upper part of a colony, where a rapid and chaotic branching is observed; newly-formed daughter corallites may grow even downwards. As a results small, often wide-crowned colonies develop in *C. kabakovitchae*. Sometimes they develop root-like shoots to support sharply deflected corallites (pl. 32: 6). In upper parts of some colonies a multiplied axial and lateral rejuvenescence of corallites is observed. This process may occur as a reaction against worsening of ecological conditions (pl. 35: 2, 3).

The basic mode of reproduction is lateral offsetting or, to be more precise, an intramural increase. At the beginning, the peripheral part of the parent corallite between two septa is separated by the tabula. Then the groove develops on the inner part of the external wall and subsequently evolves into a small cavity (0.4—0.5 mm) in the thickness of the wall. As the corallite grows, the groove becomes quickly overlapped with subsequent layers of fibrous tissue. A channel (pore) in the wall of the parent corallite is formed, connecting it with the embryonic daughter corallite. Then the wall is developed separating the two corallites.

This process was observed in detail in *Pentaphyllum dombaricum, Calophyllum dobrolyubovae* (pl. 32: 1) and *C. kabakovitchae* (pl. 32: 5, 7). The septal apparatus starts developing after the separation of a daughter corallite. Lateral offsets may remain in contact with the parent corallite but sometimes they branch off almost at the right angle (pl. 32: 6).

Intracalicinal offsetting was described in *Numidiaphyllum gillianum* and *Flagelophyllum shengi*. It was observed in *Pentaphyllum dombaricum* and *Calophyllum kabakovitchae* in addition to the lateral offsetting. The most careful study of this process was conducted on *Calophyllum kabakovitchae*. Here offsets appear more often at the periphery of the parent corallite.

The daughter's cavity (1.1 mm) is at the beginning separated by a tabula but in contrast to the lateral offsetting the tabula, septa and usually the external wall of the parent corallite serve in this case as bases for new septa of a daughter individual. An independent wall develops later (pl. 33: 1) and the daugther corallite becomes separated completely from the parent corallite (pl. 33: 5*a*). Intracalicinal offsetting does not take place in all corallites. These offsets appear more often in an upper mature part of the colony. It is not unusual to observe the simulataneous formation of several offsets by means of both lateral and intracalicinal offsettings. In the last case, the parent corallite dies (pl. 34: 2). The same is observed when an offset develops near the axial part of the calice. During intensive offsetting, lateral and intracalicinal offsets may grow simultaneously or immediately one after another. Corallites developed by means of intracalicinal offsetting show only lateral mode of reproduction. Such corallites become sometimes amplexoid; offsetting is never observed at this stage, however (pl. 34: 1*b*). The amplexoid stage is apparently gerontic. Corallites developed by means of lateral offsetting have both lateral and intracalicinal offsets. Some corallites within a colony did not develop offsets. Possibly in polyps of these corallites planulae were produced and in this case the colonies were polymorphic.

Judging from the illustration of Yü, Lin and Fan (1962: pl. 1: 5*b* reproduced herein — fig. 1) the corallites of *Flagellophyllum shengi* are often in contact with each other and sometimes fuse. Thus, these small colonies are transitional between fasciculate and massive forms.

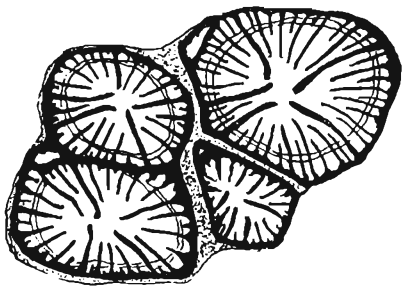

Fig. 1. *Flagellophyllum shengi* Fan, 1962 (1962: pl. 1: 5*b*). Transverse section of a massive colony, ×2; 5, China, Chinhai Province, Shinhan, Lower Carboniferous.

