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SOME ASPECTS OF CORALS

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Blastogeny in Anthozoa was compared to the parallel process in Hydrozoa with a brief discussion on the cells reorganization and genetic control of the process. Discussion on astogeny was restricted to fusion of corallites and colonies with some attention being paid to the regeneration within colonies. Four types of fusion were discussed: 1. fusion within coenenchymal colonies, regarded as a self-regulation. 2, 3. fusion within fasciculate colonies and fusion of solitary corals, interpreted as being connected with a reproductive cells exchange; 4. fusion of coenenchymal colonies, thought to be a sample of interspecific aggression. Formation of gregaria was briefly discussed as a phenomenon similar to coloniality.

K e y w o r d s: corals, coloniality, gregaria.

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INTRODUCTION

The present paper is in its larger part concentrated on some poorly known phenomena connected to coloniality. A review of the current achievements in studies on various aspects of coloniality in corals is given here only as a form of introduction to individual chapters or is omitted. Three groups of topics can be distinguished in coloniality studies: formation of offsets (blastogeny), development of colonies (astogeny), and formation of gregaria. In none of these topics all of majority of problems are solved.

BLASTOGENY

This term covers all processes leading to formation of a new individual by means of separation of part of a parent's polyp body into a daughter's polyp body. At least three different stages of this process have to be distinguished and discussed:

(1) genetic determination of the process and its regularity or random; (2) initial stage of development on the cellular level, i.e. an incipient stage of differentiation of cells and their groupping into future parts of a new animal and its bodily organs; (3) a beginning of development of organs and skeletal parts of a new individual.

1. *Genetic determination.* Investigation on various hydras provide several pieces of information which can be probably transplanted into Anthozoa. It is generally accepted by students of living Hydrozoa that the process of budding and colony formation is genetically determined on the cellular level. I believe (Fedorowski 1978) that regular or random appearance of genes that determine a colonial form of growth leads to a formation of quasi-colonies, incipient colonies and normal colonies of various types. This thesis is not confirmed by investigations of living Scleractinia.

2. *Initial stage of development.* Interpretation of genetic and cellular observations in Hydrozoa are not identical and at least two main tendencies can be distinguished: a) Budding in Hydrozoa is compared to a somatic embriogenesis, i.e. to a complete reorganization of the budding part of the body by means of the anarchy of cells (Tokin 1959; Ivanova-Kazas 1977). That early stage of differentiation is stimulated by extrinsic factors. The leading role of the interstitial cells (I-cells) is not confirmed (Diehl 1973). Further development of budds proceeds under a control of intracolony factors and can be compared to a process of organs formation (Ivanova-Kazas 1977: 221—222). b) Budding and colony organization in Hydrozoa is caused by cells migration. In contrast to the first group of students, the I-cells are highly valuated by the second group (e.g. Weiler-Stolt 1960; Campbell 1974; Breverman 1974). Not an anarchy but a migration and agglomeration of I-cells form the first stage of budding in Hydra. Well documented papers of Campbell (*l.c.*), Breverman (1969, 1974) and others advocate strongly for the second interpretation.

3. *The beginning of development of organs and skeleton.* Palaeontological studies start only somewhere on this stage of budding, where differences in a parent's polyp body are already reflected in its skeleton. It is not clear from the fossil records which part of a skeleton should be considered as being secreted already by a daughter individual. It seems very possible, however, that formation of septal swellings can be interpreted as taking place after polarisation of cells into bodily organs of a new polyp. Thus, the swellings can well be compared to the initial stage of a skeleton formation in larvae (Vandermuelen and Watabe 1973) and, consequently, classified as an initial stage of a skeleton formation in an asexually produced individual. Genetic control of the process of blastogeny in Rugosa and environmental impoulses for its initiation were deduced by Fedorowski (1978) from the study of the Lower Permian *Heritschioides.*

ASTOGENY

"Astogeny is the development of a colony and can be described in terms of form, increase, pattern and individual morphology". (Oliver 1968: 18). None of the listed topics is completely studied and in some of them only an initial work has been done. From all problems connected to astogeny only two will be discussed in more

detail: (a) fusion of corallites, polyps and colonies; (b) regeneration of colonies. The first problem has already been briefly discussed (Duerden 1903; Roniewicz 1966; Khoa 1977) but has not been systematized and was weakly documented, especially as far as rugose corals are concerned. Problems connected with regeneration in hydras were subjects of many papers. These concerning living Scleractinia and extincted groups of Anthozoa remain almost unknown.