The asexual reproduction in Polycoeliina was mainly effected through offsetting but division is also observed sometimes, e.g. in *Pentaphyllum dombaricum* and *Calophyllum kabakovitche*. The division in *Pentaphyllum dombaricum* is accomplished in the following manners: 1) A growing metaseptum divides the parent corallite into two approximately equal parts. One part retains the counter and counter-lateral protosepta, and the other — the cardinal and alar protosepta respectively (fig. 2;

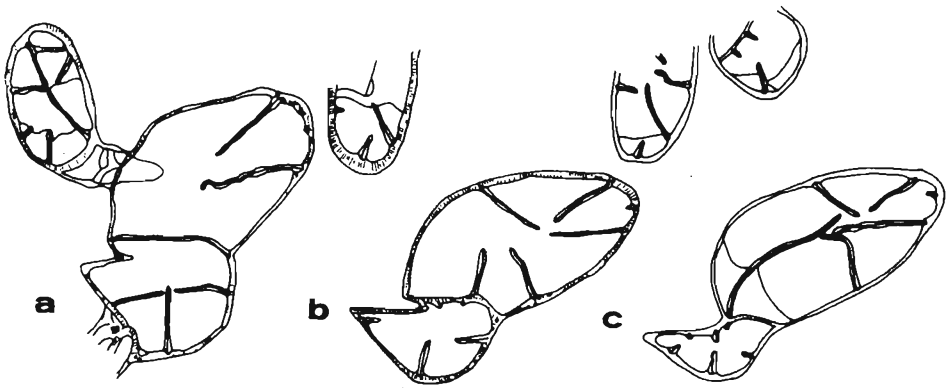


Fig. 2. *Pentaphyllum dombaricum* Iljina, 1980, PIN 2899/603. Division of a corallite, transverse sections (*a* slide 1, *b* peel 2, *c* peel 5), ×10; South Ural, Aktyubinsky region, r. Dombar, Lower Carboniferous, Serpukhovian stage.

pl. 34: 4). In daughter corallites the lacking protosepta are regenerated. But at the same time one of the separated parts gets reduced, decreasing its size. The complete separation of branches was not observed and the uncertainty remains about viability of the latter. 2) A corallite oval in section is divided into two parts by both an elongated metaseptum adjacent to one of the counter-lateral protosepta and the cardinal septum deflected towards the centre of a new corallite. As a result one of the two parts inherited two protosepta of the parent corallite: the shortened alar and deflected cardinal; the other part inherited four protosepta: the counter, one alar and two counter-laterals. One metaseptum is initially inserted in this part. In the former, poorer part, four septa are inserted at the elongated metaseptum and the inherited external wall. All of them are directed towards the centre of the new corallite (pl. 34: 5). The role of protosepta in dividing corallites is not yet clear, because no complete separation and subsequent development have been observed. The two cases mentioned above reveal the division as occurring almost simultaneously with the formation of lateral offsets or immediately after these.

During the division of *Calophyllum kabakovitchae* the parent corallite at first elongates its diameter, then in the middle of the corallite a constriction appears and a partition begins to form. In each of the two parts being formed there are three inherited protosepta and new septa are developed. Gradually, the daughter corallites break off completely (pl. 35: 1). This mode of division is analogous to that of Scleractinia. Division as a mode of reproduction is rarely observed in Polycoeliina occurring as an exception and practically having no taxonomic significance.

While the intramural (lateral) offsetting is somewhat isolated process, the intracalicinal offsetting, division and rejuvenescence are very similar. In all cases a part of the cavity of the parent corallite is used. In intracalicinal offsetting, however, this part is very small, and the daughter corallite displays the highest degree of separation developing its own septal apparatus. Rejuvenation involves larger or smaller parts of a parent corallite, together with its septal apparatus. In axial rejuvenescence the diameter of a calice decreases, its axial part does not deviate and most or all

major septa of the rejuvenating corallite continue to develop. In lateral rejuvenescence the centre of a decreasing corallite deviates and only some septa are continuing to develop. New septa appear at a new wall being directed towards the new centre. Thus the symmetry of the body of the polyp is not disturbed either in axial or in lateral rejuvenation, while in intracalicinal offsetting the symmetries of the daughter and the parent corallites do not coincide. In the case of division the connection between the two newly formed corallites is most complete. All or majority of septa of the parent corallite are continued to develop; new septa appear at the newly formed wall.

Fedorowski (1978) indicates the resemblance between peripheral offsetting and rejuvenescence. Describing asexual reproduction in *Heritshioides* sp. he noted that the colonies, figured by him in pl. 20: 2*a* and 6, represent lateral rejuvenescence. But judging from the size of young corallites disposition and septal arrangement it is intracalicinal offsetting rather than lateral rejuvenescence. In small colonies of Polycoeliina lateral and intracalicinal offsetting and sometimes division are observed, but solitary form also occur in the same species. It is interesting to note that offsetting and dividing corallites in *Pentaphyllum dombaricum* increase their diameter more rapidly than the solitary ones. They acquire a conical form, while solitary corallites have a subcylindrical, worm-like shape (pl. 32: 2, 3).

## THE RELATIONSHIP BETWEEN THE INCREASE OF SEPTA AND THE TYPE OF OFFSETTING

In the initial stage, lateral offsets are smaller in size (0.4—0.5 mm) than intracalicinal ones (1—1.5 mm). Moreover, in lateral offsetting corallites are formed with deeper calices (for example up to 5—7 mm in *Calophyllum kabakovitchae*), than in intracalicinal offsetting (up to 1.5—2 mm). In the first case the septal apparatus develops relatively slowly and individual septa appear at different levels of the calice. At the same time, in the shallow calices of corallites formed by means of intracalicinal offsetting the septal apparatus develops more quickly and septa appear one after another at short time intervals. Besides, these corallites have better developed septa. For example, during early ontogeny of *Calophyllum kabakovitchae*, the lateral offsets having a diameter of about 1.5 mm display as a rule only the cardinal and counter protosepta which protrude into the tabularium as small teeth, while the alar septa are inserted within the wall (pl. 32: 5). The intracalicinal offsets of the same diameter have all six protosepta well-developed and reaching the centre (pl. 33: 1*b*). The essential difference between corallites that developed in different ways is displayed at the mature stages as well. Corallites which developed by means of lateral offsetting have rather short metasepta and counter-lateral protosepta. These septa are often found to be reduced and to advance only as the fibrous stage. These corallites always have four well-developed protosepta that sometimes appear to be the only well-developed ones in the tabularium (pl. 33: 2, 5*c*). Corallites developing by means of intracalicinal offsetting have the first order septa reaching

the trabecular stage and usually adjoin at the centre (pl. 33: 5*b*). However, the four protosepta are not always thick which makes them difficult to be distinguished among the rest of the septa of the first order. Nevertheless, all lateral offsets developing from these corallites have four pronounced protosepta.

The most advanced development of septal apparatus is observed in corallites which evolved not only by means of intracalicinal offsetting but also in a course of the process of rapid rejuvenescence. In the first case it is probably due to the closer connection of the offsets with the parent corallite in the early stages. The second case is explained by the more favourable position of the rejuvenescent corallite which is protected by the walls of the left calice.

Thus Polycoeliina appears to have not only solitary forms but also offsetting forms, small fasciculate as well as subphaceloid colonies. Asexual reproduction in Polycoeliina was effected through lateral and intracalicinal offsetting and occasional division. Solitary and colonial corallites may be found within a single species. It suggests that the form of growth is an unimportant taxonomical feature for these corals.