The following three stages of fusion can be distinguished on a basis of the up to date studies: (1) fusion within a coenenchymal Scleractinia (Roniewicz 1966) and in pseudocerioid (= coenenchymal) colonies of Rugosa (Khoa 1977); (2) fusion within a frame of a single fasciculate colony of Rugosa (Khoa, *l.c.* and in this paper) and in the tabulate-morph corals (many records of connecting tubes, pores, etc.); (3) fusion of different pseudocerioid colonies. A problem similar to the latter one is separately discussed by Stasińska (1980) in cateniform colonies of *Halysites*. A fusion of two solitary corals is discussed to show that such a phenomenon can also be observed.

FUSION IN COENENCHYMAL COLONIES

This is the simplest stage of the process from the biological point of view. *Pseudocoenia longiseptata* (Roniewicz 1966: 172) which provides one of the discussed samples is a coenenchymal coral. Fusion in some corallites and their polyps can be interpreted as an action leading towards reduction of a number of individual gastro-vascular cavities in order to increase size of some of them. It can be tentatively speculated that large polyps produced from the fused ones served as larvae depositories similar to those observed by Duerden (1902). Fusion of very young polyps (corallites) observed by Khoa (1977) in a pseudocerioid colony of *Actinocyathus* permits to interpret the process as a simple reduction of a polyp not needed for functioning of the integrated colony. In both samples discussed there was no immunological barrier to be crossed and both the events can be considered as a kind of a self-regulation of integrated colonies.

FUSION OF CORALLITES WITHIN FASCICULATE COLONIES

Fusion in fasciculate colonies of rugose corals was for the first time described by Khoa (1977: figs. 7, 8). The process led to a complete integration of two young individuals and the reason for this is not clear. Observations of mine on *Yabeiphyllum rossi* were conducted not on a young but on the morphologically mature corallites, completely separated by epithecal walls (pl. 26: 1*a*). In the course of development some corallites on a given levels of the colony growth came into a temporary fusion by loosing their external walls and forming channels (pl. 26: 1*b*). A temporary character of fusion and its simultaneous appearance within the colony makes possible to interprete it as connnected with the breeding period. To exchange reproductive cells directly between polyps instead of having them extruded into the surrounding water was possibly a reason for that temporary fusion. Samples

are known in Actiniaria that sperm and eggs releasing individuals can temporarily get in close touch (Nyholm 1943) forming a kind of a chamber in their attached bases. Eggs and sperm are extruded into that chamber what increases a chance for fertilization. Also Spaulding (1974) observed that fertilization and brooding seems to be quiet common within the sea anemones, although a mechanism of it is uncertain. The comparatively long period of the fused growth of the here discussed specimens remains unclear. Nyholm (*l.c.*) reported of only two days of attachements of *Sagartia troglodytes*.

According to my knowledge there are no epithecae producing fascicluate colonies of Scleractinia in which connecting pores or channels were reported. Roniewicz (1976) described such a phenomenon in plocoid colonies of *Solenocoenia,* however. In fasciculate colonies of Rugosa this character is rare, but in addition to the two samples mentioned above, it can also be found in some *Waagenophyllum* (Dr. D. Weyer, personal comm.). Among cerioid colonies of Rugosa only *Parawentzelella* Fontaine is so far known as producing similar connecting channels. This character is very common among the tabulate-morph corals, majority of which produced pores or connecting tubes. Many of these structures show regularity in appearance large enough to be interpreted as being produced during more or less constant breeding periods in order to directly exchange sexual products. *Tetraporinus wittenburgi* Sokolov, *Thecostegites rossicus* Sokolov (1962: 238, 239), *Natalophyllum dubiensis* Nowiński (1976: pl. 13: 2*a*) and many other species provide spectacular illustration to this thesis. The breeding activity could have been the moon-controlled events, similar to that recognized by Atoda (1947, 1951) for planulae of living Anthozoa. A calculation similar to those made by Wells (1963) and Scrutton (1965, 1978) may answer this question.

The temporary fusion of polyps and corallites needs special investigation. It seems logical to expect a genetic control upon the process. Whatever the final explanation for these events will be, it is obvious that similarly like in the first case, no immunological barrier exists, because we are still dealing with intracolony occurrences.