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## EXPLANATION OF THE PLATES 32—35

### Plate 32

1. *Calophyllum dobrolyubovae* (Iljina) 1970. Holotype 2376/68, *a*, *b* stages of division of the lateral offset (*a* slide 48, *b* peel 71), ×10; *c* peel 35, ×. South-Eastern Pamir, Igrimyus river, Lower Permian, Artinskian stage.

2, 3. *Pentaphyllum dombaricum* Iljina, 1980. *2* Specimen N 2899/616, subcylindrical solitary coral, ×2. *3* Specimen 2899/615, offsetting corallite, ×2; South Urals, Aktyubinsk region, Lower Carboniferous, Serpukhovian stage.

4—7. *Calophyllum kabakovitchae* Iljina, 1977. *4* Specimen 2873/838A, lateral offsetting, ×4; Far East, Southern Primorie, Nahodka, Upper Permian, Dzhulfian stage, Ludyansian horizon. *5* Specimen N 2873/487, septa appearing in the lateral offset, slide 2, ×16; Far East, Southern Primorie, Lake Voltchanets, same age. *6* Specimen 2873/815A, lateral offsetting, ×8; Far East, Southern Primorie, Nahodka, same age. *7* Specimen N 2873/483, lateral offsetting, transverse sections (*a* slide 1, *b* slide 2), ×10; Far East, Southern Primorie, Lake Voltchanets, Upper Permian, Dzhulfian stage, Ludyansian horizon.

## Plate 33

1—6. *Calophyllum kabakovitchae* Iljina, 1977. *1* Specimen N 2873/490, septal development in the intracalicinal offset (*a* slide 1, *b* slide 4), ×10; Far East, Southern Primorie, Lake Voltchanets, Upper Permian, Dzhulfian stage, Ludyansian horizon. *2* Specimen 2873/838, cross section of the intracalicinal offset, slide 27, ×15; Far East, Southern Primorie, same age. *3* Specimen 2873/547A, cross section of the septum, ×50; Far East, Southern Primorie, Lake Voltchanets, same age and locality. *4* Specimen 2873/472, cross section of the corallite with intracalicinal offset, slide 2, ×15; same age and locality. *5* Specimen 2873/846, *a* cross section of corallites and an intracalicinal offset, slide 1, ×8; *b* corallite, formed by lateral offsetting; Far East, Southern Primorie, Nahodka, same age. *6* Specimen 2873/726A, simultaneous division of two intracalicinal offsets, ×10; same age and locality.