FUSION OF PSEUDOCERIOID COLONIES

Only a single specimen from the Lower Permian deposits of Spitsbergen was available for study (pl. 27: 2*a*). It has been discovered that the wall separating the two accreted colonies does not differ from walls separating particular corallites within these colonies at least in the transmitted light (pl. 27: 2*c*—*e*). In neither of these walls three layers, commonly considered as present in cerioid colonies is observed. All of them show the fine structure identical with the fine trabecular septa of densely packed but well distinguished centres of calcification (pl. 27: 2*c*—*e*). Thus, all three walls discussed have to be considered as having been secreted as partitions not dividing walls (Fedorowski and Jull 1976 distinction). Consequently, the

colonies have to be considered as pseudocerioid. This was earlier suggested by Fedorowski (1965) on the basis of blastogenetic studies. Basal, but septum-like origin of partition has been documented by Fedorowski (1978) by direct observations in calices.

If colonies discussed are pseudocerioid, as deduced, the sample under consideration represents the highest known level of fusion, because two colonies, each of which was linked by descent from different larva, were united. This should have produced an immunological barrier strong enough for making any fusion imposible, but it did not. Fusion of soft tissue and skeletons of two colonies of *Scolymia cubensis* described by Lang (1971) was interpreted as an interspecific aggresion. The sample discussed here may illustrate the same sort of events in rugose corals, because one of the fused colonies is much smaller and its peripheric corallites are obviously suppressed by these of the larger colony (pl. 27: 2*a*).

REGENERATION

All specimens discussed came from the Devonian of Belgium and belong to Dr. M. Coen-Aubert (Institut Royal des Sciences Naturelles de Belgique), who also was so kind as to take pictures illustrating the following remarks. In each case observed the walls are in normal circumstances well developed. In each case, however, when one or more polyps were wounded or destroyed, at least some of the adjacent polyps were fused with the former by stopping development of skeletal walls. In the case of larger scale of destruction a form of a colony was locally changed into plocoid. In the areas of destruction involving only parts of individual polyps (pl. 28: 1, 2) the polyps and corallites adjacent to that wounded part became completely integrated with it by loosing their external walls. This allowed easier communication and supply of the wounded individual with needed nutritions. In addition to the complete integration two kinds of reaction of individuals adjacent to the wounded polyp were observed: 1. They expanded towards it by producing offsets which gradually replaced the wounded individual (pl. 28: 2). It seems striking that no action is noted at the healthy part of the wounded individual. This is possibly because no rearrangement of the colony architecture is required there. 2. Another sample (pl. 28: 1) illustrates an advanced stage of the regeneration with new walls being already built as continuations of some septa of the wounded individual (upper arrows). These walls started to separate particular aid-bringing polyps and corallites from each other and from the remainings of the wounded individual (pl. 28: 1). The latter has probably been incorporated by the adjacent individuals in the course of their further growth. This can be deduced from the rearrangement of septa and their separation from the old external wall (lower arrow). In the either case discussed we are dealing not with the regeneration of an individual polyp and corallite for and by itself, but with the regeneration of the colony. Remainings of the wounded soft tissue were able to produce a normal skeleton (pl. 28: 2, lower left). This could have been possible only in a case of a support from

the neighbouring polyps because the gastro-vascular cavity of the wounded polyp was obviously destroyed. All these observations allow to consider the colonies discussed as being pseudocerioid in spite of apparently three-layer walls stated in these species by Sorauf (1967).

FUSION IN SOLITARY CORALS

This phenomenon was observed on two samples of *"Duplophyllum"* sp. from the Middle Permian of Texas (pl. 27: 1 and pl. 29). The specimens in question obviously tended to meet each other (pl. 27: 1*a*; pl. 29). They lost their walls after some period of growth in touch and became temporarily fused. In addition to a break of secretion of external walls there was also a wide channel formed (pl. 27: 1*b*) by a rearrangement of external parts of septa. This period of a fused growth is short and the specimens divided themselves again, continuing to grow parallel to each other, however (pl. 27: 1*a*).

The mentioned phenomenon is considered here as the ability for the exchange of reproductive cells. A comparatively short period of fusion of morphologically mature specimens and formation of a special channel strongly advocate for this suggestion. It is obvious again that no immunological barrier existed at the time of fusion. On the other hand, however, the development in fusion was unacceptable for the specimens either because of a lack of proper adaptations or because of a somatic regulations or genetic determination. It can also be speculated that the barrier was ceased only for the period of fertilization and was reactivated immediately after, pushing both polyps to separate. If a comparison between the described event and the recent Actiniaria is done, both the fused specimens could have been gymnodioecius hermaphrodites as *Epiactis prolifera* and other sea anemones described by Dunn (1977) are. The described phenomenon can also be compared with observations of Nyholm (1943), but it has to be said that no fusion among the recent sea anemones is observed.