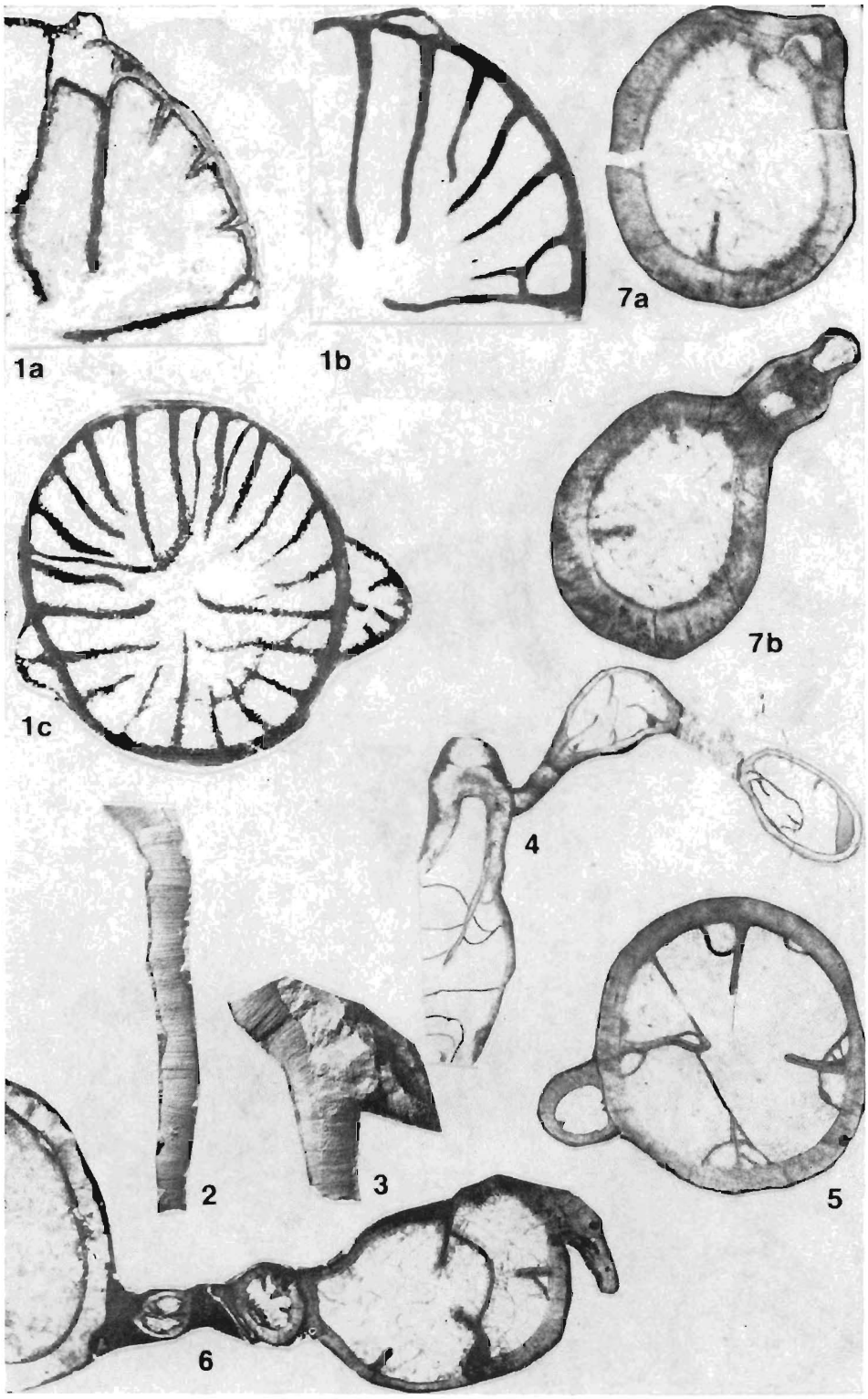
## Plate 34

1—3. *Calophyllum kabakovitchae* Iljina, 1977. *1* Specimen 2873/851, *a* intracalicinal offset with root shoot and lateral offset, slide 6, ×8; Far East, Southern Primorie, Nahodka, Upper Permian, Dzhulfian stage, Ludyansian horizon. *2* specimen 2873/838, longitudinal section of the corallite with lateral offset and two intracalicinal offsets, slide 24, ×; same age and locality. *3* Specimen 2873/811A, longitudinal section of the corallite with lateral offset, ×5; same age and locality.

4, 5. *Pentaphyllum dombaricum* Iljina, 1980. *4* Specimen 2899/603, cross section of a dividing corallite, ×10; Southern Urals, Aktyubinsk region, Dombar river, Lower Carboniferous, Serpukhovian stage. *5* Specimen 2899/59711, cross sections, division stages (*a* slide 1, *b* slide 3), ×10; same age and locality.