FORMATION OF GREGARIA

This topic represents an aspect of animal life, the coral workers seldom approach to. In spite of that, the problem seems to be very interesting from at least two points of view: biological and taxonomic. The following introductory remarks only touch the topics.

The biological aspect is mostly restricted to studies on larvae and their habits, since gregaria can be formed only be closely settled larvae. Several reasons such as substrate requirements, length of the free-swimming period of life, activity of currents, etc. have already been said as responsible for the coral distribution upon the sea bottom. All these criteria are certainly important, but there seem to exist species and possibly also genera in which formation of gregaria is so frequent that it can

be considered as a diagnostic character for taxonomy. In the case of such species I would predict an existence of a kind of tropisms inducting a given larva to settle close to the other animals of the same species. The Permo-Carboniferous genus *Carinthiaphyllum* Heritsch, 1936 forms a good example of such gregaria. The spectacular sample from the Wolfcampian of Texas (pl. 26: 2*a*, *b*), investigated in detail in serial sections makes it clear that we are dealing with a gregarium of vermitid-shaped, elongated corallites, which grew so closely to each other as to form a phaceloid type of pseudocolony. In this and in similar samples (e.g. *Koninckinaotum pseudocoloniale* Fedorowski, 1971) two facts are stricking: (1) only larvae of the same species settled together; (2) specimens are differentiated in ontogenetical development what makes clear that gregaria were acting as comparatively long-lasting larvae settlements. Consequently, it can be hypothesized that either there was a selection made by members of these gregaria, accepting larvae of only their own species to settle, or larvae themselves preferably chosen development in gregaria for some reasons. However it was, some kinds of tropisms coordinating growth of gregaria can be expected.

REFERENCES

BREVERMAN, M. 1969. Studies on hydroid differentiation. IV. Cell movements in *Podocoryne carnea* hydrants. — *Growth*, 33, 99—111.

— 1974. The cellular basis for colony form in *Podocoryne carnea*. — *Amer. Zool.*, **14**, 2, 673—698.

CAMPBELL, R. D. 1974. Cell movements in *Hydra*. — *Ibidem*, **14**, 2, 523—535.

DUERDEN, J. E. 1902. Aggregated colonies in madreporarian corals. — *Amer. Natur.*, **36**, 426, 461—471.

DUNN, D. F. 1977. Dynamics of external brooding in the sea anemone *Epiactis prolifera*. — *Marine Biol.*, **39**, 1, 41—49.

FEDOROWSKI, J. 1978. Some aspects of coloniality in rugose corals. — *Palaeontology*, **21**, 1, 177—224.

— and JULL, R. K. 1976. Review of blastogeny in Palaeozoic corals and description of lateral increase in some Upper Ordovician rugose corals. — *Acta Palaeont. Polonica*, **21**, 1, 37—78.

(IVANOVA-KAZAS, O. M.) ИВАНОВА-КАЗАС, О. М. 1977. Безполое розмножение животных. 1—240. Ленинград.

KHOA, N. D. 1977. Carboniferous Rugosa and Heterocorallia from boreholes in the Lublin region (Poland). — *Acta Palaont. Polonica*, **22**, 4, 301—404.

MATTHAI, G. 1926. Colony-formation in astraeid corals. — *Phil. Trans. Roy. Soc. London*, B, **214**, 313—367.

NOWIŃSKI, A. 1976. Tabulata and Chaetetida from the Devonian and Carboniferous of Southern Poland. — *Palaeont. Polonica*, **35**, 1—125.

NYHOLM, K. G. 1943. Zur Entwicklung und Entwicklungsbiologie der Ceriantarien und Actinien. — *Zool. Bidrag Uppsala*, **27**, 265—505.

OLIVER, W. A., Jr. 1968. Some aspects of colony development in corals. — *J. Paleont.*, **42**, 5, 16—34.

RONIEWICZ, E. 1966. Les Madréporaires du Jurassique supérieur de la bordure des Monts de Sainte-Croix, Pologne. — *Acta Palaeont. Polonica*, **11**, 2, 157—264.

— 1976. Les Scléractiniaires du Jurassique supérieur de la Dobrogea Centrale, Roumanie. — *Palaeont. Polonica*, **34**, 17—121.

RÓŻKOWSKA, M. 1960. Blastogeny and individual variations in tetracoral colonies from the Devonian of Poland. — *Acta Palaeont. Polonica*, **5**, 1, 3—63.

SORAUF, J. E. 1967. Massive Devonian Rugosa from Belgium. — *Univ. Kansas Paleont. Contrib.*, **16**, 1—41.

SPAULDING, J. E. 1974. Embryonic and larval development in sea anemones (Anthozoa, Actinaria). — *Amer. Zool.*, **14**, 2, 511—520.

(TOKIN, B. P.) ТОКИН, Б. П. 1959. Регенерация и соматический эмбриогенез. 1—268. Ленинград.

VANDERMUELEN, J. H. and WATABE, N. 1973. Studies on reef corals: I. Skeleton formation by newly settled planula larva of *Pocillopora damicornis*. — *Marine Biol.*, **23**, 1, 47—57.

EXPLANATION OF THE PLATES 26—29

Plate 26

1. *Yabeiphyllum rossi* Minato and Kato, 1965: holotype, specimen USNM 139785, Gaptank Fm., Glass Mts., Texas; *a* transverse section of the lower part of the colony with all specimens completely separated, ×3; *b* transverse section made approximately 2,5 cm above the preceding one showing several corallites connected by channels (inked and bleached photograph), ×4; *c* transverse section made approximately 0,5 cm above the preceding one with only two corallites connected by channels, ×3.
2. *Carinthiaphyllum* sp.: Specimen USNM 196692, Lower Wolfcampian, Glass Mts., Texas; *a* transverse section across the gregarium with the young corallite lowermost, ×2; *b* a part of the gregarium with some specimens attached to surfaces of the other ones, ×2.

Plate 27

1. *"Duplophyllum"* sp. 1: specimen USNM 196693, Leonardian, Glass Mts., Texas; *a* general view of the two temporarily fused specimens, ×4; *b* transverse section through the fused part of the specimen, ×5 (inked and bleached photograph).
2. *Kleopatrina* (*Porfirievella*) *permiana* (Fedorowski, 1965): specimen KGP-2/1, Lower Permian, Hornsund area, Vestspitsbergen; *a* general view of the fused colonies with the left, larger colony dominating, nat. size; *b* transverse section through the fused parts of colonies, nat. size. The line of fusion shown by an arrow, the larger colony to the left; *c*—*e* the fine structures of external walls, ×200. *c* the larger colony, *d* the common wall of the two fused colonies, *e* the smaller colony.

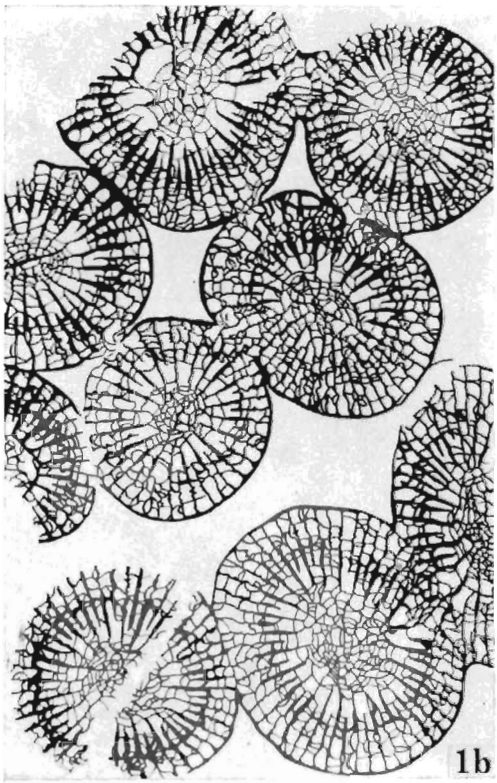
Plate 28

1. *Hexagonaria davidsoni* (M.-Edwards et Haime, 1851): specimen 1750, Frasnian, Neuville road cut, Belgium; the transverse section showing advanced regeneration of the wounded colony by means of division of the wounded polyp's body into the neighbouring polyps, ×6.
2. *Hexagonaria mirabilis* Moenke, 1954: specimen 1747, Frasnian, Pry, Belgium; the

transverse section showing regeneration of the colony by mean of expansion of offsets of the neighbouring specimens into the destroyed part of the wounded specimen ×6. The remainings of the latter develope normally due to the aid of the colony.