## Plate 35

1—3. *Calophyllum kabakovitchae* Iljina, 1977. *1* Specimen 2873/838, stages of division (*a* peel 13, *b* peel 15, *c* peel 16, *d* peel 17), ×8; Far East, Southern Primorie, Nahodka, Upper Permian, Dzhulfian stage, Ludyansian horizon. *2* Specimen 2873/718, axial rejuvenescence, slide 2, ×10; same age and locality. *3* Specimen 2873/838B, lateral rejuvenescence, slide 15, ×8; same age and locality.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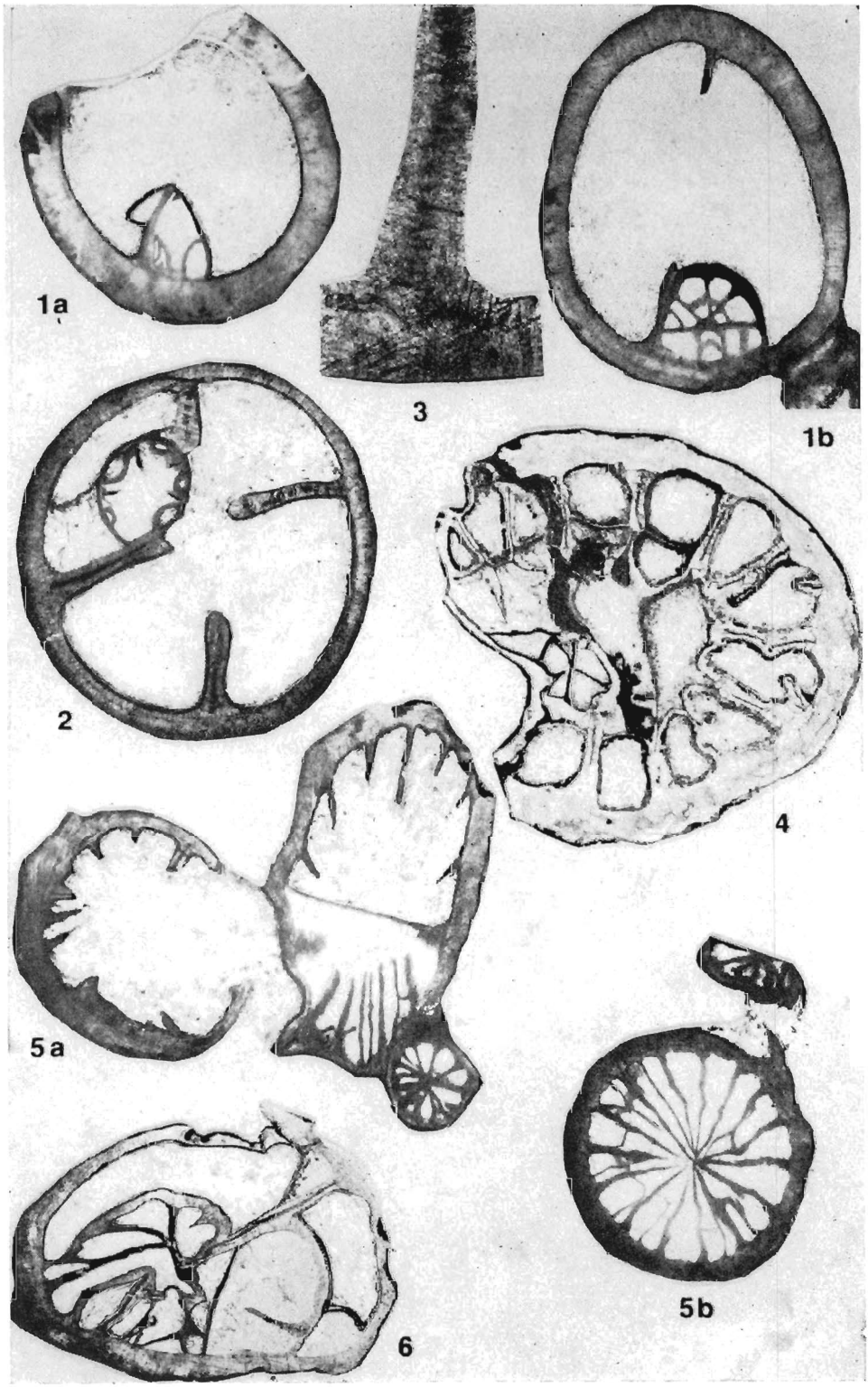