Plate 29

"Duplophyllum" sp. 2: specimen No 196694, Glass Mts, SW Texas, Skinner Ranch Fm., Wolfcampian; fusion of two solitary corallites, ×5. *a* completely integrated calices of two specimens. In the peripheral part of the new calice the rejuvenescence is developed; *b* lateral view showing a rejuvenescence, i.e. the formation of one of the future components of the fused calice; *c*, *d* lateral sides of two fused specimens showing their complete independence at the beginning (one of them developed from a larva that settled down on a lateral side of the old part of the second corallite) and complete fusion in more advanced growth, documented by common growth lines of the epitheca.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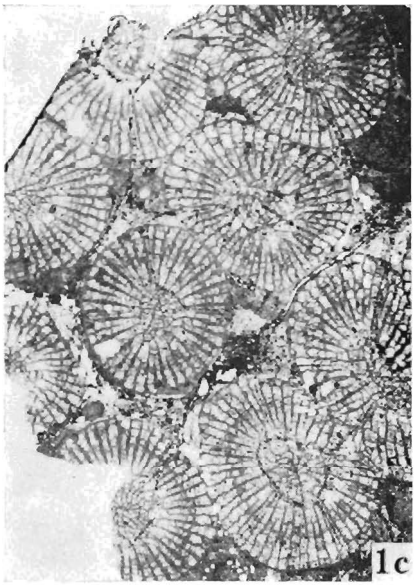
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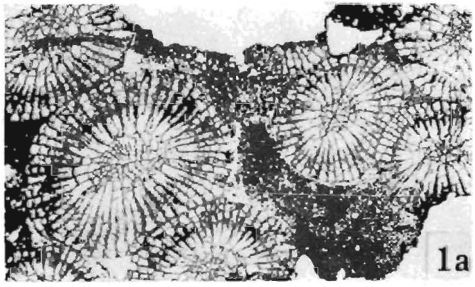
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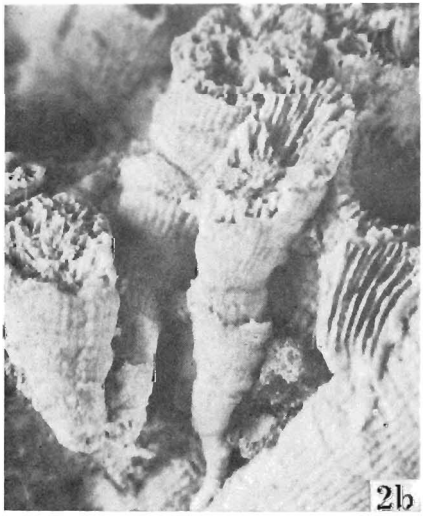
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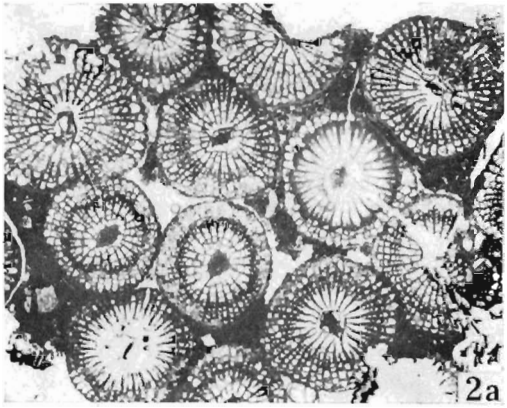
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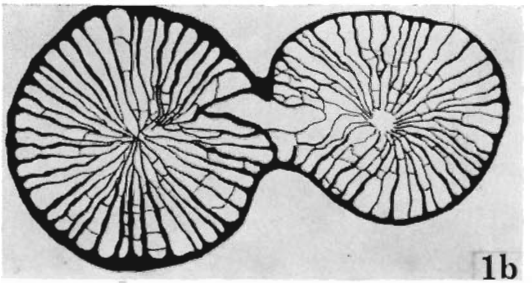
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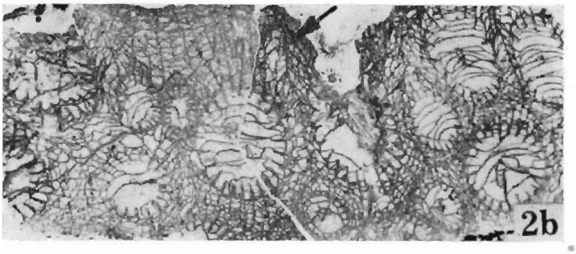
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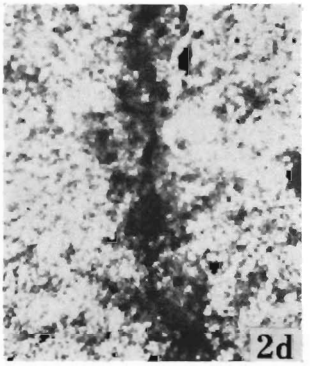