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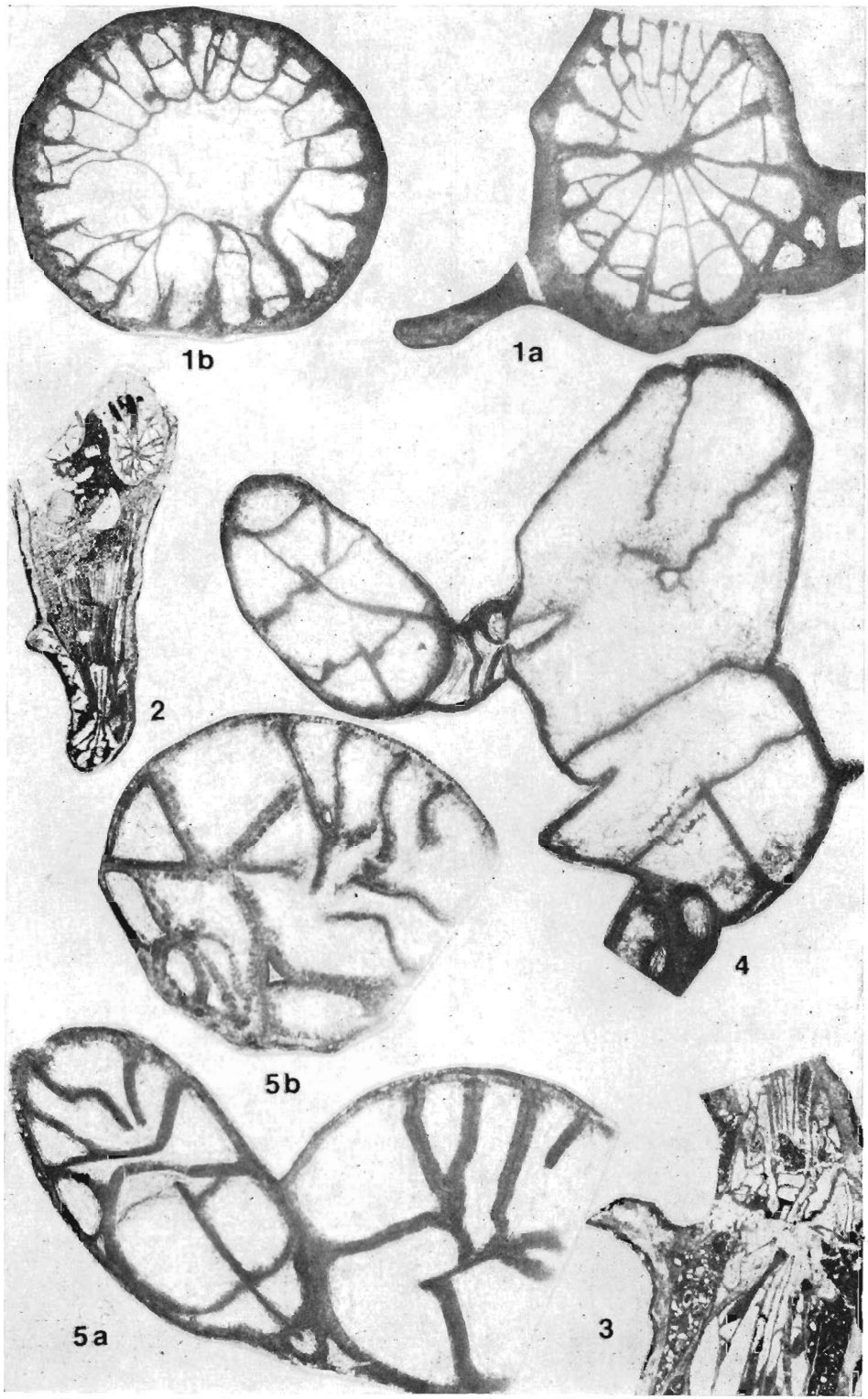
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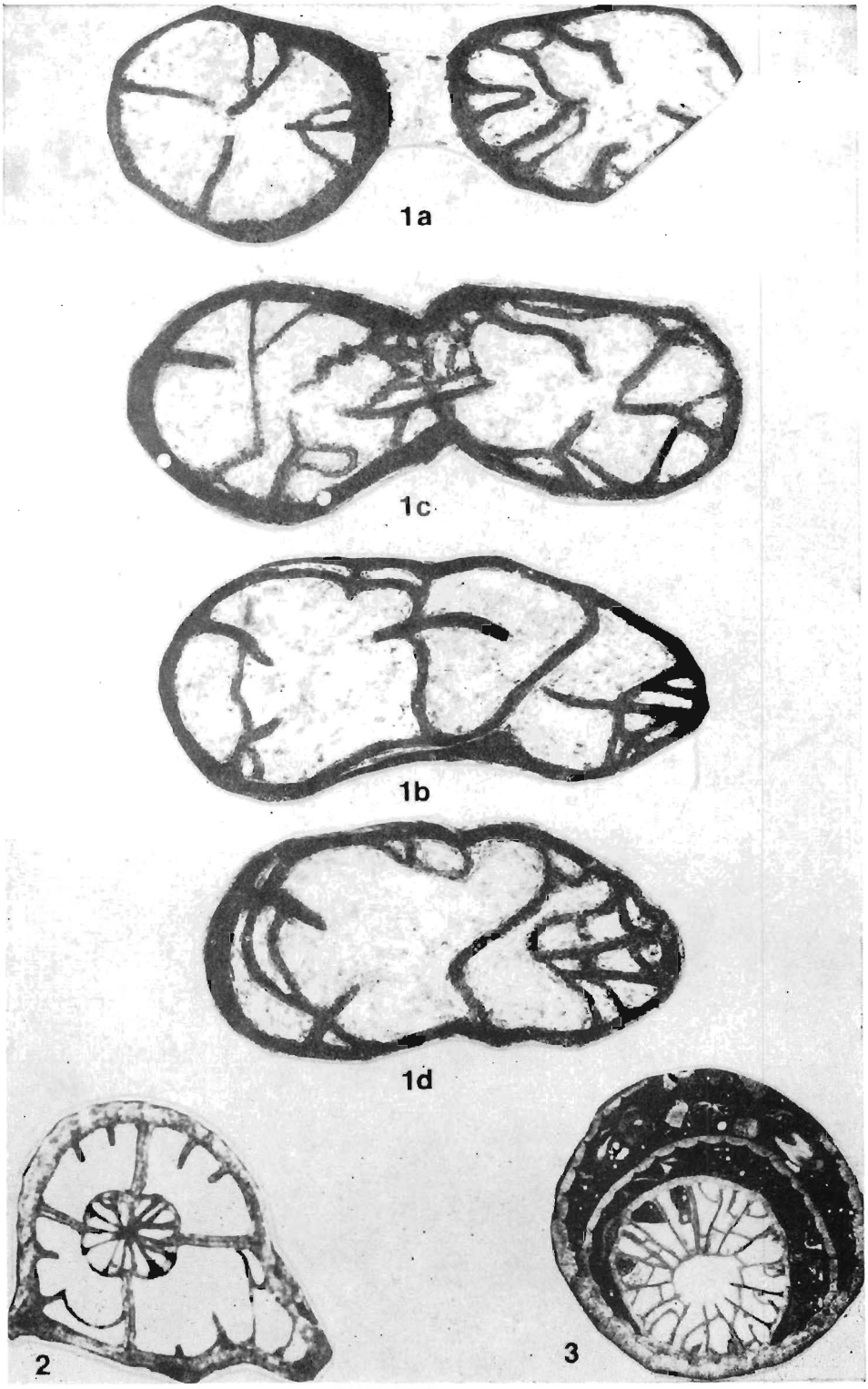
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