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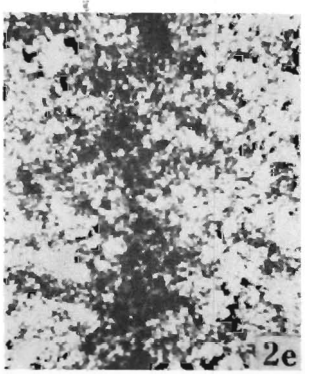
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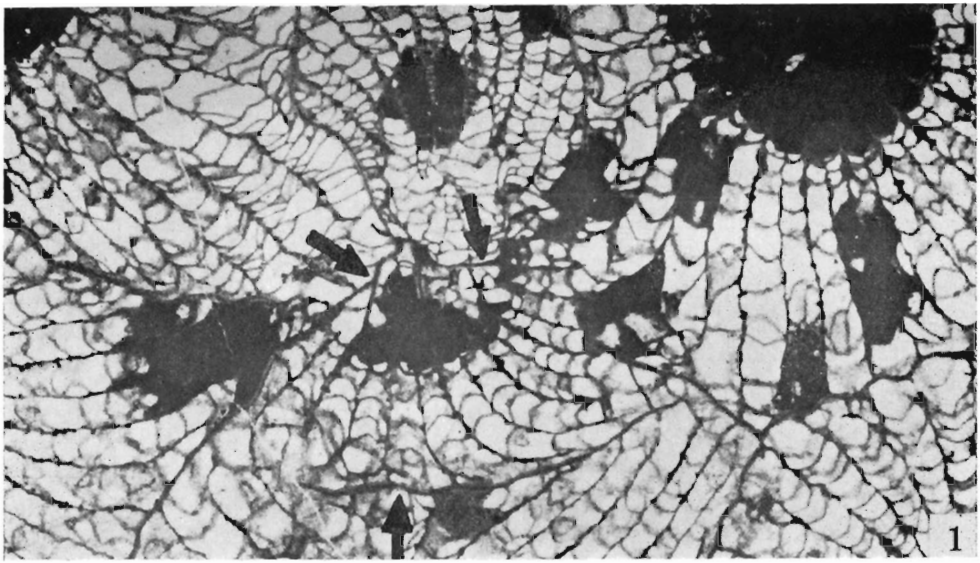
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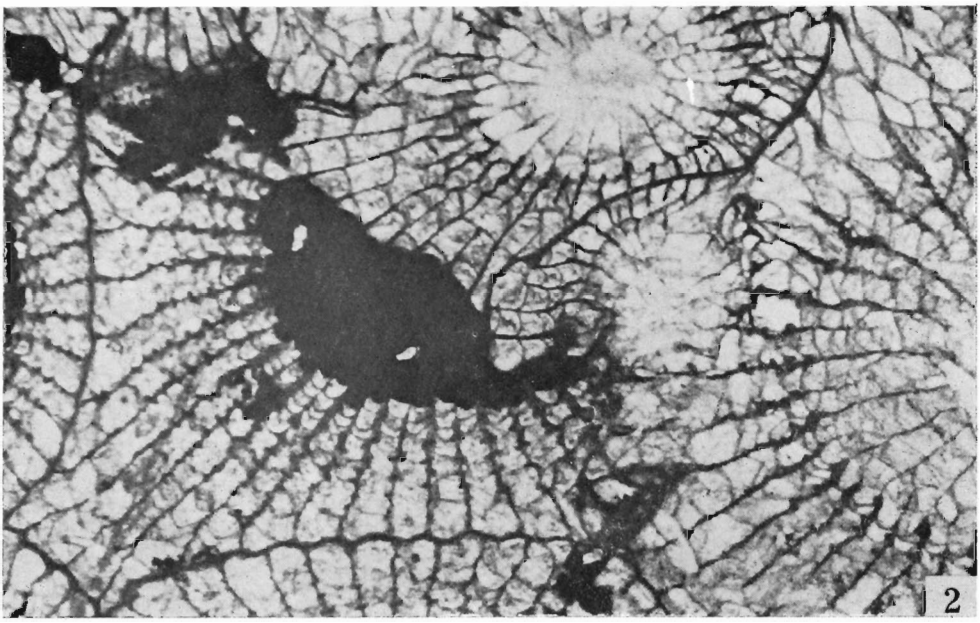
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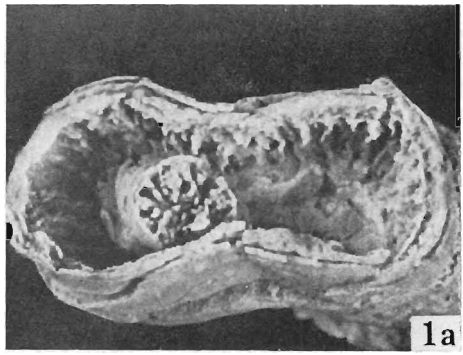
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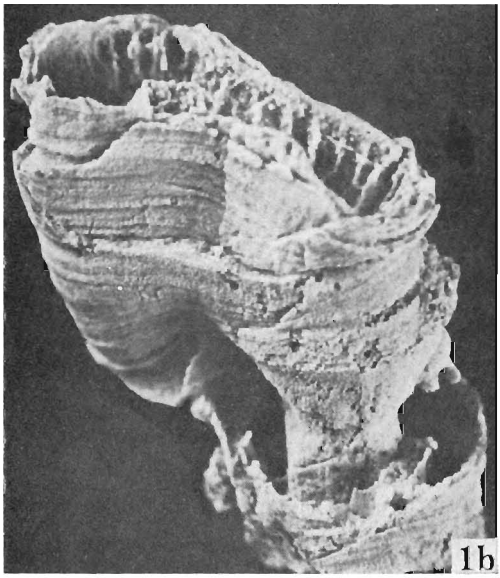
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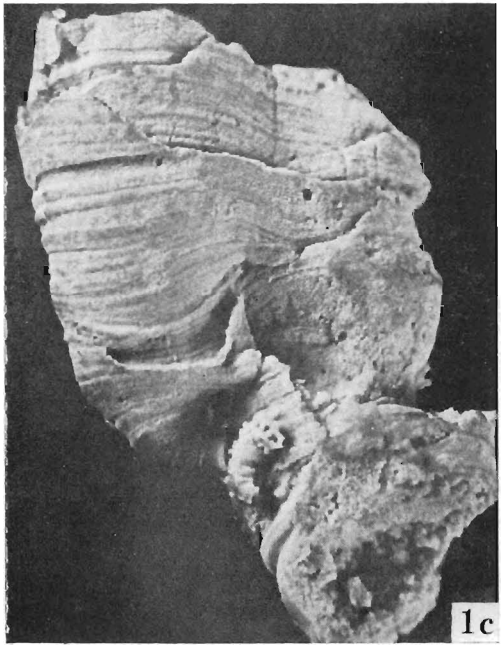
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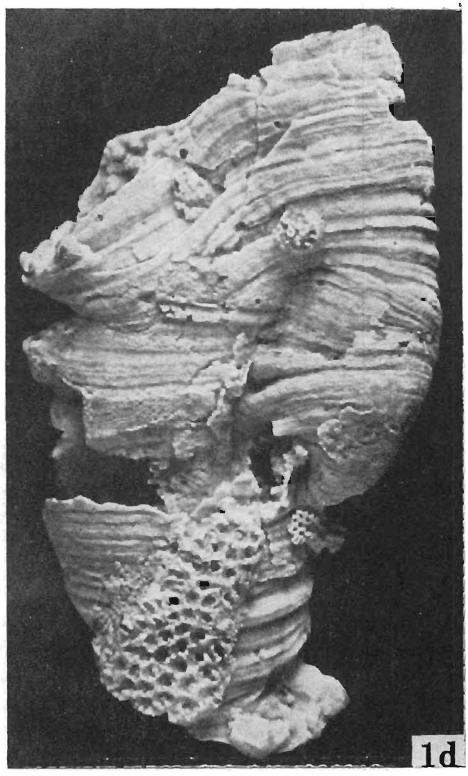
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